The covariance between metabolic rate and behaviour varies across behaviours and thermal types: meta-analytic insights

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Authorship statement: KJM, NJD and SN conceived of the study. KJM performed the literature review and extracted data estimates. SN assisted with data extractions and performed the meta-analysis. KJM and SN co-wrote the paper. All co-authors contributed to revisions.

Data accessibility statement: All data used for the analyses and all r-scripts are available from the Open Science Framework digital repository (DOI 10.17605/OSF.IO/GMVAB).

Running title: Metabolism and behaviour: a meta-analysis

Original version as submitted to Biological Reviews: 2018.05.02

Abstract

Energy metabolism has received much attention as a potential driver of repeatable among-individual differences in behaviour (animal personality). Several factors have been hypothesized to mediate this relationship. We performed a meta-analysis of >70 studies comprised of >8000 individuals reporting relationships between measures of maintenance metabolic rates (i.e., basal metabolic rate, resting metabolic rate, and standard metabolic rate) and behaviour. We evaluated support for three hypothesized mediators: 1) type of behaviour, 2) opportunities for energy re-allocation, and 3) magnitude of energetic constraints. Relationships between measures of maintenance metabolic rate (MR) and behaviour are predicted to be strongest for behaviours with strong consequences for energy turnover (acquisition or expenditure). Consistent with this, we found that behaviours with known consequences for energy gain (e.g., foraging, dominance, boldness) or expenditure (e.g., maximum sprint speed, sustained running speed, maximum distance travelled, etc.) had strong positive correlations with MR, while behaviours with putatively weak and/or inconsistent associations with net energy gain or loss (e.g., exploration, activity, sociability) were not correlated with MR. Greater opportunities for energy reallocation are predicted to weaken relationships between MR and behaviour by creating alternative pathways to balance energy budgets . We tested this by contrasting relationships between MR and behaviour in ectotherms versus endotherms, as thermoregulation in endotherms creates additional opportunities for energy reallocation compared with ectotherms. As predicted, the relationship between behaviour and metabolic rate (MR) was stronger in ectotherms compared with endotherms. However, statistical analyses of heterogeneity among effect sizes from different species did not support energy re-allocation as the main driver of these differences. Finally, we tested whether conditions where animals face greater constraints in meeting their energy budgets (e.g., field versus lab, breeding versus non-breeding) increased the strength of relationship between MR and behaviour. We found that the relationship between MR and behaviour was unaffected by either of these modifiers. This meta-analysis provides two key insights. First, we observed positive relationships of similar magnitude between MR and behaviours that bring in net energy, and behaviours that cost net energy. This result is only consistent with a performance energy management model. Given that the studies included in our meta-analysis represent a wide range of taxa, this suggests that the performance model may be the most common model in general. Second, we found that behaviours with putatively weak or inconsistent consequences for net energy gain or expenditure (exploration, activity, sociability) show no relationship with MR. This provides the first systematic demonstration of the central importance of the ecological function of traits in mediating relationships between MR and behaviour.

Keywords: among-individual differences, animal personality, basal metabolic rate, resting metabolic rate, routine metabolic rate, standard metabolic rate, energetic constraints, energy management strategy

Contents

I. Introduction

The last decade has seen a surge of interest in understanding the causes and consequences of among-individual differences in behaviour (i.e. animal personality). The majority of adaptive explanations for animal personality are based on state-dependence (Dingemanse & Wolf, 2010; Sih *et al.*, 2015; Wolf & Weissing, 2010), where state is broadly defined as any factor that influences the payoffs of a given behavioural action (Houston & McNamara, 1999). State variables related to energy metabolism in particular have been the subject of much attention in this burgeoning area of research (e.g., Biro *et al.*, 2010; Careau & Garland, 2012; Careau *et al.*, 2008; Houston, 2010; Mathot & Dall, 2013; Mathot & Dingemanse, 2015; Wolf & McNamara, 2012), and the number of empirical studies investigating links between metabolism and behaviour has grown dramatically in the last several years (reviewed in Biro & Stamps, 2010; Careau & Garland, 2012; Mathot & Dingemanse, 2015; Niemelä & Dingemanse, 2018; Royauté *et al.*, 2018).

Several papers have called attention to the fact that relationships between measures of maintenance MR (i.e., basal metabolic rate, resting metabolic rate, and standard metabolic rate) and behaviour are likely mediated by interacting factors (Biro & Stamps, 2010; Careau & Garland, 2012; Careau *et al.*, 2008; Killen *et al.*, 2013; Mathot & Dingemanse, 2015; Speakman *et al.*, 2004). For example, the energy management model of an organism (i.e., how maintenance MR covaries with total energy expenditure) (Biro & Stamps, 2010; Careau & Garland, 2012; Careau *et al.*, 2008; Mathot & Dingemanse, 2015; Speakman *et al.*, 2004), the type of behaviour (Biro & Stamps, 2010; Mathot & Dingemanse, 2015), the extent to which there are alternative allocation opportunities (Careau & Garland, 2012; Mathot & Dingemanse, 2015), and environmental stressors (Biro & Stamps, 2010; Killen *et al.*, 2013) are all expected to shape the relationships between MR and behaviour.

Here, we performed a meta-analysis of existing studies to assess the overall support for a relationship between MR and behaviour. In addition, we evaluated the importance of several of the factors that have been proposed to mediate these relationships: 1) the type of behaviour, 2) the opportunities for energy re-allocation, and 3) the degree of energetic stress. Below, we detail the rationale and predictions for each of these proposed mediators.

(1) Does covariation between MR and behaviour depend on the type of behaviour?

Assuming that variation in MR reflects variation in energy requirements, then to balance their energy budgets, variation in MR can be logically expected to be associated with variation in either behaviours that bring in net energy (e.g. foraging, food defense, foraging boldness), or cost net energy (e.g. movement, mate defense, etc.) (Biro & Stamps, 2010; Careau & Garland, 2012; Careau *et al.*, 2008; Mathot & Dingemanse, 2015; Speakman *et al.*, 2004). However, variation in MR inferred from measures of oxygen consumption may not reflect true differences in energetic requirements if organisms differ in their mitochondrial efficiency (i.e., the amount of adenosine triphosphate, ATP, generated per molecule of oxygen consumed) (Salin *et al.*, 2015). Although there is evidence for among-individual differences in mitochondrial efficiency (reviewed in Salin *et al.*, 2015), we do not address this here given that paucity of studies simultaneously recording among-individual differences in MR, mitochondrial efficiency, and behaviour.

Assuming variation in oxygen consumption does reflect variation in energy requirements, the direction of the relationship between MR and behaviours that cost net energy depends on the energy management model of the organism. Three energy management models have been described which reflect three distinct relationships between MR and daily energy expenditure (DEE). Under the allocation model (also called the compensation model), DEE does not vary as a function of MR (Careau & Garland, 2012; Careau *et al.*, 2008; Mathot & Dingemanse, 2015). Thus, logically, variation in MR is not predicted to be associated with variation in behaviours that bring in net energy (e.g., foraging) (Mathot & Dingemanse, 2015). However, because organisms work with a fixed energy budget, high MR means a relatively smaller fraction of energy available for energetically costly behaviours (e.g., sustained sprint speed) (Careau & Garland, 2012; Careau *et al.*, 2008; Mathot & Dingemanse, 2015). Under the independent model (also referred to as compensation model), the energy devoted to activity is independent of MR, i.e., the amount of energy expended on activities above basic maintenance does not vary with MR (Careau & Garland, 2012; Mathot & Dingemanse, 2015). However, this still has the consequence that total energy required, DEE, does increase with increasing MR, and therefore, a positive relationship is predicted between MR and behaviours such as foraging (Mathot & Dingemanse, 2015). Finally, under the performance model (also referred to as increased intake), the capacity of an organism to bring in energy is positively correlated with MR (Careau & Garland, 2012; Careau *et al.*, 2008; Mathot & Dingemanse, 2015). Thus, organisms adopting a performance model would be predicted to have higher expressions of both behaviours that bring in net energy, and behaviours that cost net energy.

