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

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20 and extracted data estimates. SN assisted with data extractions and performed the meta-analysis. KJM
21 and SN co-wrote the paper. All co-authors contributed to revisions.

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25

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27 **Abstract**

28 Energy metabolism has received much attention as a potential driver of repeatable among-individual
29 differences in behaviour (animal personality). Several factors have been hypothesized to mediate this
30 relationship. We performed a meta-analysis of >70 studies comprised of >8000 individuals reporting
31 relationships between measures of maintenance metabolic rates (i.e., basal metabolic rate, resting
32 metabolic rate, and standard metabolic rate) and behaviour. We evaluated support for three
33 hypothesized mediators: 1) type of behaviour, 2) opportunities for energy re-allocation, and 3)
34 magnitude of energetic constraints. Relationships between measures of maintenance metabolic rate
35 (MR) and behaviour are predicted to be strongest for behaviours with strong consequences for energy
36 turnover (acquisition or expenditure). Consistent with this, we found that behaviours with known
37 consequences for energy gain (e.g., foraging, dominance, boldness) or expenditure (e.g., maximum sprint
38 speed, sustained running speed, maximum distance travelled, etc.) had strong positive correlations with
39 MR, while behaviours with putatively weak and/or inconsistent associations with net energy gain or loss
40 (e.g., exploration, activity, sociability) were not correlated with MR. Greater opportunities for energy
41 reallocation are predicted to weaken relationships between MR and behaviour by creating alternative
42 pathways to balance energy budgets . We tested this by contrasting relationships between MR and
43 behaviour in ectotherms versus endotherms, as thermoregulation in endotherms creates additional
44 opportunities for energy reallocation compared with ectotherms. As predicted, the relationship between
45 behaviour and metabolic rate (MR) was stronger in ectotherms compared with endotherms. However,
46 statistical analyses of heterogeneity among effect sizes from different species did not support energy re-
47 allocation as the main driver of these differences. Finally, we tested whether conditions where animals
48 face greater constraints in meeting their energy budgets (e.g., field versus lab, breeding versus non-
49 breeding) increased the strength of relationship between MR and behaviour. We found that the
50 relationship between MR and behaviour was unaffected by either of these modifiers. This meta-analysis

51 provides two key insights. First, we observed positive relationships of similar magnitude between MR
52 and behaviours that bring in net energy, and behaviours that cost net energy. This result is only
53 consistent with a performance energy management model. Given that the studies included in our meta-
54 analysis represent a wide range of taxa, this suggests that the performance model may be the most
55 common model in general. Second, we found that behaviours with putatively weak or inconsistent
56 consequences for net energy gain or expenditure (exploration, activity, sociability) show no relationship
57 with MR. This provides the first systematic demonstration of the central importance of the ecological
58 function of traits in mediating relationships between MR and behaviour.

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

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85 **I. Introduction**

86 The last decade has seen a surge of interest in understanding the causes and consequences of among-
87 individual differences in behaviour (i.e. animal personality). The majority of adaptive explanations for
88 animal personality are based on state-dependence (Dingemanse & Wolf, 2010; Sih *et al.*, 2015; Wolf &
89 Weissing, 2010), where state is broadly defined as any factor that influences the payoffs of a given
90 behavioural action (Houston & McNamara, 1999). State variables related to energy metabolism in
91 particular have been the subject of much attention in this burgeoning area of research (e.g., Biro *et al.*,
92 2010; Careau & Garland, 2012; Careau *et al.*, 2008; Houston, 2010; Mathot & Dall, 2013; Mathot &
93 Dingemanse, 2015; Wolf & McNamara, 2012), and the number of empirical studies investigating links
94 between metabolism and behaviour has grown dramatically in the last several years (reviewed in Biro &
95 Stamps, 2010; Careau & Garland, 2012; Mathot & Dingemanse, 2015; Niemelä & Dingemanse, 2018;
96 Royauté *et al.*, 2018).

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

107 Here, we performed a meta-analysis of existing studies to assess the overall support for a relationship
108 between MR and behaviour. In addition, we evaluated the importance of several of the factors that have

109 been proposed to mediate these relationships: 1) the type of behaviour, 2) the opportunities for energy
110 re-allocation, and 3) the degree of energetic stress. Below, we detail the rationale and predictions for
111 each of these proposed mediators.

