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3 Linking personality and cognition: A meta-analysis4  
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**Abstract**

In the past decade, several conceptual papers have linked variation in animal personality to variation in cognition, and recent years have seen a flood of empirical studies testing this question. However, these results have not been synthesised in a quantitative way. Here, we systematically search the literature and conduct a phylogenetically-controlled meta-analysis of empirical papers that have tested the relationship between animal personality (exploration, boldness, activity, aggression and sociability) and cognition (initial learning/reversal speed, number of correct choices/errors after standard training). We find evidence for a small but significant relationship between variation in personality and

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3 25 variation in learning across species in the absolute scale, however the *direction* of this  
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5 26 relationship is highly variable and when both positive and negative effect sizes are  
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7 27 considered the average effect size does not differ significantly from zero. Importantly, this  
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9 28 variation between studies is not explained by differences in personality or learning measure,  
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11 29 or taxonomic grouping. Further, these results do not support current hypotheses suggesting  
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13 30 that that fast-explorers are fast learners or that slow explorers perform better on tests of  
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15 31 reversal learning. Rather, we find evidence that bold animals are faster learners, but only  
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17 32 when boldness is measured in response to a predator (or simulated) and not when boldness  
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19 33 is measured by exposure to a novel object (or novel food). Further, although only a small  
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21 34 sub-sample of papers reported results separately for males and females, sex explained a  
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23 35 significant amount of variation in effect size. These results therefore suggest that, while  
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25 36 personality and learning are indeed related across a range of species, the direction of this  
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27 37 relationship is highly variable. Thus further empirical work is needed to determine whether  
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29 38 there are important moderators of this relationship.  
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#### 40 Keywords

41 Behavioural syndrome, Exploration, Individual differences, Learning, Sex differences,  
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#### 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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3 48 different tasks, could form suites of correlated traits (behavioural syndromes *sensu* [4–6]).  
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5 49 Thus, the tide of studying the average behaviour of groups has ebbed, as researchers have  
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7 50 realised the importance of quantifying the variation among individuals in a group [7]. Along  
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9 51 with this upwelling of empirical papers on animal personality came a swell of conceptual,  
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11 52 terminological, and statistical papers ('data-free' papers, reviewed in [8]) linking personality  
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13 53 to many aspects of ecological and evolutionary biology (e.g., sexual selection [9];  
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15 54 conservation [10]; ecology and evolution [11]; development [2]; evolutionary genomics  
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17 55 [12]). Included in this swell are several conceptual papers linking animal personality to  
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19 56 animal cognition [13–18].

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23 57 A link between personality and cognition, albeit by different names, was first  
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25 58 established by Pavlov in the early 20<sup>th</sup> century during his work examining associative  
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27 59 processes (i.e., conditioned reflexes) and digestive physiology [14,19–21]. Pavlov described  
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29 60 four different 'types' of nervous systems based on how quickly dogs learned to form  
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31 61 different types of associations [22]. For instance, the 'Excitable type' showed strong (and  
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33 62 quick) excitatory conditioning (learning to make a response), but weak (and slow) inhibitory  
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35 63 conditioning (learning to withhold making a response). The 'Inhibited type' was the  
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37 64 opposite: showing strong and quick inhibitory conditioning, and weak and slow excitatory  
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39 65 conditioning. Both the Excitable and Inhibited type also showed low flexibility – that is,  
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41 66 alternating between excitatory and inhibitory conditioning. The 'Lively type' showed rapid  
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43 67 associative learning for both excitatory and inhibitory tasks and could make flexible  
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45 68 conversions between the two. The last type, 'Quiet', formed slow but consistent  
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47 69 associations and was less flexible, compared to the Lively type, when transitioning between  
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49 70 the different conditioning types (excitatory and inhibitory; [13,14]). In two lectures: *An*  
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51 71 *attempt to understand the symptoms of hysteria physiologically* (1932) and *The conditioned*

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3 72 *reflex* (1935; [21]), Pavlov connected the four types of nervous systems to individually  
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5 73 distinct animal ‘temperaments’. For instance, the Excitable type display general behaviour  
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7 74 that is ‘aggressive, animated and undisciplined’ (pp 105). While the Lively and Quiet type  
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9 75 behave ‘actively and lively’ and ‘inert...calm and unperturbed’ (pp 177), respectively. Lastly,  
10  
11 76 the Inhibitory type is ‘restless and constantly looking about or on the contrary, constantly  
12  
13 77 stopping and remaining motionless...’ (pp 177). Pavlov believed these four types of nervous  
14  
15 78 systems were responsible for individually distinctive and fixed behavioural phenotypes (i.e.,  
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17 79 personalities) of different dogs [21].

20  
21 80 The foremost goal of this paper is to assess if Pavlov was indeed correct by asking: is  
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23 81 an animal’s personality related to its cognitive ability? Recent years have seen a flurry of  
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25 82 empirical studies testing this question, in a range of species [e.g., mammals, 23; fish, 24;  
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27 83 birds, 25]. However, these results have not yet been synthesised in a quantitative way. We  
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29 84 address this using a meta-analytic approach. We systematically searched the literature for  
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31 85 studies testing for a relationship between animal personality and cognition across  
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33 86 individuals, finding estimates for 19 animal species, including mammals, birds, reptiles, fish  
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35 87 and insects. We use data from papers examining at least one measure of personality and at  
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37 88 least one measure of cognition from the same individuals, where these two measures were  
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39 89 derived from independent assays. Cognition, broadly defined, is the acquisition, processing,  
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41 90 storage and use of information [26], and, following Pavlov, the current meta-analysis will  
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43 91 focus on information acquisition. In the current paper variation in information acquisition is  
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45 92 quantified by either: the number of trials individuals take to learn an association to a pre-  
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47 93 determined level of expertise (the learning criteria, see methods for details and [16] Table 1  
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49 94 for a guide to measuring cognitive abilities); or, the number of correct (or incorrect)  
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51 95 responses in a standard number of training trials. The personality traits included in the  
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3 96 current meta-analysis are those broadly defined by [11, and revised by 24]: boldness,  
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5 97 exploration, activity, sociability and aggression (see methods for details and [28] for a  
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7 98 pertinent discussion regarding the naming and quantification of personality traits).

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10 99 Importantly, the relationship (correlation) between personality and cognition can be  
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12 100 either positive or negative, depending on how behaviours are coded. While the assignment  
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14 101 of a direction to these behavioural measures is somewhat arbitrary (see methods), the  
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16 102 biological meaning is not; for example: a positive relationship between cognition and  
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18 103 boldness (e.g. faster learners are bolder) is biologically and ecologically different from the  
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20 104 converse (e.g. faster learners are less bold). However, another way to examine this  
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22 105 relationship across species is to look at the absolute magnitude of the effect, irrespective of  
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24 106 the sign (in other words by making all effect sizes positive). Such an approach may be  
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26 107 needed if the sign of the relationship is not consistent across species [29,30][30]. In such a  
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28 108 case, using the absolute values may allow us to detect a strong relationship that is masked  
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30 109 when we examine the raw (positive and negative) effect sizes alone, and this result would  
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32 110 be informative in that it suggests that there are underlying factors that strongly influence  
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34 111 the direction of the relationship which we can try to uncover. In this study we therefore  
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36 112 quantify the strength of the relationship between personality and cognition both with and  
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38 113 without considering the directionality of the effect sizes.

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44 114 The secondary goal of this paper is to begin to address specific predictions regarding  
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46 115 the direction of the relationship between personality and cognition. Although it has been  
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48 116 argued elsewhere [16], making predictions about the direction of the relationship between  
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50 117 personality and cognition will depend on many factors, including, but not limited to - the  
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52 118 stimulus (e.g., tone, light, conspecific, odour), the response (e.g., making one versus  
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54 119 withholding making one), and the outcome (positive or negative). A popular prediction,  
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3 120 nonetheless, based both on conceptual [13,15,27,28] and early empirical work (e.g.,  
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5 121 [29,30]), is that fast-explorers are fast learners and excel in stable environments, whereas  
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7 122 slow explorers are more flexible and therefore should be better at reversal learning  
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9 123 compared to fast explorers. In other words, the relationship between exploration and  
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11 124 cognition may depend on the cognitive measure being used. Therefore, we predict a  
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13 125 positive relationship between personality and learning speed for newly acquired tasks (e.g.,  
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15 126 fast-explorers are fast learners) and a negative relationship between personality and  
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17 127 reversal learning (e.g., slow-explorers are fast at reversal learning).  
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21 128 Finally, the relationship between personality and cognition may also depend on  
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23 129 which personality measure is being examined. For example, Sih and Del Giudice hypothesize  
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25 130 that individual differences along the bold-aggressive-active-exploratory axis will be  
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27 131 correlated with cognition [35]. The proposed mechanism for this correlation is a risk-reward  
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29 132 trade-off that underlies both cognition and personality, that is, the more a behaviour is  
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31 133 expressed (e.g., more aggression, more boldness, fast learner) the greater the reward (e.g.,  
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33 134 more mates, more food), but also the greater the risk (e.g., being predated, injury in  
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35 135 contests, decision errors). Sih and Del Giudice [35] make a distinction between cognitive  
36  
37 136 abilities and cognitive 'style', where cognitive style refers to 'the way individuals acquire,  
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39 137 process, store or act on information, independent of cognitive ability' (pp 2762). And, while  
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41 138 the distinction between ability and style is not usually discussed or addressed in papers  
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43 139 examining cognition, the theoretical framework supplied by [35] is applied (see [16] for  
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45 140 example of measuring cognitive style). A similar view, linking personality to cognition, holds  
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47 141 that bold/explorative animals experience more of their environment, more quickly, thus  
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49 142 coming into contact with to-be-learned associations more readily than shy/less explorative  
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51 143 individuals [16,35,36]. This view therefore suggests that personality constrains cognition.  
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3 144 The same end can also be achieved by different means: animals that form associations more  
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5 145 quickly may be able to then move through their environment more quickly [learning ability  
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7 146 facilitates exploration, 26]. Despite these different proposed mechanisms, the outcome  
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9 147 remains the same – a positive link between exploration and learning speed. In the current  
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11 148 meta-analysis we ask if six different personality measures are related to learning in the  
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14 149 same way.

