



10 **Abstract**

11 Although the evolution of cognitive differences among species has long been of interest in ecology,  
12 whether natural selection acts on cognitive processes within populations has only begun to receive  
13 similar attention. One of the key challenges is to understand how consistently cognitive traits within  
14 any one domain are expressed over time and across different contexts, as this has direct implications  
15 for the way in which selection might act on this variation. Animal studies typically measure a  
16 cognitive domain using only one task in one context, and assume that this captures the likely  
17 expression of that domain in different contexts. This deficit is not surprising because, from an  
18 ecologist's perspective, cognitive tasks are notoriously laborious to employ, and for design reasons  
19 most tasks can only be deployed in a specific context. Thus our knowledge of whether individual  
20 differences in cognitive abilities are consistent across contexts is limited. Using a wild population of  
21 great tits (*Parus major*) we characterised consistency of two cognitive abilities, each in two different  
22 contexts: 1) spatial learning at two different spatial scales, and 2) behavioural flexibility as both  
23 performance in a detour reaching task and reversal learning in a spatial task. We found no evidence  
24 of a correlation between the two spatial learning speeds, or between the two measures of  
25 behavioural flexibility. This suggests that cognitive performance is highly plastic and sensitive to  
26 differences across tasks, or that variants of these well-known tasks may tap into different  
27 combinations of both cognitive and non-cognitive mechanisms, or that they simply do not  
28 adequately measure each putative cognitive domain. Our results highlight the challenges of  
29 developing standardised cognitive assays to explain natural behaviour and to understand the  
30 selective consequences of that variation.

31 **Keywords:** cognition, spatial learning, inhibitory control, great tits, consistency, repeatability

32

### 33 **Introduction**

34 The importance of evolutionary processes in explaining why individuals vary in their cognitive  
35 abilities is an emerging question in behavioural ecology. On the one hand, support for natural  
36 selection is accumulating in studies that show links between correlates of fitness and cognitive  
37 measures (Ashton et al., 2018; Cauchard et al., 2013; Cole et al., 2012; Cole & Quinn, 2012; Keagy et  
38 al., 2009; Raine & Chittka, 2008). On the other, it remains unclear whether selection on individual  
39 variation in cognitive traits will result in a meaningful response (Shaw & Schmelz, 2017). One reason  
40 for this uncertainty over the evolutionary consequences of selection on cognition is that estimates of  
41 heritability are almost entirely lacking from natural populations (Langley et al., 2020; Quinn et al.,  
42 2016; reviewed in Croston et al., 2015), partly because generating reliable estimates of heritability  
43 demand large pedigrees (Quinn et al., 2006), and instead most researchers are forced to accept the  
44 phenotypic gambit, i.e., to assume that if a trait is repeatable, it is likely to be heritable, or that if  
45 two traits are phenotypically correlated, they are also genetically correlated (but see Quinn et al.,  
46 2016).

47 A recent meta-analysis has shown that repeatability among cognitive traits is highly variable, and  
48 that behaviours in certain types of cognitive tasks are less repeatable than others, thus providing  
49 less reliable measures of cognition (Cauchoix et al., 2018). This is particularly the case for contextual  
50 repeatability whereby two different tasks or the same task in different contexts aim to test the same  
51 cognitive trait, as opposed to temporal repeatability in which the exact same task is repeated over  
52 time (Cauchoix et al., 2018). Robust measures of individual differences in cognitive abilities are  
53 generally lacking, particularly within the same cognitive domain (i.e. statistically derived group of  
54 factors that capture the variance in a set of tasks) (Shaw & Schmelz, 2017; van Horik, Langley,  
55 Whiteside, Laker, & Madden, 2018). In fact, other studies looking at the same domain-specific  
56 cognitive abilities found little evidence of contextual repeatability, particularly for associative  
57 learning (Boogert et al., 2011; Bray et al., 2014; Brucks et al., 2017; Guenther & Brust, 2017; Isden et

