Meta-analysis reveals that resting metabolic rate is not consistently related to fitness and performance in animals

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Abbreviations: RMR = resting metabolic rate; SMR = standard metabolic rate; BMR = basal metabolic rate, MR = metabolic rate; PRISMA = Preferred Reporting Items in Systematic Reviews and Meta-Analyses

Abstract

Explaining variation in the fitness of organisms is a fundamental goal in evolutionary ecology. Maintenance energy metabolism is the minimum energy required to sustain biological processes at rest (resting metabolic rate; RMR) and is proposed to drive or constrain fitness of animals, however this remains debated. Hypotheses have been proposed as to why fitness might increase with RMR (the ‘increased intake’ or ‘performance’ hypothesis), decrease with RMR (the ‘compensation’ or ‘allocation’ hypothesis), or vary among species and environmental contexts (the ‘context dependent’ hypothesis). Here, we conduct a systematic review and meta-analysis of the literature, finding 114 studies with 355 relationships between RMR and traits that may be related to fitness. We show that individuals with relatively high RMR generally have high fitness overall, which might be supported by an increased energy intake. However, fitness proxies are not interchangeable: the nature of the RMR-fitness relationship varied substantially depending on the specific trait in question, and we found no consistent relationship between RMR and those traits most closely linked with actual fitness (i.e., lifetime reproductive success). We hypothesise that maintaining high RMR is not costly when resources are unlimited, and we propose ideas for future studies to identify mechanisms underlying RMR-fitness relationships.

Introduction

Metabolic rate is the rate at which energy and materials consumed from the environment are processed and depleted within an organism (Suarez 2012). The transformed energy is allocated and expended on maintenance, growth, reproduction, and other fitness-enhancing processes and activities (Brown et al. 2004). The rate of energy expenditure on metabolic processes sets the pace of life and the demands that animals place on their environment (Brown et al. 2004), and constrains the allocation of energy (e.g., energy expended on maintenance cannot also be expended on reproduction).

Maintenance energy metabolism is one of the most widely measured physiological traits (White et al. 2012b) and has long been associated with many aspects of life-history, performance, and fitness (Metcalfe et al. 2016; Pettersen et al. 2016; Burton et al. 2011; Speakman et al. 2004; Reinhold 1999; Hayes et al. 1992; Biro and Stamps 2010). Although the fitness consequences of variation in metabolic rate have long been of interest, most studies do not measure fitness directly (the number of surviving offspring produced by an individual after a single generation), but instead measure more tractable proximate traits, often in the form of whole-organism performance (Orr 2009; Burton et al. 2011; Pettersen et al. 2018). The literature often conflates performance and fitness, because whole-organism performance is defined as a measure of how well an individual performs an ecologically relevant task, and crucially, it may include any trait that can be directly linked to, or correlated with, fitness (Lailvaux and Husak 2014). Performance traits that are likely to influence the probability that an individual of a given phenotype will contribute to subsequent generations may be meaningful components of, or proxies for, fitness itself. Hence, a vast array of traits could be measured when biologists attempt to quantify fitness in their study system. Here, we refer to survival and reproduction traits as ‘fitness’, and consider performance traits as ‘fitness-related traits’, or ‘proxies’.

Minimum rates of metabolism are defined and measured differently among taxonomic groups, but collectively aim to measure the obligatory energy cost of self-maintenance: the energy expended by an animal in an inactive state, measured at a specified temperature (resting metabolic rate; RMR). Standard metabolic rate (SMR) additionally specifies non-growing and post-absorptive states, basal metabolic rate (BMR) is specifically for adult, non-reproductive endotherms that are thermoregulating at a thermoneutral temperature, and routine metabolic rate (routine MR) does not necessarily specify an inactive state (usually in fish). Here, we inclusively refer to RMR, SMR, BMR, and routine MR as estimates of the minimum rate of metabolism, hereafter collectively referred to as resting metabolic rate (RMR) (Mathot and Dingemanse 2015; Burton et al. 2011).

There is considerable variance in RMR; orders of magnitudes among individuals of different species, but having the same body mass (White and Kearney 2013), and up to three-fold differences within species among individuals of the same body mass and physiological state (Burton et al. 2011; Schimpf et al. 2013; Johnston et al. 2007). Some of this variance can be attributed to differences in methodology, context, or taxonomy among-studies – especially between ectotherms and endotherms. The rate of energy expenditure required to generate heat and maintain body temperature in endotherms (birds and mammals) is substantial; ectotherms do not thermoregulate using endogenously generated heat, and so do not incur this cost (Bennett and Ruben 1979). The allocation of metabolic resources is therefore fundamentally different between endotherms and ectotherms, which might affect the correlation between RMR and fitness. The extensive variation in RMR – which is often repeatable within individuals (Nespolo and Franco 2007; Auer et al. 2016; White et al. 2013; Biro et al. 2020) and heritable across generations (White and Kearney 2013; Pettersen et al. 2018) – is hypothesized to have consequences for fitness due to correlations between fitness-related traits and RMR (Burton et al. 2011). Two main mechanistic hypotheses for the correlation between RMR and fitness have been proposed and tested in a variety of systems.

The ‘increased intake’ (synonymous with ‘performance’) hypothesis proposes that individuals with higher RMR would have higher fitness because they have higher energy intake and processing capacity, which facilitates increased productivity through increased activity (encompassing traits such as boldness and dominance, which are related to the likelihood of reproducing), growth, and reproduction (positive RMR-fitness correlation) (Nilsson 2002; Careau and Garland 2012). On the other hand, the 'compensation' (or 'allocation') hypothesis proposes that animals with lower RMR will have more energy available to allocate toward fitness because energy allocated to maintenance cannot also be expended on fitness-enhancing activities (negative RMR-fitness correlation) (Nilsson 2002; Careau and Garland 2012).

Evolutionary theory predicts that persistent directional selection will deplete genetic variance, and so the widespread presence of additive genetic variance in RMR (Pettersen et al. 2018) suggests that neither of the 'increased intake' and 'compensation' hypotheses can offer complete explanations for the evolution of RMR. One possible explanation for the maintenance of genetic variance is that complex genetic correlations or pleiotropy among RMR and other traits constrain directional evolution of RMR (Walsh and Blows 2009). Another explanation is the 'context dependent' hypothesis, which proposes that the relationship between RMR and fitness varies with, for example, spatiotemporal fluctuations in resource availability (Burton et al. 2011; Careau and Garland 2012). To determine which of these explanations might be more likely, and under what circumstances particular hypotheses hold, it is necessary to determine how performance and fitness vary with RMR, and how these relationships vary among species and traits. Although there is evidence for correlations between RMR and many fitness and fitness-related traits (e.g., boldness (Behrens et al. 2020), dominance (Reid et al. 2011; Røskaft et al. 1986), reproductive traits (Boratyński and Koteja 2010; Blackmer et al. 2005), growth (Sadowska et al. 2009), and survival (Larivee et al. 2010; Boratyński et al. 2010)), there are also many clear examples that show no relationship between RMR and fitness-related traits (e.g., locomotor performance (Le Galliard et al. 2013; Arnold et al. 2017), aerobic performance (Merritt et al. 2013), and reproductive traits (Schimpf et al. 2012)). The magnitude and direction of these correlations varies substantially among-studies, and support for mechanistic hypotheses remains mixed (Careau and Garland 2012; Burton et al. 2011; Glazier 2015). Accordingly, interest in this research area shows no sign of waning (Glazier 2015; Mathot and Dingemanse 2015; Metcalfe et al. 2016; Pettersen et al. 2016; Pettersen et al. 2018).

To determine how fitness and performance vary with RMR, and to test the increased intake', 'compensation', and 'context dependent' hypotheses, we compiled published relationships between fitness or fitness-related traits and RMR in ectotherms and endotherms using a systematic meta-analytical framework. We considered six broad groups of fitness-related traits: active metabolic rate, aerobic capacity, boldness, dominance, growth, movement or activity, and two fitness traits: reproduction and survival (hereafter we refer to all eight groups collectively as fitness categories). Over the course of data collection, analysis, and writing, two related meta-analyses of the relationships between MR and aerobic performance traits and behaviours in animals appeared in the literature (Auer et al. 2017; Mathot et al. 2019). We present our study as an independent replication of their work, which we expand upon with the addition of other fitness-related traits and direct measures of fitness. There have been several relevant studies published in the time since the systematic literature search and meta-analysis were conducted that were not included, but it is likely that these would serve to strengthen evidence for smaller effect sizes observed through time (see results) and therefore likely to not change our overall conclusions.

