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**Linking personality and cognition: A meta-analysis**

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Complete List of Authors:	Dougherty, Liam; University of Liverpool, Department of Evolution, Ecology and Behaviour Guillette, Lauren; University of St. Andrews, School of Biology
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3 Linking personality and cognition: A meta-analysis4  
5 Liam R. Dougherty<sup>1</sup> & Lauren M. Guillette<sup>2,3\*</sup>  
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11 <sup>1</sup>Department of Evolution, Ecology and Behaviour, University of Liverpool, Liverpool, L6912  
13 7RB, UK14  
15 <sup>2</sup>School of Biology, University of St Andrews, St Andrews, Fife, KY16 9TH, UK16  
17 <sup>3</sup>Department of Psychology, University of Alberta, Edmonton, AB, T6G 2R3, Canada  
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20  
21  
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2425  
26 \*Correspondence: L.M. Guillette, Department of Psychology, University of Alberta, P21727  
28 Biological Sciences Building, Edmonton, AB, T6G 2R3, Canada  
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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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#### 45 Introduction

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47 44 In the past 15 years research in behavioural ecology has shown that different behaviours of  
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49 45 individual animals may be stable across time or contexts (animal personality *sensu* [1–3]).  
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51 46 These different behaviours (also called personality traits), moreover, may not be  
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53 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  
36  
37 64 opposite: showing strong and quick inhibitory conditioning, and weak and slow excitatory  
38  
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  
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13 77 stopping and remaining motionless...’ (pp 177). Pavlov believed these four types of nervous  
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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  
11  
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  
15  
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  
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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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### 13 173 **Criteria for inclusion**

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16 174 We had several criteria for inclusion of a study in our analysis (see Table S1 for a list  
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18 175 of studies not included in the analysis, and the reasons for their exclusion). The main  
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20 176 criterion was that each paper needed to include at least one measure of personality and one  
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22 177 measure of cognition, which came from different tasks. For example, in a study examining  
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24 178 boldness (as measured by latency to interact with a novel object) and learning speed  
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26 179 (number of trials reach criteria for a visual discrimination task), this criterion was violated if  
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28 180 boldness was measured as latency to interact with the cognitive testing apparatus which  
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30 181 was used to assess learning speed. Second, the paper needed to present statistical  
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32 182 information so that an effect size could be calculated (though note that in several cases we  
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34 183 contacted the authors of papers that did not present appropriate statistics in order to  
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36 184 obtain such information; see below for more details).  
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42 185 Personality measure. The relatively young field of animal personality faces several  
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44 186 challenges when it comes to measuring personality, which are clearly reviewed in [28]. One  
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46 187 challenge relates to defining personality traits, a second challenge related to how these  
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48 188 traits are measured (see [41] for discussion about failure to measure repeatability in traits  
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50 189 and [42] for a meta-analysis of repeatability of personality traits). Here, we followed the  
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52 190 definition of a personality trait from [28; pp 476]: *A specific aspect of a behavioural*  
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54 191 *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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13 197 that the five outlined traits be regarded as a working tool. Thus the working definitions we  
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15 198 used are more in line with those used by [27], and consisted of the following categories:  
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17 199 Boldness – responses to novel objects, food and potential predators; Exploration –  
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19 200 responses to a novel environment or open field; Social/Aggression – reactions to conspecific  
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21 201 presentations; Activity – movement around a familiar environment (e.g., a home cage); and,  
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23 202 Exploration/Boldness – combined reactions to novel environment and novel object tests  
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25 203 (e.g., established composite scores for great tits *sensu* [43]). Note that in the analysis we  
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27 204 distinguish between boldness in response to novel objects or food and boldness in response  
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29 205 to predators, as preliminary analyses indicated that these were informative groupings. We  
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31 206 use the term 'personality measure' rather than 'personality trait' in order to distinguish  
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33 207 between these two types of boldness. In summary, the 'behaviour measures' variable  
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35 208 consists of six categories: boldness in response to novel objects/food, boldness in response  
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37 209 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  
28  
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  
12  
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  
47  
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  
8  
9 289 the phylogeny is not possible. However, the phylogenetic branching pattern of the tree still  
10  
11 290 contains important information on the relatedness between different taxa [39], and so we  
12  
13 291 estimated branch lengths based on the total length of the tree [59]. Accordingly, we first  
14  
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 28 297 **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  
33  
34 300 package MCMCglmm v2.21 [53]. We first ran a multilevel meta-analysis model in order to  
35  
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  
4  
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  
23  
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  
35  
36 326 produced a potential scale reduction factor point estimate of 1 or very close to 1, indicating  
37  
38 327 convergence. We also re-ran the intercept-only model using a flat prior for the residuals and  
39  
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.