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

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

124 Assuming variation in oxygen consumption does reflect variation in energy requirements, the direction
125 of the relationship between MR and behaviours that cost net energy depends on the energy
126 management model of the organism. Three energy management models have been described which
127 reflect three distinct relationships between MR and daily energy expenditure (DEE). Under the allocation
128 model (also called the compensation model), DEE does not vary as a function of MR (Careau & Garland,
129 2012; Careau *et al.*, 2008; Mathot & Dingemanse, 2015). Thus, logically, variation in MR is not predicted
130 to be associated with variation in behaviours that bring in net energy (e.g., foraging) (Mathot &
131 Dingemanse, 2015). However, because organisms work with a fixed energy budget, high MR means a

132 relatively smaller fraction of energy available for energetically costly behaviours (e.g., sustained sprint
133 speed) (Careau & Garland, 2012; Careau *et al.*, 2008; Mathot & Dingemanse, 2015). Under the
134 independent model (also referred to as compensation model), the energy devoted to activity is
135 independent of MR, i.e., the amount of energy expended on activities above basic maintenance does not
136 vary with MR (Careau & Garland, 2012; Mathot & Dingemanse, 2015). However, this still has the
137 consequence that total energy required, DEE, does increase with increasing MR, and therefore, a positive
138 relationship is predicted between MR and behaviours such as foraging (Mathot & Dingemanse, 2015).
139 Finally, under the performance model (also referred to as increased intake), the capacity of an organism
140 to bring in energy is positively correlated with MR (Careau & Garland, 2012; Careau *et al.*, 2008; Mathot
141 & Dingemanse, 2015). Thus, organisms adopting a performance model would be predicted to have
142 higher expressions of both behaviours that bring in net energy, and behaviours that cost net energy.

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

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

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

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

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

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

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

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

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

227

228 **II. Methods**

229 ***(1) Data collection and inclusion/exclusion criteria***

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

242 We performed the initial literature search on 30 June 2014, and later updated the search on 24 August
243 2016. The second search was restricted to articles published after 2013 to reduce the number of
244 references duplicated from the initial search. These literature searches produced a total of 2614 unique
245 references. These references were screened by reading the titles and abstract to assess their relevance
246 to the meta-analyses. We selected studies according the following five criteria:

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

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

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

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

261 (4) The correlation provided had to be either a raw (un-partitioned) phenotypic correlation or an among-
262 individual correlation. We did not consider within-individual correlations (not the targeted hierarchical
263 level) or genetic correlations. Although genetic correlations represent the relevant hierarchical level (i.e.,
264 among-individual), there were insufficient studies providing such estimates (N = 2 studies, Careau *et al.*,
265 2011; Mathot *et al.*, 2013) to allow us to compare the effects sizes of genetic correlations with either
266 among-individual or un-partitioned phenotypic correlations. One of these studies was nonetheless
267 included in the meta-analysis as it additionally provided estimates of raw un-partitioned phenotypic
268 correlations (Careau *et al.*, 2011). One study (Gifford *et al.*, 2014) presented both among-individual and
269 un-partitioned phenotypic correlations for two behavioural traits (foraging and exploration). Both types
270 of correlations were included in the meta-analysis and coded appropriately. The resultant non-
271 independence was accounted for by additionally assigning a group ID to estimates derived from the
272 same sample of individuals.

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

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

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

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

304 ***(2) Data coding and calculation of effect sizes***

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

316 Following recommendations from Noble *et al.* (2017) we preferentially collected descriptive statistics
317 (e.g. correlations, group means, standard deviations and standard errors) over inferential statistics (t , F ,
318 χ^2 , U and p). Both descriptive and inferential statistics were transformed using formulas found in the
319 following references (Krishnamoorthy, 2006; Lipsey & Wilson, 2001; Nakagawa & Cuthill, 2007) and using

320 an effect size determination program (Wilson, 2001). Note that we only retained effect sizes from
321 inferential statistics when directions could be determined (e.g., F , χ^2 , and p do not have directional
322 information), and directions of effect sizes were adjusted in a way that all positive effect sizes meant
323 strong correlations between metabolism and behaviour that either bring in or consume net energy (see
324 above). For the calculation of Zr 's sampling variance, we use the number of independent subjects (i.e.
325 $1/(i - 3)$; i = the number of subjects). For phenotypic correlations, this provides a more conservative
326 estimate of sampling variance compared with using the total number of observations. We also collected
327 more information for each data point for use as moderators to explain potential heterogeneity and bias
328 in the data (e.g., species information, ectothermic vs. endothermic, types of behaviour, publication year).
329 The details of these potential moderators are summarized in the published dataset
330 (<https://osf.io/gmvab/>).

