Linking personality and cognition: A meta-analysis

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1 Linking personality and cognition: A meta-analysis

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15

16 Abstract

17 In the past decade, several conceptual papers have linked variation in animal personality to

18 variation in cognition, and recent years have seen a flood of empirical studies testing this

19 question. However, these results have not been synthesised in a quantitative way. Here, we

20 systematically search the literature and conduct a phylogenetically-controlled meta-analysis

21 of empirical papers that have tested the relationship between animal personality

22 (exploration, boldness, activity, aggression and sociability) and cognition (initial

23 learning/reversal speed, number of correct choices/errors after standard training). We find

24 evidence for a small but significant relationship between variation in personality and

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25   variation in learning across species in the absolute scale, however the *direction* of this

26   relationship is highly variable and when both positive and negative effect sizes are

27   considered the average effect size does not differ significantly from zero. Importantly, this

28   variation between studies is not explained by differences in personality or learning measure,

29   or taxonomic grouping. Further, these results do not support current hypotheses suggesting

30   that that fast-explorers are fast learners or that slow explorers perform better on tests of

31   reversal learning. Rather, we find evidence that bold animals are faster learners, but only

32   when boldness is measured in response to a predator (or simulated) and not when boldness

33   is measured by exposure to a novel object (or novel food). Further, although only a small

34   sub-sample of papers reported results separately for males and females, sex explained a

35   significant amount of variation in effect size. These results therefore suggest that, while

36   personality and learning are indeed related across a range of species, the direction of this

37   relationship is highly variable. Thus further empirical work is needed to determine whether

38   there are important moderators of this relationship.

39

40   Keywords

41   Behavioural syndrome, Exploration, Individual differences, Learning, Sex differences,

42

43   Introduction

44   In the past 15 years research in behavioural ecology has shown that different behaviours of

45   individual animals may be stable across time or contexts (animal personality *sensu* [1–3]).

46   These different behaviours (also called personality traits), moreover, may not be

47   independent from one another and, seemingly independent behaviours, measured using

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48   different tasks, could form suites of correlated traits (behavioural syndromes *sensu* [4–6]).

49   Thus, the tide of studying the average behaviour of groups has ebbed, as researchers have

50   realised the importance of quantifying the variation among individuals in a group [7]. Along

51   with this upwelling of empirical papers on animal personality came a swell of conceptual,

52   terminological, and statistical papers ('data-free' papers, reviewed in [8]) linking personality

53   to many aspects of ecological and evolutionary biology (e.g., sexual selection [9];

54   conservation [10]; ecology and evolution [11]; development [2]; evolutionary genomics

55   [12]). Included in this swell are several conceptual papers linking animal personality to

56   animal cognition [13–18].

57   A link between personality and cognition, albeit by different names, was first

58   established by Pavlov in the early 20th century during his work examining associative

59   processes (i.e., conditioned reflexes) and digestive physiology [14,19–21]. Pavlov described

60   four different 'types' of nervous systems based on how quickly dogs learned to form

61   different types of associations [22]. For instance, the 'Excitable type' showed strong (and

62   quick) excitatory conditioning (learning to make a response), but weak (and slow) inhibitory

63   conditioning (learning to withhold making a response). The 'Inhibited type' was the

64   opposite: showing strong and quick inhibitory conditioning, and weak and slow excitatory

65   conditioning. Both the Excitable and Inhibited type also showed low flexibility – that is,

66   alternating between excitatory and inhibitory conditioning. The 'Lively type' showed rapid

67   associative learning for both excitatory and inhibitory tasks and could make flexible

68   conversions between the two. The last type, 'Quiet', formed slow but consistent

69   associations and was less flexible, compared to the Lively type, when transitioning between

70   the different conditioning types (excitatory and inhibitory; [13,14]). In two lectures: *An*

71   *attempt to understand the symptoms of hysteria physiologically* (1932) and *The conditioned*

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72   *reflex* (1935; [21]), Pavlov connected the four types of nervous systems to individually

73   distinct animal 'temperaments'. For instance, the Excitable type display general behaviour

74   that is 'aggressive, animated and undisciplined' (pp 105). While the Lively and Quiet type

75   behave 'actively and lively' and 'inert…calm and unperturbed' (pp 177), respectively. Lastly,

76   the Inhibitory type is 'restless and constantly looking about or on the contrary, constantly

77   stopping and remaining motionless…' (pp 177). Pavlov believed these four types of nervous

78   systems were responsible for individually distinctive and fixed behavioural phenotypes (i.e.,

79   personalities) of different dogs [21].

80   The foremost goal of this paper is to assess if Pavlov was indeed correct by asking: is

81   an animal's personality related to its cognitive ability? Recent years have seen a flurry of

82   empirical studies testing this question, in a range of species [e.g., mammals, 23; fish, 24;

83   birds, 25]. However, these results have not yet been synthesised in a quantitative way. We

84   address this using a meta-analytic approach. We systematically searched the literature for

85   studies testing for a relationship between animal personality and cognition across

86   individuals, finding estimates for 19 animal species, including mammals, birds, reptiles, fish

87   and insects. We use data from papers examining at least one measure of personality and at

88   least one measure of cognition from the same individuals, where these two measures were

89   derived from independent assays. Cognition, broadly defined, is the acquisition, processing,

90   storage and use of information [26], and, following Pavlov, the current meta-analysis will

91   focus on information acquisition. In the current paper variation in information acquisition is

92   quantified by either: the number of trials individuals take to learn an association to a pre-

93   determined level of expertise (the learning criteria, see methods for details and [16] Table 1

94   for a guide to measuring cognitive abilities); or, the number of correct (or incorrect)

95   responses in a standard number of training trials. The personality traits included in the

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96 current meta-analysis are those broadly defined by [11, and revised by 24]: boldness,

97 exploration, activity, sociability and aggression (see methods for details and [28] for a

98 pertinent discussion regarding the naming and quantification of personality traits).

99   Importantly, the relationship (correlation) between personality and cognition can be

100 either positive or negative, depending on how behaviours are coded. While the assignment

101 of a direction to these behavioural measures is somewhat arbitrary (see methods), the

102 biological meaning is not; for example: a positive relationship between cognition and

103 boldness (e.g. faster learners are bolder) is biologically and ecologically different from the

104 converse (e.g. faster learners are less bold). However, another way to examine this

105 relationship across species is to look at the absolute magnitude of the effect, irrespective of

106 the sign (in other words by making all effect sizes positive). Such an approach may be

107 needed if the sign of the relationship is not consistent across species [29,30][30]. In such a

108 case, using the absolute values may allow us to detect a strong relationship that is masked

109 when we examine the raw (positive and negative) effect sizes alone, and this result would

110 be informative in that it suggests that there are underlying factors that strongly influence

111 the direction of the relationship which we can try to uncover. In this study we therefore

112 quantify the strength of the relationship between personality and cognition both with and

113 without considering the directionality of the effect sizes.