45  
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  
6  
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  
12  
13 339 and high respectively, though heterogeneity in ecological and evolutionary meta-analyses is  
14  
15 340 typically very high [65].

16  
17  
18 341 This first analysis was used to estimate both the magnitude and the direction of the  
19  
20 342 relationship between cognition and personality. However, given that the sign of the effect  
21  
22 343 was highly variable (see below), and there are not always clear predictions for which  
23  
24 344 direction this relationship should be, we also wanted to estimate the absolute magnitude of  
25  
26 345 the relationship between personality and cognition ( $|r|$ ), irrespective of the sign. We did  
27  
28 346 this by applying the folded normal distribution to the posterior mean estimate derived from  
29  
30 347 the intercept-only model, in order to estimate the average effect size and credible intervals  
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32 348 on the absolute scale (i.e. the 'analyse and transform' approach recommended by  
33  
34 349 [29,30,41,66]).

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37 350 We next examined the extent to which variation in effect size was related to five  
38  
39 351 categorical moderator variables. These were: personality measure, cognitive measure,  
40  
41 352 taxonomic class, sex, and training type (see 'criteria for inclusion' for category details). We  
42  
43 353 used a model-selection approach to determine the importance of potential moderators of  
44  
45 354 mean effect size [40]. We performed a series of meta-regression models, each of which  
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47 355 included study, species, and phylogeny as random effects, and one of the five categorical  
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49 356 fixed effects. Model fit was then determined using the deviance information criterion (DIC),  
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51 357 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  
14  
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  
30  
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  
34  
35 373 method to test for asymmetry in the 'funnel plot' of residual effect size against sample  
36  
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  
42  
43 377 between effect size and the year the study was published, which may be indicative of  
44  
45 378 publication bias. For example, the commonly observed negative relationship between effect  
46  
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  
20  
21 389 [73], fish [50,74–78], reptiles [79], birds [46,51,88,89,80–87], and mammals [90–94].  
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23 390

### 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  
30  
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 ( $I^2$ =  
34  
35 396 67.09%, HPD interval= 49.1% - 80.39%). It is therefore unlikely that this heterogeneity has  
36  
37 397 arisen due to sampling error alone. The three random factors explained little of the  
38  
39 398 heterogeneity in effect sizes (Study  $I^2$ = 8.46%, HPD interval= 0.16% - 31.98%; Species  $I^2$ =  
40  
41 399 5.21%, HPD interval= 0.12% - 17.52%; Phylogeny  $I^2$ = 10.71%, HPD interval= 0.24% - 37.69%).  
42  
43 400 The absolute mean effect size ( $|r|$ ) was 0.268 (95% CI = 0.179- 0.368, significantly different  
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45 401 from zero,  $N$ = 66 effect sizes, 652 individuals), which is considered medium to small (small  
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47 402 effect size of 0.1, medium effect size of 0.3; Cohen, 1992).  
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### 50 51 404 **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  
13  
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  
21  
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  
31  
32 442 (animals that were more bold, aggressive, explorative, active and social were slower to  
33  
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  
19  
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  
23  
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  
15  
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.  
21  
22 485 Further, the absolute size of the relationship between personality and cognition was more  
23  
24 486 positive when males or females were tested separately, compared to when individuals of  
25  
26 487 both sexes were combined. This result is somewhat surprising, given that there have been  
27  
28 488 few studies examining sex differences in the relationship between personality and  
29  
30 489 cognition, and indeed only a single study in our sample tested for this relationship in males  
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32 490 and females separately [96]. For this reason, and the fact that this effect is primarily driven  
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34 491 by the presence of a relatively few effect sizes of large effect (4 and 8 effect sizes for males  
35  
36 492 only and females only, respectively), we interpret this result cautiously. Nevertheless, we  
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38 493 suggest that this pattern merits further investigation, and that researchers should test for  
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40 494 sex differences, including interactions between sex and personality, in the relationship  
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42 495 between personality and cognition before data from males and females are combined, and  
43  
44 496 report this in the methods or results sections even when there is no significant difference.  
45  
46 497 Sex differences in cognitive abilities has long been a well-studies area in human psychology  
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48 498 [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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51 520           In conclusion, our results show that Pavlov was correct: animal personality and  
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53 521 cognition are related. However, our analysis also revealed high among-study heterogeneity  
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55 522 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  
20  
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,  
36  
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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50