331 **(3) Meta-analysis and meta-regression analysis**

332 We employed phylogenetic multilevel meta-analysis (PMMA) to control the effect of phylogeny and
333 other types of non-independence (Hadfield & Nakagawa, 2010; Nakagawa & Santos, 2012). We used the
334 function, *rma.mv* from the R package, *metafor* (Viechtbauer, 2010). A PMMA requires a phylogenetic
335 tree so we constructed a tree using the R package *rotl* (Michonneau *et al.*, 2016) which uses the Open
336 Tree of Life data (Hinchliff *et al.*, 2015). The resulting phylogenetic tree did not have tree branch length
337 estimates. Therefore, we used the function *compute.brlen*, in the R package *ape* (Paradis *et al.*, 2004) to
338 estimate branch lengths. With this function, we used the method of Grafen (1989), setting the power to
339 1, to create an ultrametric tree closely imitating the Brownian motion model of evolution. We used this
340 ultrametric tree for PMMA by converting it to a correlation matrix (using the *vcv* function from *ape*).

341 We first constructed a meta-analytic model (only with the intercept) with four random factors: 1) species
342 identity (a non-phylogenetic component of species), 2) phylogeny (a phylogenetic component of

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

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

366 repository (R-markdown file along with our data set: DOI 10.17605/OSF.IO/GMVAB; web address:
367 <https://osf.io/gmvab/>).

368 **(4) Publication bias analysis and sensitivity analysis**

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

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

387 III. Results

388 Overall, a phylogenetic multilevel meta-analytic model revealed that MR and behaviour were
389 significantly and moderately correlated ($\beta_0 = 0.261$, 95% confidence interval, CI = [0.053, 0.469]; Table 1
390 and Figure 3A). However, the observed total heterogeneity was high ($I^2_{[total]} = 93.00\%$), implying that this
391 correlation was contingent upon moderators; this set the stage for our meta-regression models (see
392 Table 2). Notably, approximately 21% of variation in the data were explained by phylogeny (Table 2). The
393 first meta-regression model showed that the type of behaviour accounted around 20% of the variation
394 ($R^2 = 19.06\%$), with boldness, dominance, foraging and stress showing moderate to large, significant
395 correlations with metabolic rate, MR (Figure 3A), while activity, exploration and sociability showed little
396 or zero correlation with MR. Though not significant, courtship and performance showed moderate
397 correlations with MR (complete contrasts among the behaviour types are in the ESM, Figure S1).

398 The second meta-regression on the thermal types showed that the mean effect for ectotherms was
399 significant and moderate ($\beta_{[ectotherm]} = 0.301$, 95% CI = [0.102, 0.500]), and that for endotherms the effect
400 was non-significant and weak ($\beta_{[endotherm]} = 0.151$, 95% CI = [-0.076, 0.378]; Figure 4; also see Figure S2),
401 although the contrast between the two was not significant ($\beta_{[contrast]} = -0.150$, 95% CI = [-0.355, 0.056],
402 $Q_{M[df = 68]} = 2.031$, $p = 0.15$; $R^2 = 3.88\%$; Figure 4). The separate meta-analytic models mirrored the results
403 from the meta-regression, apart from the mean effect for endotherms being significant ($\beta_{[ectotherm]} =$
404 0.297 , 95% IC = [0.0445, 0.548]; Figure 3B; $\beta_{[endotherm]} = 0.101$, 95% CI = [0.033, 0.200]; Table 1, Figure 3C).
405 In the corresponding meta-regression models incorporating the different behaviour types, we found
406 similar patterns observed in the meta-regression model with all data, but the patterns were, in general,
407 stronger for ectotherms and weaker for endotherms than for all species together (compare panels A, B
408 and C in Figure 3). The magnitude of heterogeneity was high for both meta-analytic models ($I^2_{[total]} =$
409 94.16% for ectotherms and $I^2_{[total]} = 81.22\%$ for endotherms). Notably, much of heterogeneity in the
410 ectotherm data came from the phylogenetic and non-phylogenetic effects of species ($I^2_{[phylogeny]} = 18.20\%$