Few studies directly assess the relationship between MR and DEE (but see Portugal *et al.*, 2016), thus the energy management model is typically an untested assumption (Mathot & Dingemanse, 2015). Assuming that existing studies comprise a mix of study species that adopting each of the three potential energy management models, we would predict that there should generally be stronger support for a positive relationship between behaviours that are associated with increased intake rate or increased access to resources (e.g. foraging, foraging boldness, foraging dominance) compared with behaviours that cost net energy (e.g. courtship/mating, stress responses and performance measures such as maximum sprint speed). This is because two of the three energy management models predict a positive relationship between MR and resource acquisition (independent and performance models) while the third predicts no relationship (allocation model). In contrast, only one of the three energy management models predicts a positive relationship between MR and behaviours that consume net energy (performance model), the others predict either no relationship (independent model), or a negative relationship (allocation model).

Notably, many studies investigating relationships between behaviour and metabolic rate quantify behaviours for which the functional significance in terms of net energy gain/loss is unclear. For example, exploration behaviour in novel environmental conditions and general activity, are two commonly measured behaviours in studies of repeatable among-individual variation. Activity measures the speed with which an organism moves through a familiar environment, and exploration is typically defined as the speed with which an individual moves through a novel environment (Réale *et al.*, 2007). Although the expression of these behaviours undoubtedly involve energetic costs, they are often also assumed to determine the rate with which organisms encounter resources. Thus, depending on the intensity of activity and exploration and the extent to which they determine encounter rates with food, a high expression of activity or exploration may be associated with large net energy costs, large net energy gains, or anything in between (Biro & Stamps, 2010; Careau & Garland, 2012; Carter *et al.*, 2013). Thus, relationships between activity or exploration and MR will likely differ for different species, or under different ecological contexts, therefore, overall relationships between MR and exploration or activity are predicted to be weak or non-existent (Careau & Garland, 2012; Carter *et al.*, 2013; Mathot & Dingemanse, 2015). Similarly, it is unclear how sociability (the propensity to affiliate with congeners) should influence net energy gain or loss. On the one hand, being more strongly affiliated with congeners may decrease expected intake through resource competition. On the other hand, it may allow for increased feeding rates if sociable animals can reduce their relative investment in vigilance due to dilution or group vigilance effects. Thus, we do not predict a consistent net effect of sociability on energy gain or energy loss, and therefore, predict either no or weak relationships between sociability and MR.

(2) Do opportunities for alternative energy allocation decisions weaken relationships between MR and behaviour?

Assuming that the energy management model of a study system is known, we can predict how metabolic rate should covary with behaviours that facilitate net energy gain versus net energy loss *in general*.

However, animals are able to allocate the energy available for such behaviours to a variety of different behaviours (e.g. foraging, foraging boldness, food defense). The ability to allocate among multiple behaviours means that even if metabolic rate is predicted to covary positively with behaviours that bring in net energy, it need not covary positively with *all* behaviours that bring in net energy (Mathot & Dingemanse, 2015). Opportunities to reallocate energy across different behaviours that have the same net consequence for energy balance means that associations between MR and specific behaviours may not match the relationship between MR and behaviours in general. Consider the following, very simplified, example. In a system with an independent energy management model, higher MR is predicted to be associated with greater expression of behaviours that bring in net energy (see Figure 1, Mathot & Dingemanse, 2015). Imagine that an organism has the ability to allocate between just two behaviours that bring in net energy; foraging boldness (green) or resource defense (blue). Note that resource defense is only predicted to occur when organism experience net benefits from defense (i.e., the resource is economically defendable), thus, despite costs associated with territory defense, the behaviour would still be associated with net energetic gains (Davies *et al.*, 2012). In this simplified scenario, alternative allocation decisions between these two behaviours may create scenarios where both behaviours show the predicted positive correlation with MR (Figure 1a), or only one behaviour shows the predicted relationship (i.e., resource defense, Figures 1b-c). Note that it is even possible for specific behaviours (i.e., foraging boldness) to show relationships with MR that are opposite to the predicted relationship for a given energy management model (in this case, the independent model), so long as other behaviours (i.e., resource defense) are sufficiently upregulated to offset this (Figure 1c).

We test the idea that a greater number of alternative options for energy allocation will weaken the strength of relationships between MR and behaviour by contrasting endotherms with ectotherms. Thermoregulation introduces additional allocation opportunities for endotherms, for example, because heat produced through activity can be used to offset thermoregulation costs (Careau & Garland, 2012;

Careau *et al.*, 2014; Humphries & Careau, 2011). Thus, we predict that the relationships between MR and behaviour will be weaker in endotherms compared with ectotherms.

(3) Does energetic stress promote stronger relationships between metabolic rate and behaviour?

Environmental stressors can alter the relationship between MR and behaviour, though the direction of the effect may differ for different types of stressors (Killen *et al.*, 2013). However, the rationale for relationships between MR and behaviour is based in part on the assumption that balancing one's energy budget is challenging. Environmental stressors that create greater challenges for organisms in terms of balancing their energy budgets (e.g., reduced food availability, breeding), are expected to strengthen the relationships between MR and behaviour (Mathot & Dingemanse, 2015; Ricklefs & Wikelski, 2002). We test this prediction in two ways: 1) by testing for an effect of reproductive status (reproductive versus non-reproductive), and 2) by testing for an effect of captivity (free-living versus wild-caught captive animal versus lab-reared captive animal). We assume that animals face greater challenges in balancing their energy budgets during reproduction due to increased energetic costs (e.g., production of offspring, parental care). For animals that engage in parental care, reproduction may also decrease time available for self-feeding, and thereby further challenge animals to balance their energy budgets. Consequently, we predicted that the strength of the relationship between MR and behaviour would be greater in reproductive versus non-reproductive animals. We also assume that free-living animals face greater challenges in balancing their energy budgets compared with captive animals, because captive animals are typically provided with predictable, *ad libitum*, access to food. Therefore, we predicted that relationships between MR and behaviour would be stronger in free-living animals compared with lab-reared animals. We also distinguished wild-caught animals that were tested in captivity, as they may be expected to be intermediate to free-living and lab-reared animals depending on the time-scale across which animals adjust to ad-libitum food conditions in captivity.

II. Methods

(1) Data collection and inclusion/exclusion criteria

We followed the steps outlined in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocol (Moher *et al.*, 2009) for our meta-analysis as closely as possible, as recommended by Nakagawa and Poulin (2012). We performed a literature search using two online databases; *Scopus* (subject area: Life Sciences) and Web of Science. We included all available years up to August 2016 (when the search was last updated). We had both behavioural and metabolism search terms. The behavioural search terms used were: behavio*, “coping strategy”, “coping style”, personality, and temperament. The metabolism search terms were: “basal metabolic rate”, BMR, “resting metabolic rate”, RMR, “standard metabolic rate”, SMR and “routine metabolic rate”. We searched for articles including these terms in the “Topic” field. Articles had to include at least one of the behavioural search terms and one of the metabolism search terms. Our meta-analysis was focused on non-human animals thus, to eliminate human studies, we additionally excluded articles that had any of the following terms in the Topic field: child*, infant, baby, patient, women, men, student, person, elderly, boy or girl.