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#### 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

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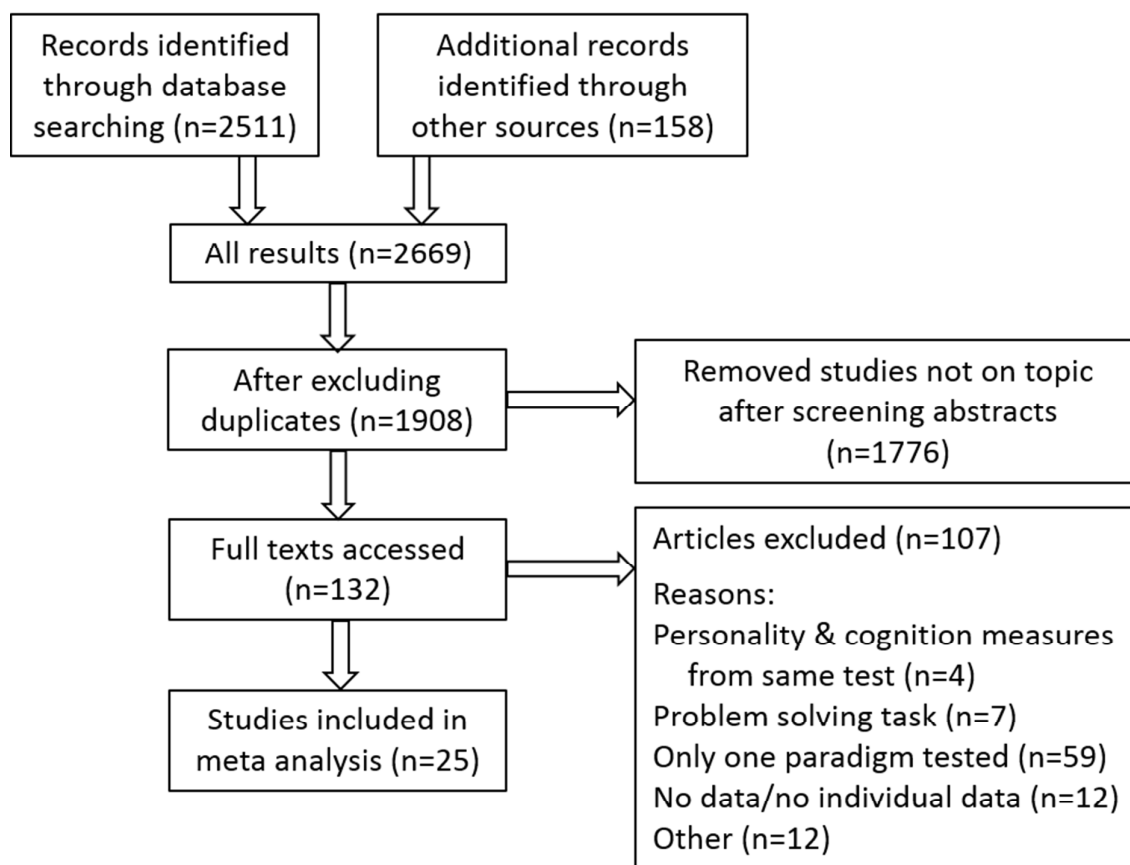
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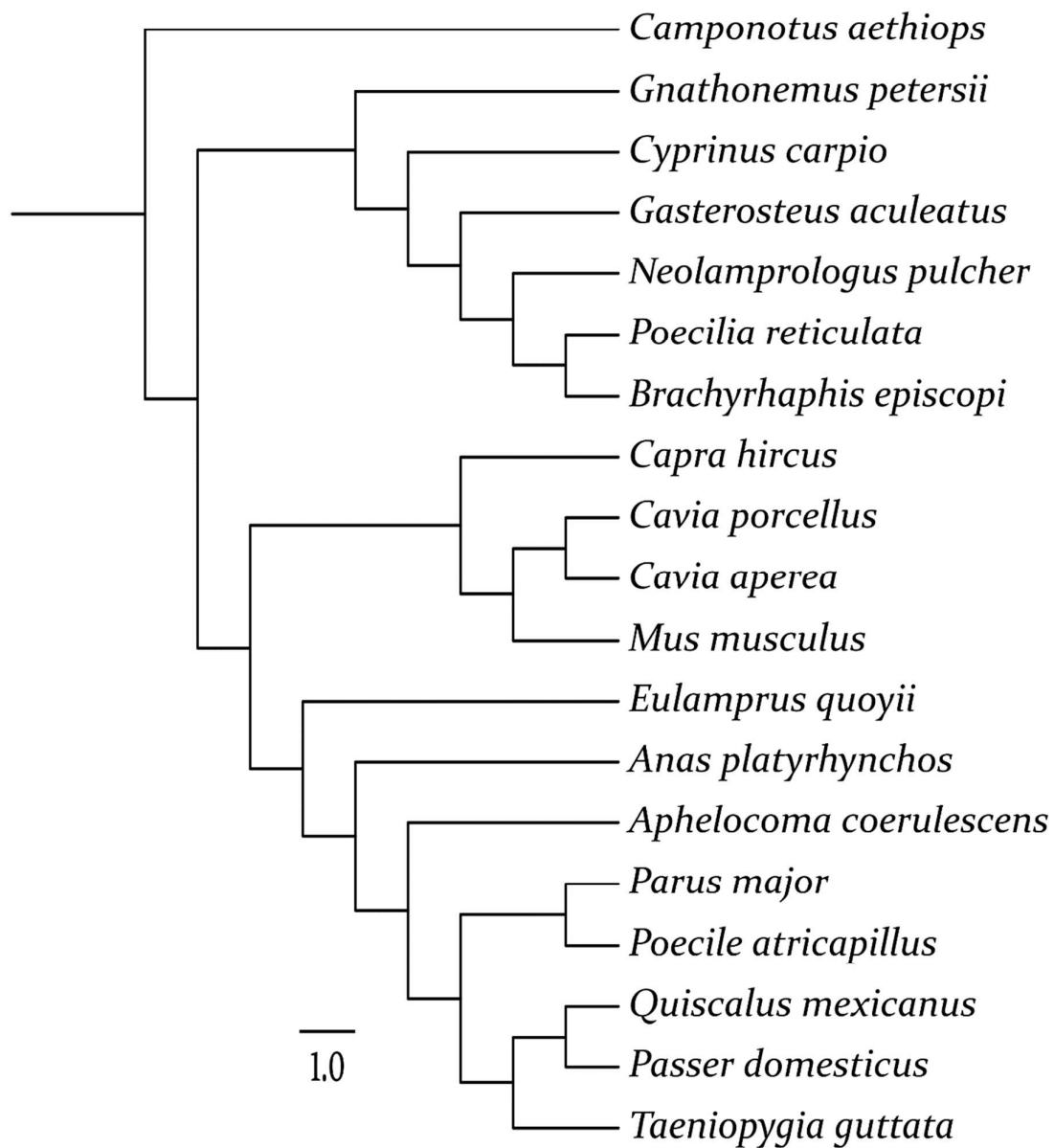
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**Figure 1.** PRISMA diagram showing systematic search process. See supplementary material for complete list of search terms used in different databases and Table S1 for a list of relevant papers not included in the final analysis. For the articles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