58 al., 2013; Keagy et al., 2009; Morand-Ferron et al., 2011; Shaw et al., 2015; van Horik et al., 2019;  
59 van Horik, Langley, Whiteside, Laker, Beardsworth, et al., 2018; van Horik, Langley, Whiteside, Laker,  
60 & Madden, 2018; Vernouillet et al., 2018). While a handful of studies have adopted test batteries to  
61 measure individual differences in cognitive abilities (Anderson et al., 2017; Ashton et al., 2018;  
62 Boogert et al., 2011; Guenther & Brust, 2017; Isden et al., 2013; Shaw et al., 2015; Soha et al., 2019;  
63 van Horik, Langley, Whiteside, Laker, & Madden, 2018), this approach remains relatively rare and  
64 few studies have explicitly tested contextual repeatability in multiple cognitive abilities. The gold  
65 standard would be to measure multiple traits across time and contexts in order to validate those  
66 measures of cognition (Völter et al., 2018). In this study we examined performance of two cognitive  
67 traits of key functional significance in behavioural ecology, spatial learning across contexts (i.e.  
68 spatial scale) and behavioural flexibility across two types of cognitive tasks.

69 Spatial learning, a form of learning relating to information about orientation and location, is a  
70 fundamental cognitive process that affects many aspects of an animal's ecology. For example, spatial  
71 learning helps individuals to find food and mates, to monitor their territory boundaries, and at a  
72 larger scale to navigate their migration routes (Healy & Hurly, 2004). Several processes are involved  
73 in different navigational methods or attention to different cues. Animals can use view-matching  
74 strategies, such as landmark-matching or panorama-matching, where the apparent size or distance  
75 of landmarks, or the shape of the surroundings are important in matching a remembered view  
76 (Pritchard et al., 2018; Pritchard & Healy, 2018). Animals may also use strategies where the absolute  
77 distance or direction of a goal from a landmark is of importance (Pritchard et al., 2018; Pritchard &  
78 Healy, 2018). Moreover, these methods are not mutually exclusive and can be applied  
79 simultaneously in different environments or during different stages of navigation (Pritchard & Healy,  
80 2018). In fact, evidence in the field and in captivity suggests that individuals rely on different  
81 information depending on the scale of their environment or the size of their enclosure (Chiandetti et  
82 al., 2007; Healy & Hurly, 1998; Sovrano et al., 2005, 2006). Although spatial learning is commonly  
83 referred to as a domain specific cognitive trait, such results question whether spatial learning should

84 in fact be broken down into even more specific mechanisms. In humans, spatial abilities measured at  
85 different scales, have been shown to be underlined by some common processes for encoding,  
86 maintaining and transforming spatial representation, as well as some unique processes not shared at  
87 different scales of space (Hegarty et al., 2006; Montello, 1993). Yet the majority of studies in non-  
88 human animals adopt tasks that are relatively small in scale and do not differ in context (e.g. Branch  
89 et al., 2019; Sewall et al., 2013; Sonnenberg et al., 2019). If animals use different cues depending on  
90 the spatial scale, we may expect performance in a spatial learning task to differ across contexts.  
91 Nevertheless, the use of different navigational mechanisms does not preclude individual consistency  
92 across contexts, which would be suggestive of a meaningful trait that has the potential to be  
93 heritable.