We performed the initial literature search on 30 June 2014, and later updated the search on 24 August 2016. The second search was restricted to articles published after 2013 to reduce the number of references duplicated from the initial search. These literature searches produced a total of 2614 unique references. These references were screened by reading the titles and abstract to assess their relevance to the meta-analyses. We selected studies according the following five criteria:

(1) The study had to include one of the following measures of metabolic rate: resting metabolic rate, standard metabolic rate, basal metabolic rate, routine metabolic rate. We excluded studies that only reported metabolic rates in active animals (except in fish, because water must flow over the gills for fish

to respire), such as summit metabolic rate, daily energy expenditure, sustained metabolic rate, etc. This was to reduce the extent to which the measured MR was confounded with behaviour.

(2) The behaviour had to be measured outside of the MR measurements. For example, activity during MR was not considered a valid behaviour. Again, this was to avoid scenarios where the MR measure and behaviour were confounded.

(3) The study had to present a correlation between the appropriate measure of MR and a behaviour, or present statistics that allowed for the correlation to be estimated indirectly. Thus, studies which only presented categorical data on MR or behaviour were not included with the exception of studies investigating links between dominance and MR. This is because dominance is not an individual trait, but a relative trait, thus paired comparisons of MR rate in relation to dominance status (categorical: dominant or subordinate) were also included.

(4) The correlation provided had to be either a raw (un-partitioned) phenotypic correlation or an among-individual correlation. We did not consider within-individual correlations (not the targeted hierarchical level) or genetic correlations. Although genetic correlations represent the relevant hierarchical level (i.e., among-individual), there were insufficient studies providing such estimates (N = 2 studies, Careau *et al.*, 2011; Mathot *et al.*, 2013) to allow us to compare the effects sizes of genetic correlations with either among-individual or un-partitioned phenotypic correlations. One of these studies was nonetheless included in the meta-analysis as it additionally provided estimates of raw un-partitioned phenotypic correlations (Careau *et al.*, 2011). One study (Gifford *et al.*, 2014) presented both among-individual and un-partitioned phenotypic correlations for two behavioural traits (foraging and exploration). Both types of correlations were included in the meta-analysis and coded appropriately. The resultant non-independence was accounted for by additionally assigning a group ID to estimates derived from the same sample of individuals.

(5) The study had to provide sufficient information to allow for sample size, estimated effect size via descriptive or inferential statistics, and uncertainty to be extracted. In some cases, the study did not directly report the relevant information, but the information could be extracted from data provided in the supplementary material, from the published data set, or from data presented in figures.

These selection criteria resulted in a list of 71 papers and 5 published datasets that were appropriate for our meta-analysis (ESM Table S1). Studies that did not fulfill our selection criteria are listed in the electronic supplementary material (ESM Table S2) along with the reason for their exclusion. When the relevant data was presented in figures, we extracted the data using WebPlotDigitizer 3.8 (http://arohatgi.info/WebPlotDigitizer/). The 76 sources (71 articles and 5 published data sets) for relevant effect size estimates produced a total of 163 estimates from 48 species (Table 1). The full PRISMA flow chart is provided in Figure 2.

Our meta-analysis was intended to focus on among-individual correlations between MR and behaviour. We nonetheless included studies that reported both among-individual correlations and raw (i.e., un-partitioned phenotypic) correlations. Raw correlations represent a mix of within- and among-individual correlations and may not accurately reflect the correlation structure at the level of interest (in our case, among-individual) when within- and among-individual correlations are qualitatively different (e.g., positive versus negative) (Dingemanse *et al.*, 2012). We tested whether estimates derived from among-individual (N = 41 estimates) versus phenotypic correlations (N = 122 estimates) differed and found no support for a difference. Importantly, the estimated difference was close to zero (the contrast between the two: $\beta_{[\text{difference in } Zr]} = 0.003$, 95% confidence interval, CI = [-0.165, 0.170]; see the section '*Meta-analysis and meta-regression analysis*' below for the details of the statistical model). This suggests that in our data set, within- and among-individual correlations are quantitatively and qualitatively similar, otherwise, estimated phenotypic correlations would not be identical to estimated among-individual correlations.

A previous meta-analysis found that within-individual correlations between state and behaviour were significantly weaker than among-individual correlations (Niemelä & Dingemanse, 2018). However, when considering only correlations between MR and behaviour, the contrast between among- and within-individual correlations were not significantly different (P. Niemelä, personal comment). Further, based on the strong support for lack of difference between phenotypic and among-individual correlations in the present dataset, we did not treat among-individual correlations and un-partitioned phenotypic correlations separately in any subsequent analyses.

(2) Data coding and calculation of effect sizes

We collected and transformed relevant study results into the standardised effect statistic, Fisher's *z*-transformation statistic (*Zr*); *Zr* (a transformation of correlation) was chosen because we were interested in the relationship between two variables, metabolism and behaviour (c.f. Nakagawa *et al.*, 2017). Behaviours were grouped into nine broad categories and were always coded such that higher values represented higher expression of behaviours associated with greater energy expenditure and/or acquisition (see ESM Table S3 for behaviours and definitions). Thus, effect size estimates obtained for relationships between MR and behaviours such as latency scores (e.g., latency to resume feeding) were multiplied by -1 so that positive estimates indicated that higher MR was associated with higher expression of behaviours that bring in net energy (resuming feeding). For behaviours that we presumed to have weak or inconsistent relationships with energy turnover (activity, exploration, sociability), data were coded such that higher values indicated higher expression of those traits.

Following recommendations from Noble *et al.* (2017) we preferentially collected descriptive statistics (e.g. correlations, group means, standard deviations and standard errors) over inferential statistics (t, F, χ^2, U and p). Both descriptive and inferential statistics were transformed using formulas found in the following references (Krishnamoorthy, 2006; Lipsey & Wilson, 2001; Nakagawa & Cuthill, 2007) and using an effect size determination program (Wilson, 2001). Note that we only retained effect sizes from inferential statistics when directions could be determined (e.g., F, χ^2, and p do not have directional information), and directions of effect sizes were adjusted in a way that all positive effect sizes meant strong correlations between metabolism and behaviour that either bring in or consume net energy (see above). For the calculation of *Zr*'s sampling variance, we use the number of independent subjects (i.e. $1/(i - 3)$; i = the number of subjects). For phenotypic correlations, this provides a more conservative estimate of sampling variance compared with using the total number of observations. We also collected more information for each data point for use as moderators to explain potential heterogeneity and bias in the data (e.g., species information, ectothermic *vs*. endothermic, types of behaviour, publication year). The details of these potential moderators are summarized in the published dataset (https://osf.io/gmvab/).

(3) Meta-analysis and meta-regression analysis

We employed phylogenetic multilevel meta-analysis (PMMA) to control the effect of phylogeny and other types of non-independence (Hadfield & Nakagawa, 2010; Nakagawa & Santos, 2012). We used the function, *rma.mv* from the R package, *metafor* (Viechtbauer, 2010). A PMMA requires a phylogenetic tree so we constructed a tree using the R package rotl (Michonneau *et al.*, 2016) which uses the Open Tree of Life data (Hinchliff *et al.*, 2015). The resulting phylogenetic tree did not have tree branch length estimates. Therefore, we used the function compute.brlen, in the R package ape (Paradis *et al.*, 2004) to estimate branch lengths. With this function, we used the method of Grafen (1989), setting the power to 1, to create an ultrametric tree closely imitating the Brownian motion model of evolution. We used this ultrametric tree for PMMA by converting it to a correlation matrix (using the vcv function from ape).