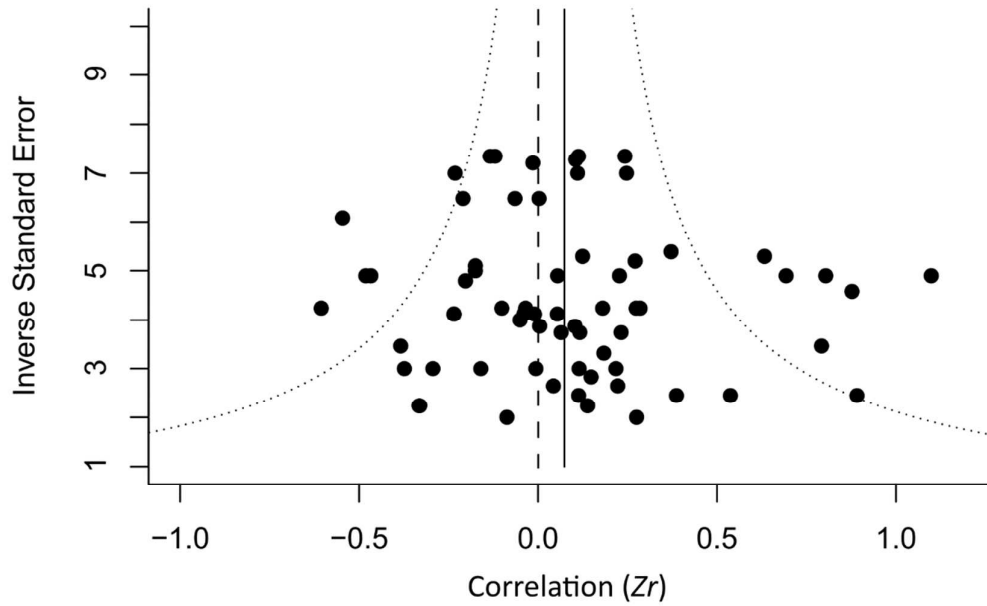
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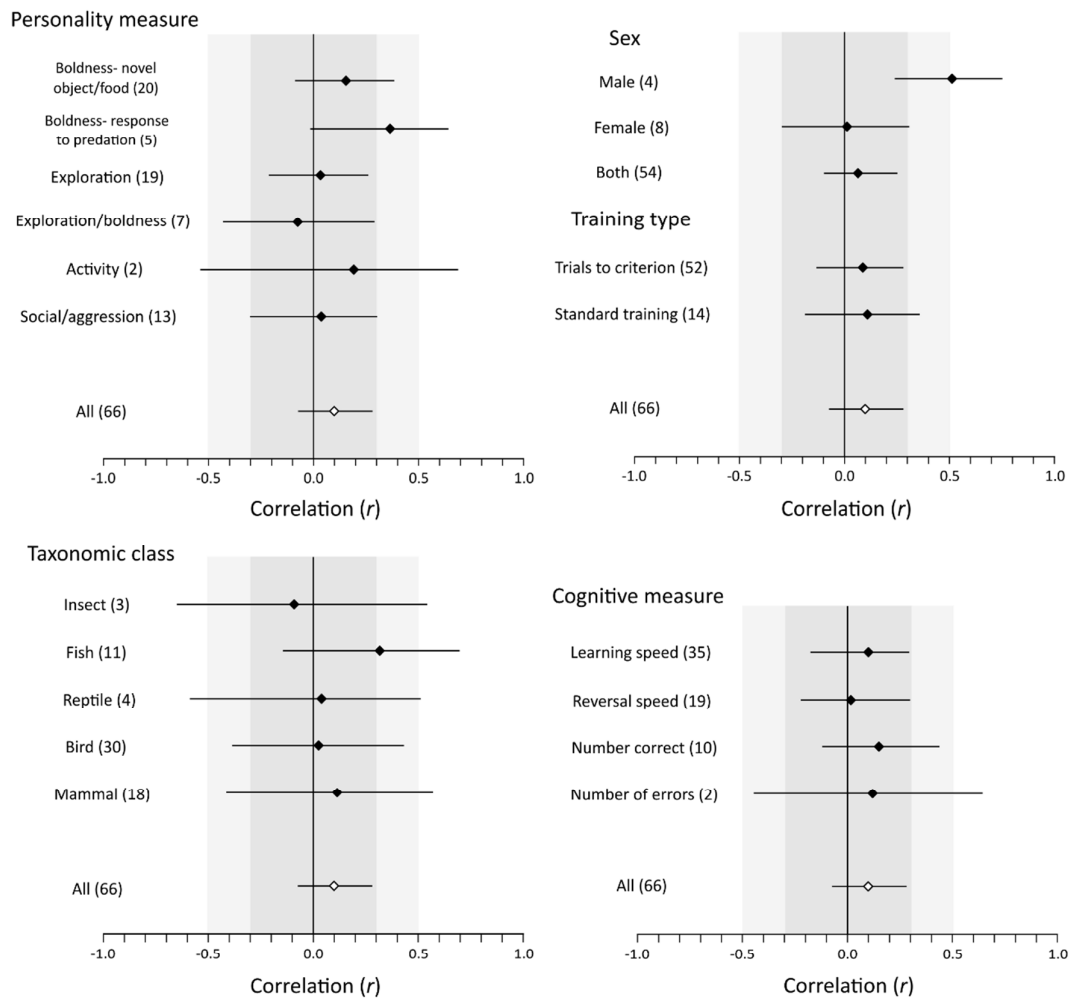
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**Figure 2.** Phylogeny used in meta-analysis (see main text for details).