411 and $I^2_{[\text{species}]} = 44.52\%$, respectively) whereas there was virtually zero variation resulting from phylogeny
412 or species in the endotherm data (Table 2). In our final meta-regression models, in contrast to our
413 predictions, we did not find significant effects of the breeding status ($Q_{M[df=2]} = 1.047$, $p = 0.592$; $R^2 =$
414 0.70%) or testing conditions (i.e., free-living, wild-caught and tested in captivity, captive reared and
415 tested) ($Q_{M[df=2]} = 0.592$, $p = 0.744$, $R^2 = 0.45\%$; Figure 4; Figure S2).

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

432

433 **IV. Discussion**

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

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

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

453 The strongest relationship between MR and behaviour was found for stress response (response to
454 human handling), a putatively energetically costly trait (Koolhaas *et al.*, 2011; Manzur *et al.*, 2014).

455 Higher metabolic rates were associated with quicker escape latencies from observers, greater struggle

456 rates and higher breath rates. There was also a moderately strong, albeit non-significant, correlation
457 between 'performance' traits (e.g., maximum sprint speed, maximum sustained activity, etc.), which are
458 also energetically demanding behaviours. Although courtship behaviour is often assumed to be
459 energetically costly, we found a weak and non-significant relationship between MR and
460 courtship/mating behaviours. However, our analysis of courtship behaviour was based on only three
461 studies (Figure 3); two studies of calling rates, and one study of copulation duration. This is not a
462 comprehensive sample of courtship behaviours. Given that the relationship between courtship
463 behaviours and net energy expenditure may vary for different types of courtship behaviours and as a
464 function of both the intensity and duration of the behaviour (Clark, 2012), the number of existing studies
465 ($N = 3$), is insufficient to draw strong conclusions at this time.

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

470 In contrast, there was little or no support for significantly positive correlations between MR and
471 behaviours with unknown or putatively weak and/or inconsistent relationships with net energy gain or
472 net energy expenditure. As predicted, there was no support for a relationship between sociability and
473 MR. Although the sociability estimate was derived from only three studies, the point estimate lies at
474 zero, as predicted. There was also no support for a relationship between MR and either activity or
475 exploration. Activity and exploration are two commonly measured behaviours in animal personality
476 research; both provide some measure of the movement behaviour of animals, and so may be assumed
477 to involve some net energetic costs. However, these movements can range from very low (e.g., periodic
478 slow walking) to very high gross energetic costs (e.g., continuous running, flying). Further, these
479 behaviours are assumed to increase encounter rates with resources. Thus, the net consequences of

480 these behaviours could range from high net energetic costs to high net gains. Thus, the lack of
481 correlation between MR and exploration/activity is not surprising (Mathot & Dingemanse, 2015), and
482 further substantiates recent criticism of the use of standardized behavioural assays in animal personality
483 research without careful consideration of the functional significance of the traits being studied (Carter *et al.*,
484 2013). We are not suggesting that exploration and activity are not associated with net energetic costs
485 or gains, but rather that the relationship likely differs in different organisms or under different conditions
486 (Carter *et al.*, 2013; Mathot *et al.*, 2012). The consequences of greater activity or exploration on net
487 energy expenditure or gain should not remain untested assumptions in studies aimed at understanding
488 functional linkages between metabolism and behaviour, but should be evaluated directly if we are to
489 better understand why they are (or are not) associated with MR.

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

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

503 relationships between MR and behaviour appear to differ for endotherms and ectotherms, the
504 mechanism underlying this variation is unclear.

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

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

519 We also found little effect of captivity on the strength of the relationship between MR and behaviour,
520 despite the fact that food availability and predictability are almost always higher under captive
521 compared with free-living conditions. Animals with increased access to food for prolonged periods may
522 exhibit metabolic adjustments (e.g., increased metabolic rate under increased food availability, Mueller
523 & Diamond, 2001), such that energetic constraints are similar in the field versus the lab. However, there
524 were also no differences between wild-caught animals tested in captivity shortly after capture and either
525 free-living or lab-reared animals. Thus, although some studies have found that increased energetic
526 constraints strengthen the relationship between MR and behaviour (e.g., Killen *et al.*, 2011), our analyses

527 suggest that this may not generally true. Although unexpected, this result is also promising in that it
528 implies that the results from studies investigating links between MR and behaviour in the lab can be
529 generalizable to free-living organisms.