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16 150 In summary, in this study we ask several questions. First, is there a significant  
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18 151 relationship between personality and learning, either in the absolute or raw scale? Second,  
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20 152 is the strength or direction of this relationship influenced by additional factors, such as the  
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22 153 personality measure or cognitive test used, or the sex of the subjects? Third, is there any  
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24 154 evidence of publication bias against studies showing certain results (e.g. those that  
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26 155 counteract prevailing theory)?  
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## 31 157 **Methods**

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35 158 Our methods followed the PRISMA standards for reporting meta-analyses ([36–39];  
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37 159 see Figure 1 for a diagram of the search results and study selection) as closely as possible.  
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### 41 161 **Search protocol**

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44 162 We used three methods to search the literature for relevant studies. First, keyword  
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46 163 searches were performed using three databases on 17 October 2017 (Web of Science,  
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48 164 PsychINFO, and Scopus, see Supplementary Material for complete list of search terms used  
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50 165 for each database). Second, Web of Science was used to search for papers that had cited  
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52 166 two influential papers in this area: a review on behavioural syndromes and cognition [15];  
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54 167 and an opinion paper on cognition and personality [16]. After these searches, we excluded  
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3 168 duplicate results, and then accessed the abstracts of 1776 papers and screened them for  
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5 169 inclusion. Full texts of papers that were deemed relevant were read ( $n= 129$ ). Finally, the full  
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7 170 texts of three additional papers that were not located by the initial search were accessed  
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9 171 because they were cited in the papers that were deemed relevant (final  $n= 132$ , Figure 1).  
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### 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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3 192 *individual consistency (such as boldness, aggression, activity)*. We included studies that  
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5 193 report personality measures from one or several behavioural episodes. The terminology for  
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7 194 the specific personality traits used here is based on [11], sometimes referred to as the 'Big  
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9 195 Five': boldness, exploration, activity, aggressiveness and sociability [6]. However, [11]  
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11 196 explicitly addressed the limitation of this over-simplification of terminology and suggested  
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14 197 that the five outlined traits be regarded as a working tool. Thus the working definitions we  
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16 198 used are more in line with those used by [27], and consisted of the following categories:  
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18 199 Boldness – responses to novel objects, food and potential predators; Exploration –  
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20 200 responses to a novel environment or open field; Social/Aggression – reactions to conspecific  
21  
22 201 presentations; Activity – movement around a familiar environment (e.g., a home cage); and,  
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24 202 Exploration/Boldness – combined reactions to novel environment and novel object tests  
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26 203 (e.g., established composite scores for great tits *sensu* [43]). Note that in the analysis we  
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28 204 distinguish between boldness in response to novel objects or food and boldness in response  
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30 205 to predators, as preliminary analyses indicated that these were informative groupings. We  
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32 206 use the term 'personality measure' rather than 'personality trait' in order to distinguish  
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34 207 between these two types of boldness. In summary, the 'behaviour measures' variable  
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36 208 consists of six categories: boldness in response to novel objects/food, boldness in response  
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38 209 to predators, exploration/boldness, activity, exploration, and social/aggression.  
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44 210 *Cognitive measure and training type*. We included studies that examined four  
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46 211 different cognitive measures (learning speed, reversal learning speed, number of errors,  
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48 212 number of correct responses) – which we grouped into two different training types: 'trials to  
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50 213 criterion' and 'standard training'. In the first type of study (trials to criterion), animals were  
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52 214 trained until they reached a pre-determined learning criteria for: (1) initial acquisition of a  
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54 215 task (learning speed); or, (2) during a subsequent phase when the initial reward  
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3 216 contingencies (those in place during initial acquisition) were reversed (reversal learning).  
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5 217 Animals trained to criteria are at the same level of asymptotic performance (e.g., in  
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7 218 associative learning, the maximum associative value a Conditioned Stimulus [CS] can  
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9 219 gain[44]). In the second type of study (standard training), animals were trained for a  
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11 220 standard number of trials and the cognitive measures were: (3) the number of errors; or, (4)  
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13 221 the number of correct responses. In these latter two measures, it is unclear *if or how much*  
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15 222 an animal has learned (i.e., where an individual's performance falls on a learning curve that  
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17 223 culminates, theoretically, in asymptotic learning). We therefore have separated these from  
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19 224 the cases where animals are trained until they reach learning criteria. There are a dearth of  
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21 225 studies that examine the link between cognitive abilities beyond information acquisition  
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23 226 (i.e., information use, but see [45] for a test of generalization of previously learned rules in a  
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25 227 pigeon and [46] for a test of performance accuracy on novel exemplars following initial  
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27 228 acquisition). We did not include studies that tested motor learning or problem solving  
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29 229 (extractive foraging task) as it is unclear which cognitive mechanism may underpin  
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31 230 performance in these tasks (for in-depth treatment of this topic see [47–49]).  
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33 231 Supplementary Table S3 contains the *Cognitive measure* and *Training type* for all effect sizes  
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35 232 in the meta-analysis (see reference [16] Table 1 for overview of measurement of cognitive  
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37 233 abilities).  
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44 234 Sex. We included both studies that tested for sex differences in behaviour and those  
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46 235 that did not, with sex classified as 'both' when sex differences were not assessed. In one  
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48 236 case, the sex of the subjects was not specified [50]; therefore we classed this as 'both'.  
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53 238 **Calculating effect sizes**  
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3 239 In order to quantify the relationship between personality and learning, the  
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5 240 experimental results first need to be converted into a standardised effect size. We used  
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7 241 Pearson's product moment correlation coefficient ( $r$ ) as the measure of effect size, as the  
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9 242 majority of studies in our sample measured both personality and learning on a continuous  
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11 243 scale (though there were nine cases in which subjects were classified into discrete groups  
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13 244 based on a personality or cognition score). Here,  $r$  represents the magnitude of the  
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15 245 association between one of several personality measures and some cognitive measure.  
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17 246 Given that  $r$  can range from +1 to -1, we need to determine the sign of the relationship for  
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19 247 each study. We classified correlations as either positive or negative depending on the  
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21 248 following criteria. Positive effect sizes were assigned when individuals that had faster  
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23 249 learning (or reversal) speeds, more correct choices, or fewer mistakes were also: more  
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25 250 active, more explorative, bolder, more aggressive or more sociable. Negative effect sizes  
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27 251 were assigned when individuals that had faster learning (or reversal) speeds, more correct  
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29 252 choices, or fewer mistakes were also: less active, less bold, less aggressive or less sociable.  
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31 253 Note that individuals that were classed as 'faster' at learning took fewer trials to reach the  
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33 254 learning criterion, but this is still classed as a positive effect size. The direction of effect was  
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35 255 determined either using the sign of test statistics presented in the papers, the descriptions  
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37 256 given by the authors, or by examining the raw data.  
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44 257 If studies did not report  $r$ , it was computed from the available statistical information,  
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46 258 or from additional information provided by the authors, using the procedures in [37]. See  
47  
48 259 supplementary Table S2 for full details on the calculation of effect sizes when  $r$  was not  
49  
50 260 reported. Only one paper (2 effect sizes) reported  $r$  directly. Twenty one effect sizes (from 9  
51  
52 261 papers) were obtained by converting statistical data presented in the text. For the remaining  
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54 262 45 effect sizes, new calculations were made using descriptive statistics presented in the text  
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3 263 (2 papers) or raw data provided in the paper, the accompanying supplementary material, or  
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5 264 by the authors (13 papers).

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7 265 In 17 out of 25 studies we obtained more than one effect size. In all but one study  
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9 266 [51] this was due to multiple tests being performed on the same sample of individuals.  
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11 267 However, note that sample sizes often varied between tests from the same study, usually  
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13 268 because some tests could not be performed using all individuals. When calculating the total  
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15 269 number of individuals used in any study or data subset (Table S4) we were therefore careful  
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17 270 to avoid pseudoreplication by not counting any individual more than once. For all analyses,  
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19 271 we used Fisher's Z transform of the correlation coefficient ( $Z_r$ ), as this has better statistical  
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21 272 properties when  $r$  approaches  $\pm 1$  [37]. The associated variance for  $Z_r$  ( $\text{var}_z$ ) was calculated  
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23 273 as  $1/(n - 3)$  [52].  
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### 29 30 275 **Generating the phylogeny**

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32 276 Our sample included data from multiple species across several taxonomic classes,  
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34 277 and as such one potential confounding factor is similarity due to shared evolutionary history  
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36 278 [37]. Modern meta-analytic methods allow for the phylogenetic relatedness of species to be  
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38 279 taken into account during the analysis [53]. However, as our sample includes a wide range  
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40 280 of species, spanning several vertebrate orders (as well as a single invertebrate species),  
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42 281 there is currently no single phylogeny available that incorporates every species included. We  
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44 282 therefore constructed a supertree by manually combining multiple smaller trees from the  
45  
46 283 literature. We used taxonomic groupings for species for which phylogenetic data were not  
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48 284 available [53]. We obtained phylogenetic trees from several sources: for the relationship  
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50 285 among birds we used [54,55]; for the relationship among fish we used [56]; for the  
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3 286 relationship among mammals we used [57].; and for the relationship among vertebrates we  
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5 287 used [58].  
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7 288 The supertree approach also means that obtaining accurate branch length data for  
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9 289 the phylogeny is not possible. However, the phylogenetic branching pattern of the tree still  
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11 290 contains important information on the relatedness between different taxa [39], and so we  
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13 291 estimated branch lengths based on the total length of the tree [59]. Accordingly, we first  
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15 292 assigned all branch lengths a value of one. The tree was then made ultrametric (all tips  
16  
17 293 contemporaneous), and branch lengths estimated, using Grafen's method [59], using the  
18  
19 294 Analysis of Phylogenetics and Evolution (APE) package v3.3 [60] in R v3.5. The final  
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21 295 ultrametric tree used in the analysis is shown in Figure 2.  
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### 27 297 **Statistical analysis**

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30 298 All analyses were performed using R v3.5 (R Core Development Team, 2018) and  
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32 299 Metafor v1.9 [61]. Meta-analysis models were run using a Bayesian approach, using the  
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34 300 package MCMCglmm v2.21 [53]. We first ran a multilevel meta-analysis model in order to  
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36 301 estimate the mean effect size across all studies in the sample. We use the term 'multilevel'  
37  
38 302 to refer to random-effects meta-analysis models (in traditional meta-analysis classification;  
39  
40 303 see [37,52]) that include additional random factors in order to control for potential non-  
41  
42 304 independence between effect sizes (following [40]). We included study, species and  
43  
44 305 phylogenetic relatedness (using the phylogenetic tree shown above) as random factors in  
45  
46 306 these models. Study was included as a random factor because we extracted more than one  
47  
48 307 effect size from most studies (average of 2.64 effect sizes per study, range= 1- 6). Species  
49  
50 308 was included as a random factor because four species (*Cavia porcellus*, *Parus major*, *Poecile*  
51  
52 309 *atricapillus*, and *Taeniopygia guttata*) were tested in more than one study. Phylogeny was  
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3 310 included as a random factor as our sample included several species in the same  
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5 311 genus/family. Removing any of these random factors did not significantly improve model fit,  
6  
7 312 or influence the significance of any categorical factors in meta-regression models (see  
8  
9 313 below) therefore we included all the three random factors in all models.