94 Another cognitive trait that has received a lot of attention in cognitive ecology is behavioural  
95 flexibility, which allows individuals to adapt their behaviour to changes in their environment (Brown  
96 & Tait, 2014). In psychology, behavioural flexibility refers specifically to attentional shifting, rule  
97 switching and response reversal (Brown & Tait, 2014). Recently, behavioural and cognitive ecologists  
98 have been criticised for adopting the term to broadly describe any flexible behaviour, thus grouping  
99 behaviours that may be guided by different cognitive mechanisms (Audet & Lefebvre, 2017). As  
100 such, different assays of behavioural flexibility may involve different cognitive mechanisms,  
101 therefore limiting our ability to make broad inferences about what an animal's performance in a  
102 particular context might mean for adaptive responses in the wild. Two tasks have been frequently  
103 used to test how well animals respond to changes in their environment – the detour reaching and  
104 reverse learning tasks. The detour task is thought to measure inhibitory control - an executive  
105 cognitive function that determines the ability to overcome a prepotent but disadvantageous  
106 response in favour of a more advantageous but less instinctive response. In this task animals must  
107 avoid a transparent barrier by inhibiting a motor response to go the most direct route towards a  
108 reward and instead move around the barrier (Boogert et al., 2011; MacLean et al., 2014). Reversal  
109 learning tasks are thought to measure how flexibly animals can adjust to changes in learned

110 contingencies, whereby a novel response is rewarded and the previously rewarded response is not.  
111 While reverse learning can involve inhibitory control (Bari & Robbins, 2013) (particularly on the first  
112 reversal as opposed to multiple reversals in which rules are formed), it also involves instrumental  
113 conditioning (extinction and relearning of reinforced stimuli) (Brown & Tait, 2014). Previous work  
114 has directly tested the relationship between individual performance in a detour reach and a reversal  
115 learning task, with mixed results (Anderson et al., 2017; Ashton et al., 2018; Boogert et al., 2011;  
116 Brucks et al., 2017; Shaw et al., 2015; Soha et al., 2019; van Horik, Langley, Whiteside, Laker, &  
117 Madden, 2018). Moreover, all of the reversal learning tasks were based on object or colour  
118 associations, so it is still unclear how detour reach performance relates to reversal learning in a  
119 spatial context. Therefore, there is good reason to expect overlap in a domain general cognitive  
120 mechanism (i.e. inhibitory control) for both detour reaching and reverse learning, but there are also  
121 potentially some mechanisms that are exclusive to one task only, raising uncertainty as to whether  
122 one might expect these two traits to predict similar behaviours.

123 The great tit (*Parus major*) is a model species for ecological and behavioural studies (e.g. Aplin et al.,  
124 2015; Cole et al., 2011; Dutour et al., 2020; Loukola et al., 2020; Morand-Ferron et al., 2011). Great  
125 tits adapt well to temporary captivity, allowing for their use in controlled experiments on individual  
126 differences. Here we investigated consistency in spatial learning and behavioural flexibility across  
127 contexts. We measured spatial learning at two different spatial scales: at a large scale within an  
128 experimental room, and at a smaller scale within the birds' individual home cages. We also  
129 measured behavioural flexibility across two different tasks (also at different scales): reversal  
130 learning, using a spatial feeder array in the experimental room and a detour apparatus in the home  
131 cage (MacLean et al., 2014). Our study had two objectives: first, to examine whether a learning task  
132 conducted in a home cage predicts measures of the same putative cognitive domain at a larger  
133 scale. Second, to investigate whether behavioural flexibility measured by the detour reach task  
134 predicts the behaviour of birds in a reversal learning task. If learning at different spatial scales is  
135 underlined by a general cognitive mechanism, then we would expect our measure of spatial learning

136 in the home cage to be correlated to our measure of spatial learning in the experimental room. By  
137 contrast, if spatial learning at different scales requires different mechanisms, or attention to  
138 different cues, then we would not expect such a correlation. Similarly, if behavioural flexibility is  
139 underlined by inhibitory control, then we would expect measures coming from our two tasks to be  
140 correlated. However, if behavioural flexibility is a consolidated measure of different cognitive  
141 processes, then we expected measures emerging from those tasks be uncorrelated with each other  
142 (Miyake et al., 2000).