530 ***(4) Energy management model inferences***

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

546 We found support for an overall positive relationship between MR and behaviour. This is consistent with
547 a previous meta-analysis focused exclusively on among-individual correlations between state (including
548 MR measures) and behaviour (Niemelä & Dingemanse, 2018). More specifically, we found the strongest
549 support for positive relationship between MR and behaviours that bring in net energy or cost net energy,
550 with no support for relationships between MR and behaviours with putatively weak or inconsistent

551 consequences for energy gain/expenditure. Further, effect sizes were comparable for behaviours that
552 bring in net energy and behaviours that cost net energy. The performance model is the only one to
553 predict similar effects for both types of behaviour, suggesting that our sample of studies is comprised
554 primarily of organisms with a performance energy management model. As this meta-analysis includes a
555 taxonomically diverse set of organism, this suggests that the performance model may be most common.
556 In a recent paper, Portugal *et al.* (2016) compiled estimates of MR and daily energy expenditure in 7
557 birds and 4 mammals to evaluate support for alternative energy management models. Although they
558 observed heterogeneity in estimates across species, a meta-analysis of the reported slopes reveals that
559 the best supported model is in fact the performance model (see ESM Text S1), as the overall slope of the
560 relationship between MR and DEE is > 1 ($\beta = 1.11$, 95% CI = 1.00, 1.22).

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

575

576 **V. Conclusions**

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

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

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

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

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

592

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599

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736 **VIII. Supporting information**

737 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

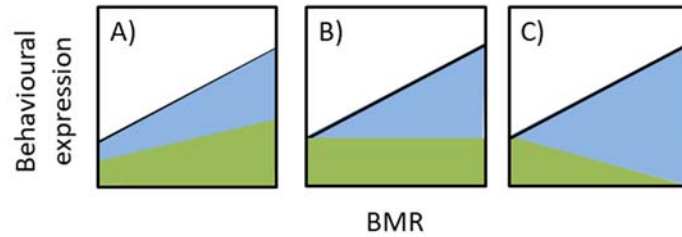


Figure 1: Illustration of how opportunities to allocate among alternative options can create scenarios where the relationship between specific behaviours and MR do not match the more general predictions for the energy management model. Consider an example where an organism can express two behaviours 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).