114   The secondary goal of this paper is to begin to address specific predictions regarding

115 the direction of the relationship between personality and cognition. Although it has been

116 argued elsewhere [16], making predictions about the direction of the relationship between

117 personality and cognition will depend on many factors, including, but not limited to - the

118 stimulus (e.g., tone, light, conspecific, odour), the response (e.g., making one versus

119 withholding making one), and the outcome (positive or negative). A popular prediction,

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120   nonetheless, based both on conceptual [13,15,27,28] and early empirical work (e.g.,

121   [29,30]), is that fast-explorers are fast learners and excel in stable environments, whereas

122   slow explorers are more flexible and therefore should be better at reversal learning

123   compared to fast explorers. In other words, the relationship between exploration and

124   cognition may depend on the cognitive measure being used. Therefore, we predict a

125   positive relationship between personality and learning speed for newly acquired tasks (e.g.,

126   fast-explorers are fast learners) and a negative relationship between personality and

127   reversal learning (e.g., slow-explorers are fast at reversal learning).

128   Finally, the relationship between personality and cognition may also depend on

129   which personality measure is being examined. For example, Sih and Del Giudice hypothesize

130   that individual differences along the bold-aggressive-active-exploratory axis will be

131   correlated with cognition [35]. The proposed mechanism for this correlation is a risk-reward

132   trade-off that underlies both cognition and personality, that is, the more a behaviour is

133   expressed (e.g., more aggression, more boldness, fast learner) the greater the reward (e.g.,

134   more mates, more food), but also the greater the risk (e.g., being predated, injury in

135   contests, decision errors). Sih and Del Giudice [35] make a distinction between cognitive

136   abilities and cognitive 'style', where cognitive style refers to 'the way individuals acquire,

137   process, store or act on information, independent of cognitive ability' (pp 2762). And, while

138   the distinction between ability and style is not usually discussed or addressed in papers

139   examining cognition, the theoretical framework supplied by [35] is applied (see [16] for

140   example of measuring cognitive style). A similar view, linking personality to cognition, holds

141   that bold/explorative animals experience more of their environment, more quickly, thus

142   coming into contact with to-be-learned associations more readily than shy/less explorative

143   individuals [16,35,36]. This view therefore suggests that personality constrains cognition.

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144   The same end can also be achieved by different means: animals that form associations more

145   quickly may be able to then move through their environment more quickly [learning ability

146   facilitates exploration, 26]. Despite these different proposed mechanisms, the outcome

147   remains the same – a positive link between exploration and learning speed. In the current

148   meta-analysis we ask if six different personality measures are related to learning in the

149   same way.

150   In summary, in this study we ask several questions. First, is there a significant

151   relationship between personality and learning, either in the absolute or raw scale? Second,

152   is the strength or direction of this relationship influenced by additional factors, such as the

153   personality measure or cognitive test used, or the sex of the subjects? Third, is there any

154   evidence of publication bias against studies showing certain results (e.g. those that

155   counteract prevailing theory)?

156

157   Methods

158   Our methods followed the PRISMA standards for reporting meta-analyses ([36–39];

159   see Figure 1 for a diagram of the search results and study selection) as closely as possible.

160

161   **Search protocol**

162   We used three methods to search the literature for relevant studies. First, keyword

163   searches were performed using three databases on 17 October 2017 (Web of Science,

164   PsychINFO, and Scopus, see Supplementary Material for complete list of search terms used

165   for each database). Second, Web of Science was used to search for papers that had cited

166   two influential papers in this area: a review on behavioural syndromes and cognition [15];

167   and an opinion paper on cognition and personality [16]. After these searches, we excluded

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168   duplicate results, and then accessed the abstracts of 1776 papers and screened them for

169   inclusion. Full texts of papers that were deemed relevant were read (*n*= 129). Finally, the full

170   texts of three additional papers that were not located by the initial search were accessed

171   because they were cited in the papers that were deemed relevant (final *n*= 132, Figure 1).

172

173   **Criteria for inclusion**

174   We had several criteria for inclusion of a study in our analysis (see Table S1 for a list

175   of studies not included in the analysis, and the reasons for their exclusion). The main

176   criterion was that each paper needed to include at least one measure of personality and one

177   measure of cognition, which came from different tasks. For example, in a study examining

178   boldness (as measured by latency to interact with a novel object) and learning speed

179   (number of trials reach criteria for a visual discrimination task), this criterion was violated if

180   boldness was measured as latency to interact with the cognitive testing apparatus which

181   was used to assess learning speed. Second, the paper needed to present statistical

182   information so that an effect size could be calculated (though note that in several cases we

183   contacted the authors of papers that did not present appropriate statistics in order to

184   obtain such information; see below for more details).

185   *Personality measure.* The relatively young field of animal personality faces several

186   challenges when it comes to measuring personality, which are clearly reviewed in [28]. One

187   challenge relates to defining personality traits, a second challenge related to how these

188   traits are measured (see [41] for discussion about failure to measure repeatability in traits

189   and [42] for a meta-analysis of repeatability of personality traits). Here, we followed the

190   definition of a personality trait from [28; pp 476]: *A specific aspect of a behavioural*

191   *repertoire that can be quantified and that shows between-individual variation and within-*

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192   *individual consistency (such as boldness, aggression, activity).* We included studies that

193   report personality measures from one or several behavioural episodes. The terminology for

194   the specific personality traits used here is based on [11], sometimes referred to as the 'Big

195   Five': boldness, exploration, activity, aggressiveness and sociability [6]. However, [11]

196   explicitly addressed the limitation of this over-simplification of terminology and suggested

197   that the five outlined traits be regarded as a working tool. Thus the working definitions we

198   used are more in line with those used by [27], and consisted of the following categories:

199   Boldness – responses to novel objects, food and potential predators; Exploration –

200   responses to a novel environment or open field; Social/Aggression – reactions to conspecific

201   presentations; Activity – movement around a familiar environment (e.g., a home cage); and,

202   Exploration/Boldness – combined reactions to novel environment and novel object tests

203   (e.g., established composite scores for great tits *sensu* [43]). Note that in the analysis we

204   distinguish between boldness in response to novel objects or food and boldness in response

205   to predators, as preliminary analyses indicated that these were informative groupings. We

206   use the term 'personality measure' rather than 'personality trait' in order to distinguish

207   between these two types of boldness. In summary, the 'behaviour measures' variable

208   consists of six categories: boldness in response to novel objects/food, boldness in response

209   to predators, exploration/boldness, activity, exploration, and social/aggression.