11  
12 314 All models were fitted using an inverse-Wishart prior for all fixed and random effects  
13  
14 315 ( $V=1$ ,  $\nu=0.002$ , [30,62]). All models were run for 3 million iterations, with a thinning  
15  
16 316 interval of 2000 and a burn-in period of 2 million iterations. We present our results as mean  
17  
18 317 posterior estimates of  $r$  (back-converted from  $Zr$  after analysis), as well as 95% credible  
19  
20 318 intervals (also known as the posterior density intervals). We consider an estimate to be  
21  
22 319 significantly different from zero if the 95% credible intervals do not overlap zero. We  
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24 320 checked the convergence of all models by examining the MCMC time series; the number of  
25  
26 321 iterations was sufficient to result in no trend for any of the models. We checked model  
27  
28 322 mixing by checking the autocorrelation between the stored samples in the chain  
29  
30 323 (representing the end of the MCMC run). Values for all models were less than 0.1, indicating  
31  
32 324 good mixture. We ran all models three times using identical parameters, and used Gelman-  
33  
34 325 Rubin diagnostics to check for convergence between the three runs [63]). These diagnostics  
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36 326 produced a potential scale reduction factor point estimate of 1 or very close to 1, indicating  
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38 327 convergence. We also re-ran the intercept-only model using a flat prior for the residuals and  
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40 328 random effects ( $V = 1e-16$ ,  $\nu = -2$ ), with the same number of iterations as all previous  
41  
42 329 models. This model gave a very similar mean estimate as those using an inverse gamma  
43  
44 330 prior, though the credible interval was significantly wider, and we do not present it here.

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46 331 We assessed the amount of heterogeneity in effect sizes for the intercept-only  
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48 332 model using the  $I^2$  statistic [64]. This statistic estimates the percentage of overall variation in  
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50 333 the sample that is due to heterogeneity between studies (or effect sizes in this case)

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3 334 compared to sampling error (variation within studies). The  $I^2$  value is generally preferred  
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5 335 over Cochran's Q test, as it gives an estimate of the degree of heterogeneity, rather than  
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7 336 just a  $P$  value, and is less affected by sample size. We present  $I^2$  values associated with the  
8  
9 337 overall model, and each of the three random factors, following [40]. We follow the  
10  
11 338 recommendations of [64] in considering  $I^2$  values of 25%, 50% and 75% as low, moderate  
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13 339 and high respectively, though heterogeneity in ecological and evolutionary meta-analyses is  
14  
15 340 typically very high [65].

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19 341 This first analysis was used to estimate both the magnitude and the direction of the  
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21 342 relationship between cognition and personality. However, given that the sign of the effect  
22  
23 343 was highly variable (see below), and there are not always clear predictions for which  
24  
25 344 direction this relationship should be, we also wanted to estimate the absolute magnitude of  
26  
27 345 the relationship between personality and cognition ( $|r|$ ), irrespective of the sign. We did  
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29 346 this by applying the folded normal distribution to the posterior mean estimate derived from  
30  
31 347 the intercept-only model, in order to estimate the average effect size and credible intervals  
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33 348 on the absolute scale (i.e. the 'analyse and transform' approach recommended by  
34  
35 349 [29,30,41,66]).

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39 350 We next examined the extent to which variation in effect size was related to five  
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41 351 categorical moderator variables. These were: personality measure, cognitive measure,  
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43 352 taxonomic class, sex, and training type (see 'criteria for inclusion' for category details). We  
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45 353 used a model-selection approach to determine the importance of potential moderators of  
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47 354 mean effect size [40]. We performed a series of meta-regression models, each of which  
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49 355 included study, species, and phylogeny as random effects, and one of the five categorical  
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51 356 fixed effects. Model fit was then determined using the deviance information criterion (DIC),  
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53 357 which is a Bayesian equivalent of traditional information theoretic criteria. Lower values  
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3 358 indicate a better fit, and a change in DIC of 2 or more (compared to the multilevel model  
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5 359 without moderators) was considered to indicate a significant improvement in model fit [67].  
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7 360 In order to obtain mean effect size estimates for each factor level we also ran five mixed-  
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9 361 effects models, each including only a single fixed effect, and with the intercept excluded.  
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11 362 Again, we consider an estimate to be significantly different from zero if the 95% credible  
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13 363 intervals do not overlap zero. We also applied the folded normal distribution to the  
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15 364 posterior mean estimates from these models in order to estimate the average magnitude  
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17 365 ( $|r|$ ) for each category of the five moderator variables. Finally, we calculated the amount of  
18  
19 366 variance explained by the fixed factors (marginal  $R^2$ ) using the method of [68].  
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23 367 We examined the dataset for two types of publication bias. First, we looked for  
24  
25 368 evidence of bias against publishing studies with small or negative effect sizes, or with small  
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27 369 sample sizes. To do this we tested for a relationship between effect size and variance using a  
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29 370 rank correlation test [69] and a linear regression test [70]. However, these methods assume  
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31 371 that effect sizes are independent, which does not apply to our dataset. Therefore, we used  
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33 372 meta-analytic residuals rather than the raw effect size [40]. We also used the trim-and-fill  
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35 373 method to test for asymmetry in the 'funnel plot' of residual effect size against sample  
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37 374 variance. Asymmetry in the funnel plot is assumed to be indicative of publication bias  
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39 375 against the 'missing' effect sizes on either side of the plot [71], although there are other  
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41 376 reasons for such asymmetry [40]. Second, we tested whether there is a relationship  
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43 377 between effect size and the year the study was published, which may be indicative of  
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45 378 publication bias. For example, the commonly observed negative relationship between effect  
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47 379 size and year may be due to a greater bias against publishing studies of small effect in the  
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49 380 early stages of the development of a new theory [37,72]. We examined this temporal trend  
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3 381 by performing a meta-regression of the raw correlations, with year of publication added as a  
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5 382 fixed factor and study, species and phylogeny as random factors.  
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## 8 9 384 **Results**

### 10 11 385 12 13 386 **Final dataset**

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17 387 The final dataset consisted of 25 studies and 66 effect sizes, testing 652 individuals in  
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19 388 total. This included data for 19 species across a broad taxonomic range, including insects  
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21 389 [73], fish [50,74–78], reptiles [79], birds [46,51,88,89,80–87], and mammals [90–94].  
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### 24 25 391 **Overall relationship**

26  
27 392 The overall mean effect size was not significantly different from zero ( $r$  mean= 0.098,  
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29 393 95% CI = -0.074 - 0.281,  $N$ = 66 effect sizes, 652 individuals). It can be seen from the funnel  
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31 394 plot (Figure 3) that the sample consists of an approximately equal number of positive and  
32  
33 395 negative effect sizes. The overall heterogeneity of effect sizes ( $I^2$ ) was moderate to high ( $I^2$ =  
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35 396 67.09%, HPD interval= 49.1% - 80.39%). It is therefore unlikely that this heterogeneity has  
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37 397 arisen due to sampling error alone. The three random factors explained little of the  
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39 400 heterogeneity in effect sizes (Study  $I^2$ = 8.46%, HPD interval= 0.16% - 31.98%; Species  $I^2$ =  
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41 401 5.21%, HPD interval= 0.12% - 17.52%; Phylogeny  $I^2$ = 10.71%, HPD interval= 0.24% - 37.69%).  
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43 402 The absolute mean effect size ( $|r|$ ) was 0.268 (95% CI = 0.179- 0.368, significantly different  
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45 403 from zero,  $N$ = 66 effect sizes, 652 individuals), which is considered medium to small (small  
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47 404 effect size of 0.1, medium effect size of 0.3; Cohen, 1992).  
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### 56 404 **Moderator variables**

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3 405           Given the high heterogeneity in effect sizes, we searched for potential moderators of  
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5 406   this heterogeneity using a model selection approach. The variance explained by the fixed  
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7 407   factors was low for all models, and sex was the only categorical factor which significantly  
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9 408   improved model DIC (Table S5). Accordingly, there is a significantly positive relationship  
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11 409   between learning and personality when males are tested ( $r = 0.511$ , HPD interval = 0.239 -  
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13 410   0.75,  $N = 4$  effect sizes, 90 individuals; Figure 4), but not when females were tested ( $r =$   
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15 411   0.012, HPD interval = -0.298 - 0.308,  $N = 8$  effect sizes, 103 individuals), or when the sexes  
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17 412   were not considered separately ( $r = 0.064$ , HPD interval = -0.098 - 0.251,  $N = 54$  effect sizes,  
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19 413   511 individuals). However, the positive effect seen in males is due to only four effect sizes of  
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21 414   large effect. When examining the personality measures category separately, there was a  
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23 415   marginally significant positive relationship between learning and boldness in response to  
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25 416   predators ( $r$  mean= 0.363, HPD interval = -0.016 - 0.641,  $N = 5$  effect sizes, 98 individuals;  
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27 417   Figure 4). All other categories tested had mean effect size estimates that did not  
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29 418   significantly differ from zero (Figure 4). The absolute average effect size ( $|r|$ ) across all  
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31 419   behavioural measure categories was generally between 0.2- 0.4, with the exception of  
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33 420   effect sizes considering males ( $|r| = 0.549$ , 95% CI= 0.298- 0.744), females ( $|r| = 0.44$ , 95%  
34  
35 421   CI= 0.242- 0.713), and fish ( $|r| = 0.451$ , 95% CI= 0.261- 0.725,  $N = 11$  effect sizes, 154  
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37 422   individuals; Figure 5).  
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#### 424 **Publication bias**

425           There was no significant relationship between residual effect size ( $Z_r$ ) 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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3 428 funnel plot. There was no significant relationship between raw effect size ( $Z_r$ ) and year  
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5 429 (Meta-regression, fixed effect of year,  $\beta = -0.024$ , HPD interval =  $-0.054$ -  $0.007$ ; Figure S1).  
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## 9 431 Discussion