### 143 **Methods**

144 Wild-caught great tits (n= 36) from the Bandon Valley, County Cork, Ireland, were brought into  
145 captivity, and later released at their capture site upon finishing the experiments (O'Shea et al.,  
146 2018). Birds were fitted with BTO rings for individual identification and a Passive Integrated  
147 Transponder (PIT) tag. Birds were housed in 57(h) x 56(d) x 46(w) cm plywood cages with two  
148 perches each and with an internal light set from 7:30 to 18:00. Birds had *ad libitum* access to food  
149 and water. Food consisted of sunflower hearts, peanuts, mealworms and waxworms. Out of the 36  
150 birds brought into captivity, 28 birds learned the large-scale spatial learning task, and 25 of those  
151 also learned the reverse learning task. Out of the 36 birds, 30 learned the small-scale spatial learning  
152 task, and 32 completed all 10 trials of the detour reach task. Data collection took place between  
153 January and March 2019, and the mean time that birds were in captivity was 12 days.

#### 154 Large-scale spatial learning task

155 The large-scale spatial learning task took place in an experimental room of 460 (W) x 310 (L) x 265  
156 (H) cm, with four feeders containing sunflower seeds placed in a square with sides of one meter, and  
157 a small plastic Christmas tree (150 cm high) placed in the centre for birds to rest and hide. Feeders  
158 were equipped with RFID readers to remotely log each visit by detecting the individual's PIT tag.

159 The task consisted of a habituation phase, training and test phases. Each trial within a phase lasted 1  
160 hour, and birds were food deprived 1 hour beforehand. Each phase took place at least 12 hours  
161 apart (i.e. typically the following day). In the habituation phase, birds were released into the  
162 experimental room from a small opening in their home cage. Food was accessible and visible in all  
163 four feeders. Birds had to eat 10 seeds within 1 hour (based on seed husk collected on the floor after  
164 the trial) before progressing to the training phase. In the training phase, birds were once again  
165 released into the experimental room, but this time the seeds in each feeder were concealed by an  
166 opaque paper sheet so the food was no longer visible by the birds except from the RFID reader  
167 platform, from which it was also accessible. Once a bird visited any of the four feeders a total of 10  
168 times (based on logged visits from RFID reader), they were advanced to the initial learning phase of  
169 the testing trials. During the testing trials, all feeders remained wrapped in paper but only one  
170 (randomly assigned) feeder contained food. The criterion for having learned the feeder position was  
171 to have visited the correct feeder 8 times within a moving window of 10 visits (Guenther & Brust,  
172 2017). The number of visits to reach criterion was used as a measure of learning. Once the birds met  
173 the criterion, they were advanced to the reverse learning phase, in which a new feeder was  
174 allocated as the rewarded feeder. The same criterion was used as for the initial learning phase: 8  
175 visits to the correct feeder within a moving window of 10 visits.

176 In all phases, birds were given one hour to visit the feeders before being returned to their home  
177 cage. Data from the loggers were reviewed on the same day to determine whether birds had met  
178 the criterion. If the birds did not reach their criterion within 6 trials, they were excluded as non-  
179 learners.

180 These data were collected as part of another experiment (Cooke et al., In prep) in which birds were  
181 exposed to different levels of simulated predation risk (treatment), during both the initial learning  
182 and reversal learning part of the experiment. We found no evidence that treatment in the previous  
183 experiment (Cooke et al., In prep) affected behaviour in the current one, so we analysed all

184 individuals together (but see supplementary material for analysis of birds with no perceived  
185 predation risk (control birds)).