210   *Cognitive measure and training type*. We included studies that examined four

211   different cognitive measures (learning speed, reversal learning speed, number of errors,

212   number of correct responses) – which we grouped into two different training types: 'trials to

213   criterion' and 'standard training'. In the first type of study (trials to criterion), animals were

214   trained until they reached a pre-determined learning criteria for: (1) initial acquisition of a

215   task (learning speed); or, (2) during a subsequent phase when the initial reward

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216   contingencies (those in place during initial acquisition) were reversed (reversal learning).

217   Animals trained to criteria are at the same level of asymptotic performance (e.g., in

218   associative learning, the maximum associative value a Conditioned Stimulus [CS] can

219   gain[44]). In the second type of study (standard training), animals were trained for a

220   standard number of trials and the cognitive measures were: (3) the number of errors; or, (4)

221   the number of correct responses. In these latter two measures, it is unclear *if* or *how much*

222   an animal has learned (i.e., where an individual's performance falls on a learning curve that

223   culminates, theoretically, in asymptotic learning). We therefore have separated these from

224   the cases where animals are trained until they reach learning criteria. There are a dearth of

225   studies that examine the link between cognitive abilities beyond information acquisition

226   (i.e., information use, but see [45] for a test of generalization of previously learned rules in a

227   pigeon and [46] for a test of performance accuracy on novel exemplars following initial

228   acquisition). We did not include studies that tested motor learning or problem solving

229   (extractive foraging task) as it is unclear which cognitive mechanism may underpin

230   performance in these tasks (for in-depth treatment of this topic see [47–49]).

231   Supplementary Table S3 contains the *Cognitive measure* and *Training type* for all effect sizes

232   in the meta-analysis (see reference [16] Table 1 for overview of measurement of cognitive

233   abilities).

234   *Sex.* We included both studies that tested for sex differences in behaviour and those

235   that did not, with sex classified as 'both' when sex differences were not assessed. In one

236   case, the sex of the subjects was not specified [50]; therefore we classed this as 'both'.

237

238   **Calculating effect sizes**

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239   In order to quantify the relationship between personality and learning, the

240   experimental results first need to be converted into a standardised effect size. We used

241   Pearson's product moment correlation coefficient (*r*) as the measure of effect size, as the

242   majority of studies in our sample measured both personality and learning on a continuous

243   scale (though there were nine cases in which subjects were classified into discrete groups

244   based on a personality or cognition score). Here, *r* represents the magnitude of the

245   association between one of several personality measures and some cognitive measure.

246   Given that *r* can range from +1 to -1, we need to determine the sign of the relationship for

247   each study. We classified correlations as either positive or negative depending on the

248   following criteria. Positive effect sizes were assigned when individuals that had faster

249   learning (or reversal) speeds, more correct choices, or fewer mistakes were also: more

250   active, more explorative, bolder, more aggressive or more sociable. Negative effect sizes

251   were assigned when individuals that had faster learning (or reversal) speeds, more correct

252   choices, or fewer mistakes were also: less active, less bold, less aggressive or less sociable.

253   Note that individuals that were classed as 'faster' at learning took fewer trials to reach the

254   learning criterion, but this is still classed as a positive effect size. The direction of effect was

255   determined either using the sign of test statistics presented in the papers, the descriptions

256   given by the authors, or by examining the raw data.

257   If studies did not report *r*, it was computed from the available statistical information,

258   or from additional information provided by the authors, using the procedures in [37]. See

259   supplementary Table S2 for full details on the calculation of effect sizes when *r* was not

260   reported. Only one paper (2 effect sizes) reported *r* directly. Twenty one effect sizes (from 9

261   papers) were obtained by converting statistical data presented in the text. For the remaining

262   45 effect sizes, new calculations were made using descriptive statistics presented in the text

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263   (2 papers) or raw data provided in the paper, the accompanying supplementary material, or

264   by the authors (13 papers).

265   In 17 out of 25 studies we obtained more than one effect size. In all but one study

266   [51] this was due to multiple tests being performed on the same sample of individuals.

267   However, note that sample sizes often varied between tests from the same study, usually

268   because some tests could not be performed using all individuals. When calculating the total

269   number of individuals used in any study or data subset (Table S4) we were therefore careful

270   to avoid pseudoreplication by not counting any individual more than once. For all analyses,

271   we used Fisher's *Z* transform of the correlation coefficient (*Zr*), as this has better statistical

272   properties when *r* approaches ±1 [37]. The associated variance for *Zr* (varz) was calculated

273   as $1/ (n - 3)$ [52].

274

Generating the phylogeny

276   Our sample included data from multiple species across several taxonomic classes,

277   and as such one potential confounding factor is similarity due to shared evolutionary history

278   [37]. Modern meta-analytic methods allow for the phylogenetic relatedness of species to be

279   taken into account during the analysis [53]. However, as our sample includes a wide range

280   of species, spanning several vertebrate orders (as well as a single invertebrate species),

281   there is currently no single phylogeny available that incorporates every species included. We

282   therefore constructed a supertree by manually combining multiple smaller trees from the

283   literature. We used taxonomic groupings for species for which phylogenetic data were not

284   available [53]. We obtained phylogenetic trees from several sources: for the relationship

285   among birds we used [54,55]; for the relationship among fish we used [56]; for the

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286   relationship among mammals we used [57].; and for the relationship among vertebrates we

287   used [58].

288   The supertree approach also means that obtaining accurate branch length data for

289   the phylogeny is not possible. However, the phylogenetic branching pattern of the tree still

290   contains important information on the relatedness between different taxa [39], and so we

291   estimated branch lengths based on the total length of the tree [59]. Accordingly, we first

292   assigned all branch lengths a value of one. The tree was then made ultrametric (all tips

293   contemporaneous), and branch lengths estimated, using Grafen's method [59], using the

294   Analysis of Phylogenetics and Evolution (APE) package v3.3 [60] in R v3.5. The final

295   ultrametric tree used in the analysis is shown in Figure 2.

296

297   **Statistical analysis**

298   All analyses were performed using R v3.5 (R Core Development Team, 2018) and

299   Metafor v1.9 [61]. Meta-analysis models were run using a Bayesian approach, using the

300   package MCMCglmm v2.21 [53]. We first ran a multilevel meta-analysis model in order to

301   estimate the mean effect size across all studies in the sample. We use the term 'multilevel'

302   to refer to random-effects meta-analysis models (in traditional meta-analysis classification;

303   see [37,52]) that include additional random factors in order to control for potential non-

304   independence between effect sizes (following [40]). We included study, species and

305   phylogenetic relatedness (using the phylogenetic tree shown above) as random factors in

306   these models. Study was included as a random factor because we extracted more than one

307   effect size from most studies (average of 2.64 effect sizes per study, range= 1- 6). Species

308   was included as a random factor because four species (*Cavia porcellus*, *Parus major*, *Poecile*

309   *atricapillus*, and *Taeniopygia guttata*) were tested in more than one study. Phylogeny was

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310 included as a random factor as our sample included several species in the same

311 genus/family. Removing any of these random factors did not significantly improve model fit,

312 or influence the significance of any categorical factors in meta-regression models (see

313 below) therefore we included all the three random factors in all models.