We first constructed a meta-analytic model (only with the intercept) with four random factors: 1) species identity (a non-phylogenetic component of species), 2) phylogeny (a phylogenetic component of species), 3) group (i.e., unique set of individuals because the same individuals could be used to estimate multiple relationships between MR and behaviour) and 4) observation (effect size) level random effect (equivalent to the residual term in a normal linear model). The species term captures the similarities of effect sizes within the same species, while the phylogenetic term represents the similarity due to common ancestors (Hadfield & Nakagawa, 2010). For a meta-analysis, the quantification of variance not due to sampling errors, known as heterogeneity or I^2 (Higgins & Thompson, 2002). We calculated the multilevel-model version of heterogeneity, which quantify I^2 for each random effect as well as the total heterogeneity, following Nakagawa and Santos (2012).

We then created a set of meta-regression models, which address our three main questions (see Introduction). The first model added nine behavioural types (activity, boldness, courtship, dominance, exploration, foraging, performance, sociability, and stress response) as a categorical moderator to the meta-analytic model above (see ESM Table S3 for definitions). The second model had the thermal types (endotherms and ectotherms) as a moderator along with an extra random factor, behavioural types (because the first model showed that this categorical variable was important; we also note that the same random-factor structure was used for the model comparing among-individual and phenotypic correlations, above). We also created meta-analytic models for endotherms and ectotherms separately to quantify heterogeneity for both thermal types (total I^2 and I^2 for the four different random terms). Finally, we tested the effects of the breeding statuses (breeding versus non-breeding) and the testing conditions (free-living, wild-caught and tested in captivity, captive reared and tested) by constructing two separate models with the same random factors as the second model. For meta-regression models, we calculated R^2 as the marginal R^2 in mixed models described in Nakagawa and Schielzeth (2013); in meta-analysis, R^2 consisted of variance accounted for after taking away sampling error. Complete details of meta-analytic and meta-regression models are available through the Open Science Framework repository (R-markdown file along with our data set: DOI 10.17605/OSF.IO/GMVAB; web address: https://osf.io/gmvab/).

(4) Publication bias analysis and sensitivity analysis

In the past, meta-analyses often identified temporal tends of declining effect size over time, known as the time-lag effect (Jennions & Møller, 2002; Trikalinos & Ioannidis, 2006). We tested this as a part of our publication bias analysis, by including the publication year as a moderator; we created a uni-moderator model with only the publication year as a moderator (along with the five random factors as described above) and a full model with publication year, thermal type, breeding status, and place of origin/testing conditions fitted as fixed effects. The analysis of the time-lag effect showed an important effect of the publication year (see below). Thus, we decided to add a set of sensitivity analyses where we repeated the analysis using meta-analyses and meta-regression with the data since 2007, because this represented the year with a marked increase in the number of studies per year that met the criteria for inclusion in our meta-analysis and because the time trend was not significant after 2007 (see Results for further details).

Publication bias analysis often includes Egger regression tests along with funnel plots (Egger *et al.*, 1997) and trim-and-fill tests (Duval & Tweedie, 2000a; Duval & Tweedie, 2000b). However, multilevel (non-independent) data are not amenable to these methods in their original forms. We applied these two methods to the meta-analytic residuals, which consist of the effect-size level effects (equivalent to normal residuals) and sampling errors (sensu Nakagawa & Santos, 2012). The meta-analytic residuals were taken from the full model above as this model should have accounted for most heterogeneity in our data set.

III. Results

Overall, a phylogenetic multilevel meta-analytic model revealed that MR and behaviour were significantly and moderately correlated ($\beta_0 = 0.261$, 95% confidence interval, CI = [0.053, 0,469]; Table 1 and Figure 3A). However, the observed total heterogeneity was high ($I^2_{[total]} = 93.00\%$), implying that this correlation was contingent upon moderators; this set the stage for our meta-regression models (see Table 2). Notably, approximately 21% of variation in the data were explained by phylogeny (Table 2). The first meta-regression model showed that the type of behaviour accounted around 20% of the variation ($R^2 = 19.06\%$), with boldness, dominance, foraging and stress showing moderate to large, significant correlations with metabolic rate, MR (Figure 3A), while activity, exploration and sociability showed little or zero correlation with MR. Though not significant, courtship and performance showed moderate correlations with MR (complete contrasts among the behaviour types are in the ESM, Figure S1).

The second meta-regression on the thermal types showed that the mean effect for ectotherms was significant and moderate ($\beta_{[ectotherm]} = 0.301$, 95% CI = [0.102, 0.500]), and that for endotherms the effect was non-significant and weak ($\beta_{[endotherm]} = 0.151$, 95% CI = [-0.076, 0.378]; Figure 4; also see Figure S2), although the contrast between the two was not significant ($\beta_{[contrast]} = -0.150$, 95% CI = [-0.355, 0.056], $Q_{M[df = 68]} = 2.031$, p = 0.15; $R^2 = 3.88\%$; Figure 4). The separate meta-analytic models mirrored the results from the meta-regression, apart from the mean effect for endotherms being significant ($\beta_{[ectotherm]} = 0.297$, 95% IC = [0.0445, 0.548]; Figure 3B; $\beta_{[endotherm]} = 0.101$, 95% CI = [0.033, 0.200]; Table 1, Figure 3C). In the corresponding meta-regression models incorporating the different behaviour types, we found similar patterns observed in the meta-regression model with all data, but the patterns were, in general, stronger for ectotherms and weaker for endotherms than for all species together (compare panels A, B and C in Figure 3). The magnitude of heterogeneity was high for both meta-analytic models ($I^2_{[total]} = 94.16\%$ for ectotherms and $I^2_{[total]} = 81.22\%$ for endotherms). Notably, much of heterogeneity in the ectotherm data came from the phylogenetic and non-phylogenetic effects of species ($I^2_{[phylogeny]} = 18.20\%$

and $I^2_{[species]}$ = 44.52%, respectively) whereas there was virtually zero variation resulting from phylogeny or species in the endotherm data (Table 2). In our final meta-regression models, in contrast to our predictions, we did not find significant effects of the breeding status ($Q_{M[df = 2]}$= 1.047, p = 0.592; R^2 = 0.70%) or testing conditions (i.e., free-living, wild-caught and tested in captivity, captive reared and tested) ($Q_{M[df = 2]}$ = 0.592, p = 0.744, R^2 = 0.45%; Figure 4; Figure S2).

We found a time-lag effect in our data set: there was a significant trend of decreasing effect size with publication year ($\beta_{[year]}$ = -0.0132, 95% IC = [-0.0250, -0.0015]; $Q_{M[df = 1]}$ = 4.8644, p = 0.027; R^2 = 4.62%; Figure 5). As a sensitivity analysis, we repeated the main analyses (the analyses shown in Figure 3 and Table 2) using only data points published from 2007 onwards, because 2007 was the year in which the number of studies on this topic showed a sharp increase and because the time trend was not significant after 2007 ($\beta_{[year]}$ = 0.0123, 95% IC = -0.0185, 0.0431); $Q_{M[df = 1]}$ = 0.610, p = 0.434; see Figure 5 & Figure S3). The results of these analyses were quantitatively very similar to the original analyses (see ESM Figure S4, Table S4 & Table S5). An Egger's regression test on the meta-analytic residuals from our full model suggested no evidence for funnel asymmetry ($\underline{t}_{[df = 161]}$ = 0.225, p = 0.822). However, a visual inspection of the funnel plot showed some hint of asymmetry (Figure 6) and this was corroborated by the results from a trim-and-fill test. The trim-and-fill test indicated that seven data points were potentially missing (p = 0.0039 for the hypothesis for no missing data points). The meta-analytic mean incorporating these seven filled points was -0.022 (95% CI = [-0.066, 0.022]; Figure 6B). This result means we could have overestimate the meta-analytic mean in the original model by 0.022, but this amount is negligible (see Figure 3 and Table 2). Taken together, we conclude that our results are robust against publication bias.