We present this work as a tribute to Frapps, because our collective interest in this area began when he asked one of us (CRW) why BMR matters, at the 18th annual meeting of the Australian and New Zealand Society for Comparative Physiology and Biochemistry in 2001. Frapps and Pat Butler then asked the same question of the field as a whole at the International Congress of Comparative Physiology and Biochemistry in 2003 (Frappell and Butler 2004). This marked the first time we tried to answer the question of how and why metabolic rate varies (White and Seymour 2004). In the nearly 20 years since this first interaction, we have undertaken a range of empirical and comparative studies to address this question (e.g., White et al. 2007; Schimpf et al. 2012; Merritt et al. 2013; Arnold et al. 2017; White et al. 2019), including several that involved Frapps directly (White et al. 2012a; White et al. 2012b). This question had an enduring impact – CRW still remembers the colour of the shirt that Frapps was wearing when he asked it – as did every subsequent interaction with Frapps.

Methods

Literature search

We used the Preferred Reporting Items in Systematic Reviews and Meta-Analyses (PRISMA) framework (Moher et al. 2009) to compile a database of published studies on relationships between fitness (components) and maintenance metabolic rate. We systematically searched the Web of Science database Core Collection with access through Monash University in November 2016 using the following search terms in the ‘topic’ field (title, abstract, and extended keywords): ((*metabolic rate**) and (*aerob** or *surviv** or *locomot** or *domin** or *grow** or *reprod** or *bold** or *personal** or *perform** or *behav** or *fitness* or *move** or *longev** or *thermal* or *tolerance* or *home range*) and (*insect** or *fish** or *amphib** or *reptil** or *aves* or *bird** or *mammal** or *gastropod** or *arachnid** or *crustacea**) not (*human** or *pharma** or *metabolic syndrome**)). We included studies from a previous non-systematic search by CRW conducted in 2013, and studies from relevant previously published literature surveys (Metcalfe et al. 2016; Hayes and Garland 1995; Mathot and Dingemanse 2015). The systematic review approach is clearly defined and reduces potential biases to result in an objective overview of the available literature that is then quantitatively assessed through meta-analysis to synthesise evidence (Gurevitch et al. 2018). Although we recognise that there have been numerous relevant studies since this literature search was initially conducted, ours still represents the most complete systematic review and meta-analysis covering both performance and fitness traits in relation to metabolic rate.

Inclusion and exclusion criteria

The search results were first screened by title and abstract, where the inclusion criteria were studies that 1) measured basal, standard, resting, or routine metabolic rates, 2) measured fitness or some component or proxy of fitness (e.g., aerobic capacity, survival, reproduction, or growth), and 3) appeared to assess an intraspecific relationship between the measure of maintenance metabolic rate and fitness. Studies that were retained after this first level of screening were then excluded when 1) they were interspecific comparisons, unless the data for each species were presented separately, 2) they were reviews or meta-analyses, 3) the data was not appropriate for this meta-analysis (e.g., did not actually measure maintenance metabolic rate or fitness, or included experimental manipulation of hormone levels), or 4) they did not measure or specify mean body mass.

Our initial Web of Science search returned 6459 publications. The database compiled by CRW contained 62 publications, 29 of which were not identified in the Web of Science search. The previously published literature surveys included 43 papers, 23 of which were not identified in the Web of Science search or CRW database. We removed 55 duplicates from the combined total of 6564 publications, leaving 6509 records. The first level screening of publication abstracts removed 6078 records, leaving 431 remaining to be assessed as full-text publications. A further 317 records were removed through this eligibility assessment, including those studies that did not provide a body mass estimate, leaving 114 studies that had appropriate, extractable data for this meta-analysis (Fig. S1).

Data extraction

We extracted data from 114 studies that assessed 355 correlations between metabolic rate and fitness across 94 species and 25 taxonomic orders. Overall, we collected data from eight fitness categories: active metabolic rate (*n* = 97), aerobic capacity (*n* = 30), boldness (*n* = 31), dominance (*n* = 39), growth (*n* = 15), movement/activity (*n* = 67), reproduction (*n* = 50), and survival (*n* = 26), across four metabolic rate categories: BMR (*n* = 102), RMR (*n* = 198), routine MR (*n* = 23), and SMR (*n* = 42). Studies were categorized as field studies when the fitness trait was measured in the field (*n* = 44). The remaining measurements were from laboratory studies (*n* = 311). For each included study, we also extracted the taxonomic class and species used in the study, exact fitness trait, within study sample size (*n*), correlation coefficient (Pearson's *r*) or test statistics (*t*, *F*, χ^2, *Z*, or R^2), whether the relationship was originally reported as significant or not ($\alpha = 0.05$), and moderator variables of thermoregulation strategy (ectotherm or endotherm), mean body mass, the fitness category, and publication details.

Statistical analyses

Effect size standardization

All statistical analyses were conducted in the R environment for statistical and graphical computing (v3.4.1) (R Development Core Team 2017). For the meta-regressions and meta-analyses, we standardized correlation coefficient measures across the published studies by calculating Fisher's *Z*-transformed correlation coefficient (*Zr*), which converts the skewed distribution of the sample correlation coefficient (Pearson's *r*) to an approximately normal distribution. For studies that did not provide a correlation coefficient (Pearson's *r*) estimate, we obtained it from *t*, *F*, χ^2, *Z*, or R^2 statistics using established equations (Lajeunesse 2013; Nakagawa et al. 2007), or by data-mining figures using a plot digitizing tool (WebPlotDigitizer) (Rohatgi 2017), and then by fitting a linear regression. For six latency-related boldness traits, we changed the sign of *r* to ensure that higher values indicated more positive associations between RMR with fitness (Table S1). We used the meta-analysis package *metafor* (Viechtbauer 2010) in R to transform *r* into *Zr* to obtain unbiased estimates of effect sizes and sampling variances (Hedges and Olkin 1985) using the *escalc* function. Mean body mass (M) and within-study sample size (*n*) were $\log_{10}$-transformed prior to analyses. R code for statistical analyses is available at https://github.com/pieterarnold/fitness-rmr-meta.

Meta-analyses and meta-regressions

We took a meta-regression approach to fit a series of random-effects multi-level models using the *rma.mv* function in *metafor*. These models were built with *a priori* determined combinations of fixed effect moderator variables (fitness category, thermoregulation, and mean body mass) that included random effects to account for among- and within-study variation (i.e., multiple *r* values contributed by individual studies). One estimate for South American sea lions (*Otaria flavescens*) had M, RMR, and *Zr* values at the extreme tail of the distribution, which had significant leverage on model selection, therefore we excluded this single estimate from further analysis. We used Akaike Information Criterion corrected for small sample sizes (AIC_C) to evaluate the relative rankings of these candidate models, then quantified relative support for each model using Akaike's weights (w_i). We assessed the highest ranked model for consistency of effect sizes among- and within-studies, and quantified this heterogeneity using I^2 statistics from analyses of the meta-regression model. We considered effects that had 95% CIs that were non-overlapping with zero to be significant.

Publication bias, missing data, and sensitivity

We evaluated the evidence for publication bias in our meta-analysis by constructing funnel plots of standard error and effect size, to visually identify asymmetry in the data. We also applied a rank correlation test (Kendall's τ) on the meta-regression model to measure asymmetry. To determine other sources of bias, we also plotted *Zr* against sample size (*n*), and absolute values of *Zr* (|*Zr*|) against journal impact factor, and |*Zr*| against publication year, grouping the data by studies that originally reported the correlation as either significant or non-significant at $p = 0.05$. Finally, we checked the sensitivity of our overall effect size to the removal of active MR from the fitness categories, as active MR was expected to be partially correlated with RMR for functional reasons described by the aerobic capacity model for the evolution of endothermy (Bennett and Ruben 1979; Hayes and Garland 1995; Hayes 2010).

Results

Data description

The quantitative meta-analysis revealed 114 studies that investigated 355 correlations between metabolic rate and one of eight fitness or fitness-related traits (for full dataset see Table S1). The dataset was dominated by laboratory-based measurements of fitness (88%), where active MR was the most common fitness-related trait category (27%), and mammals were the most commonly measured taxonomic group (39%). The data structure is summarized in Table S2 and Table S3. We did not apply a phylogenetically informed analysis because of the considerable over-dispersion and sparseness of related taxa (Table S2), however representation of endotherms and ectotherms was more balanced (n = 201 and n = 154, respectively). We therefore considered thermoregulatory strategy (endotherm or ectotherm) to be a fundamental moderator variable for taxonomic differences in RMR.