314   All models were fitted using an inverse-Wishart prior for all fixed and random effects

315 (V=1, nu= 0.002, [30,62]). All models were run for 3 million iterations, with a thinning

316 interval of 2000 and a burn-in period of 2 million iterations. We present our results as mean

317 posterior estimates of r (back-converted from Zr after analysis), as well as 95% credible

318 intervals (also known as the posterior density intervals). We consider an estimate to be

319 significantly different from zero if the 95% credible intervals do not overlap zero. We

320 checked the convergence of all models by examining the MCMC time series; the number of

321 iterations was sufficient to result in no trend for any of the models. We checked model

322 mixing by checking the autocorrelation between the stored samples in the chain

323 (representing the end of the MCMC run). Values for all models were less than 0.1, indicating

324 good mixture. We ran all models three times using identical parameters, and used Gelman-

325 Rubin diagnostics to check for convergence between the three runs [63]). These diagnostics

326 produced a potential scale reduction factor point estimate of 1 or very close to 1, indicating

327 convergence. We also re-ran the intercept-only model using a flat prior for the residuals and

328 random effects (V = 1e-16, nu = -2), with the same number of iterations as all previous

329 models. This model gave a very similar mean estimate as those using an inverse gamma

330 prior, though the credible interval was significantly wider, and we do not present it here.

331   We assessed the amount of heterogeneity in effect sizes for the intercept-only

332 model using the I^2 statistic [64]. This statistic estimates the percentage of overall variation in

333 the sample that is due to heterogeneity between studies (or effect sizes in this case)

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334 compared to sampling error (variation within studies). The I^2 value is generally preferred

335 over Cochran's Q test, as it gives an estimate of the degree of heterogeneity, rather than

336 just a P value, and is less affected by sample size. We present I^2 values associated with the

337 overall model, and each of the three random factors, following [40]. We follow the

338 recommendations of [64] in considering I^2 values of 25%, 50% and 75% as low, moderate

339 and high respectively, though heterogeneity in ecological and evolutionary meta-analyses is

340 typically very high [65].

341   This first analysis was used to estimate both the magnitude and the direction of the

342 relationship between cognition and personality. However, given that the sign of the effect

343 was highly variable (see below), and there are not always clear predictions for which

344 direction this relationship should be, we also wanted to estimate the absolute magnitude of

345 the relationship between personality and cognition ($|r|$), irrespective of the sign. We did

346 this by applying the folded normal distribution to the posterior mean estimate derived from

347 the intercept-only model, in order to estimate the average effect size and credible intervals

348 on the absolute scale (i.e. the 'analyse and transform' approach recommended by

349 [29,30,41,66]).

350   We next examined the extent to which variation in effect size was related to five

351 categorical moderator variables. These were: personality measure, cognitive measure,

352 taxonomic class, sex, and training type (see 'criteria for inclusion' for category details). We

353 used a model-selection approach to determine the importance of potential moderators of

354 mean effect size [40]. We performed a series of meta-regression models, each of which

355 included study, species, and phylogeny as random effects, and one of the five categorical

356 fixed effects. Model fit was then determined using the deviance information criterion (DIC),

357 which is a Bayesian equivalent of traditional information theoretic criteria. Lower values

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358 indicate a better fit, and a change in DIC of 2 or more (compared to the multilevel model

359 without moderators) was considered to indicate a significant improvement in model fit [67].

360 In order to obtain mean effect size estimates for each factor level we also ran five mixed-

361 effects models, each including only a single fixed effect, and with the intercept excluded.

362 Again, we consider an estimate to be significantly different from zero if the 95% credible

363 intervals do not overlap zero. We also applied the folded normal distribution to the

364 posterior mean estimates from these models in order to estimate the average magnitude

365 ($|r|$) for each category of the five moderator variables. Finally, we calculated the amount of

366 variance explained by the fixed factors (marginal R^2) using the method of [68].

367   We examined the dataset for two types of publication bias. First, we looked for

368 evidence of bias against publishing studies with small or negative effect sizes, or with small

369 sample sizes. To do this we tested for a relationship between effect size and variance using a

370 rank correlation test [69] and a linear regression test [70]. However, these methods assume

371 that effect sizes are independent, which does not apply to our dataset. Therefore, we used

372 meta-analytic residuals rather than the raw effect size [40]. We also used the trim-and-fill

373 method to test for asymmetry in the 'funnel plot' of residual effect size against sample

374 variance. Asymmetry in the funnel plot is assumed to be indicative of publication bias

375 against the 'missing' effect sizes on either side of the plot [71], although there are other

376 reasons for such asymmetry [40]. Second, we tested whether there is a relationship

377 between effect size and the year the study was published, which may be indicative of

378 publication bias. For example, the commonly observed negative relationship between effect

379 size and year may be due to a greater bias against publishing studies of small effect in the

380 early stages of the development of a new theory [37,72]. We examined this temporal trend

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381   by performing a meta-regression of the raw correlations, with year of publication added as a

382   fixed factor and study, species and phylogeny as random factors.

383

384   Results

385

386   **Final dataset**

387   The final dataset consisted of 25 studies and 66 effect sizes, testing 652 individuals in

388   total. This included data for 19 species across a broad taxonomic range, including insects

389   [73], fish [50,74–78], reptiles [79], birds [46,51,88,89,80–87], and mammals [90–94].

390

391   **Overall relationship**

392   The overall mean effect size was not significantly different from zero (r mean= 0.098,

393   95% CI = -0.074 - 0.281, N= 66 effect sizes, 652 individuals). It can be seen from the funnel

394   plot (Figure 3) that the sample consists of an approximately equal number of positive and

395   negative effect sizes. The overall heterogeneity of effect sizes (I^2) was moderate to high (I^2=

396   67.09%, HPD interval= 49.1% - 80.39%). It is therefore unlikely that this heterogeneity has

397   arisen due to sampling error alone. The three random factors explained little of the

398   heterogeneity in effect sizes (Study I^2= 8.46%, HPD interval= 0.16% - 31.98%; Species I^2=

399   5.21%, HPD interval= 0.12% - 17.52%; Phylogeny I^2= 10.71%, HPD interval= 0.24% - 37.69%).

400   The absolute mean effect size ($|r|$) was 0.268 (95% CI = 0.179- 0.368, significantly different

401   from zero, N= 66 effect sizes, 652 individuals), which is considered medium to small (small

402   effect size of 0.1, medium effect size of 0.3; Cohen, 1992).