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12 432 Our analysis provides the first quantitative test of the relationship between  
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14 433 personality and cognition in animals, using a sample of 25 studies and 19 species. We find  
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16 434 evidence for a small but significant relationship between variation in personality and  
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18 435 variation in learning across species in the absolute scale (i.e. irrespective of the sign of the  
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20 436 effect sizes). However, the *direction* of this relationship is highly variable, so that the  
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22 437 average effect size for the raw data is not significantly different from zero. This means that  
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24 438 our sample includes an approximately equal number of studies showing a positive  
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26 439 relationship between personality and cognition (e.g. animals that were more bold,  
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28 440 aggressive, explorative, active and social were quicker to learn, or had fewer errors, or more  
29  
30 441 correct responses after a standard amount of training) as showing a negative relationship  
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32 442 (animals that were more bold, aggressive, explorative, active and social were slower to  
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34 443 learn, had more errors, or fewer correct responses after a standard amount of training).  
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36 444 Further, taking into account the type of personality measure or cognitive measure did not  
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38 445 significantly explain the variation in the direction of this relationship seen across studies.  
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40 446 Taken together, these results show that that, while personality and learning co-vary  
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42 447 significantly across the studies sampled here, there is currently no evidence for a consistent  
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44 448 positive or negative relationship across species.  
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49 449 Given the large amount of variation in effect sizes seen in our sample, we included  
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51 450 several categorical moderator variables in our analysis in order to examine whether they  
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53 451 could significantly explain some of the variation in the size or direction of the relationship  
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3 452 between personality and cognition. We had two key predictions regarding how these  
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5 453 variables might influence this relationship. Our first prediction was that the relationship  
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7 454 between personality and cognition should depend on the type of learning test used to  
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9 455 measure cognition: with a positive relationship predicted between personality and initial  
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11 456 learning speed, and a negative relationship predicted between personality and reversal  
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14 457 speed. However, this prediction was not supported: cognitive measure did not significantly  
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16 458 influence the direction of the relationship between personality and cognition. This finding is  
17  
18 459 in direct contrast with conceptual work which suggests 'fast' personality types are 'fast' and  
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20 460 'inflexible' learners. With 'inflexible' meaning animals that persevere in previously rewarded  
21  
22 461 patterns of behaviour (early empirical paper: [33]) or fail to produce new, correct behaviour  
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24 462 when the rules of a task or the environment changes or is altered (conceptual papers:  
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26 463 [15,32,77]; empirical paper: [65]).

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30 464 Our second prediction was that certain personality measures, notably exploration,  
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32 465 are more likely to co-vary with cognition than others. However, this was not seen to be the  
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34 466 case, with personality measure explaining little of the heterogeneity in effect sizes seen  
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36 467 across species. However, we did find evidence for a marginally significant positive  
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38 468 relationship between cognition and boldness in response to predators: animals that are  
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40 469 bolder are able to learn new associations (and reverse previously-learned associations)  
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42 470 more quickly, and show more correct responses (and fewer errors) during standard training,  
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44 471 compared to animals that are less bold. Though it should also be noted that this category  
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46 472 consists of only five effect sizes from three studies, and so should be investigated further  
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48 473 before any strong conclusions are made. Nevertheless, this result was in contrast to the  
49  
50 474 other personality measures (activity, exploration, sociality and aggression) which all have  
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52 475 mean effect sizes that are not significantly different from zero (including boldness when  
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3 476 measured as a response to novel objects or food), and it is not clear why boldness in  
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5 477 response to predation shows a significant directional relationship with cognition while the  
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7 478 others do not. It is worth stressing here that we do not assume a causal direction for this  
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9 479 relationship – for example, it is equally likely that being a fast learner could lead individuals  
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12 480 to be bolder.

13  
14 481 The only categorical factor which explained a significant amount of the variation in  
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16 482 effect sizes in our sample was the sex of the subject. For the directional data, the  
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18 483 relationship was significantly positive when only males were tested, whereas the  
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20 484 relationship for females and both sexes combined did not significantly differ from zero.  
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23 485 Further, the absolute size of the relationship between personality and cognition was more  
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25 486 positive when males or females were tested separately, compared to when individuals of  
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27 487 both sexes were combined. This result is somewhat surprising, given that there have been  
28  
29 488 few studies examining sex differences in the relationship between personality and  
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31  
32 489 cognition, and indeed only a single study in our sample tested for this relationship in males  
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34 490 and females separately [96]. For this reason, and the fact that this effect is primarily driven  
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36 491 by the presence of a relatively few effect sizes of large effect (4 and 8 effect sizes for males  
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38 492 only and females only, respectively), we interpret this result cautiously. Nevertheless, we  
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40 493 suggest that this pattern merits further investigation, and that researchers should test for  
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42 494 sex differences, including interactions between sex and personality, in the relationship  
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44 495 between personality and cognition before data from males and females are combined, and  
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46 496 report this in the methods or results sections even when there is no significant difference.  
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48  
49 497 Sex differences in cognitive abilities has long been a well-studied area in human psychology  
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52 498 [97] and is beginning to receive attention in studies of animal cognition [e.g., 97,98].  
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3 499           Importantly, the majority of the variation in effect size and direction in our sample  
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5 500   remains unexplained, with effect size not influenced by differences in personality measure,  
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7 501   cognitive measure, or phylogenetic history across studies. There are two potential  
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9 502   explanations for this: either the relationship between personality and cognition does not  
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11 503   have a consistent 'direction', in which case we need to adapt current theory in order to  
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13 504   explain this; or there are additional moderating factors which we have not identified that  
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15 505   strongly influence the direction of the relationship. For example, given the limited sample  
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17 506   size of our sample we did not test the effect of any ecological or life history factors that may  
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19 507   influence this relationship (e.g. sociality, breeding system, habitat type). Further, many of  
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21 508   these studies tested a relatively small number of individuals; the average sample size across  
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23 509   all studies was 26.08 (s.d.= 13.89), with eight studies testing less than 20 individuals. This  
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25 510   means that many of the trait categories we examined consisted of a very small number of  
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27 511   individuals (e.g. 45 individual insects and 57 individual reptiles). Therefore, we suggest that  
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29 512   more empirical tests are needed to investigate these potential explanations, using larger  
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31 513   sample sizes if possible. This is still a relatively young field, as exemplified by the fact that 19  
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33 514   of the 25 studies included in our analysis were published in the past five years, and there is  
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35 515   much we still do not know. Nevertheless, other meta-analyses have shown that personality  
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37 516   is related to an individual's intrinsic state (i.e., body mass, size, metabolic rate and hormone  
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39 517   levels; [41]) and has fitness consequences (e.g., reproductive success and survival; [27]).  
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41 518   Taken together with the current results, this suggests that personality is a measure worth  
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43 519   examining in the future.

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45 520           In conclusion, our results show that Pavlov was correct: animal personality and  
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47 521   cognition are related. However, our analysis also revealed high among-study heterogeneity  
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49 522   in the direction of this relationship. This means that knowing the personality of an animal  
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3 523 (where an individual's behavioural scores fall along a continuum ranging from inactive to  
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5 524 active, for example) does not consistently allow you to predict how quickly that animal will  
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7 525 learn. Further, we failed to find support for several key hypotheses regarding the  
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9 526 relationship between personality and cognition, and we hope that these hypotheses will be  
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11 527 re-assessed accordingly. Specifically, researchers may need to abandon the primary  
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13 528 assumption that fast-explorers should be fast-learners, while slow-explorers should be  
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15 529 better at reversal learning tasks. Finally, further work is needed in order to identify whether  
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17 530 there are other factors which influence the direction of the relationship between cognition  
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19 531 and personality. In light of these results, we have several recommendations. First, we urge  
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21 532 research undertaking future work to test for sex differences and interactions between sex,  
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23 533 personality and cognitive measures. Secondly, we suggest researchers measure both  
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25 534 personality and cognition across several different time points, or in several different  
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27 535 contexts in the same individuals (see [16] for details, and Cauchoix this issue). Lastly, our  
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29 536 hope is that this meta-analysis stimulates empirical work where formulation of study-  
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31 537 specific predictions should take into account not only the evolutionary pressures that have  
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33 538 shaped different species cognitive abilities, but also the different developmental histories  
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35 539 among discrete populations of the same species (e.g., pond snails, *Lymnaea stagnalis* [88,  
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37 540 Dalesman current issue], sticklebacks, *Gasterosteus aculeatus*, [101,102]) along with the  
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39 541 nature of the cognitive testing paradigm (the stimuli, the behavioural response, and the  
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41 542 outcomes [16]).  
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#### 20 21 555 Data Accessibility

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24 556 The dataset supporting this article has been uploaded as part of the Supplementary  
25  
26 557 Material.  
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29 558

#### 30 31 559 Authors’ Contribution

32  
33  
34 560 LMG conceived the idea. LMG and LRD designed and collected the data and wrote the  
35  
36 561 paper. LRD analysed the data. All authors give final approval for this publication.  
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39 562

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42  
43 564 We have no competing interests.  
44

45  
46 565

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**References**

572

573 1. Dingemanse N, Réale D. 2005 Natural selection and animal personality. *Behaviour*574 **142**, 1165–1190.

575 2. Stamps J, Groothuis TGG. 2010 The development of animal personality: relevance,

576 concepts and perspectives. *Biol. Rev. Camb. Philos. Soc.* **85**, 301–325.

577 (doi:10.1111/j.1469-185X.2009.00103.x)

578 3. Dall SRX, Houston AI, McNamara JM. 2004 The behavioural ecology of personality:

579 consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739.

580 (doi:10.1111/j.1461-0248.2004.00618.x)

581 4. Sih A, Bell AM, Johnson JC. 2004 Behavioral syndromes: an ecological and

582 evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378.

583 (doi:10.1016/j.tree.2004.04.009)

584 5. Bell AM, Sih A. 2008 Insights for behavioral ecology from behavioral syndromes. *Adv.*585 *Study Behav.* **38**, 227–281.

586 6. Garamszegi LZ, Markó G, Herczeg G. 2013 A meta-analysis of correlated behaviors

587 with implications for behavioral syndromes: Relationships between particular

588 behavioral traits. *Behav. Ecol.* **24**, 1068–1080. (doi:10.1093/beheco/art033)589 7. Wilson DS. 1998 Adaptive individual differences within single populations. *Philos.*590 *Trans. R. Soc. B Biol. Sci.* **353**, 199–205. (doi:10.1098/rstb.1998.0202)

591 8. DiRienzo N, Montiglio P-O. 2015 Four ways in which data-free papers on animal

592 personality fail to be impactful. *Front. Ecol. Evol.* **3**, 1–5.