Meta-regression

The complete table of meta-regression models and their rankings are presented in Table S4. The highest-ranking model (output presented in Table S5) included the moderator variables of fitness category, thermoregulation, and their interactions. The overall effect size of the relationship between RMR and all fitness categories for the highest ranked meta-regression model was positive ($Zr = 0.157 \pm 0.049$). The null meta-regression model that included study identification as a random factor had the highest heterogeneity among-studies (I^2_{among} = 55.0%) compared to the moderate heterogeneity within-studies (I^2_{within} = 36.4%). The highest ranked meta-regression model was similarly heterogeneous (I^2_{among} = 57.3% and I^2_{within} = 33.1%), such that the inclusion of moderator variables did not change among- and within-studies variance substantially. Forest plots showing the heterogeneity in Zr among-studies are presented separately for ectotherms (Fig. 1) and endotherms (Fig. 2).

Moderator variable – fitness category × thermoregulation

The effect size of the relationship between RMR and fitness was strongly dependent on the fitness categories (Fig. 3; Table S5). At a standardized body size (median endotherm body mass: $\log_{10}M = 1.38$), the mean effect sizes for fitness-related traits were positive on average, except for aerobic capacity for both ectotherms and endotherms, and movement/activity for endotherms (Fig. 3). Active MR and dominance both positively correlated with RMR, and their 95% CIs were non-overlapping with zero for both endotherms and ectotherms. Boldness in endotherms had a strongly positive effect on RMR, but also had a relatively large 95% CI. Movement/activity had opposing relationships with RMR dependent on thermoregulation strategy, where active ectotherms had a weakly positive relationship with RMR, and active endotherms had a weakly negative relationship with RMR (Fig. 3). Confidence intervals around *Zr* estimates for aerobic capacity and growth substantially overlapped with zero. We did not find strong evidence to suggest that fitness (reproduction and survival traits) is related to RMR (Fig. 3). For both endotherms and ectotherms, the confidence intervals for both reproduction and survival substantially overlapped with zero, where the estimate for survival was remarkably close to zero (Fig. 3).

Evidence for publication bias, missing data, and sensitivity

The effect size within each study had a distinct relationship with the sample size of the study, where large *Zr* values were only detected at low *n*, and at high sample size the effect size converged toward zero in a funnel-like pattern (Fig. 4). There is likely some publication bias toward large, positive relationships, particularly at smaller sample sizes, where there is a notable absence of data for $Zr = 0$ and strong negative relationships at the lowest sample sizes (Fig. 4). We detected some publication bias in our data. Visually, there were high numbers of published positive effects and an absence of published non-significant high variance data, particularly for endotherms (Fig. S2). Statistically, the rank correlation test for funnel asymmetry suggested marginal publication bias (Kendall's $\tau = 0.068$, $p = 0.059$). Together, these suggest that there may be publication bias in the endotherm literature, which if accounted for, would reduce the overall effect size of the relationship between RMR and fitness or fitness-related traits. Interestingly, we identified weak negative correlations between |*Zr*| and journal impact factor (Pearson's *r* = -0.224 [-0.459, 0.006 95% CI]; Fig. S3), and |*Zr*| and publication year (Pearson's *r* = -0.196 [-0.295, -0.094 95% CI]; Fig. S4), such that some studies finding large effect sizes were published earlier or in lower impact journals. The finding that RMR was overall positively related to fitness was relatively insensitive to excluding active MR from the dataset, where the overall effect size estimate was only marginally reduced (*Zr* = 0.154 ± 0.059 compared to *Zr* = 0.157 ± 0.049 from the full dataset).

Discussion

Our systematic and quantitative meta-analysis provides evidence that resting metabolic rate (RMR) has a positive relationship with fitness-related traits, but no consistent relationship with the fitness components of reproduction and survival. The relationships we observe are complex, and dependent upon the type of fitness measure and the biology of the animal. We found significant effects of moderator variables including fitness category, and interactions between fitness category, thermoregulation, and body mass. Our findings resolve the gap in knowledge of how some RMR-fitness relationships vary across different fitness traits and biological contexts, but also identify very significant gaps in our understanding of the relationship between RMR and fitness. Here, we discuss explanations for the empirical patterns we observed and suggest future key directions for the field to pursue to resolve outstanding questions.

Patterns of RMR correlations with fitness-related traits differ markedly by trait, but generally support the increased intake hypothesis

RMR is the energy required to maintain 'metabolic machinery' and is an inherent biological cost of living. The 'context dependent' hypothesis predicts that the relationship between RMR and fitness will change dependent on context because resource availability fluctuates spatially and temporally

(Careau and Garland 2012; Burton et al. 2011). Sometimes, RMR will be positively correlated with fitness, such as when higher RMR represents increased capacity and the higher maintenance costs associated with a fast metabolism are outweighed by fitness benefits (‘increased intake’ hypothesis). Other times (e.g., under resource limitation), RMR will be negatively correlated with fitness if lower RMR represents lower maintenance costs and greater allocation of energy to fitness-related traits (‘compensation’ hypothesis). We found that many fitness-related traits and reproduction were positively correlated with RMR, which provides stronger support for the ‘increased intake’ hypothesis (13 out of 16 estimates were positive and five of these were clearly different from zero). Another recent meta-analysis also found generally positive covariation between MR and behaviour, providing greater support to the ‘increased intake’ hypothesis (Mathot et al. 2019). Although different types of behaviours altered the covariation with MR, these findings are congruent with our general findings that also include performance traits and fitness proxies. Below, we outline some testable hypotheses to explain our findings.

Unsurprisingly, we found that active MR was positively and significantly correlated with RMR. Another recent meta-analysis that investigated the relationship between minimum MR and maximum MR across vertebrate taxa found positive intra- and inter-specific correlations between the traits (Auer et al. 2017). This correlation is hypothesized to arise due to a mechanistic link between resting and maximum metabolic rates (Killen et al. 2016). Importantly, the exclusion of this mechanistic correlation between RMR and active MR did not significantly change the overall positive RMR-fitness relationship, despite active MR being one of the most frequently studied fitness-related traits in our meta-analysis. Although RMR and active MR are positively correlated, their relationship is allometric (less than proportional) (Killen et al. 2016) and consequently individuals that have a high RMR relative to their active MR could have a reduced aerobic scope. Across both ectotherms and endotherms, the relationship between RMR and aerobic capacity (here which includes aerobic scope and costs of transport) is negative but also overlaps with zero. The different relationships between active MR and RMR (positive) and aerobic capacity and RMR (negative but overlapping with zero) suggests that the positive relationship between RMR and aerobic capacity may arise because active MR represents and additive combination of RMR and an "activity energy expenditure (AEE)" component of active MR (e.g. active MR = RMR + AEE; Portugal et al. 2016; White et al. 2011). In such a scenario, active MR and RMR may be positively correlated even when there is no correlation between AEE and RMR (White et al. 2011; Portugal et al. 2016).

'Boldness' is not a single trait, but rather a complex axis of personality (Réale et al. 2007). Here, we categorized a range of traits that includes exploration-avoidance, escape behaviour, and 'boldness' measures because sample size was too low to make meaningful comparisons if boldness was subdivided into different personality axes or proactive-reactive behaviour categories. The significant positive RMR-boldness correlation in endotherms could imply that individuals that have an increased energy intake to maintain high RMR are those that are in relatively good condition and have less to fear (Careau et al. 2008), however this correlation had large associated error and is estimated from a small sample (n = 8). Although the association between RMR and boldness was weakly positive for ectotherms, this was less consistent between studies. For example, in our dataset there were opposing signs of effect sizes for the association between RMR and latency to emerge from a shelter into a novel habitat and time remaining in an open arena (e.g., Herrera et al. 2014; Martins et al. 2011). In contrast, dominance was clearly positively correlated with RMR for both ectotherms and endotherms. Dominant individuals are often those that can acquire more resources (territory, food, or mates), and in accordance with the increased intake hypothesis, these individuals should be able to maintain high RMR in non-limiting conditions (Careau et al. 2008; Careau and Garland 2012; Turbill et al. 2013). However, the relatively large effect size may be inflated by early studies that found large effects from small samples (e.g., Røskaft et al. 1986), as more recent studies with much larger samples sizes typically identify far smaller effects (e.g., Radwan et al. 2004).

The correlation between RMR and movement/activity was significantly affected by thermoregulatory strategy; it was negative for endotherms and positive for ectotherms. Transport costs do not differ between endotherms and ectotherms (White et al. 2016), but reptiles expend a smaller proportion of their non-resting daily energy expenditure on locomotion than mammals (Christian et al. 1997), presumably because reptiles travel shorter distances each day. The different relationships between RMR and movement/activity for endotherms and ectotherms therefore might arise because of the differences in energy allocation to movement/activity between these groups. For example, RMR and activity levels might be correlated in ectotherms because they expend relatively little on movement/activity such that they can increase their intake to facilitate a more productive lifestyle (Careau et al. 2008; Le Galliard et al. 2013).