403

404   **Moderator variables**

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405   Given the high heterogeneity in effect sizes, we searched for potential moderators of

406   this heterogeneity using a model selection approach. The variance explained by the fixed

407   factors was low for all models, and sex was the only categorical factor which significantly

408   improved model DIC (Table S5). Accordingly, there is a significantly positive relationship

409   between learning and personality when males are tested (r = 0.511, HPD interval = 0.239 -

410   0.75, N= 4 effect sizes, 90 individuals; Figure 4), but not when females were tested (r =

411   0.012, HPD interval = -0.298 - 0.308, N = 8 effect sizes, 103 individuals), or when the sexes

412   were not considered separately (r = 0.064, HPD interval = -0.098 - 0.251, N= 54 effect sizes,

413   511 individuals). However, the positive effect seen in males is due to only four effect sizes of

414   large effect. When examining the personality measures category separately, there was a

415   marginally significant positive relationship between learning and boldness in response to

416   predators (r mean= 0.363, HPD interval = -0.016 - 0.641, N= 5 effect sizes, 98 individuals;

417   Figure 4). All other categories tested had mean effect size estimates that did not

418   significantly differ from zero (Figure 4).The absolute average effect size ($|r|$) across all

419   behavioural measure categories was generally between 0.2- 0.4, with the exception of

420   effect sizes considering males ($|r|$= 0.549, 95% CI= 0.298- 0.744), females ($|r|$= 0.44, 95%

421   CI= 0.242- 0.713), and fish ($|r|$= 0.451, 95% CI= 0.261- 0.725, N= 11 effect sizes, 154

422   individuals; Figure 5).

423

424   **Publication bias**

425   There was no significant relationship between residual effect size (Zr) and study

426   precision (Egger's test: t_{64}= -0.473, P= 0.64; Begg-Mazumdar test: Kendall's tau= 0.033, P=

427   0.7). Further, trim and fill analysis did not detect missing effect sizes on either side of the

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428   funnel plot. There was no significant relationship between raw effect size (*Zr*) and year

429   (Meta-regression, fixed effect of year, *β*= -0.024, HPD interval = -0.054- 0.007; Figure S1).

430

431   Discussion

432   Our analysis provides the first quantitative test of the relationship between

433   personality and cognition in animals, using a sample of 25 studies and 19 species. We find

434   evidence for a small but significant relationship between variation in personality and

435   variation in learning across species in the absolute scale (i.e. irrespective of the sign of the

436   effect sizes). However, the *direction* of this relationship is highly variable, so that the

437   average effect size for the raw data is not significantly different from zero. This means that

438   our sample includes an approximately equal number of studies showing a positive

439   relationship between personality and cognition (e.g. animals that were more bold,

440   aggressive, explorative, active and social were quicker to learn, or had fewer errors, or more

441   correct responses after a standard amount of training) as showing a negative relationship

442   (animals that were more bold, aggressive, explorative, active and social were slower to

443   learn, had more errors, or fewer correct responses after a standard amount of training).

444   Further, taking into account the type of personality measure or cognitive measure did not

445   significantly explain the variation in the direction of this relationship seen across studies.

446   Taken together, these results show that that, while personality and learning co-vary

447   significantly across the studies sampled here, there is currently no evidence for a consistent

448   positive or negative relationship across species.

449   Given the large amount of variation in effect sizes seen in our sample, we included

450   several categorical moderator variables in our analysis in order to examine whether they

451   could significantly explain some of the variation in the size or direction of the relationship

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452   between personality and cognition. We had two key predictions regarding how these

453   variables might influence this relationship. Our first prediction was that the relationship

454   between personality and cognition should depend on the type of learning test used to

455   measure cognition: with a positive relationship predicted between personality and initial

456   learning speed, and a negative relationship predicted between personality and reversal

457   speed. However, this prediction was not supported: cognitive measure did not significantly

458   influence the direction of the relationship between personality and cognition. This finding is

459   in direct contrast with conceptual work which suggests 'fast' personality types are 'fast' and

460   'inflexible' learners. With 'inflexible' meaning animals that persevere in previously rewarded

461   patterns of behaviour (early empirical paper: [33]) or fail to produce new, correct behaviour

462   when the rules of a task or the environment changes or is altered (conceptual papers:

463   [15,32,77]; empirical paper: [65]).

464   Our second prediction was that certain personality measures, notably exploration,

465   are more likely to co-vary with cognition than others. However, this was not seen to be the

466   case, with personality measure explaining little of the heterogeneity in effect sizes seen

467   across species. However, we did find evidence for a marginally significant positive

468   relationship between cognition and boldness in response to predators: animals that are

469   bolder are able to learn new associations (and reverse previously-learned associations)

470   more quickly, and show more correct responses (and fewer errors) during standard training,

471   compared to animals that are less bold. Though it should also be noted that this category

472   consists of only five effect sizes from three studies, and so should be investigated further

473   before any strong conclusions are made. Nevertheless, this result was in contrast to the

474   other personality measures (activity, exploration, sociality and aggression) which all have

475   mean effect sizes that are not significantly different from zero (including boldness when

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476 measured as a response to novel objects or food), and it is not clear why boldness in

477 response to predation shows a significant directional relationship with cognition while the

478 others do not. It is worth stressing here that we do not assume a causal direction for this

479 relationship – for example, it is equally likely that being a fast learner could lead individuals

480 to be bolder.

481   The only categorical factor which explained a significant amount of the variation in

482 effect sizes in our sample was the sex of the subject. For the directional data, the

483 relationship was significantly positive when only males were tested, whereas the

484 relationship for females and both sexes combined did not significantly differ from zero.

485 Further, the absolute size of the relationship between personality and cognition was more

486 positive when males or females were tested separately, compared to when individuals of

487 both sexes were combined. This result is somewhat surprising, given that there have been

488 few studies examining sex differences in the relationship between personality and

489 cognition, and indeed only a single study in our sample tested for this relationship in males

490 and females separately [96]. For this reason, and the fact that this effect is primarily driven

491 by the presence of a relatively few effect sizes of large effect (4 and 8 effect sizes for males

492 only and females only, respectively), we interpret this result cautiously. Nevertheless, we

493 suggest that this pattern merits further investigation, and that researchers should test for

494 sex differences, including interactions between sex and personality, in the relationship

495 between personality and cognition before data from males and females are combined, and

496 report this in the methods or results sections even when there is no significant difference.

497 Sex differences in cognitive abilities has long been a well-studies area in human psychology

498 [97] and is beginning to receive attention in studies of animal cognition [e.g., 97,98].