593 (doi:10.3389/fevo.2015.00023)

- 1  
2  
3 594 9. Schuett W, Tregenza T, Dall SRX. 2009 Sexual selection and animal personality. *Biol.*  
4  
5 595 *Rev.* **84**. (doi:10.1111/j.1469-185X.2009.00101.x)  
6  
7 596 10. McDougall PT, Réale D, Sol D, Reader SM. 2006 Wildlife conservation and animal  
8  
9 597 temperament: Causes and consequences of evolutionary change for captive,  
10  
11 598 reintroduced, and wild populations. *Anim. Conserv.* **9**, 39–48. (doi:10.1111/j.1469-  
12  
13 599 1795.2005.00004.x)  
14  
15  
16 600 11. Reale D, Reader SM, Sol D, Mcdougall PT, Dingemanse N. 2007 Integrating animal  
17  
18 601 temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318.  
19  
20 602 (doi:10.1111/j.1469-185X.2007.00010.x)  
21  
22  
23 603 12. van Oers K, Mueller JC. 2010 Evolutionary genomics of animal personality. *Philos.*  
24  
25 604 *Trans. R. Soc. B Biol. Sci.* **365**, 3991–4000. (doi:10.1098/rstb.2010.0178)  
26  
27  
28 605 13. Carere C, Locurto C. 2011 Interaction between animal personality and animal  
29  
30 606 cognition. *Curr. Zool.* **57**, 491–498.  
31  
32  
33 607 14. Locurto C. 2007 Individual differences and animal personality. *Comp. Cogn. Behav.*  
34  
35 608 *Rev.* **2**, 67–78.  
36  
37  
38 609 15. Sih A, Del Giudice M. 2012 Linking behavioural syndromes and cognition: a  
39  
40 610 behavioural ecology perspective. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2762–2772.  
41  
42 611 (doi:10.1098/rstb.2012.0216)  
43  
44 612 16. Griffin AS, Guillette LM, Healy SD. 2015 Cognition and personality: An analysis of an  
45  
46 613 emerging field. *Trends Ecol. Evol.* **30**, 207–214. (doi:10.1016/j.tree.2015.01.012)  
47  
48  
49 614 17. Guillette LM, Naguib M, Griffin AS. 2017 Individual differences in cognition and  
50  
51 615 personality. *Behav. Processes* **134**, 1–3. (doi:10.1016/j.beproc.2016.12.001)  
52  
53  
54 616 18. van Oers K, Naguib M. 2013 Avian personality. In *Animal Personalities: Behavior,*  
55  
56 617 *Physiology, and Evolution* (eds C Carere, D Maestriperi), pp. 66–95. Chicago, IL: The  
57  
58  
59  
60

- 1  
2  
3 618 University of Chicago Press.  
4  
5 619 19. Pavlov IP. 2010 Conditioned reflexes: An investigation of the physiological activity of  
6  
7 620 the cerebral cortex. *Ann. Neurosci.* **17**, 136–141.  
8  
9  
10 621 20. Pavlov IP. 1906 The scientific investigation of the psychical faculties or processes in  
11  
12 622 the higher animals. *Science (80- )*. **620**, 613–619.  
13  
14 623 21. Pavlov IP. 1941 Lectures on conditioned reflexes. Vol. II. Conditioned reflexes and  
15  
16 624 psychiatry. In (ed HW Gantt), London, UK: Lawrence & Wishart, LTD.  
17  
18  
19 625 22. Gray JA. 1964 *Pavlov's Typology*. New York, NY: Pergamon Press.  
20  
21 626 23. Mazza V, Eccard JA, Zaccaroni M, Jacob J, Dammhahn M. 2018 The fast and the  
22  
23 627 flexible: cognitive style drives individual variation in cognition in a small mammal.  
24  
25 628 *Anim. Behav.* **137**, 119–132. (doi:10.1016/j.anbehav.2018.01.011)  
26  
27  
28 629 24. Etheredge RI, Avenas C, Armstrong MJ, Cummings ME. 2018 Sex-specific cognitive–  
29  
30 630 behavioural profiles emerging from individual variation in numerosity discrimination  
31  
32 631 in *Gambusia affinis*. *Anim. Cogn.* **21**, 37–53. (doi:10.1007/s10071-017-1134-2)  
33  
34  
35 632 25. Jha NA, Kumar V. 2017 Effect of no-night light environment on behaviour, learning  
36  
37 633 performance and personality in zebra finches. *Anim. Behav.* **132**, 29–47.  
38  
39 634 (doi:10.1016/j.anbehav.2017.07.017)  
40  
41  
42 635 26. Shettleworth SJ. 2010 *Cognition, Evolution and Behavior*. 2nd edn. New York: Oxford  
43  
44 636 University Press.  
45  
46 637 27. Smith BR, Blumstein DT. 2007 Fitness consequences of personality: a meta-analysis.  
47  
48 638 *Behav. Ecol.* **19**, 448–455. (doi:10.1093/beheco/arm144)  
49  
50  
51 639 28. Carter AJ, Feeney WE, Marshall HH, Cowlshaw G, Heinsohn R. 2013 Animal  
52  
53 640 personality: What are behavioural ecologists measuring? *Biol. Rev.* **88**.  
54  
55 641 (doi:10.1111/brv.12007)  
56  
57  
58  
59  
60

- 1  
2  
3 642 29. Morrissey MB. 2016 Meta-analysis of magnitudes, differences and variation in  
4  
5 643 evolutionary parameters. *J. Evol. Biol.* **29**, 1882–1904. (doi:10.1111/jeb.12950)  
6  
7 644 30. Noble DWA, Stenhouse V, Schwanz LE. 2018 Developmental temperatures and  
8  
9 645 phenotypic plasticity in reptiles: a systematic review and meta-analysis. *Biol. Rev.* **93**,  
10  
11 646 72–97. (doi:10.1111/brv.12333)  
12  
13  
14 647 31. Cockrem JF. 2007 Stress, corticosterone responses and avian personalities. *J. für*  
15  
16 648 *Ornithol.* **148**, 169–178. (doi:10.1007/s10336-007-0175-8)  
17  
18  
19 649 32. Cockrem JF. 2013 Corticosterone responses and personality in birds: Individual  
20  
21 650 variation and the ability to cope with environmental changes due to climate change.  
22  
23 651 *Gen. Comp. Endocrinol.* **190**, 156–163. (doi:10.1016/j.ygcen.2013.02.021)  
24  
25  
26 652 33. Verbeek MEM, Drent PJ, Wiepkema PR. 1994 Consistent individual differences in  
27  
28 653 early exploratory behaviour in male great tits. *Anim. Behav.* **48**, 1113–1121.  
29  
30  
31 654 34. Bolhuis JE, Schouten WG., Leeuw JA d., Schrama JW, Wiegant VM. 2004 Individual  
32  
33 655 coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behav.*  
34  
35 656 *Brain Res.* **152**, 351–360.  
36  
37 657 35. Sih A, Del Giudice M. 2012 Linking behavioural syndromes and cognition: a  
38  
39 658 behavioural ecology perspective. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2762–2772.  
40  
41 659 (doi:10.1098/rstb.2012.0216)  
42  
43  
44 660 36. Carere C, Locurto C. 2011 Interaction between animal personality and animal  
45  
46 661 cognition. *Curr. Zool.* **57**, 491–498. (doi:10.1093/czoolo/57.4.491)  
47  
48  
49 662 37. Koricheva J, Gurevitch J, Mengersen K. 2013 *Handbook of meta-analysis in ecology*  
50  
51 663 *and evolution*. Princeton, NJ: Princeton University Press.  
52  
53 664 38. Liberati A *et al.* 2009 The PRISMA statement for reporting systematic reviews and  
54  
55 665 meta-analyses of studies that evaluate healthcare interventions: explanation and  
56  
57  
58  
59  
60

- 1  
2  
3 666 elaboration. *Bmj* **339**, b2700–b2700. (doi:10.1136/bmj.b2700)  
4  
5 667 39. Nakagawa S, Poulin R. 2012 Meta-analytic insights into evolutionary ecology: An  
6  
7 668 introduction and synthesis. *Evol. Ecol.* **26**, 1085–1099. (doi:10.1007/s10682-012-  
8  
9 669 9593-z)  
10  
11  
12 670 40. Nakagawa S, Santos ESA. 2012 Methodological issues and advances in biological  
13  
14 671 meta-analysis. *Evol. Ecol.* **26**, 1253–1274. (doi:10.1007/s10682-012-9555-5)  
15  
16  
17 672 41. Niemelä PT, Dingemanse NJ. 2018 Meta-analysis reveals weak associations between  
18  
19 673 intrinsic state and personality. *Proc. R. Soc. B Biol. Sci.* **285**, 20172823.  
20  
21 674 (doi:10.1098/rspb.2017.2823)  
22  
23  
24 675 42. Bell AM, Hankison SJ, Laskowski KL. 2009 The repeatability of behaviour: a meta-  
25  
26 676 analysis. *Anim. Behav.* **77**, 771–783. (doi:10.1016/j.anbehav.2008.12.022)  
27  
28  
29 677 43. van Oers K, Drent PJ, de Goede P, van Noordwijk AJ. 2004 Realized heritability and  
30  
31 678 repeatability of risk-taking behaviour in relation to avian personalities. *Proc. Biol. Sci.*  
32  
33 679 **271**, 65–73. (doi:10.1098/rspb.2003.2518)  
34  
35  
36 680 44. Rescorla RA, Wagner AR. 1972 A theory of Pavlovian conditioning: Variations in the  
37  
38 681 effectiveness of reinforcement and nonreinforcement. In *Classical Conditioning II:*  
39  
40 682 *Current Theory and Research* (eds AH Black, WF Prokasy), pp. 64–99. New York:  
41  
42 683 Appleton-Century-Crofts.  
43  
44  
45 684 45. Guillette LM, Baron DM, Sturdy CB, Spetch ML. 2017 Fast- and slow-exploring pigeons  
46  
47 685 differ in how they use previously learned rules. *Behav. Processes* **134**.  
48  
49 686 (doi:10.1016/j.beproc.2016.07.006)  
50  
51  
52 687 46. Guillette LM, Hahn AH, Hoeschele M, Przyslupski A-M, Sturdy CB. 2015 Individual  
53  
54 688 differences in learning speed, performance accuracy and exploratory behaviour in  
55  
56 689 black-capped chickadees. *Anim. Cogn.* **18**, 165–178. (doi:10.1007/s10071-014-0787-3)  
57  
58  
59  
60