Patterns of RMR correlations with direct measures of fitness are non-significant

The two categories that are most direct measures of fitness, reproduction and survival, both exhibited non-significant correlations with RMR. The weak positive correlation of reproduction with RMR, particularly in endotherms, again suggests that individuals that can maintain a high RMR could sustain a more productive lifestyle and allocate more resources to reproduction, however this is not a consistent correlation between studies. Genetic correlations have even revealed positive associations between RMR and reproductive traits when phenotypic correlations show the opposite association (Boratyński et al. 2013). Different reproductive traits within the same study system can even show support for both positive and negative relationships with RMR within- and between-individuals, illustrating the complexities of the bioenergetics of reproduction (Ameri et al. 2020). Survival had an essentially zero correlation with RMR, which could be explained by context-dependent probabilities for low and high RMR individuals to die. A high RMR individual could die from engaging in risky activities or from shifts in conditions that limit resources to maintain high RMR, and a low RMR individual might die from starvation or predation if they have low performance values, as might be plausible for the RMR-fitness-related traits relationships we have described above. Further, survival probability may simply be related to stochastic processes that acts indiscriminately on individuals with any RMR, or because stabilizing selection removes individuals with extreme high or low RMR (e.g., Artacho and Nespolo 2009). Recent studies published after our systematic search demonstrate a range of correlations that further suggest taxa- and context-dependence; snails demonstrate a positive, stabilising correlation between RMR and survival probability (Bech et al. 2020), many tropical birds show a negative correlation between BMR and survival (Boyce et al. 2020; Scholer et al. 2019), and BMR has no correlation with survival in root voles (Książek et al. 2017). More pertinently, why more direct measures of ‘true’ fitness do not correlate with RMR remains to be tested, and these findings places the relevance of statements about traits that are ‘fitness proxies’ in doubt as reasonable proxies for fitness, unless they are validated within the study itself.

Moving forward with testable hypotheses in evolutionary physiology

Most explanations of the patterns we observe rely on the increased intake hypothesis; individuals that can acquire and process adequate energetic resources to maintain a relatively high cost of maintenance metabolism should also perform well or have higher fitness. Testing this hypothesis relies on variation in resource availability, so that resource acquisition and intake can vary. Yet, laboratory experiments (which constitute most studies in our meta-analysis) typically provide food *ad libitum*, which is unlikely to cause trade-offs for energetic allocation (Burton et al. 2011). Even if the experimental organisms have their RMR measured under a post-absorptive or food deprived state, the general abundance of resources outside of this measurement period will likely not induce a physiological response akin to resource limitation. RMR may not represent a substantial enough energy cost that would cause these organisms to divide resource allocation between RMR and fitness-enhancing traits. If sampling is inherently biased toward the tail of the distribution of fit (or high condition) individuals, where only those that have already survived to adulthood and are inherently more active are measured, then the true relationship between fitness and RMR could be under- or over-estimated.

Reconciling whether differences in RMR-fitness relationships across taxa are a function of resource limitation (or lack thereof) or artefacts of other experimental conditions requires controlled experiments to replicate conditions that are experienced by natural populations. Model systems could measure the effects of fluctuating resource availability and environmental conditions on the RMR-fitness relationship (Norin and Metcalfe 2019). Likewise, the relationship between RMR and fitness has been postulated to be context-dependent (Burton et al. 2011), but explicit tests for the effect of context within a study system are only recently gaining traction (e.g., Liu and Fu 2017; Auer et al. 2018; Zeng et al. 2017; Killen et al. 2013). These empirical studies have so far demonstrated support for the context-dependence of the MR and performance trait relationships, particularly when food availability is manipulated, which might weaken the generally positive relationship between RMR and fitness-related traits. To explore how context mediates the RMR-fitness relationship, it needs to be assessed across a range of environments (e.g., thermal, nutritional, or social) to disentangle contextual variation that is currently confounded by taxonomy, variation in experimental conditions, and in methodology of both RMR and fitness measures. For example, RMR-fitness component relationships can be sex-dependent, where males and females could differ in their energetic requirements, which will also vary with age (Boratyński et al. 2018). Important contextual information such as sex and age but likely contribute to residual variation, but these are not often determined or reported. Experimental designs that test RMR-fitness relationships within multiple environmental or treatment levels can also examine the slope of the RMR-fitness relationship across these levels from a reaction norm perspective to identify whether the relationship is plastic (Norin and Metcalfe 2019). Similarly, undertaking tests of the RMR-fitness relationship for a single species at multiple points in space and time would make it possible to determine if the RMR-fitness relationship shows spatiotemporal variability under natural conditions.

Whatever approach is taken, our meta-analysis highlights the need for careful replication. Some of the strongest RMR-fitness correlations were in earlier studies that used few samples; a compelling example of the ‘winner’s curse’, where early detection of a significant effect leads to inflated estimates, and subsequent findings of similar effects are much reduced or closer to zero (Button et al. 2013).

Conclusion: is metabolic rate related to fitness?

Through undertaking a systematic meta-analysis, we have identified substantial gaps in empirical studies investigating the links between RMR and fitness traits for both ectotherms (i.e., growth, reproduction, survival) and endotherms (i.e., boldness, growth, survival). Overall, we found a positive relationship between RMR and fitness traits, which was inconsistent between different trait categories. Two recent meta-analyses (Mathot et al. 2019; Auer et al. 2017) both demonstrate positive but variable relationships between MR and aerobic performance traits and behaviours in animals, to which our meta-analysis adds on other fitness-related traits and fitness directly and substantiates their findings. We identified that biases include insufficient taxonomic representation in empirical studies apart from mammals, birds, and fish, and a concerning magnification effect of small sample sizes on the strength of correlations. Additional studies that are appropriately replicated are required to reduce publication bias, and to achieve more precise estimates of the effect sizes for these trait categories and within under-represented taxa.

‘Fitness’ has often been used as a vague term in comparative evolutionary physiology that constitutes both direct measures of fitness (lifetime reproductive success) and a vast array of traits that are more appropriately described as measures of performance, as well as proxies for fitness, or components of fitness. Our meta-analysis demonstrates decisively that a given fitness-related trait cannot be substituted for another *ad hoc* to necessarily retain a similar relationship with fitness and nor should they explicitly be considered to be related to fitness. Reproduction and survival are also not freely interchangeable measures of fitness (present findings; see also (Pettersen et al. 2015)). Here, we have summarized the current state of knowledge from the available empirical literature: RMR is often positively related to fitness-related traits, but we are unable to determine the relationship between RMR and fitness *per se*, because our systematic meta-analysis includes no studies that determined the relationship between RMR and lifetime reproductive success. The only study of the relationship between RMR and lifetime reproductive success that we are aware of found that the relationship was complex, and that fitness was highest for individuals that exhibited high RMR in one life stage and low RMR in another (Pettersen et al. 2016). More studies examining the relationship between RMR and actual fitness (lifetime reproductive success) are sorely needed. There is now opportunity for future studies to discern the conditions under which RMR does and does not affect fitness and the mechanisms of these relationships.

References

Ameri M, Kemp DJ, Barry KL, Herberstein ME (2020) Is resting metabolic rate related to reproductive output in an orb-web spider, *Argiope radon*? Ecol Entomol 45 (5):1044-1052. doi:10.1111/een.12882

Arnold PA, Cassey P, White CR (2017) Functional traits in red flour beetles: the dispersal phenotype is associated with leg length but not body size nor metabolic rate. Funct Ecol 31 (3):653-661. doi:10.1111/1365-2435.12772

Artacho P, Nespolo RF (2009) Natural selection reduces energy metabolism in the garden snail, *Helix aspersa* (*Cornu aspersum*). Evolution 63 (4):1044-1050. doi:10.1111/j.1558-5646.2008.00603.x

Auer SK, Anderson GJ, McKelvey S, Bassar RD, McLennan D, Armstrong JD, Nislow KH, Downie HK, McKelvey L, Morgan TAJ, Salin K, Orrell DL, Gauthey A, Reid TC, Metcalfe NB (2018) Nutrients from salmon parents alter selection pressures on their offspring. Ecol Lett 21 (2):287-295. doi:10.1111/ele.12894

Auer SK, Bassar RD, Salin K, Metcalfe NB (2016) Repeatability of metabolic rate is lower for animals living under field versus laboratory conditions. J Exp Biol 219 (5):631-634. doi:10.1242/jeb.133678

Auer SK, Killen SS, Rezende EL (2017) Resting vs. active: a meta-analysis of the intra- and inter-specific associations between minimum, sustained, and maximum metabolic rates in vertebrates. Funct Ecol 31 (9):1728-1738. doi:10.1111/1365-2435.12879