IV. Discussion

We used meta-analyses to test for general relationships between MR and behaviour, as well as the importance of several putative modifiers of the relationship. We demonstrate the importance of two moderators of the magnitude of the relationship between MR and behaviour; the type of behaviour, and the thermal type of the organism (endotherm versus ectotherm). However, we did not find any support for the notion that conditions that impose greater energetic stress on organisms (breeding versus non-breeding or captive vs. free-living), strengthen the relationship between MR and behaviour. Unexpectedly, despite identifying several important moderators for the relationship between MR and behaviour, we found support for an overall relationship between MR and behaviour even when not accounting for any moderators. We discuss the implications of these findings for understanding the functional significance MR and its relationship with behaviour.

(1) Covariation between MR and behaviour depends on the type of behaviour

Several recent conceptual papers have highlighted the fact that both the magnitude and direction of the relationship between MR and behaviour are likely to be influenced by several moderators (Careau & Garland, 2012; Killen *et al.*, 2013; Mathot & Dingemanse, 2015). For example, the strength of the relationship should differ for different types of behaviour. In particular, behaviours associated with net energy expenditure or net energy gain are expected to have the strongest functional linkage with MR (Biro & Stamps, 2010; Careau & Garland, 2012; Mathot & Dingemanse, 2015). Our results support this prediction. Behaviours that cost net energy or brought in net energy were positively correlated with MR, consistent with a performance energy management model.

The strongest relationship between MR and behaviour was found for stress response (response to human handling), a putatively energetically costly trait (Koolhaas *et al.*, 2011; Manzur *et al.*, 2014). Higher metabolic rates were associated with quicker escape latencies from observers, greater struggle rates and higher breath rates. There was also a moderately strong, albeit non-significant, correlation between ‘performance’ traits (e.g., maximum sprint speed, maximum sustained activity, etc.), which are also energetically demanding behaviours. Although courtship behaviour is often assumed to be energetically costly, we found a weak and non-significant relationship between MR and courtship/mating behaviours. However, our analysis of courtship behaviour was based on only three studies (Figure 3); two studies of calling rates, and one study of copulation duration. This is not a comprehensive sample of courtship behaviours. Given that the relationship between courtship behaviours and net energy expenditure may vary for different types of courtship behaviours and as a function of both the intensity and duration of the behaviour (Clark, 2012), the number of existing studies (*N* = 3), is insufficient to draw strong conclusions at this time.

We also found moderate to strong and significant correlations between MR and each of the traits assumed to be associated with net energy gain (dominance, boldness, foraging). Animals with higher MR were more dominant (i.e., had priority access to food), bolder (i.e., resumed feeding more quickly after a disturbance), and foraged more intensively.

In contrast, there was little or no support for significantly positive correlations between MR and behaviours with unknown or putatively weak and/or inconsistent relationships with net energy gain or net energy expenditure. As predicted, there was no support for a relationship between sociability and MR. Although the sociability estimate was derived from only three studies, the point estimate lies at zero, as predicted. There was also no support for a relationship between MR and either activity or exploration. Activity and exploration are two commonly measured behaviours in animal personality research; both provide some measure of the movement behaviour of animals, and so may be assumed to involve some net energetic costs. However, these movements can range from very low (e.g., periodic slow walking) to very high gross energetic costs (e.g., continuous running, flying). Further, these behaviours are assumed to increase encounter rates with resources. Thus, the net consequences of these behaviours could range from high net energetic costs to high net gains. Thus, the lack of correlation between MR and exploration/activity is not surprising (Mathot & Dingemanse, 2015), and further substantiates recent criticism of the use of standardized behavioural assays in animal personality research without careful consideration of the functional significance of the traits being studied (Carter *et al.*, 2013). We are not suggesting that exploration and activity are not associated with net energetic costs or gains, but rather that the relationship likely differs in different organisms or under different conditions (Carter *et al.*, 2013; Mathot *et al.*, 2012). The consequences of greater activity or exploration on net energy expenditure or gain should not remain untested assumptions in studies aimed at understanding functional linkages between metabolism and behaviour, but should be evaluated directly if we are to better understand why they are (or are not) associated with MR.

(2) Relationships between MR and behaviour differ across thermal types

We also tested the idea that greater opportunities for energy (re-)allocation (Humphries & Careau, 2011) could obscure relationships between MR and behaviour (Careau & Garland, 2012; Mathot & Dingemanse, 2015) by contrasting ectotherms with endotherms. Because endotherms can offset thermoregulation costs by substituting heat produced through activity (Careau & Garland, 2012; Humphries & Careau, 2011), we predicted that endotherms would show weaker relationships between MR and behaviour compared with ectotherms. Although our meta-analysis confirmed this prediction, we suggest that thermal substitution alone cannot account for this observed differences. Within endotherms, opportunities for heat substitution vary both taxonomically and allometrically (Humphries & Careau, 2011). Thus, if heat substitution was a primary reason for a weaker relationship between MR and behaviours in endotherms, we would expect to observe strong phylogenetic- or species-related heterogeneity. However, this was not the case. In fact, the proportion of heterogeneity associated with phylogeny and species in endotherms was close to zero (Table 2). Thus, although the strength of the relationships between MR and behaviour appear to differ for endotherms and ectotherms, the mechanism underlying this variation is unclear.

(3) No evidence that greater energetic stress strengthens relationships between MR and behaviour

The rationale for predicting relationships between MR and behaviour hinges on the assumption that animals face constraints in balancing their energy budgets. We tested whether conditions that create greater energetic stress for organisms (reduced access to food and reproduction) strengthen the relationship between MR and behaviour but found no support for this. There was no support for differences in mean effect sizes for breeding versus non-breeding animals, nor for contrasts between studies in captive versus free-living organisms (which we assume covaries with access to resource, as captive studies typically provide ad libitum access to food) (Figure 4, Figure S2). The lack of an effect of breeding status may reflect that breeding does not actually impose greater challenges on organisms in terms of balancing their energy budgets. This could occur if animals adjust their metabolic profiles during breeding, for example, supressing resting MR to offset energetic costs associated with breeding behaviour (Welcker *et al.*, 2015), if increased energetic costs of breeding are easily offset by increased food availability, or if breeders represent non-random sample of the populations (i.e., animals that are the least energetically stressed).

We also found little effect of captivity on the strength of the relationship between MR and behaviour, despite the fact that food availability and predictability are almost always higher under captive compared with free-living conditions. Animals with increased access to food for prolonged periods may exhibit metabolic adjustments (e.g., increased metabolic rate under increased food availability, Mueller & Diamond, 2001), such that energetic constraints are similar in the field versus the lab. However, there were also no differences between wild-caught animals tested in captivity shortly after capture and either free-living or lab-reared animals. Thus, although some studies have found that increased energetic constraints strengthen the relationship between MR and behaviour (e.g., Killen *et al.*, 2011), our analyses suggest that this may not generally true. Although unexpected, this result is also promising in that it implies that the results from studies investigating links between MR and behaviour in the lab can be generalizable to free-living organisms.