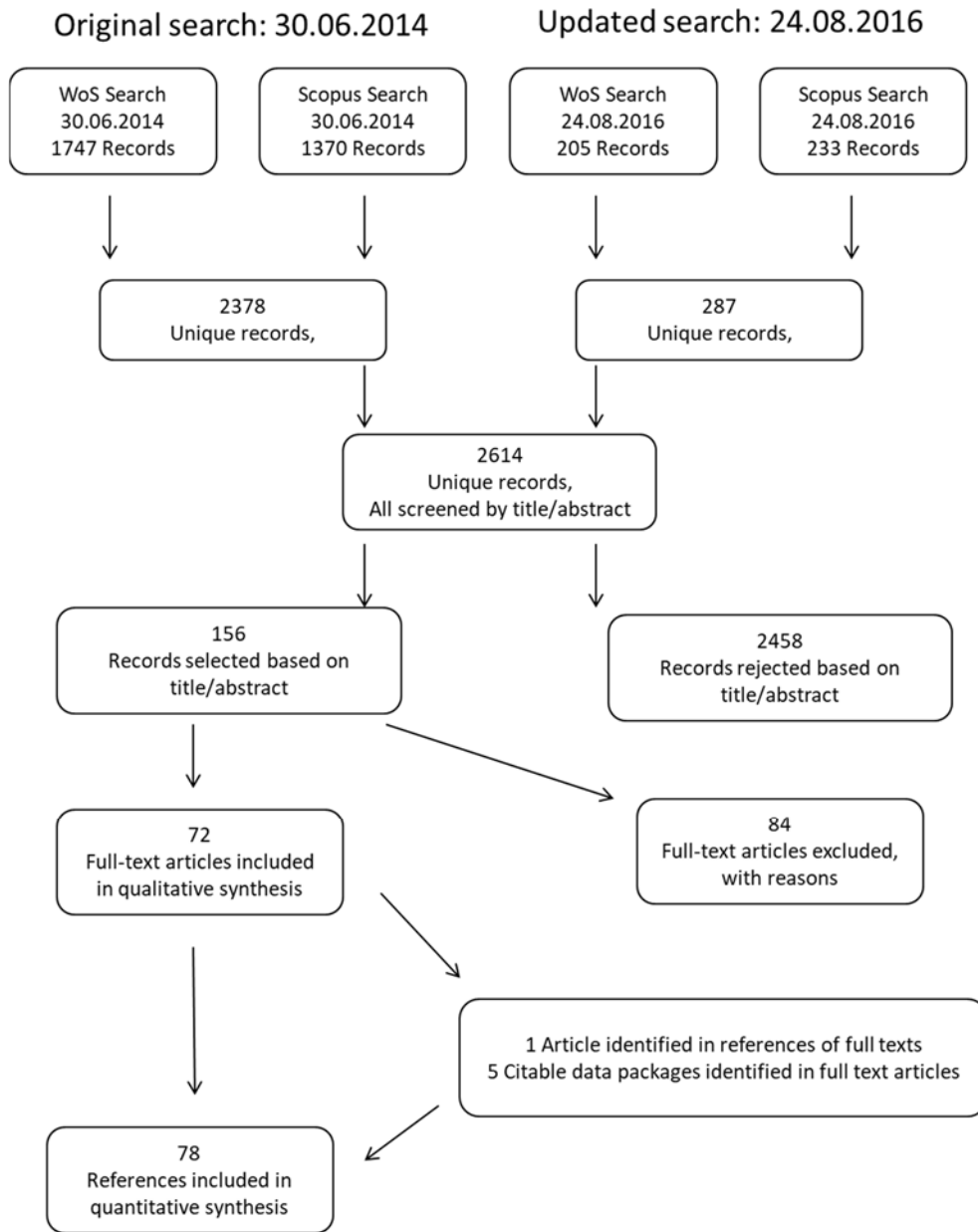


Figure 2: PRISMA flow chart indicating articles identified during different phases of the systematic review.

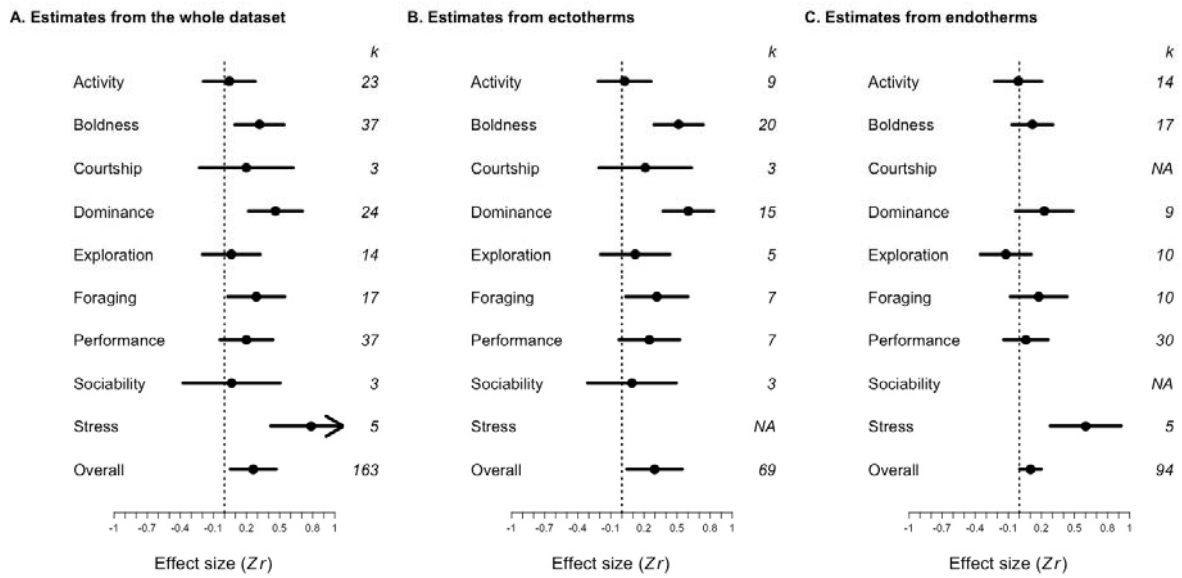


Figure 3: Effect sizes for the relationship between metabolic rate and behaviour separated for different types of behaviours, including an overall estimate (bottom). Panel (A) combines the full data set, panel (B) presents estimates from ectotherms, and panel (C) presents estimates from endotherms. Circles 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.