Bech C, Christiansen MT, Kvernland P, Nygård RM, Rypdal E, Sneltorp SK, Trondrud LM, Tvedten ØG (2020) The standard metabolic rate of a land snail (*Cepaea hortensis*) is a repeatable trait and influences winter survival. Comp Biochem Physiol A Mol Integr Physiol 249:110773. doi:10.1016/j.cbpa.2020.110773

Behrens JW, von Friesen LW, Brodin T, Ericsson P, Hirsch PE, Persson A, Sundelin A, van Deurs M, Nilsson PA (2020) Personality- and size-related metabolic performance in invasive round goby (*Neogobius melanostomus*). Physiol Behav 215:112777. doi:10.1016/j.physbeh.2019.112777

Bennett AF, Ruben JA (1979) Endothermy and activity in vertebrates. Science 206 (4419):649. doi:10.1126/science.493968

Biro PA, Stamps JA (2010) Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends Ecol Evol 25 (11):653-659. doi:10.1016/j.tree.2010.08.003

Biro PA, Thomas F, Ujvari B, Adriaenssens B, Beckmann C (2020) Spontaneous activity rates and resting metabolism: Support for the allocation model of energy management at the among-individual level. Ethology 126 (1):32-39. doi:10.1111/eth.12957

Blackmer AL, Mauck RA, Ackerman JT, Huntington CE, Nevitt GA, Williams JB (2005) Exploring individual quality: basal metabolic rate and reproductive performance in storm-petrels. Behav Ecol 16 (5):906-913. doi:10.1093/beheco/ari069

Boratyński Z, Koskela E, Mappes T, Mills SC, Mokkonen M (2018) Maintenance costs of male dominance and sexually antagonistic selection in the wild. Funct Ecol 32 (12):2678-2688. doi:10.1111/1365-2435.13216

Boratyński Z, Koskela E, Mappes T, Oksanen TA (2010) Sex-specific selection on energy metabolism - selection coefficients for winter survival. J Evol Biol 23 (9):1969-1978. doi:10.1111/j.1420-9101.2010.02059.x

Boratyński Z, Koskela E, Mappes T, Schroderus E (2013) Quantitative genetics and fitness effects of basal metabolism. Evol Ecol 27 (2):301-314. doi:10.1007/s10682-012-9590-2

Boratyński Z, Koteja P (2010) Sexual and natural selection on body mass and metabolic rates in free-living bank voles. Funct Ecol 24 (6):1252-1261. doi:10.1111/j.1365-2435.2010.01764.x

Boyce AJ, Mouton JC, Lloyd P, Wolf BO, Martin TE (2020) Metabolic rate is negatively linked to adult survival but does not explain latitudinal differences in songbirds. Ecol Lett 23 (4):642-652. doi:10.1111/ele.13464

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85 (7):1771-1789. doi:10.1890/03-9000

Burton T, Killen SS, Armstrong JD, Metcalfe NB (2011) What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proc Roy Soc Lond B Biol Sci 278 (1724):3465-3473. doi:10.1098/rspb.2011.1778

Button KS, Ioannidis JPA, Mokrysz C, Nosek BA, Flint J, Robinson ESJ, Munafo MR (2013) Power failure: why small sample size undermines the reliability of neuroscience. Nat Rev Neurosci 14 (5):365-376. doi:10.1038/nrn3475

Careau V, Garland T (2012) Performance, personality, and energetics: correlation, causation, and mechanism. Physiol Biochem Zool 85 (6):543-571. doi:10.1086/666970

Careau V, Thomas D, Humphries MM, Réale D (2008) Energy metabolism and animal personality. Oikos 117 (5):641-653. doi:10.1111/j.0030-1299.2008.16513.x

Christian KA, Baudinette RV, Pamula Y (1997) Energetic costs of activity by lizards in the field. Funct Ecol 11 (3):392-397. doi:10.1046/j.1365-2435.1997.00099.x

Frappell PB, Butler PJ (2004) Minimal metabolic rate, what it is, its usefulness, and its relationship to the evolution of endothermy: a brief synopsis. Physiol Biochem Zool 77 (6):865-868

Glazier DS (2015) Is metabolic rate a universal 'pacemaker' for biological processes? Biol Rev 90:377-407. doi:10.1111/brv.12115

Gurevitch J, Koricheva J, Nakagawa S, Stewart G (2018) Meta-analysis and the science of research synthesis. Nature 555 (7695):175-182. doi:10.1038/nature25753

Hayes JP (2010) Metabolic rates, genetic constraints, and the evolution of endothermy. J Evol Biol 23 (9):1868-1877. doi:10.1111/j.1420-9101.2010.02053.x

Hayes JP, Garland T (1995) The evolution of endothermy - testing the aerobic capacity model. Evolution 49 (5):836-847. doi:10.2307/2410407

Hayes JP, Garland T, Dohm MR (1992) Individual variation in metabolism and reproduction of *Mus*: are energetics and life-history linked? Funct Ecol 6 (1):5-14. doi:10.2307/2389765

Hedges LV, Olkin I (1985) Statistical methods for meta-analysis. Academic Press, San Diego, CA, U.S.A.

Herrera M, Castanheira MF, Conceicao LEC, Martins CI (2014) Linking risk taking and the behavioral and metabolic responses to confinement stress in gilthead seabream *Sparus aurata*. Appl Anim Behav Sci 155:101-108. doi:10.1016/j.applanim.2014.03.001

Johnston SL, Souter DM, Erwin SS, Tolkamp BJ, Yearsley JM, Gordon IJ, Illius AW, Kyriazakis I, Speakman JR (2007) Associations between basal metabolic rate and reproductive performance in C57BL/6J mice. J Exp Biol 210 (1):65-74. doi:10.1242/jeb.02625

Killen SS, Glazier DS, Rezende EL, Clark TD, Atkinson D, Willener AST, Halsey LG (2016) Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. Am Nat 187 (5):592-606. doi:10.1086/685893

Killen SS, Marras S, Metcalfe NB, McKenzie DJ, Domenici P (2013) Environmental stressors alter relationships between physiology and behaviour. Trends Ecol Evol 28 (11):651-658. doi:10.1016/j.tree.2013.05.005

Książek A, Zub K, Szafrańska PA, Wieczorek M, Konarzewski M (2017) The nexus of hair corticosterone level, immunocompetence, metabolic rates and overwinter survival in the root vole, *Microtus oeconomus*. Gen Comp Endocrinol 250:46-53. doi:10.1016/j.ygcen.2017.05.021

Lailvaux SP, Husak JF (2014) The life history of whole-organism performance. Q Rev Biol 89 (4):285-318. doi:10.1086/678567

Lajeunesse MJ (2013) Recovering missing or partial data from studies: a survey of conversions and imputations for meta-analysis. In: Koricheva J, Gurevitch J, Mengersen K (eds) Handbook of Meta-analysis in Ecology and Evolution. Princeton University Press, New Jersey, USA, pp 195-206

Larivee ML, Boutin S, Speakman JR, McAdam AG, Humphries MM (2010) Associations between over-winter survival and resting metabolic rate in juvenile North American red squirrels. Funct Ecol 24 (3):597-607. doi:10.1111/j.1365-2435.2009.01680.x

Le Galliard J-F, Paquet M, Cisel M, Montes-Poloni L (2013) Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances. Funct Ecol 27 (1):136-144. doi:10.1111/1365-2435.12017

Liu S, Fu S-J (2017) Effects of food availability on metabolism, behaviour, growth and their relationships in a triploid carp. J Exp Biol 220 (24):4711. doi:10.1242/jeb.167783

Martins CIM, Castanheira MF, Engrola S, Costas B, Conceicao LEC (2011) Individual differences in metabolism predict coping styles in fish. Appl Anim Behav Sci 130 (3-4):135-143. doi:10.1016/j.applanim.2010.12.007

Mathot KJ, Dingemanse NJ (2015) Energetics and behavior: unrequited needs and new directions. Trends Ecol Evol 30 (4):199-206. doi:10.1016/j.tree.2015.01.010

Mathot KJ, Dingemanse NJ, Nakagawa S (2019) The covariance between metabolic rate and behaviour varies across behaviours and thermal types: meta-analytic insights. Biol Rev 94 (3):1056-1074. doi:10.1111/brv.12491

Merritt L, Matthews PGD, White CR (2013) Performance correlates of resting metabolic rate in garden skinks *Lampropholis delicata*. J Comp Physiol B Biochem Syst Environ Physiol 183 (5):663-673. doi:10.1007/s00360-012-0736-x

Metcalfe NB, Van Leeuwen TE, Killen SS (2016) Does individual variation in metabolic phenotype predict fish behaviour and performance? J Fish Biol 88 (1):298-321. doi:10.1111/jfb.12699