(4) Energy management model inferences

The energy management model of the organism is believed to be critical in shaping both the magnitude and direction of relationships between MR and behaviour (Careau & Garland, 2012; Mathot & Dingemanse, 2015). Predicted correlations between MR and specific behaviours are contingent on the energy management strategy, with positive, negative and zero correlations all possible depending on the type of behaviour being considered, and the energy management strategy. Alternative energy management models do not always make exclusive predictions (e.g., both the independent model and the performance model predict positive correlations between behaviours that bring in net energy and MR). Further, where relationships are predicted between MR and a class of behaviours such as behaviours that bring in net energy, the relationship need not exist for every type of behaviour that brings in net energy, but may be present for only a subset of them. Thus, in an earlier opinion (Mathot & Dingemanse, 2015), we pointed out that a single estimate of the relationship between MR and a single behaviour provides weak inference. In this meta-analytical review, by combining estimates from multiple studies and explicitly taking into account the support for relationships between MR and different types of behaviours, we can establish the overall support for the alternative energy management strategies across all published studies.

We found support for an overall positive relationship between MR and behaviour. This is consistent with a previous meta-analysis focused exclusively on among-individual correlations between state (including MR measures) and behaviour (Niemelä & Dingemanse, 2018). More specifically, we found the strongest support for positive relationship between MR and behaviours that bring in net energy or cost net energy, with no support for relationships between MR and behaviours with putatively weak or inconsistent consequences for energy gain/expenditure. Further, effect sizes were comparable for behaviours that bring in net energy and behaviours that cost net energy. The performance model is the only one to predict similar effects for both types of behaviour, suggesting that our sample of studies is comprised primarily of organisms with a performance energy management model. As this meta-analysis includes a taxonomically diverse set of organism, this suggests that the performance model may be most common. In a recent paper, Portugal *et al.* (2016) compiled estimates of MR and daily energy expenditure in 7 birds and 4 mammals to evaluate support for alternative energy management models. Although they observed heterogeneity in estimates across species, a meta-analysis of the reported slopes reveals that the best supported model is in fact the performance model (see ESM Text S1), as the overall slope of the relationship between MR and DEE is > 1 ($\beta = 1.11$, 95% CI = 1.00, 1.22).

Finally, we assessed evidence for publication biases in the studies compiled for this meta-analysis using several tests (e.g., Egger's regression and trim-and-fill tests). Overall, the evidence for publication bias distorting our main results was weak (see Figure 6). However, our time-lag analysis revealed two notable patterns (Figure 5). First, the number of studies published per year increased dramatically from 2007 onwards, and second, there was a significant trend towards decrease effect sizes estimates over time. We propose that both of these patterns may be explained by the rapid growth of the field of animal personality research in the last two decades. A major aim of the field of animal personality research is to understand the factors that promote consistent among-individual differences in behaviour, with several influential papers proposing links between among-individual differences in MR and behaviour around this time (Biro & Stamps, 2008; Biro & Stamps, 2010; Careau *et al.*, 2008). The second consequence of the boom of animal personality studies is that there was a shift in the types of behaviours studied. In particular, there was a rapid increase in the number of studies using standardized assays of exploration and activity behaviour, two of the behaviours revealed by our current analyses to exhibit no relationship with MR.

V. Conclusions

(1) The likelihood of any overarching relationship between MR and behaviour has been questioned given that such relationships are likely to be shaped by a variety of factors (Careau & Garland, 2012; Killen *et al.*, 2013; Mathot & Dingemanse, 2015). Our current analysis identified two important moderators; the thermal type of the organism, and the type of behaviour.

(2) Relationships between MR and behaviour were in the same direction for endotherms and ectotherms (positive relationship between MR and behaviours that either bring in or cost net energy), but the strength of the relationship was weaker in endotherms compared with ectotherms.

(3) We also found that the types of behaviours that showed the strongest (positive) associations with MR were behaviours with clear consequences for net energy expenditure (e.g., maximum sprint speed, sustained running speed, maximum distance travelled, etc.) or gain (e.g., foraging, dominance, boldness).

(4) In contrast, common behavioural assays used in animal personality research (exploration and activity) which have unknown or putatively weak consequences for net energy cost or gain showed no relationship with MR.

(5) Taken together, the results of our meta-analysis highlight the importance of studying behaviours that are functionally relevant in the context of the research question.

VI. Acknowledgements

We wish to thank Jan Wijmenga for assisting with the literature review and locating references (while funded by an MPG grant to NJD) and Renate Alton for assisting in locating references. NJD was funded by the Max Planck Society, KJM was funded by an NSERC postdoctoral fellowship and Veni Fellowship (no.863.14.021) from the Netherlands Organisation for Scientific Research (NWO, Netherlands Organisation for Scientific Research). SN was supported by a Future Fellowship (FT130100268).

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VIII. Supporting information

Additional supporting information may be found in the online version of this article.

Table 1: Summaries and results from phylogenetic multilevel meta-analyses of the overall data set, and the data set separated for ectotherms and endotherms. Note that the number of individuals ($N_{[\text{individuals}]}$) represents the sum of individuals making up each effect size estimate, not the total number of unique individuals (which is over 8000 for the whole data set). This non-independence is accounted for in our analyses (see the text). LCI and UCI denotes the lower and upper confidence limits, respectively, for 95% confidence intervals.

Data	$N_{[\text{individuals}]}$	$N_{[\text{effect sizes}]}$	$N_{[\text{groups}]}$	$N_{[\text{species}]}$	Estimate	SE	z value	p value	LCI	UCI
Overall	11849	163	87	48	0.261	0.106	2.459	0.014	0.053	0.469
Ectotherm	7539	69	47	28	0.297	0.128	2.314	0.021	0.045	0.548
Endotherm	4310	94	40	20	0.101	0.050	2.026	0.043	0.003	0.199

Table 2: Total heterogeneities (I^2, which can vary between 0 and 1) and heterogeneities at each hierarchical level (fitted as random effects; see the text) for meta-analytic models with phylogeny for the overall dataset, and separated for ectotherms and endotherms.

Data	$I^2_{\text{[species]}}$	$I^2_{\text{[phylogeny]}}$	$I^2_{\text{[group]}}$	$I^2_{\text{[effect size]}}$	$I^2_{\text{[total]}}$
Overall	0.138	0.209	0.068	0.517	0.930
Ectotherm	0.445	0.182	<0.001	0.311	0.942
Endotherm	<0.001	<0.001	0.186	0.626	0.812

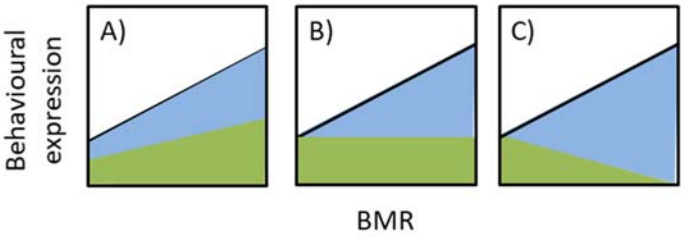

Figure 1: Illustration of how opportunities to allocate among alternative options can create scenarios where the relationship between specific behaviours and MR do not match the more general predictions for the energy management model. Consider an example where an organism can express two behaviours that both have net positive effects on energy intake: foraging boldness (green) or resource defense (blue). The total expression of each behaviour is indicated by their area under the black line. In a) expression of both behaviours increases with increasing MR (i.e., the area occupied by both green and blue increases from left to right across the x-axis), matching the more general prediction. However, in b) only one behaviour shows the predicted relationship with MR (blue, but not green), and in c) one behaviour shows the predicted relationship (blue) while the other behaviour shows the opposite relationship to the one predicted (green).