- 1  
2  
3 690 47. Griffin AS, Guez D. 2016 Bridging the Gap Between Cross-Taxon and Within-Species  
4  
5 691 Analyses of Behavioral Innovations in Birds: Making Sense of Discrepant Cognition-  
6  
7 692 Innovation Relationships and the Role of Motor Diversity. In *Advances in the Study of*  
8  
9 693 *Behavior* (eds M Naguib, JC Mitani, LW Simmons, L Barrett, S Healy, M Zuk), pp. 1–40.  
10  
11 694 (doi:10.1016/bs.asb.2016.02.001)  
12  
13  
14 695 48. Griffin AS, Guez D. 2017 Solving Foraging Problems: Top-Down and Bottom-Up  
15  
16 696 Perspectives on the Role of Cognition. In *Avian Cognition* (eds C Ten Cate, SD Healy),  
17  
18 697 pp. 119–140. Cambridge, UK: Cambridge: Cambridge University Press.  
19  
20 698 (doi:10.1017/9781316135976.008)  
21  
22  
23 699 49. van Horik JO, Madden JR. 2016 A problem with problem solving: motivational traits,  
24  
25 700 but not cognition, predict success on novel operant foraging tasks. *Anim. Behav.* **114**,  
26  
27 701 189–198. (doi:10.1016/j.anbehav.2016.02.006)  
28  
29  
30 702 50. Mesquita FO, Borcato FL, Huntingford FA. 2015 Cue-based and algorithmic learning in  
31  
32 703 common carp: A possible link to stress coping style. *Behav. Processes* **115**, 25–29.  
33  
34 704 (doi:10.1016/j.beproc.2015.02.017)  
35  
36  
37 705 51. Bebus SE, Small TW, Jones BC, Elderbrock EK, Schoech SJ. 2016 Associative learning is  
38  
39 706 inversely related to reversal learning and varies with nestling corticosterone  
40  
41 707 exposure. *Anim. Behav.* **111**, 251–260. (doi:10.1016/j.anbehav.2015.10.027)  
42  
43  
44 708 52. Borenstein M, Hedges L V, Higgins JP, H R. 2009 *Introduction to meta-analysis*.  
45  
46 709 Chichester, UK: John Wiley.  
47  
48  
49 710 53. Hadfield JD, Nakagawa S. 2010 General quantitative genetic methods for comparative  
50  
51 711 biology: Phylogenies, taxonomies and multi-trait models for continuous and  
52  
53 712 categorical characters. *J. Evol. Biol.* **23**, 494–508. (doi:10.1111/j.1420-  
54  
55 713 9101.2009.01915.x)  
56  
57  
58  
59  
60

- 1  
2  
3 714 54. Ericson PG. *et al.* 2006 Diversification of Neoaves: integration of molecular sequence  
4  
5 715 data and fossils. *Biol. Lett.* **2**, 543–547. (doi:10.1098/rsbl.2006.0523)  
6  
7 716 55. Hackett SJ *et al.* 2008 A phylogenomic study of birds reveals their evolutionary  
8  
9 717 history. *Science (80-. )*. **320**, 1763–1768. (doi:10.1126/science.1157704)  
10  
11  
12 718 56. Near TJ, Eytan RI, Dornburg A, Kuhn KL, Moore JA, Davis MP, Wainwright PC,  
13  
14 719 Friedman M, Smith WL. 2012 Resolution of ray-finned fish phylogeny and timing of  
15  
16 720 diversification. *Proc. Natl. Acad. Sci.* **109**, 13698–13703.  
17  
18 721 (doi:10.1073/pnas.1206625109)  
19  
20  
21 722 57. Murphy WJ *et al.* 2001 Resolution of the early placental mammal radiation using  
22  
23 723 bayesian phylogenetics. *Science (80-. )*. **294**, 2348–2351.  
24  
25 724 (doi:10.1126/science.1067179)  
26  
27  
28 725 58. Xia X, Xie Z, Kjer KM. 2003 18S ribosomal RNA and tetrapod phylogeny. *Syst. Biol.* **52**,  
29  
30 726 283–295. (doi:10.1080/10635150309331)  
31  
32  
33 727 59. Grafen A. 1989 The phylogenetic regression. *Philos. Trans. R. Soc. B* **326**, 119–157.  
34  
35 728 60. Paradis E, Claude J, Strimmer K. 2004 APE: Analyses of phylogenetics and evolution in  
36  
37 729 R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)  
38  
39  
40 730 61. Viechtbauer W. 2010 Conducting Meta-Analyses in R with the metafor Package. **36**.  
41  
42 731 62. Lim JN, Senior AM, Nakagawa S. 2014 Heterogeneity in individual quality and  
43  
44 732 reproductive trade-offs within species. *Evolution (N. Y.)*. **68**, 2306–2318.  
45  
46 733 (doi:10.1111/evo.12446)  
47  
48  
49 734 63. Gelman A, Rubin DB, Gelman A, Rubin DB. 1992 Inference from Iterative Simulation  
50  
51 735 Using Multiple Sequences. *Stat. Sci.* **7**, 457–472.  
52  
53  
54 736 64. Higgins JPT, Thompson SG, Deeks JJ, Altman DG. 2003 Measuring inconsistency in  
55  
56 737 meta-analyses. *BMJ* **327**, 557–560. (doi:10.1136/bmj.327.7414.557)  
57  
58  
59  
60



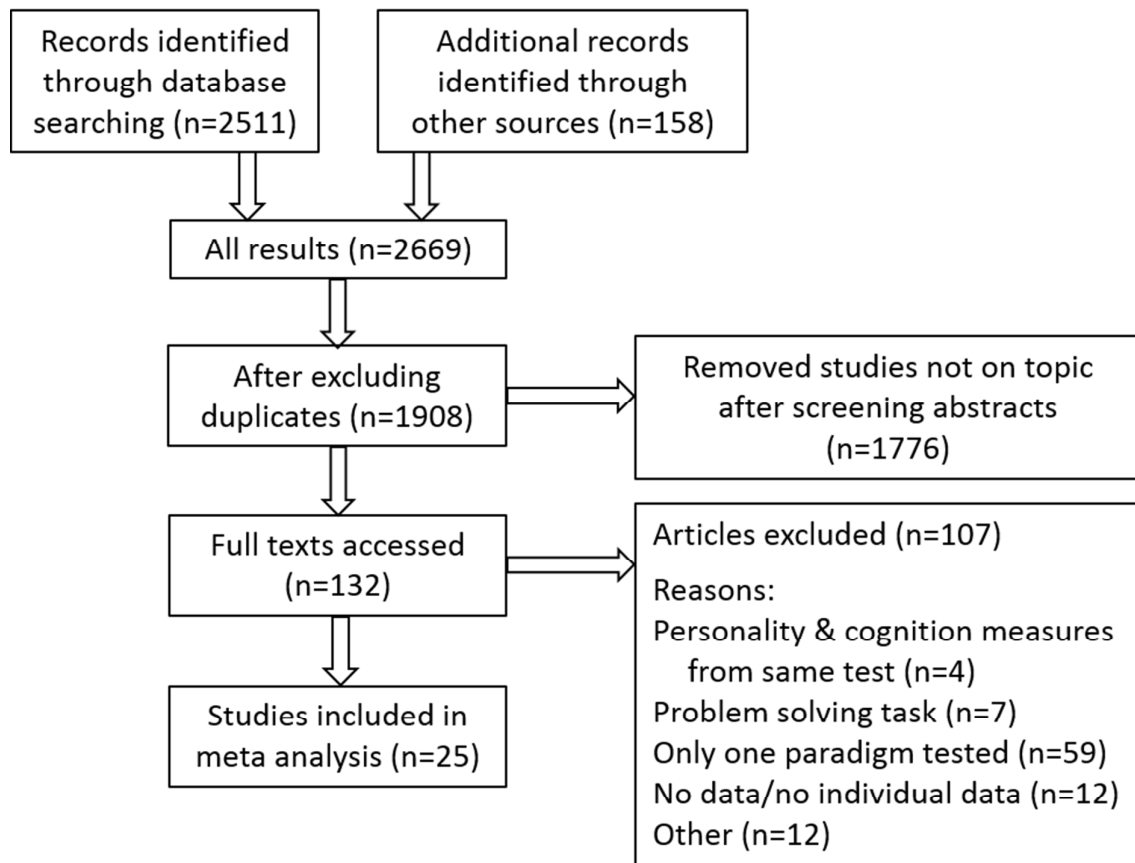
- 1  
2  
3 738 65. Senior AM, Grueber CE, Kamiya T, Lagisz M, O'Dwyer K, Santos ESA, Nakagawa S.  
4  
5 739 2016 Heterogeneity in ecological and evolutionary meta-analyses: its magnitude and  
6  
7 740 implication. *Ecology* **97**, 3293–3299.  
8  
9  
10 741 66. Morrissey MB, Hadfield JD. 2012 Directional selection in temporally replicated studies  
11  
12 742 is remarkably consistent. *Evolution (N. Y.)* **66**, 435–442. (doi:10.1111/j.1558-  
13  
14 743 5646.2011.01444.x)  
15  
16 744 67. Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A. 2002 Bayesian Measures of  
17  
18 745 Model Complexity and Fit. *J. R. Stat. Soc. Ser. B* **64**, 583–639. (doi:10.1111/1467-  
19  
20 746 9868.00353)  
21  
22  
23 747 68. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining R<sup>2</sup> from  
24  
25 748 generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142.  
26  
27 749 (doi:10.1111/j.2041-210x.2012.00261.x)  
28  
29  
30 750 69. Begg CB, Mazumdar M. 1994 Operating Characteristics of a Rank Correlation Test for  
31  
32 751 Publication Bias. *Biometrics* **50**, 1088. (doi:10.2307/2533446)  
33  
34  
35 752 70. Egger M, Smith GD, Schneider M, Minder C. 1997 Bias in meta - analysis detected by a  
36  
37 753 simple , graphical test. *BMJ Clin. Res.* **315**, 629–634.  
38  
39 754 (doi:http://dx.doi.org/10.1136/bmj.315.7109.629)  
40  
41  
42 755 71. Duval S, Tweedie R. 2000 Trim and Fill: A Simple Funnel-Plot-Based Method of Testing  
43  
44 756 and Adjusting for Publication Bias in Meta-Analysis. *Biometrics* **56**, 455–463.  
45  
46 757 72. Jennions MD, Moller AP. 2002 Relationships fade with time: a meta-analysis of  
47  
48 758 temporal trends in publication in ecology and evolution. *Proc. R. Soc. B Biol. Sci.* **269**,  
49  
50 759 43–48. (doi:10.1098/rspb.2001.1832)  
51  
52  
53 760 73. Udino E, Perez M, Carere C, D'Ettoire P. 2017 Active explorers show low learning  
54  
55 761 performance in a social insect. *Curr. Zool.* **63**, 555–560. (doi:10.1093/cz/zow101)  
56  
57  
58  
59  
60