Moher D, Liberati A, Tetzlaff J, Altman DG, The Prisma Group (2009) Preferred Reporting Items for Systematic Reviews and Meta-Analyses: the PRISMA statement. PLoS Med 6 (7):e1000097. doi:10.1371/journal.pmed.1000097

Nakagawa S, Ockendon N, Gillespie DOS, Hatchwell BJ, Burke T (2007) Assessing the function of house sparrows' bib size using a flexible meta-analysis method. Behav Ecol 18 (5):831-840. doi:10.1093/beheco/arm050

Nespolo RF, Franco M (2007) Whole-animal metabolic rate is a repeatable trait: a meta-analysis. J Exp Biol 210:2000-2005. doi:10.1242/jeb.02780

Nilsson J-Å (2002) Metabolic consequences of hard work. Proc Roy Soc Lond B Biol Sci 269 (1501):1735-1739. doi:10.1098/rspb.2002.2071

Norin T, Metcalfe NB (2019) Ecological and evolutionary consequences of metabolic rate plasticity in response to environmental change. Phil Trans Roy Soc Lond B Biol Sci 374 (1768):20180180. doi:10.1098/rstb.2018.0180

Orr HA (2009) Fitness and its role in evolutionary genetics. Nat Rev Genet 10:531-539. doi:10.1038/nrg2603

Pettersen AK, Marshall DJ, White CR (2018) Understanding variation in metabolic rate. J Exp Biol 221 (1):jeb166876. doi:10.1242/jeb.166876

Pettersen AK, White CR, Marshall DJ (2015) Why does offspring size affect performance? Integrating metabolic scaling with life-history theory. Proc Roy Soc Lond B Biol Sci 282 (1819). doi:10.1098/rspb.2015.1946

Pettersen AK, White CR, Marshall DJ (2016) Metabolic rate covaries with fitness and the pace of the life history in the field. Proc Roy Soc Lond B Biol Sci 283 (1831):20160323. doi:10.1098/rspb.2016.0323

Portugal SJ, Green JA, Halsey LG, Arnold W, Careau V, Dann P, Frappell PB, Grémillet D, Handrich Y, Martin GR, Ruf T, Guillemette MM, Butler PJ (2016) Associations between resting, activity, and daily metabolic rate in free-living endotherms: no universal rule in birds and mammals. Physiol Biochem Zool 89 (3):251-261. doi:10.1086/686322

R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing.Vienna, Austria

Radwan J, Kruczek M, Labocha MK, Katarzyna G, Koteja P (2004) Contest winning and metabolic competence in male bank voles *Clethrionomys glareolus*. Behaviour 141 (3):343-354. doi:10.1163/156853904322981897

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. Biol Rev 82 (2):291-318. doi:10.1111/j.1469-185X.2007.00010.x

Reid D, Armstrong JD, Metcalfe NB (2011) Estimated standard metabolic rate interacts with territory quality and density to determine the growth rates of juvenile Atlantic salmon. Funct Ecol 25 (6):1360-1367. doi:10.1111/j.1365-2435.2011.01894.x

Reinhold K (1999) Energetically costly behaviour and the evolution of resting metabolic rate in insects. Funct Ecol 13 (2):217-224. doi:10.1046/j.1365-2435.1999.003000.x

Rohatgi A (2017) WebPlotDigitizer https://automeris.io/WebPlotDigitizer.v4.0

Røskaft E, Järvi T, Bakken M, Bech C, Reinertsen RE (1986) The relationship between social status and resting metabolic rate in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). Anim Behav 34 (3):838-842. doi:10.1016/S0003-3472(86)80069-0

Sadowska ET, Baliga-Klimczyk K, Labocha MK, Koteja P (2009) Genetic correlations in a wild rodent: grass-eaters and fast-growers evolve high basal metabolic rates. Evolution 63 (6):1530-1539. doi:10.1111/j.1558-5646.2009.00641.x

Schimpf NG, Matthews PGD, White CR (2012) Standard metabolic rate is associated with gestation duration, but not clutch size, in speckled cockroaches *Nauphoeta cinerea*. Biol Open 1 (12):1185-1191. doi:10.1242/bio.20122683

Schimpf NG, Matthews PGD, White CR (2013) Discontinuous gas exchange exhibition is a heritable trait in speckled cockroaches *Nauphoeta cinerea*. J Evol Biol 26 (7):1588-1597. doi:10.1111/jeb.12093

Scholer MN, Arcese P, Puterman ML, Londoño GA, Jankowski JE (2019) Survival is negatively related to basal metabolic rate in tropical Andean birds. Funct Ecol 33 (8):1436-1445. doi:10.1111/1365-2435.13375

Speakman JR, Król E, Johnson MS (2004) The functional significance of individual variation in basal metabolic rate. Physiol Biochem Zool 77 (6):900-915. doi:10.1086/427059

Suarez RK (2012) Energy and metabolism. Compr Physiol 2:2527-2540. doi:10.1002/cphy.c110009

Turbill C, Ruf T, Rothmann A, Arnold W (2013) Social dominance is associated with individual differences in heart rate and energetic response to food restriction in female red deer. Physiol Biochem Zool 86 (5):528-537. doi:10.1086/672372

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. J Stat Softw 36 (3):1-48. doi:10.18637/jss.v036.i03

Walsh B, Blows MW (2009) Abundant genetic variation + strong selection = Multivariate genetic constraints: A geometric view of adaptation. Ann Rev Ecol Evol Syst 40:41-59. doi:10.1146/annurev.ecolsys.110308.120232

White CR, Alton LA, Crispin TS, Halsey LG (2016) Phylogenetic comparisons of pedestrian locomotion costs: confirmations and new insights. Ecol Evol 6:6712-6720. doi:10.1002/ece3.2267

White CR, Alton LA, Frappell PB (2012a) Metabolic cold adaptation in fishes occurs at the level of whole animal, mitochondria and enzyme. Proc Roy Soc Lond B Biol Sci 279 (1734):1740-1747

White CR, Blackburn TM, Martin GR, Butler PJ (2007) Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. Proc Roy Soc Lond B Biol Sci 274 (1607):287

White CR, Frappell PB, Chown SL (2012b) An information-theoretic approach to evaluating the size and temperature dependence of metabolic rate. Proc Roy Soc Lond B Biol Sci 279 (1742):3616-3621. doi:10.1098/rspb.2012.0884

White CR, Grémillet D, Green JA, Martin GR, Butler PJ (2011) Metabolic rate throughout the annual cycle reveals the demands of an Arctic existence in Great Cormorants. Ecology 92 (2):475-486

White CR, Kearney MR (2013) Determinants of inter-specific variation in basal metabolic rate. J Comp Physiol B Biochem Syst Environ Physiol 183 (1):1-26. doi:10.1007/s00360-012-0676-5

White CR, Marshall DJ, Alton LA, Arnold PA, Beaman JE, Bywater CL, Condon C, Crispin TS, Janetzki A, Pirtle E, Winwood-Smith HS, Angilletta MJ, Chenoweth SF, Franklin CE, Halsey LG, Kearney MR, Portugal SJ, Ortiz-Barrientos D (2019) The origin and maintenance of metabolic allometry in animals. Nat Ecol Evol 3 (4):598-603. doi:10.1038/s41559-019-0839-9

White CR, Schimpf NG, Cassey P (2013) The repeatability of metabolic rates declines with time. J Exp Biol 216:1763-1765. doi:10.1242/jeb.076562

White CR, Seymour RS (2004) Does BMR contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological and life history variables. Physiol Biochem Zool 77:929-941

Zeng L-Q, Wang L, Wang G-N, Zeng Y, Fu S-J (2017) The relationship between growth performance and metabolic rate flexibility varies with food availability in juvenile qingbo (*Spinibarbus sinensis*). Comp Biochem Physiol A Mol Integr Physiol 212:56-63. doi:10.1016/j.cbpa.2017.07.005