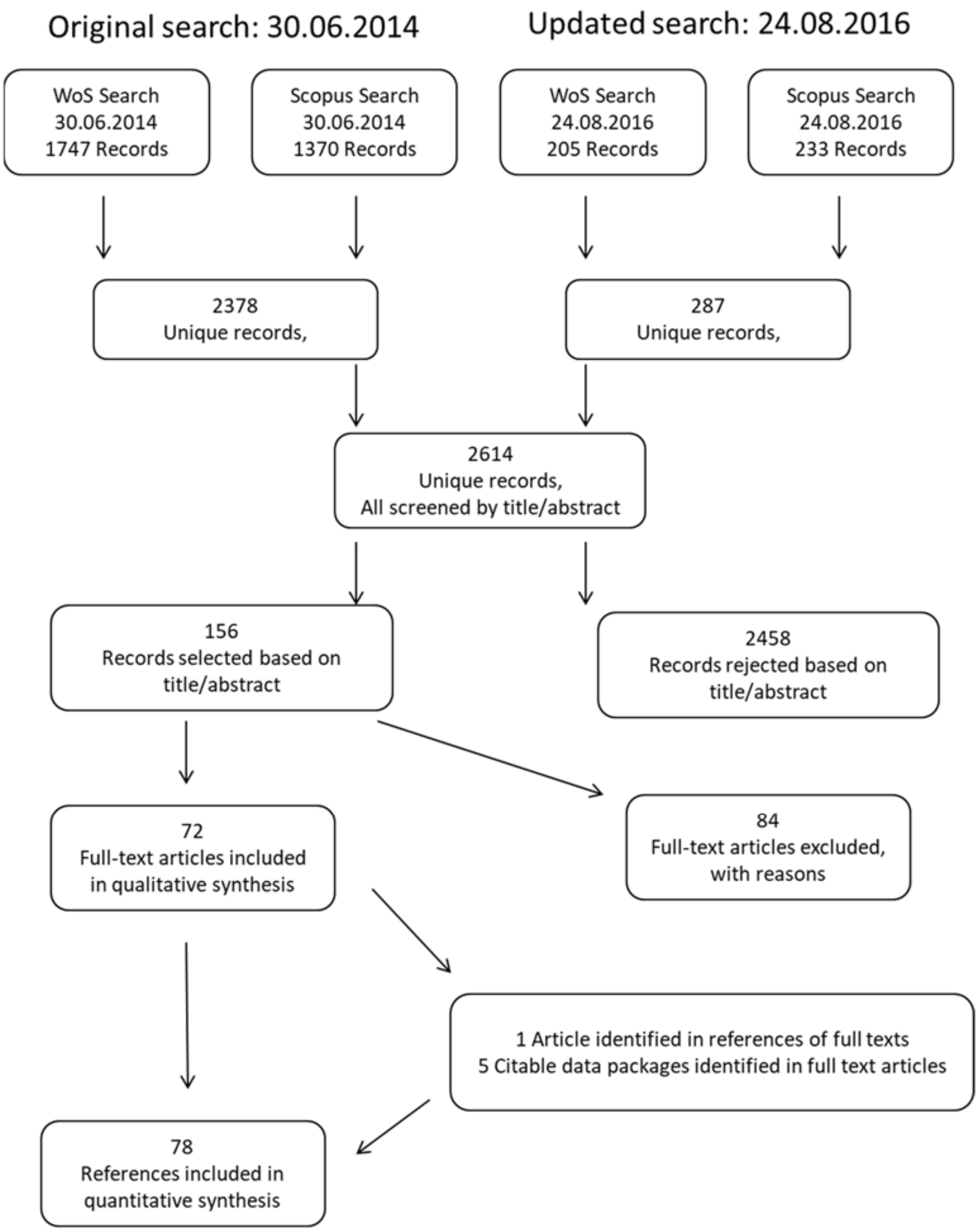

Figure 2: PRISMA flow chart indicating articles identified during different phases of the systematic review.

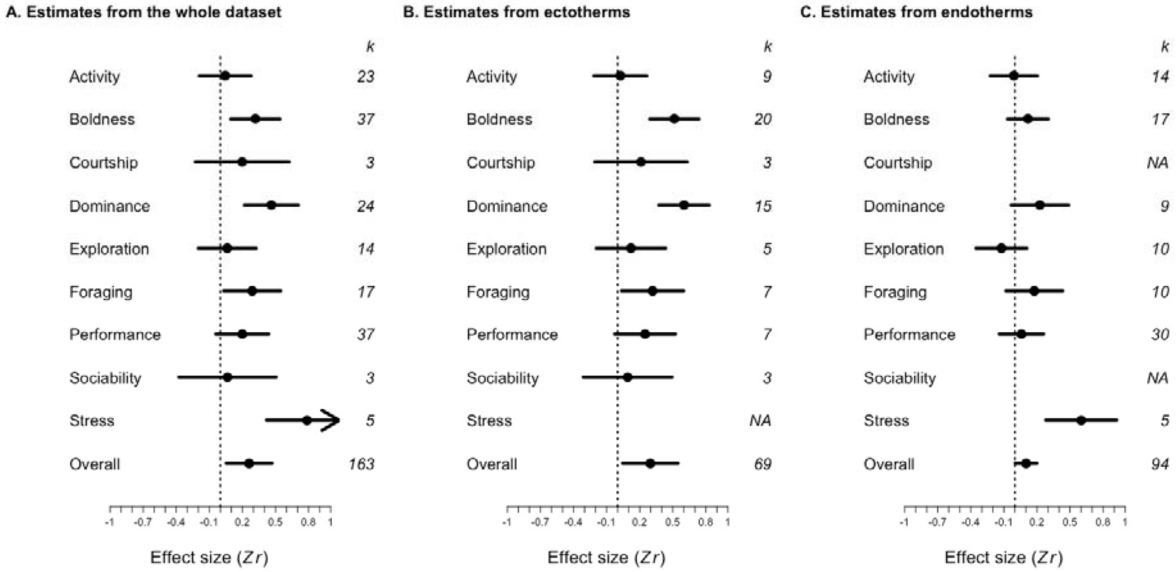

Figure 3: Effect sizes for the relationship between metabolic rate and behaviour separated for different types of behaviours, including an overall estimate (bottom). Panel (A) combines the full data set, panel (B) presents estimates from ectotherms, and panel (C) presents estimates from endotherms. Circles denote point estimates, whiskers denote 95% confidence intervals (the arrow tip indicates the end point is beyond the scale), and *k* is the number of effect sizes (NA = not available; see Table 1). Note that estimates derived from identical data (e.g., stress behaviours in panel A and panel C) may not be identical because model structures differed for each analysis.