- 1  
2  
3 762 74. Dugatkin LA, Alfieri MS. 2003 Boldness, behavioral inhibition and learning. *Ethol. Ecol.*  
4  
5 763 *Evol.* **15**, 43–49.  
6  
7 764 75. DePasquale C, Wagner T, Archard GA, Ferguson B, Braithwaite VA. 2014 Learning rate  
8  
9 765 and temperament in a high predation risk environment. *Oecologia* **176**, 661–667.  
10  
11 766 (doi:10.1007/s00442-014-3099-z)  
12  
13  
14 767 76. Bannier F, Tebbich S, Taborsky B. 2017 Early experience affects learning performance  
15  
16 768 and neophobia in a cooperatively breeding cichlid. *Ethology* **123**, 712–723.  
17  
18 769 (doi:10.1111/eth.12646)  
19  
20  
21 770 77. Bensky MKMK, Paitz R, Pereira L, Bell AMAM. 2017 Testing the predictions of coping  
22  
23 771 styles theory in threespined sticklebacks. *Behav. Processes* **136**, 1–10.  
24  
25 772 (doi:10.1016/j.beproc.2016.12.011)  
26  
27  
28 773 78. Kareklas K, Elwood RW, Holland RA. 2017 Personality effects on spatial learning:  
29  
30 774 Comparisons between visual conditions in a weakly electric fish. *Ethology* **123**, 551–  
31  
32 775 559. (doi:10.1111/eth.12629)  
33  
34  
35 776 79. Carazo P, Noble DWA, Chandrasoma D, Whiting MJ. 2014 Sex and boldness explain  
36  
37 777 individual differences in spatial learning in a lizard. *Proc. R. Soc. B Biol. Sci.* **281**,  
38  
39 778 20133275–20133275. (doi:10.1098/rspb.2013.3275)  
40  
41  
42 779 80. Guillette LM, Reddon AR, Hurd PL, Sturdy CB. 2009 Exploration of a novel space is  
43  
44 780 associated with individual differences in learning speed in black-capped chickadees,  
45  
46 781 *Poecile atricapillus*. *Behav. Processes* **82**. (doi:10.1016/j.beproc.2009.07.005)  
47  
48  
49 782 81. Exnerová A, Svádová KH, Fucíková E, Drent PJ, Stys P. 2010 Personality matters:  
50  
51 783 individual variation in reactions of naive bird predators to aposematic prey. *Proc. R.*  
52  
53 784 *Soc. B Biol. Sci.* **277**, 723–728. (doi:10.1098/rspb.2009.1673)  
54  
55  
56 785 82. Guillette LM, Reddon AR, Hoeschele M, Sturdy CB. 2011 Sometimes slower is better:  
57  
58  
59  
60

- 1  
2  
3 786 slow-exploring birds are more sensitive to changes in a vocal discrimination task.  
4  
5 787 *Proc. R. Soc. B Biol. Sci.* **278**, 767–773. (doi:10.1098/rspb.2010.1669)  
6  
7 788 83. Titulaer M, van Oers K, Naguib M. 2012 Personality affects learning performance in  
8  
9 789 difficult tasks in a sex-dependent way. *Anim. Behav.* **83**, 723–730.  
10  
11 790 (doi:10.1016/j.anbehav.2011.12.020)  
12  
13  
14 791 84. Brust V, Wuerz Y, Krüger O. 2013 Behavioural Flexibility and Personality in Zebra  
15  
16 792 Finches. *Ethology* **119**, 559–569. (doi:10.1111/eth.12095)  
17  
18  
19 793 85. Bousquet CAH, Petit O, Arrive M, Robin J-P, Sueur C. 2015 Personality tests predict  
20  
21 794 responses to a spatial-learning task in mallards, *Anas platyrhynchos*. *Anim. Behav.*  
22  
23 795 **110**, 145–154. (doi:10.1016/j.anbehav.2015.09.024)  
24  
25  
26 796 86. Moiron M, Mathot KJ, Dingemans NJ. 2016 A multi-level approach to quantify  
27  
28 797 speed-accuracy trade-offs in great tits (*Parus major*). *Behav. Ecol.* **27**, 1539–1546.  
29  
30 798 (doi:10.1093/beheco/arw077)  
31  
32  
33 799 87. Logan CJ. 2016 Behavioral flexibility and problem solving in an invasive bird. *PeerJ* **4**,  
34  
35 800 e1975. (doi:10.7717/peerj.1975)  
36  
37  
38 801 88. Moldoff DE, Westneat DF. 2017 Foraging sparrows exhibit individual differences but  
39  
40 802 not a syndrome when responding to multiple kinds of novelty. *Behav. Ecol.* **28**.  
41  
42 803 (doi:10.1093/beheco/arx014)  
43  
44  
45 804 89. Gibelli J, Dubois F. 2017 Does personality affect the ability of individuals to track and  
46  
47 805 respond to changing conditions? *Behav. Ecol.* **28**, 101–107.  
48  
49 806 (doi:10.1093/beheco/arw137)  
50  
51  
52 807 90. Kazlauskas V, Schuh J, Dall'Igna OP, Pereira GS, Bonan CD, Lara DR. 2005 Behavioral  
53  
54 808 and cognitive profile of mice with high and low exploratory phenotypes. *Behav. Brain*  
55  
56 809 *Res.* **162**, 272–278. (doi:10.1016/j.bbr.2005.03.021)  
57  
58  
59  
60

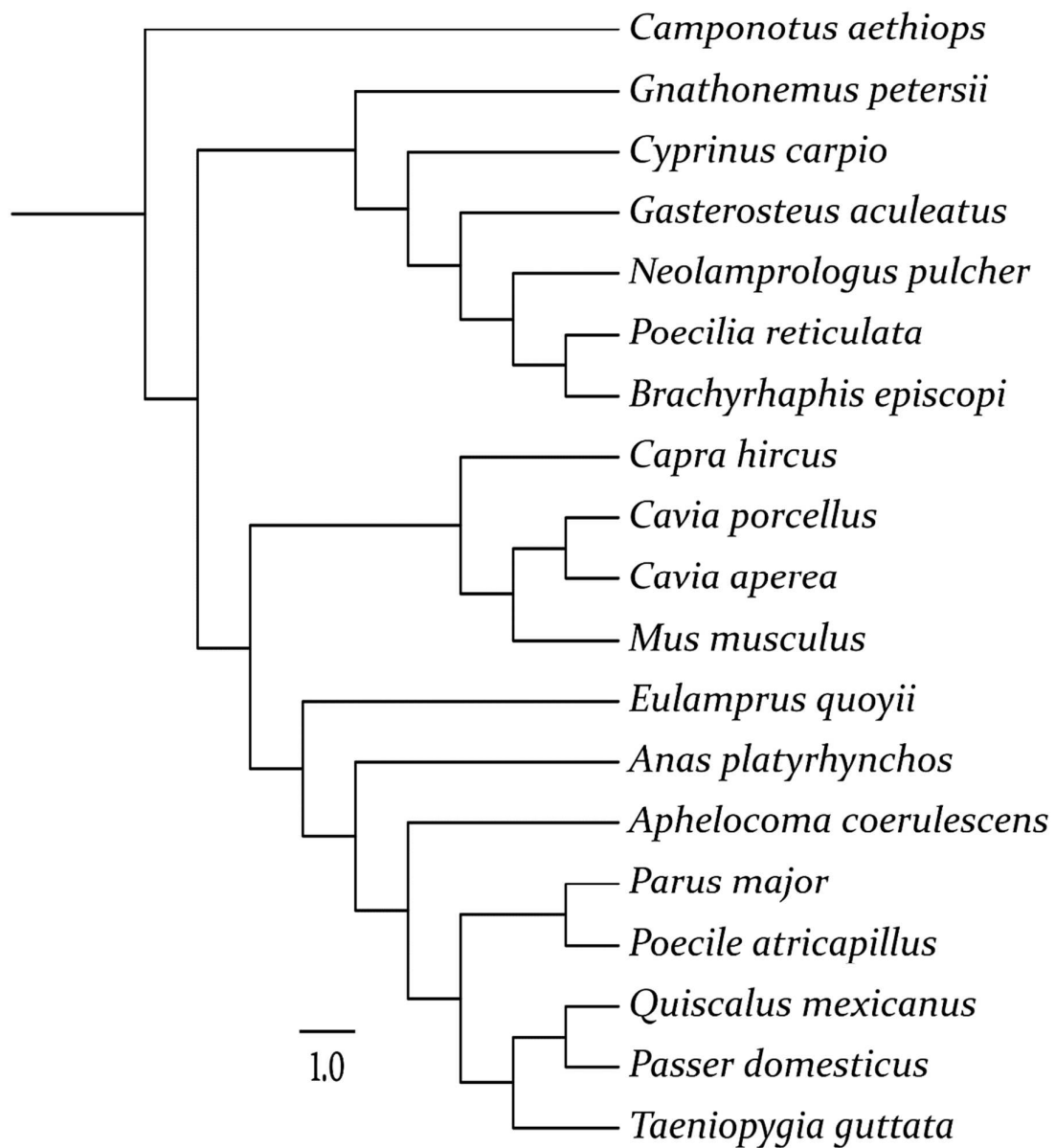
- 1  
2  
3 810 91. Guenther A, Brust V, Dersen M, Trillmich F. 2014 Learning and personality types are  
4 related in caviies (*Cavia aperea*). *J. Comp. Psychol.* **128**, 74–81.  
5 811  
6  
7 812 (doi:10.1037/a0033678)  
8  
9  
10 813 92. Brust V, Guenther A. 2015 Domestication effects on behavioural traits and learning  
11 performance: comparing wild caviies to guinea pigs. *Anim. Cogn.* **18**, 99–109.  
12 814  
13  
14 815 (doi:10.1007/s10071-014-0781-9)  
15  
16  
17 816 93. Nawroth C, Prentice PM, McElligott AG. 2017 Individual personality differences in  
18 goats predict their performance in visual learning and non-associative cognitive tasks.  
19 817  
20  
21 818 *Behav. Processes* **134**, 43–53. (doi:10.1016/j.beproc.2016.08.001)  
22  
23  
24 819 94. Guenther A, Brust V. 2017 Individual consistency in multiple cognitive performance:  
25 behavioural versus cognitive syndromes. *Anim. Behav.* **130**, 119–131.  
26 820  
27  
28 821 (doi:10.1016/j.anbehav.2017.06.011)  
29  
30  
31 822 95. Cockrem JF. 2007 Stress, corticosterone responses and avian personalities. *J. Ornithol.*  
32  
33 823 **148**, 169–178. (doi:10.1007/s10336-007-0175-8)  
34  
35 824 96. Titulaer M, van Oers K, Naguib M. 2012 Personality affects learning performance in  
36 difficult tasks in a sex-dependent way. *Anim. Behav.* **83**, 723–730.  
37 825  
38  
39 826 (doi:10.1016/j.anbehav.2011.12.020)  
40  
41  
42 827 97. Halpern DF. 2000 *Sex differences in cognitive abilities*. Mahwah, N.J.: L. Erlbaum  
43 Associates.  
44 828  
45  
46 829 98. Muller CA, Mayer C, Dorrenberg S, Huber L, Range F. 2011 Female but not male dogs  
47 respond to a size constancy violation. *Biol. Lett.* **7**, 689–691.  
48 830  
49  
50 831 (doi:10.1098/rsbl.2011.0287)  
51  
52  
53 832 99. Brown GR, Cullum P, Martin S, Healy SD. 2016 Sex differences in performance on a  
54 cognitive bias task in Norway rats. *Behav. Processes* **133**, 52–55.  
55 833  
56  
57  
58  
59  
60