Figure legends

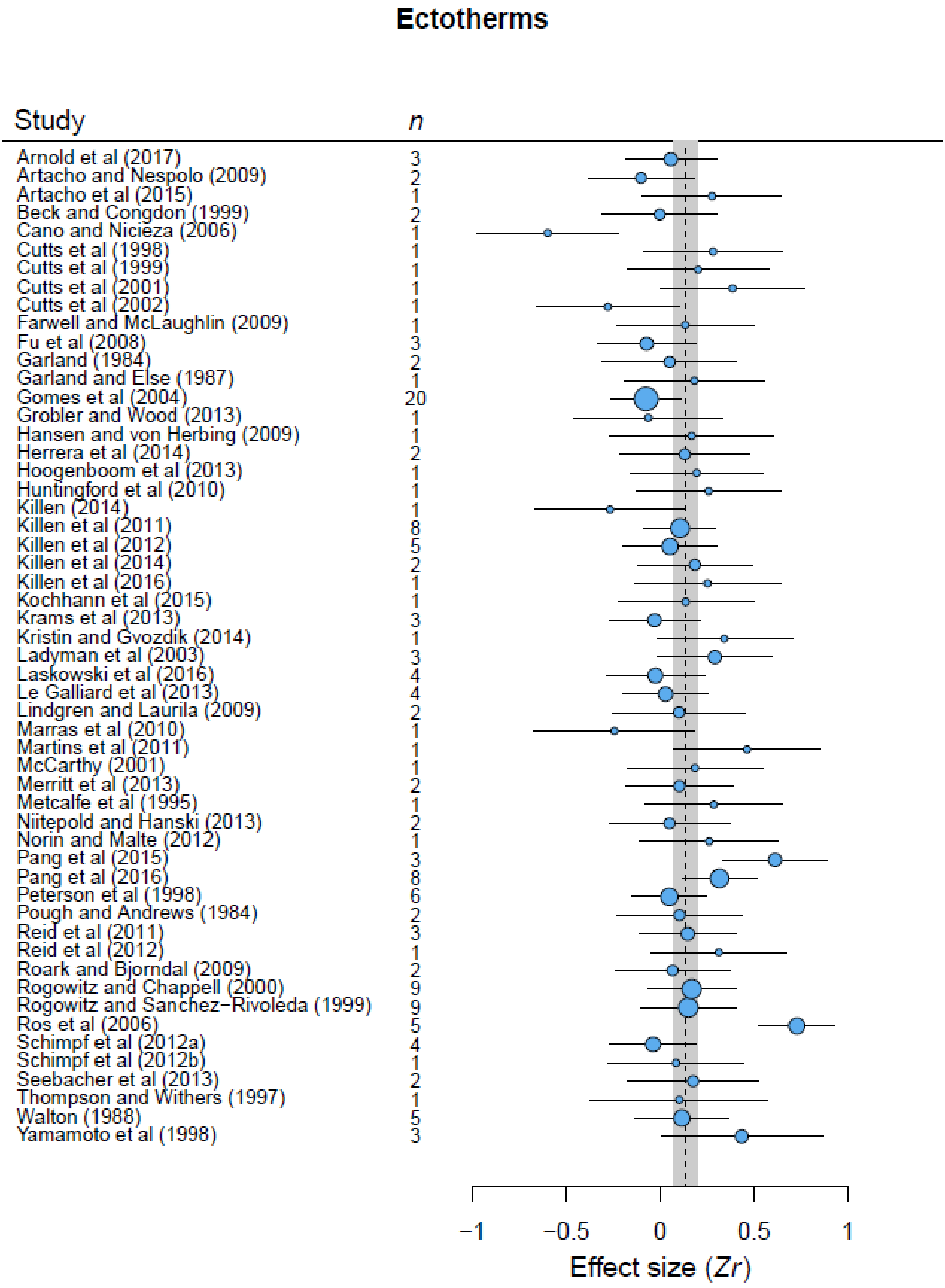
Fig. 1 Forest plot showing heterogeneity in effect size (*Zr*) among-studies on ectotherms included in the meta-analysis. *n* = number of RMR-fitness relationships observed within each study, and error bars show 95% CIs. The overall meta-analysis *Zr* value (±95% CIs) is shown with the dashed black line and grey shaded area. Size of data points reflects *n* within each study

Fig. 2 Forest plot showing heterogeneity in effect size (*Zr*) among-studies on endotherms included in the meta-analysis. *n* = number of RMR-fitness relationships observed within each study, and error bars show 95% CIs. The overall meta-analysis *Zr* value (±95% CIs) is shown with the dashed black line and grey shaded area. Size of data points reflects *n* within each study

Fig. 3 Effect size (*Zr*) estimates and 95% CIs of RMR-fitness relationships predicted from the highest-ranked meta-regression model (see main text, Table S4 and Table S5) across eight fitness categories (six fitness-related trait categories and two fitness categories) and between ectotherms (blue) and endotherms (red)

Fig. 4 Relationship between sample size (*n*) and effect size (*Zr*) of the relationship between metabolic rate and fitness components. Effect size is expressed as Fisher's *Z*-standardized correlation coefficients. Relationships reported as significant ($p < 0.05$) in their original publication are shown in orange and non-significant ($p > 0.05$) are shown in blue. Dashed black line represents $Zr = 0$, solid orange line is the intercept of the null meta-regression for reported significant relationships (± 95% CI; dashed orange line, $n = 133$), and solid blue line is the intercept of the null meta-regression for reported non-significant relationships (± 95% CI; dashed blue line, $n = 221$)