#### 186 Small-scale spatial learning task

187 Individuals were given artificial food items designed to mimic seeds/insect prey enclosed in an outer  
188 shell (Ihalainen et al., 2007). In our study, these artificial food items consisted of a sunflower seed  
189 encased in a paper parcel (1.8 cm x 1.8 cm). Adapting from Ihalainen et al. (2007), all birds were  
190 trained to handle the artificial food in their home cages in four steps in which they had to consume  
191 the seeds before advancing to the next step: (i) five food items with the seed sticking out from each  
192 parcel; (ii) five food items with the seed inside each parcel, but with a hole in the middle showing the  
193 seed inside; (iii) five food items with the seed completely hidden inside each parcel; and finally (iv)  
194 five food items with the seed completely hidden inside of each parcel with three rewarded (i.e. seed)  
195 and two unrewarded (i.e. made the reward inaccessible once the parcel was opened by wrapping  
196 the seed in duct tape). In this last step shielded items were used so that the birds would learn that  
197 not all parcels had accessible food. The birds had to eat all items before the training progressed to  
198 the next phase, or eat three rewarded food items and open two unrewarded food items in the last  
199 phase of training to proceed to the testing phase. In each training step parcels were placed centrally  
200 in the home cage in a small dish.

201 The testing phase consisted of ten parcels placed in each corner of the cage, in a small dish. Three of  
202 those locations contained only parcels that were unrewarded, while all parcels from the rewarded  
203 location contained seeds. The rewarded corner was allocated to each bird randomly. Every time the  
204 bird made 10 choices, irrespective of their location, each corner was rebaited to have 10 total  
205 parcels, so that the amount of parcels at each corner would not act as a cue for the bird.

206 During training and testing, birds had no *ad libitum* access to food, and only had access to food  
207 through the parcels. Individuals were not food deprived beforehand to allow for longer training and  
208 testing sessions. Water was still available *ad libitum*. Birds were trained and tested for a maximum of

209 three hours consecutively. After three hours their *ad libitum* food was replaced in their cages. During  
210 training and testing, if a bird had not eaten any food for the last 1.5 hours, or less than 10 seeds for  
211 the last 2 hours, then the training/testing was stopped, and *ad libitum* food was placed back in their  
212 cages.

213 Trials stopped either once the bird had learned where to find seeds, based on a criterion of 8 correct  
214 visits in a moving window of 10 visits, or if they were not eating enough (see above). The number of  
215 choices to reach criterion was used as a measure of learning.

#### 216 Detour reach task:

217 For this task, birds were required to retrieve a waxworm from inside a transparent cylinder,  
218 requiring them to make a detour around the cylinder to obtain the reward (Boogert et al., 2011;  
219 MacLean et al., 2014). The cylinder (3 cm length, 3.5 cm diameter) was made from plastic sheeting,  
220 open at both ends, and glued onto a cardboard base (7 cm x 20 cm). We also added a small perch (8  
221 cm wide, 8 cm high) parallel to the cylinder, to avoid any biases in approach direction. The task had  
222 three phases: habituation, training and testing, and a waxworm was used as a reward in all phases.  
223 During the habituation and training phases the cylinder was opaque (black plastic), whereas it was  
224 transparent during the test. Before habituation and training birds were food deprived for 1 hour. For  
225 habituation, training and testing birds had *ad libitum* access to water and only had access to food  
226 through the task.

227 Birds were first habituated to the apparatus to reduce their fear towards the novel apparatus. For  
228 habituation birds were required to eat a waxworm placed in front of the opaque cylinder. Once they  
229 had completed this three times, birds advanced to the training phase of the experiment. During  
230 training birds were required to eat a waxworm placed in the middle of the opaque apparatus, by  
231 reaching around the cylinder into the open end without touching the exterior of the tube. Birds had  
232 to complete this four times to advance to the next phase. During the test phase, birds were  
233 presented the transparent apparatus with a waxworm placed in the middle. Birds were scored either

234 a success (obtaining the worm without touching the tube) or a failure (touching the tube) and the  
235 tube was removed from the cage. This was repeated ten times in succession. Performance on this  
236 task was quantified as the number of successes out of ten. The test phase always occurred at least  
237 the day after the training phase was completed.