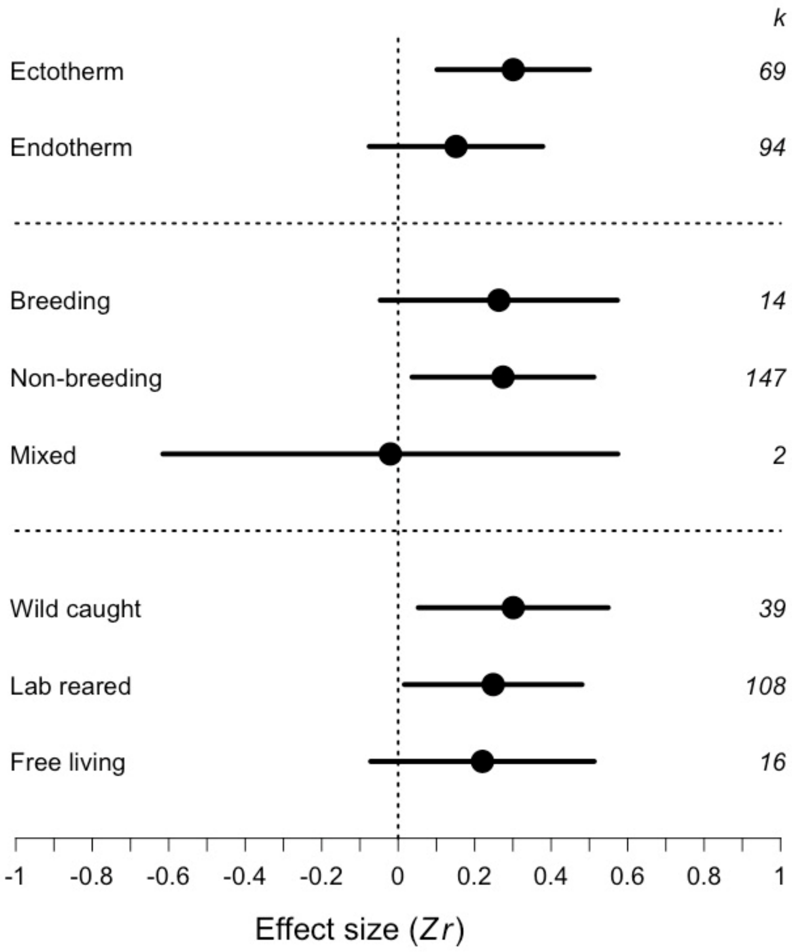

Figure 4: Effect sizes for the relationship between metabolic rate and behaviour for three potential moderators: thermal type of the organism (ectotherm or endotherm), breeding context (breeding, non-breeding, or mixed/unspecified), and testing condition (wild-caught animals tested in the lab, lab-reared animals tested in the lab, free-living animals tested under natural conditions). Circles denote point estimates, whiskers denote 95% confidence intervals and *k* is the number of effect sizes.

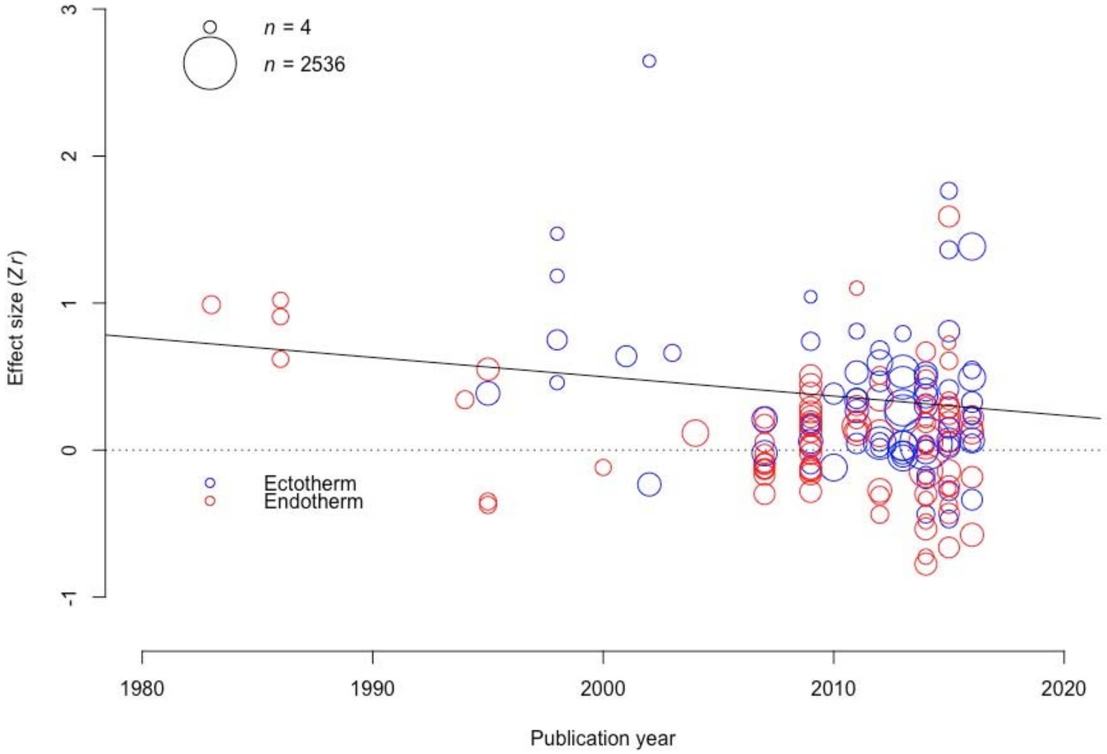

Figure 5: A bubble plot showing a time-lag effect characterised by effect sizes as a function of publication year. After the first study (for an endotherm) in the early 80's, the number of studies remains sparse until 2007, when there is a notable increase in the number of studies for both ectoterms and endotherms (see the text). The size of the circle represents the sample size (on a linear scale), with the largest circle representing the sample size of 2536 animals and the smallest circle representing a sample size of 4 animals.

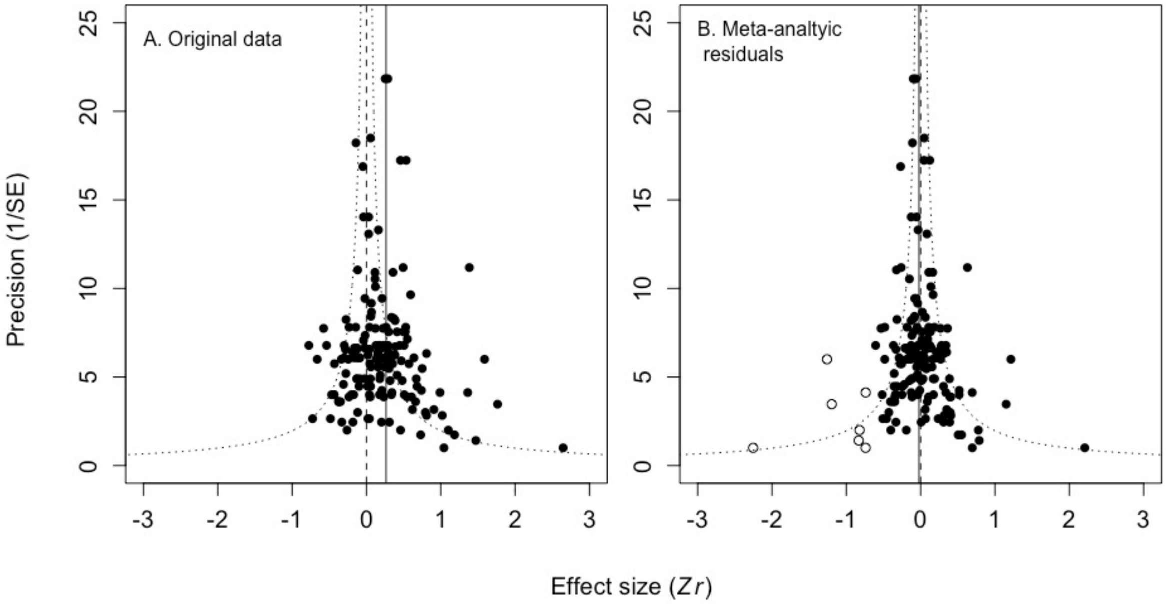

Figure 6: Funnels plots showing effect size and its precision which is the inverse of the square-root of the sampling variance (or standard error, which is the standard deviation of the estimate/effect size). Panel (A) shows the original (raw) data and the meta-analytic mean (the solid vertical line), but note that the original data, which has a non-independent data structure is not appropriate for assessment of funnel asymmetry. Panel (B) shows the meta-analytic residuals (see the text) and data points added by a trim-and-fill test (empty dots) along with the meta-analytic mean (note that the meta-analytic residuals have a mean of zero).