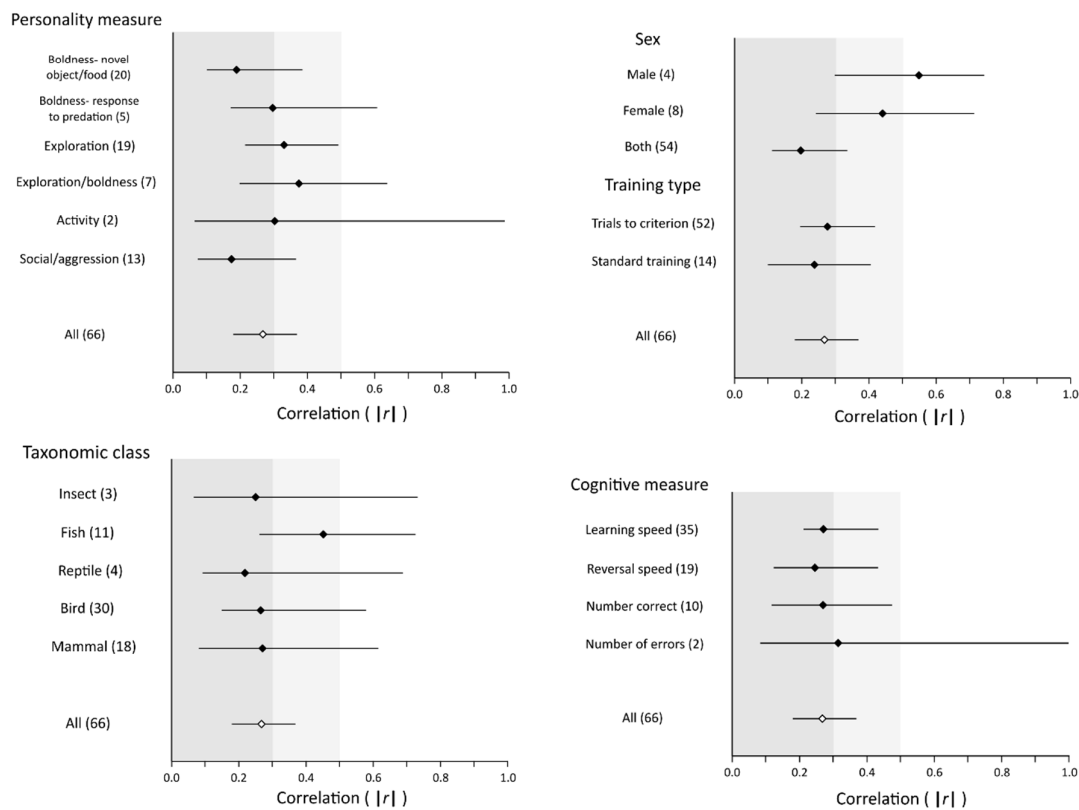


**Figure 3.** Funnel plot showing the relationship between sample size (inverse standard error; studies with larger sample sizes have larger values) and raw effect size ( $Z_r$ ). The solid line shows the overall mean effect size estimate from a multilevel meta-analysis including all 66 effect sizes.





**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.