#### 238 Statistical Analysis

239 All analyses were conducted in R (R Core Team, 2019). Data followed a Poisson distribution, and  
240 therefore Kendall's Tau correlations were conducted for non-normal distributions. We conducted a  
241 correlation test between the learning speed at the large and small scale, and between the  
242 performance on the detour reach task and reversal learning. In all analyses we excluded birds that  
243 learned on their first choice, as we cannot say whether they learned or made a choice by chance  
244 (large-scale spatial learning task  $n = 1$ ; large-scale spatial reversal learning task  $n = 3$ ; small-scale  
245 spatial learning task  $n = 2$ ) (but see supplementary material for analysis of all birds). For the two  
246 spatial learning tasks, we also compared overall learning speeds in terms of number of visits, and  
247 time, using generalised linear mixed-models with a Poisson error distribution and log function (Bates  
248 et al., 2015). Model assumptions were checked using DHARMA (Hartig, 2020).

#### 249 Data Availability

250 The dataset analysed during the current study, and the R code used to analyse them are available as  
251 supplementary material, and will be made available on the Open Science Framework upon  
252 publication.

#### 253 Ethics

254 We performed the experiment in accordance with the Association for the Study of Animal Behaviour  
255 guidelines, and the Animal Experimentation Ethics Committee of the University College Cork  
256 approved the study, under the number 2014/014 "The evolutionary and behavioural ecology of  
257 birds". The Health Products Regulatory Authority approved the ethics for the project number

258 AE19130/P017, and the National Park and Wildlife Services approved the capture of birds under the  
259 licence C01/2019.

## 260 **Results**

261 On average, birds made 30.07 (SE = 4.48) choices before learning the large-scale spatial learning task  
262 (N=27), and 26.04 (SE = 3.09) choices before learning the small-scale spatial learning task (N=28).

263 Although birds needed to make more choices to learn the large-scale spatial learning task (model  
264 estimate = 0.27; C.I. = 0.15-0.37; p-value <0.001), they took slightly less time (seconds) to learn it

265 (model estimate = -0.03; C.I. = -0.03; -0.02; p-value <0.001), compared to the small-scale spatial

266 learning task. Birds took on average 131.98 (SE = 12.29) minutes to learn the large-scale spatial

267 learning task, while it took them 139.64 (SE = 19.91) minutes to learn the small-scale spatial learning

268 task. There was no evidence of a correlation between the two measures ( $z = 0.22$ ;  $\tau = 0.03$ ;  $p =$

269  $0.823$ ,  $n=24$ ; Figure 1.A).

270 On average, birds made 19.68 (SE = 3.07) choices before reverse learning (N=22), and made 3.81 (SE

271 = 0.41) correct choices in the detour reach task (N=32). There was no evidence of a correlation

272 between the detour reach and reversal learning ( $z = 0.23$ ;  $\tau = 0.04$ ;  $p = 0.819$ ,  $n=22$ ; Figure 1.B).

## 273 **Discussion**

### 274 Spatial learning speed

275 We did not find a correlation between spatial learning performance in the small scale setting of the  
276 home cage and spatial learning in the larger scale setting of the experimental room. As far as we are

277 aware, this is the first attempt to directly compare performance on a spatial learning task at

278 different scales in non-human animals (but see Hegarty et al., 2006; Montello, 1993 for work in

279 humans). Theoretically both tasks we used should measure spatial learning because they required

280 individuals to use and remember specific location cues with food rewards, allowing them to return

281 to that location more often than one would expect by chance (Olton, 1977). One possible