Figure 1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Pough and Andrews (1984) 2
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Rogowitz and Chappell (2000) 9
Rogowitz and Sanchez-Rivoleda (1999) 9
Ros et al (2006) 5
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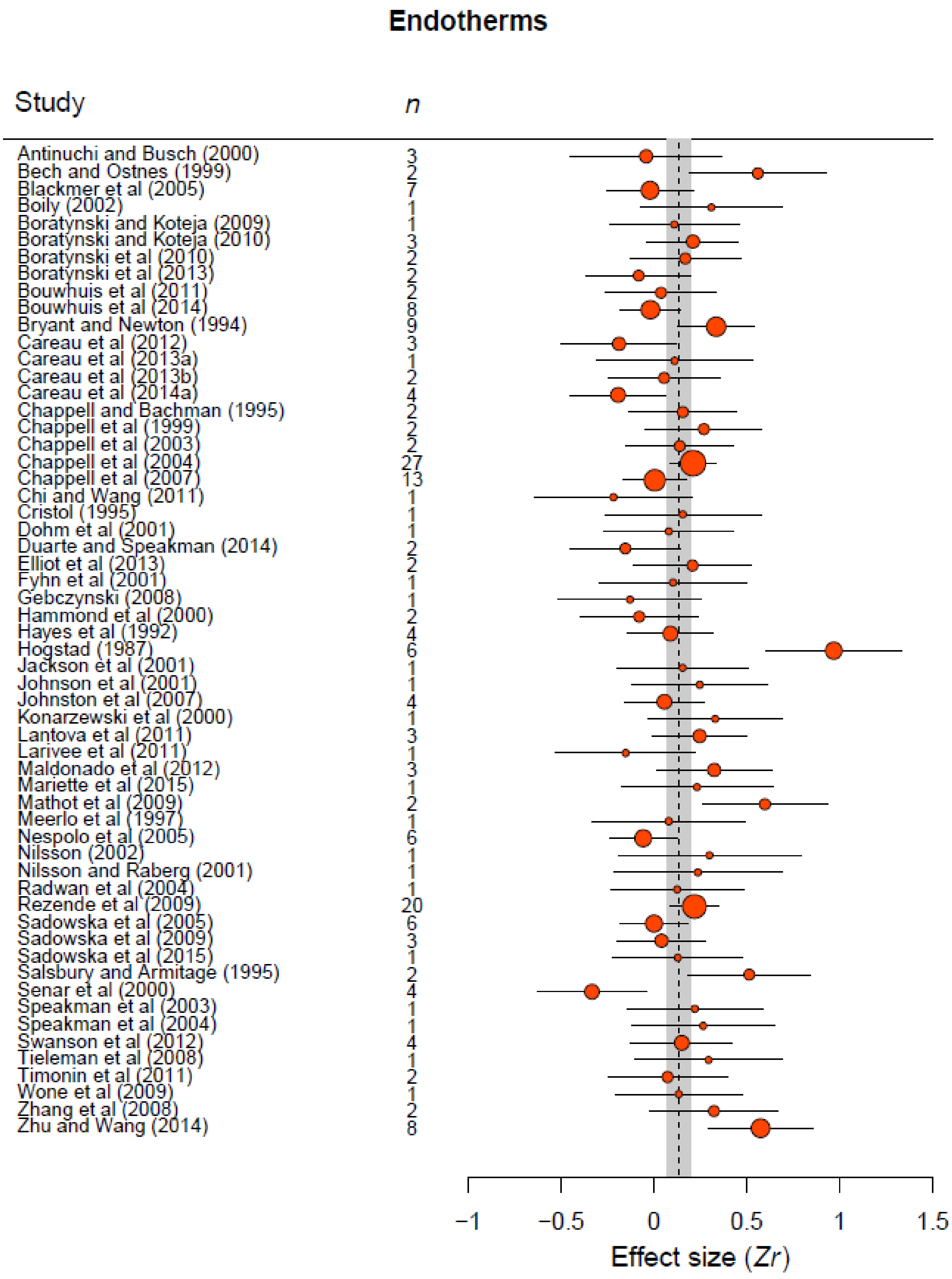
Figure 2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Bryant and Newton (1994) 9
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Elliot et al (2013) 2
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Hogstad (1987) 6
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Johnson et al (2001) 1
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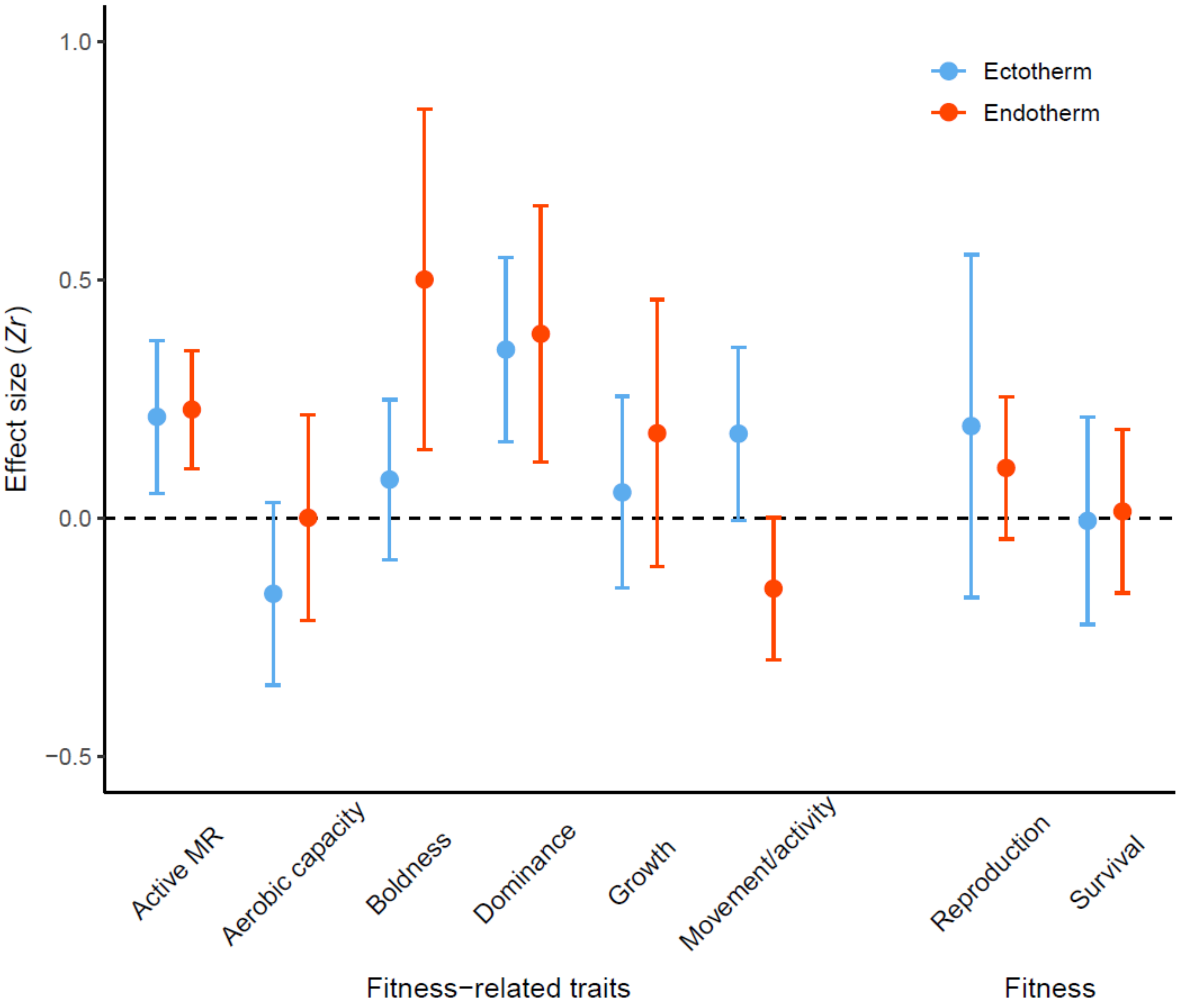
Konarzewski et al (2000) 1
Lantova et al (2011) 3
Larivee et al (2011) 1
Maldonado et al (2012) 3
Mariette et al (2015) 1
Mathot et al (2009) 2
Meerlo et al (1997) 1
Nespolo et al (2005) 6
Nilsson (2002) 1
Nilsson and Raberg (2001) 1
Radwan et al (2004) 1
Rezende et al (2009) 20
Sadowska et al (2005) 6
Sadowska et al (2009) 3
Sadowska et al (2015) 1
Salsbury and Armitage (1995) 2
Senar et al (2000) 4
Speakman et al (2003) 1
Speakman et al (2004) 1
Swanson et al (2012) 4
Tieleman et al (2008) 1
Timonin et al (2011) 2
Wone et al (2009) 1
Zhang et al (2008) 2
Zhu and Wang (2014) 8
−1
−0.5
0
0.5
1
1.5
Effect size (Zr)

753 **Figure 3**



754

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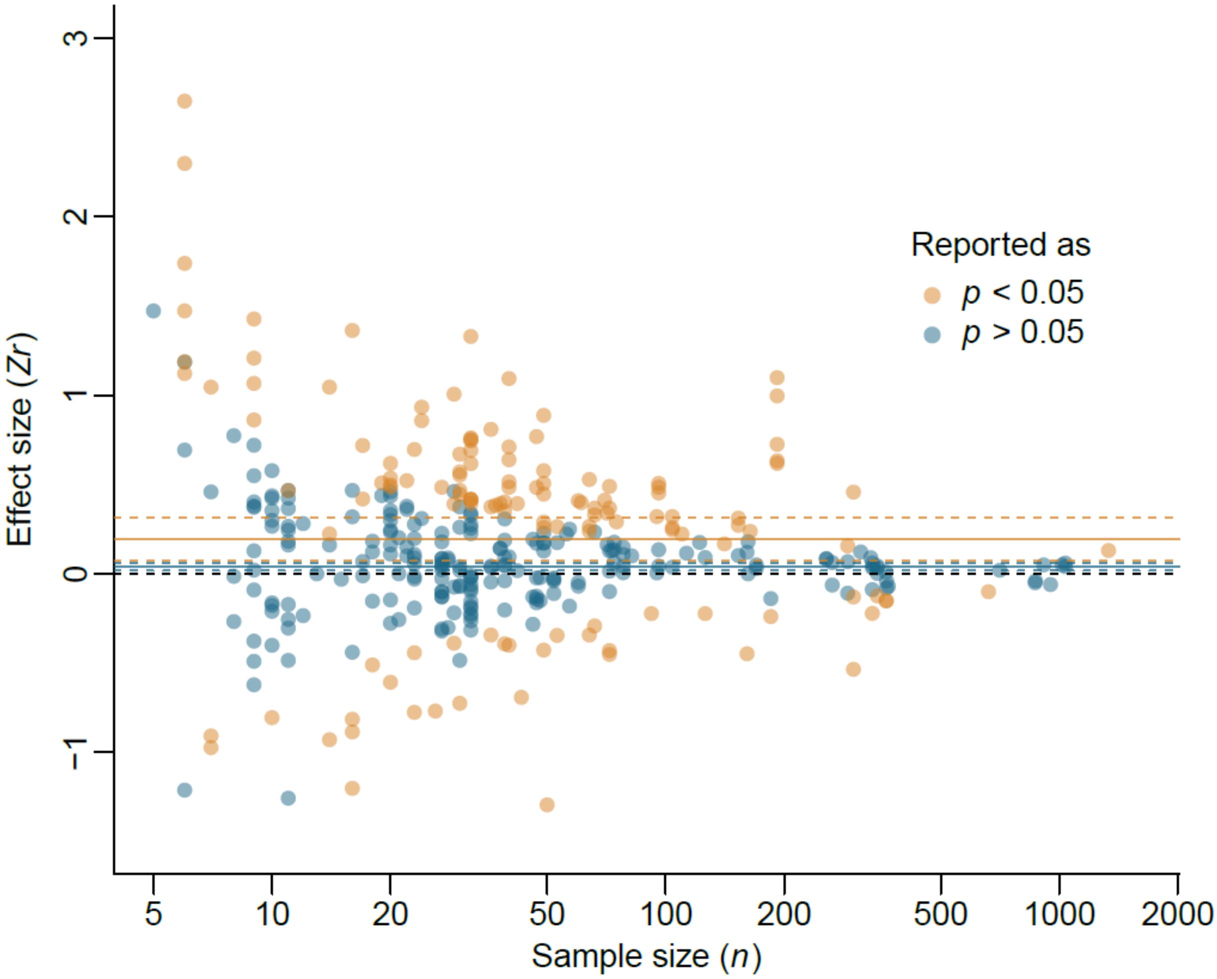
756 **Figure 4**



757