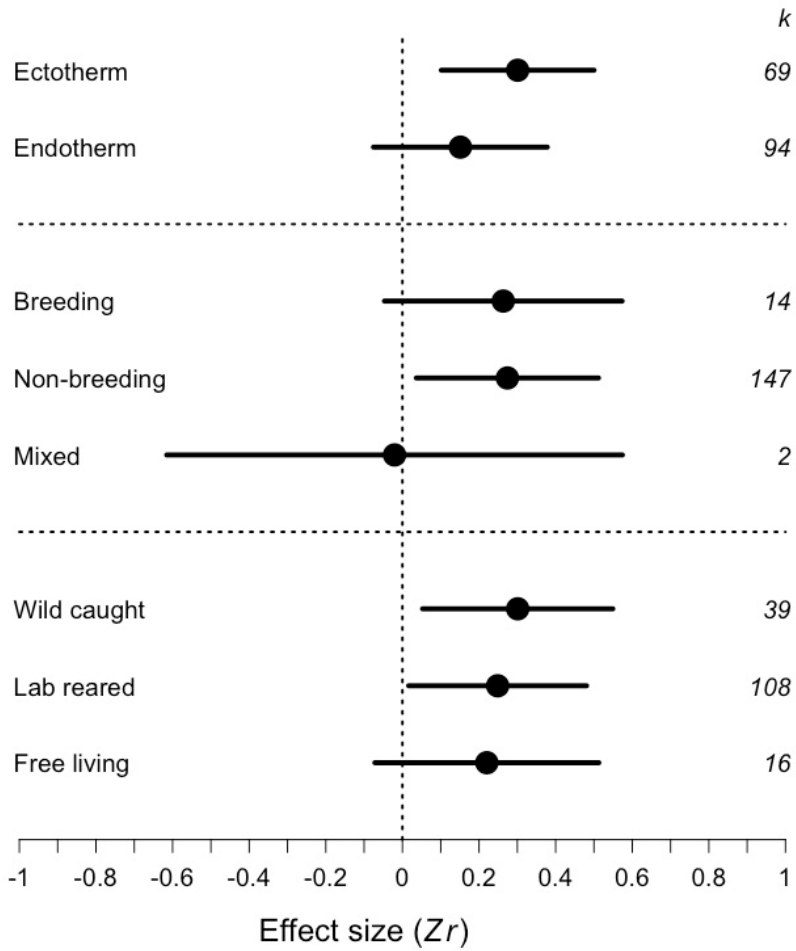


Figure 4: Effect sizes for the relationship between metabolic rate and behaviour for three potential moderators: thermal type of the organism (ectotherm or endotherm), breeding context (breeding, non-breeding, or mixed/unspecified), and testing condition (wild-caught animals tested in the lab, lab-reared 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.