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499   Importantly, the majority of the variation in effect size and direction in our sample

500   remains unexplained, with effect size not influenced by differences in personality measure,

501   cognitive measure, or phylogenetic history across studies. There are two potential

502   explanations for this: either the relationship between personality and cognition does not

503   have a consistent 'direction', in which case we need to adapt current theory in order to

504   explain this; or there are additional moderating factors which we have not identified that

505   strongly influence the direction of the relationship. For example, given the limited sample

506   size of our sample we did not test the effect of any ecological or life history factors that may

507   influence this relationship (e.g. sociality, breeding system, habitat type). Further, many of

508   these studies tested a relatively small number of individuals; the average sample size across

509   all studies was 26.08 (s.d.= 13.89), with eight studies testing less than 20 individuals. This

510   means that many of the trait categories we examined consisted of a very small number of

511   individuals (e.g. 45 individual insects and 57 individual reptiles). Therefore, we suggest that

512   more empirical tests are needed to investigate these potential explanations, using larger

513   sample sizes if possible. This is still a relatively young field, as exemplified by the fact that 19

514   of the 25 studies included in our analysis were published in the past five years, and there is

515   much we still do not know. Nevertheless, other meta-analyses have shown that personality

516   is related to an individual's intrinsic state (i.e., body mass, size, metabolic rate and hormone

517   levels; [41]) and has fitness consequences (e.g., reproductive success and survival; [27]).

518   Taken together with the current results, this suggests that personality is a measure worth

519   examining in the future.

520   In conclusion, our results show that Pavlov was correct: animal personality and

521   cognition are related. However, our analysis also revealed high among-study heterogeneity

522   in the direction of this relationship. This means that knowing the personality of an animal

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523 (where an individual's behavioural scores fall along a continuum ranging from inactive to

524 active, for example) does not consistently allow you to predict how quickly that animal will

525 learn. Further, we failed to find support for several key hypotheses regarding the

526 relationship between personality and cognition, and we hope that these hypotheses will be

527 re-assessed accordingly. Specifically, researchers may need to abandon the primary

528 assumption that fast-explorers should be fast-learners, while slow-explorers should be

529 better at reversal learning tasks. Finally, further work is needed in order to identify whether

530 there are other factors which influence the direction of the relationship between cognition

531 and personality. In light of these results, we have several recommendations. First, we urge

532 research undertaking future work to test for sex differences and interactions between sex,

533 personality and cognitive measures. Secondly, we suggest researchers measure both

534 personality and cognition across several different time points, or in several different

535 contexts in the same individuals (see [16] for details, and Cauchoix this issue). Lastly, our

536 hope is that this meta-analysis stimulates empirical work where formulation of study-

537 specific predictions should take into account not only the evolutionary pressures that have

538 shaped different species cognitive abilities, but also the different developmental histories

539 among discrete populations of the same species (e.g., pond snails, *Lymnaea stagnalis* [88,

540 Dalesman current issue], sticklebacks, *Gasterosteus aculeatus*, [101,102]) along with the

541 nature of the cognitive testing paradigm (the stimuli, the behavioural response, and the

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543

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554

Data Accessibility

556 The dataset supporting this article has been uploaded as part of the Supplementary

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558

Authors' Contribution

560 LMG conceived the idea. LMG and LRD designed and collected the data and wrote the

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562

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564 We have no competing interests.

565

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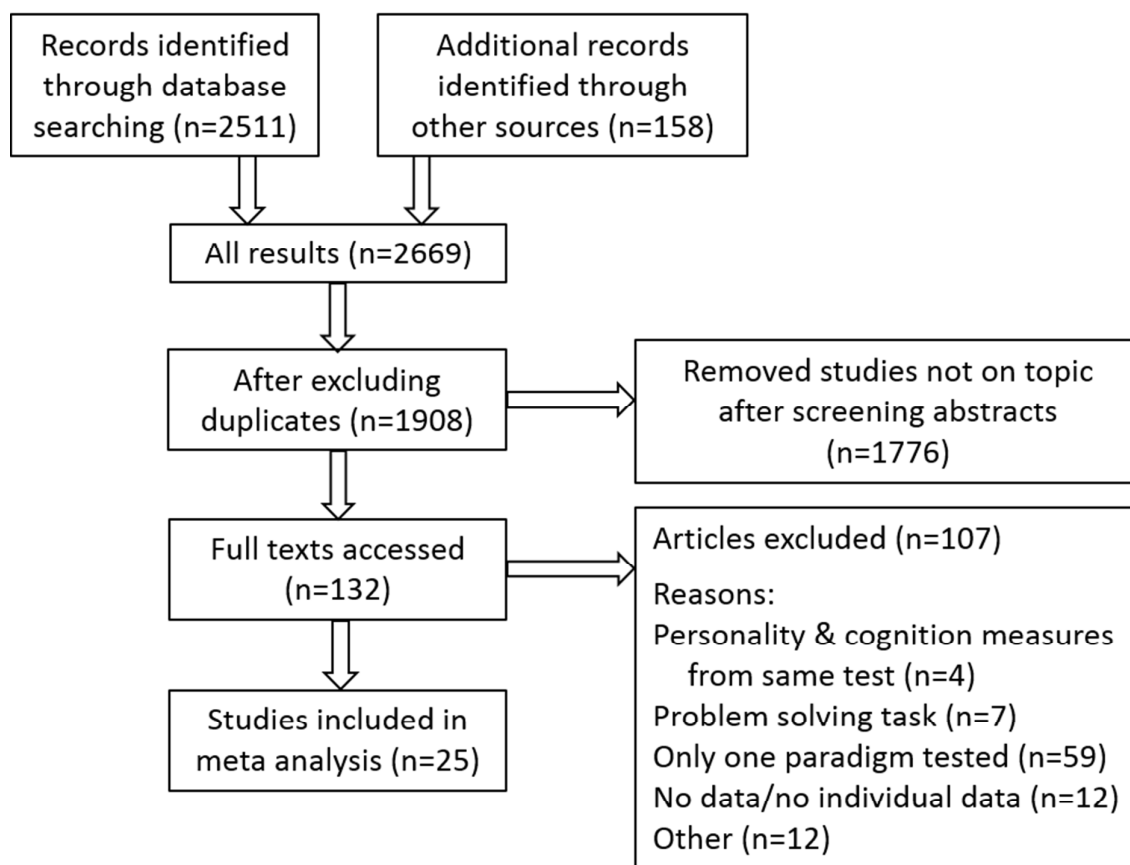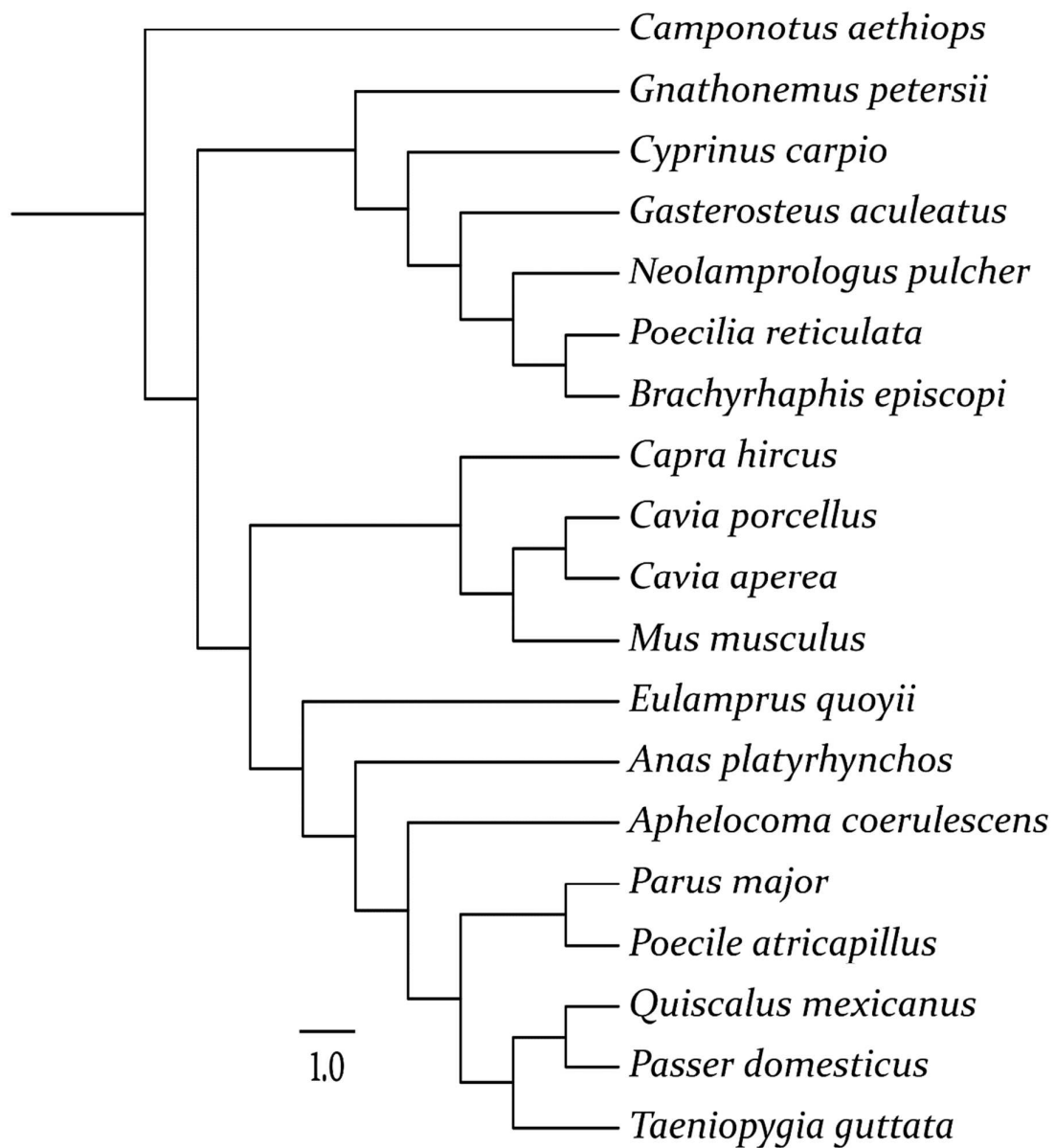
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Figure 1. PRISMA diagram showing systematic search process. See supplementary material for complete list of search terms used in different databases and Table S1 for a list of relevant papers not included in the final analysis. For the articles excluded 'Only one paradigm tested' refers to papers where only personality, or cognition, but not both, were tested.