- 1  
2  
3 834 (doi:10.1016/j.beproc.2016.11.005)  
4  
5 835 100. Dalesman S, Rendle A, Dall SRX. 2015 Habitat stability, predation risk and ‘memory  
6  
7 836 syndromes’. *Sci. Rep.* **5**. (doi:10.1038/srep10538)  
8  
9  
10 837 101. Bell AM. 2005 Behavioural differences between individuals and two populations of  
11  
12 838 stickleback (*Gasterosteus aculeatus*). *J. Evol. Biol.* **18**, 464–73. (doi:10.1111/j.1420-  
13  
14 839 9101.2004.00817.x)  
15  
16  
17 840 102. Bell AM, Sih A. 2007 Exposure to predation generates personality in threespined  
18  
19 841 sticklebacks (*Gasterosteus aculeatus*). *Ecol. Lett.* **10**, 828–834. (doi:10.1111/j.1461-  
20  
21 842 0248.2007.01081.x)  
22  
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24 843  
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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.

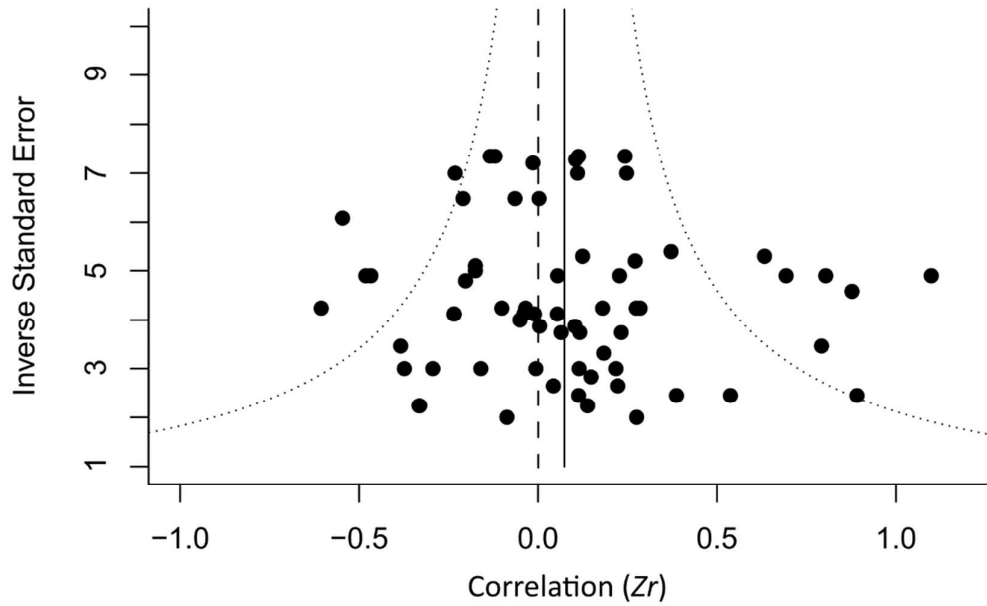
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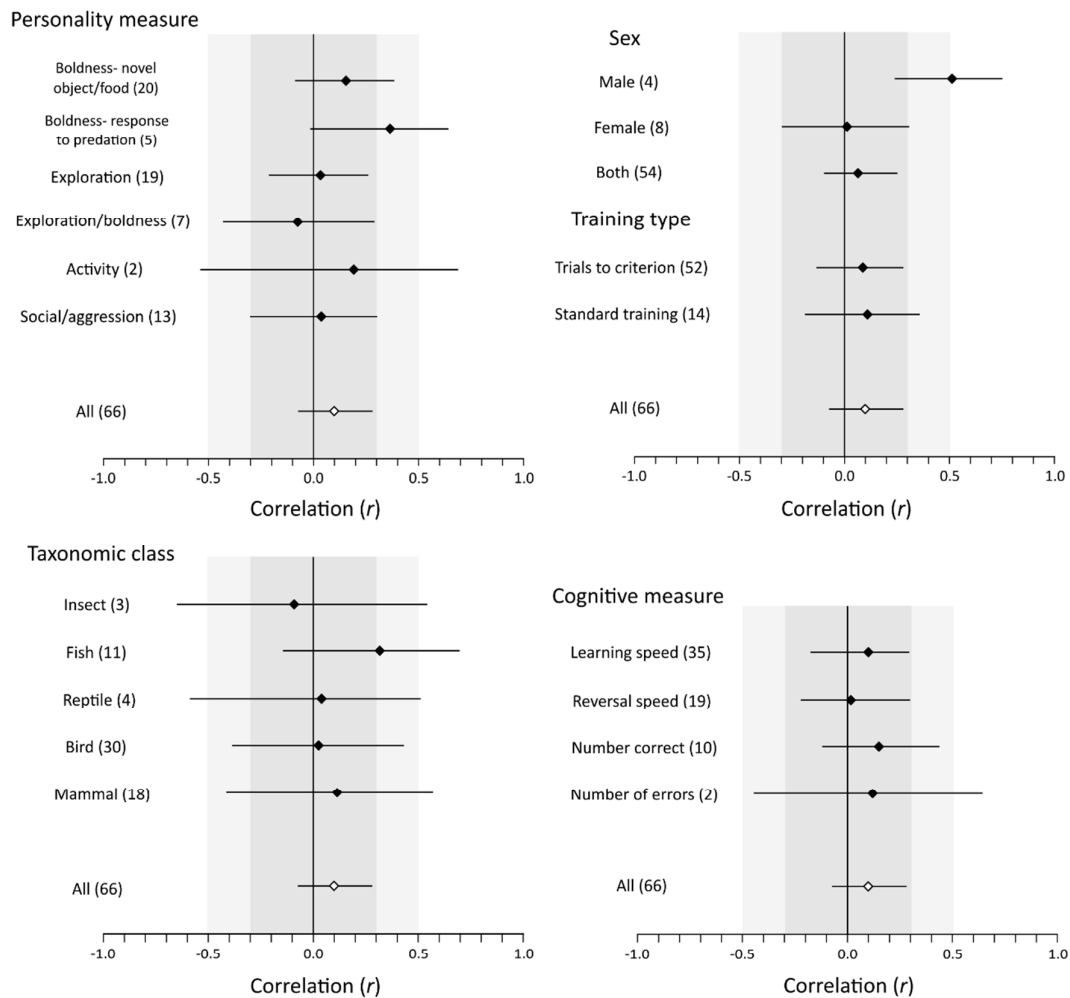
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**Figure 2.** Phylogeny used in meta-analysis (see main text for details).

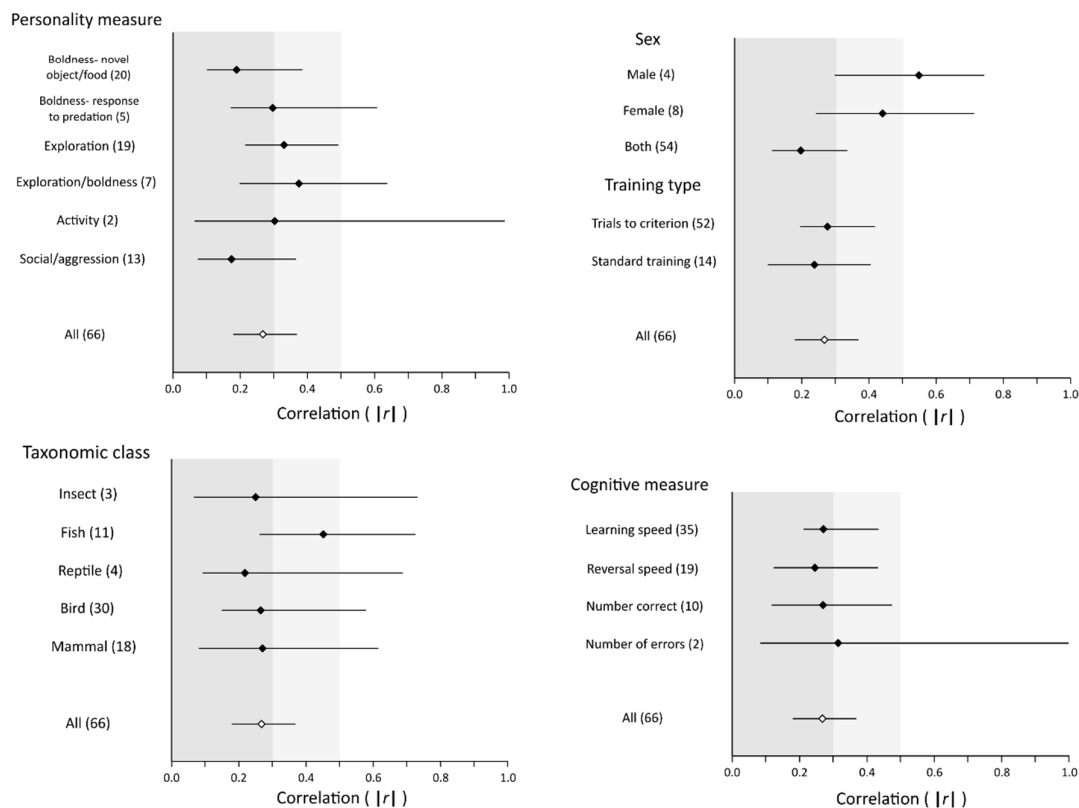


**Figure 3.** Funnel plot showing the relationship between sample size (inverse standard error; studies with larger sample sizes have larger values) and raw effect size ( $Z_r$ ). The solid line shows the overall mean effect size estimate from a multilevel meta-analysis including all 66 effect sizes.





**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.



**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.