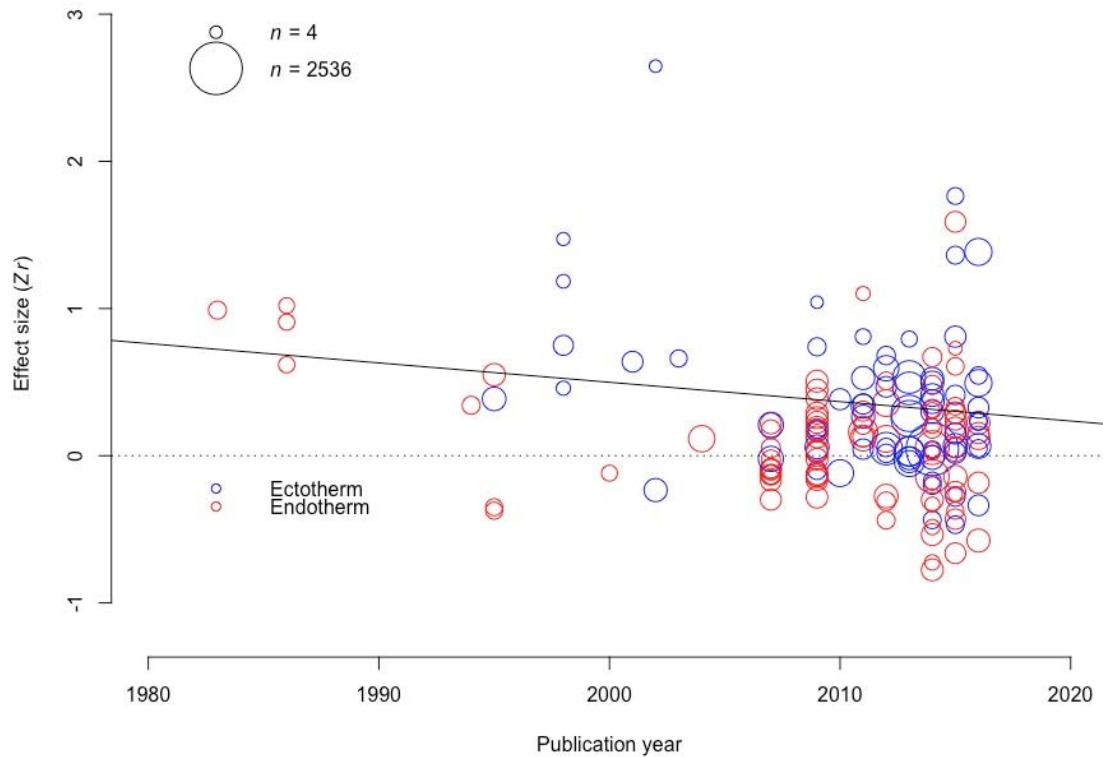


Figure 5: A bubble plot showing a time-lag effect characterised by effect sizes as a function of publication year. After the first study (for an endotherm) in the early 80's, the number of studies remains sparse until 2007, when there is a notable increase in the number of studies for both ectotherms 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.

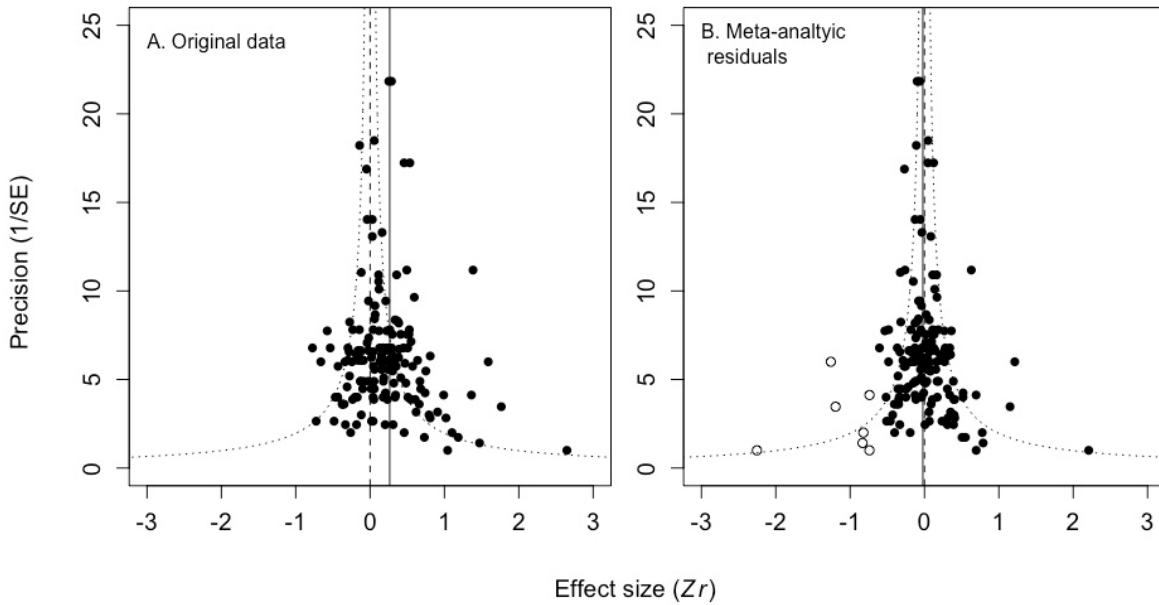


Figure 6: Funnel plots showing effect size and its precision which is the inverse of the square-root of the sampling variance (or standard error, which is the standard deviation of the estimate/effect size). Panel (A) shows the original (raw) data and the meta-analytic mean (the solid vertical line), 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).