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Camponotus aethiops

Gnathonemus petersii

Cyprinus carpio

Gasterosteus aculeatus

Neolamprologus pulcher

Poecilia reticulata

Brachyrhaphis episcopi

Capra hircus

Cavia porcellus

Cavia aperea

Mus musculus

Eulamprus quoyii

Anas platyrhynchos

Aphelocoma coerulescens

Parus major

Poecile atricapillus

Quiscalus mexicanus

Passer domesticus

Taeniopygia guttata

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3   **Figure 2**. Phylogeny used in meta-analysis (see main text for details).
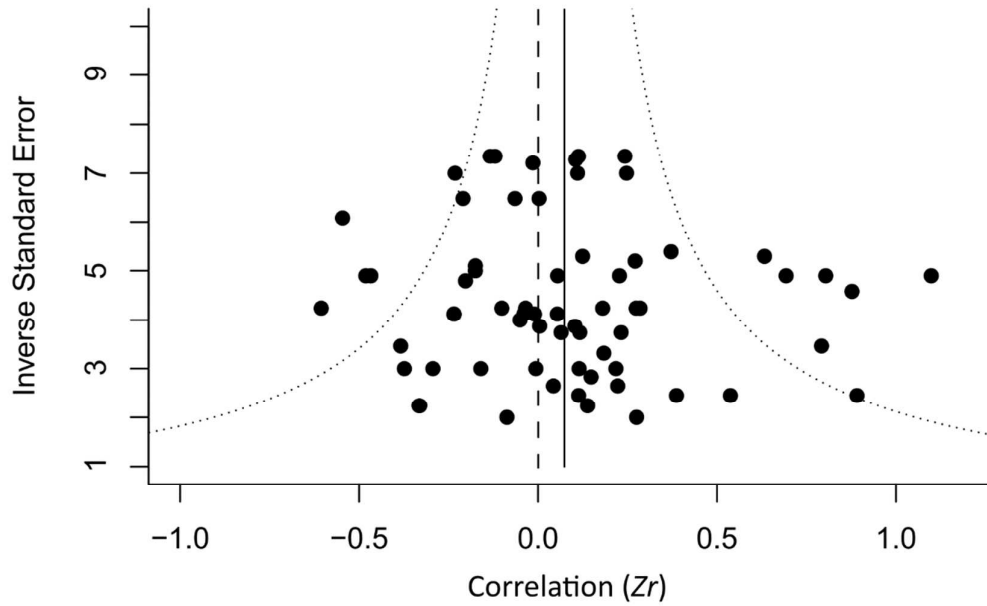
Figure 3. Funnel plot showing the relationship between sample size (inverse standard error;

studies with larger sample sizes have larger values) and raw effect size (*Zr*). The solid line

shows the overall mean effect size estimate from a multilevel meta-analysis including all 66
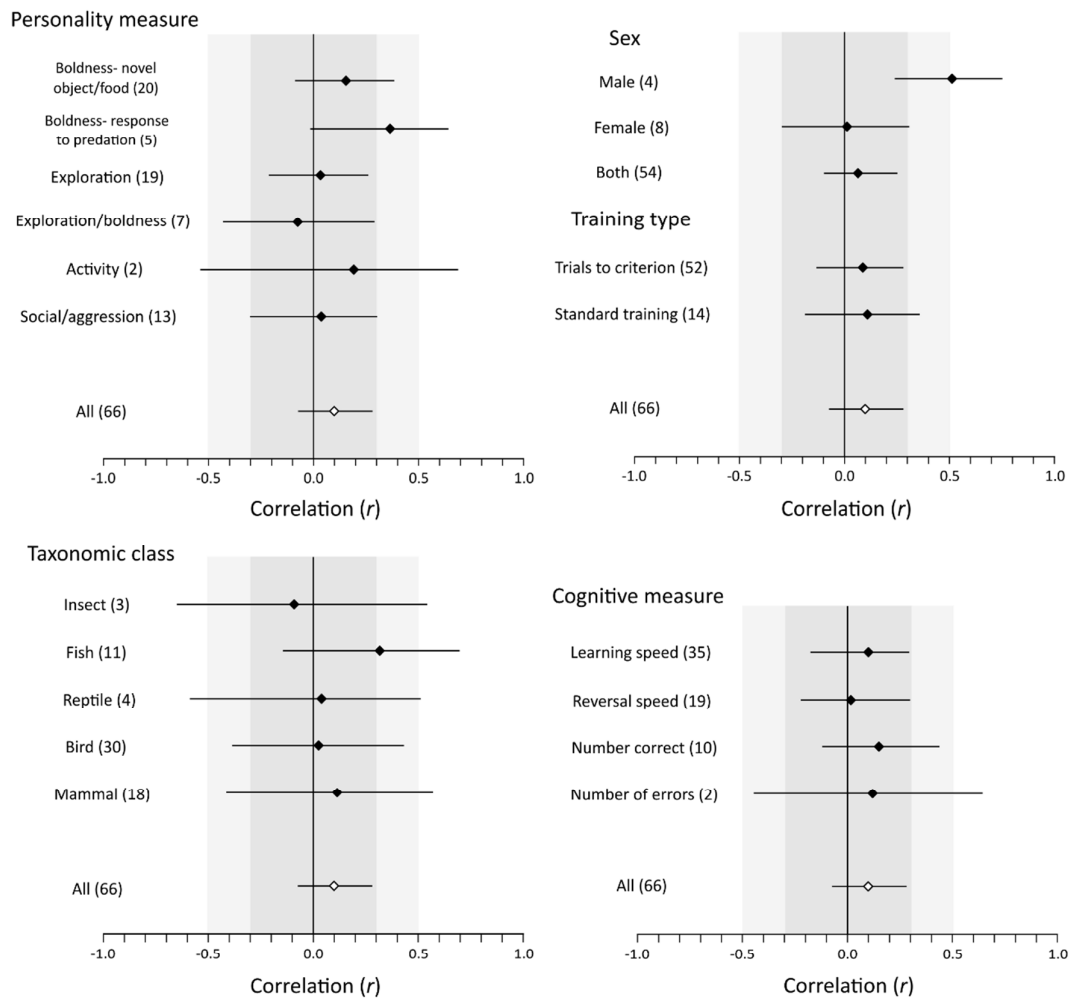
effect sizes.

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Figure 4. Mean effect size estimates (*r*) and 95% credible intervals for each moderator category. Numbers in parentheses show the number of effect sizes for each category. Estimates come from meta-regression models including three random factors (study, species, and phylogeny) and a single fixed factor, with models run separately for each moderator variable. The overall mean effect size for the entire dataset is represented by a white diamond in each plot for comparison. Shading corresponds to benchmark values for small (dark grey; < 0.3), medium (light grey; 0.3- 0.5), and large (white; >0.5) effects.
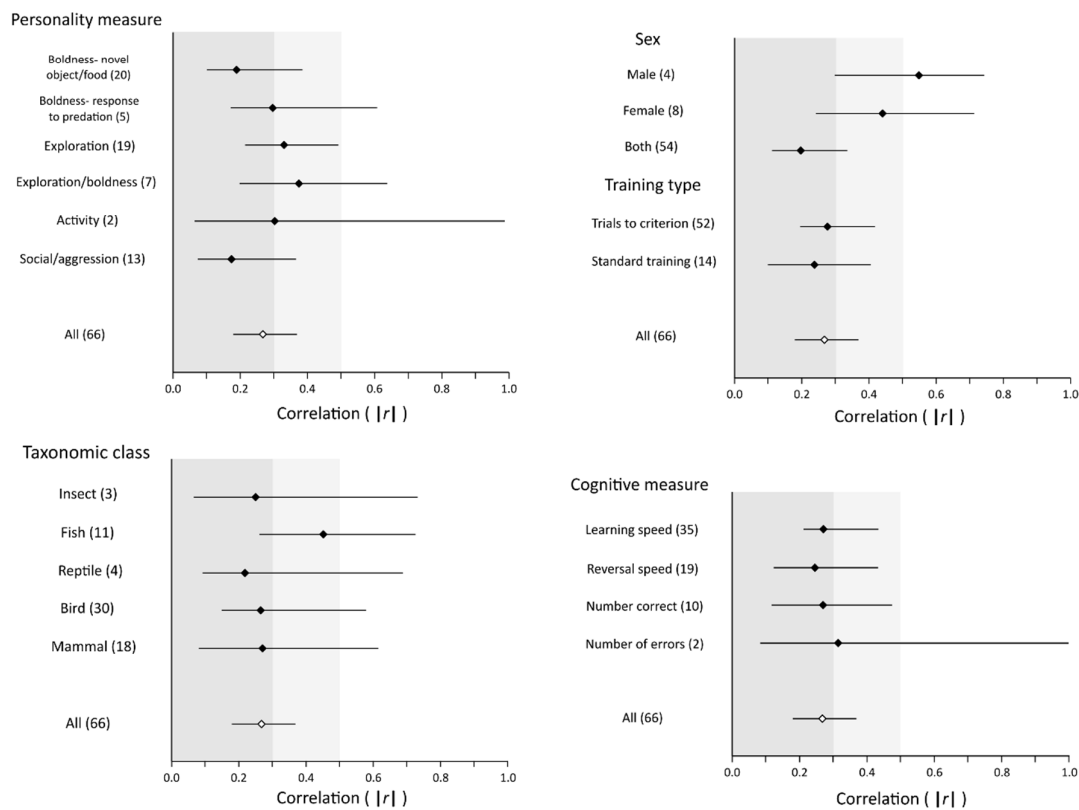
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Figure 5. Mean absolute effect size estimates ($|r|$) and 95% credible intervals for each moderator category. Numbers in parentheses show the number of effect sizes for each category. Estimates come from applying the folded-normal distribution to results from meta-regression models including three random factors (study, species, and phylogeny) and a single fixed factor, with models run separately for each moderator variable. The overall absolute mean effect size ($|r|$) for the entire dataset is represented by a white diamond in each plot for comparison. Shading corresponds to benchmark values for small (dark grey; < 0.3), medium (light grey; 0.3- 0.5), and large (white; >0.5) effects.