282 explanation for the lack of correlation between cognitive tasks is that non-cognitive factors - for  
283 example motivation, personality, stress, and motor skills - influenced performance differently across  
284 tasks. Although we had no a priori reason to expect this might be the case, it must remain a  
285 possibility. Another plausible explanation is that different kinds of cues or strategies were used to  
286 recognise locations in our two tasks and that this confounded any correlation in cognitive  
287 performance (Morgan et al., 2014). Work in captivity has shown that several species are more reliant  
288 on cues from the geometry of the room when they have to navigate in small enclosures, and  
289 absolute direction to landmarks when they have to navigate large enclosures (Chiandetti et al., 2007;  
290 Sovrano et al., 2005, 2006). Visual information might also change at a faster pace in the home cage  
291 than in the exploration room, creating a potential bias against relying on optical-flow in the home  
292 cage. If these different perceptual abilities are either not correlated among individuals (Healy et al.,  
293 2009; Jones & Healy, 2006; Pike et al., 2018; Sovrano et al., 2003) or are independent of other  
294 processes involved with spatial learning, for example memory (Tello-Ramos et al., 2018), this could  
295 readily explain the lack of a correlation in our data (Rowe & Healy, 2014b). In this case categorising  
296 the sensory information available to the individuals could explain individuals' spatial learning  
297 performances (Pritchard et al., 2017). Our results are in contrasts to findings that, despite having  
298 some different mechanisms, learning at different spatial scale was still found to be, to some extent,  
299 partly underlined by a common process for encoding, maintaining and transforming spatial  
300 representation (Hegarty et al., 2006; Montello, 1993).

301 Whatever the reason for the lack of correlation, subtle differences in experimental design may  
302 preclude meaningful comparison across studies (Thornton & Lukas, 2012). Furthermore, using only  
303 one task is unlikely to capture the expression of spatial learning in different contexts (Pritchard et al.,  
304 2017). For example, a current focus of research in food caching species is to measure spatial learning  
305 under standardised conditions, usually on a small scale, to infer performance in cache retrieval at a  
306 larger spatial scale, or to predict fitness, but it remains unclear whether observed associations relate  
307 to navigation through the environment or cache retrieval at a fine spatial scale (Healy, 2019; Healy

308 et al., 2005, 2009; Krebs et al., 1990; McGregor & Healy, 1999). Similarly, work on parasitic cowbirds  
309 in which the females, but not males, need to locate and remember potential host nests, have found  
310 that females out-perform males in some spatial learning tasks, but not others, further suggesting  
311 that individual differences in spatial ability may depend on task design and scale of spatial location  
312 (Sherry & Guigueno, 2019). This limitation mirrors the more general problem in evolutionary  
313 ecological studies of cognition where there is often a lack of a clear link between standardised  
314 cognitive tests (e.g. problem solving) and functional behaviour (innovative foraging) under natural  
315 conditions (Morand-Ferron et al., 2016; Rowe & Healy, 2014a, 2014b; Thornton et al., 2014).

### 316 Behavioural flexibility

317 We did not find any evidence of a relationship between the performance of the birds on a detour-  
318 reach and reversal learning task, despite the prediction that both measures of behavioural flexibility  
319 involve inhibitory control. This lack of correlation is in keeping with previous work in wild and captive  
320 birds, which have also used single reversals (song sparrow, *Melospiza melodia*: Boogert et al., 2011;  
321 New Zealand robin, *Petroica longipes*: Shaw et al., 2015). Our study increases the generality of this  
322 finding because these previous studies focussed on colour discrimination reversal rather than the  
323 spatial discrimination reversal we used here. There are multiple possible explanations for why these  
324 putative measures of inhibitory control may not necessarily correlate. One is that these different  
325 tasks in reality measure different components of inhibitory control (namely stopping, delaying, or  
326 withholding motor responses) (Bari & Robbins, 2013; Bray et al., 2014; Brucks et al., 2017; van Horik,  
327 Langley, Whiteside, Laker, Beardsworth, et al., 2018; Vernouillet et al., 2018). Moreover, although  
328 our results suggest that components of inhibitory control do not fall under the same general domain  
329 umbrella of behavioural flexibility, the lack of correlation may also be explained by the reversal  
330 learning task requiring a spatial learning component (Boogert et al., 2018; Brucks et al., 2017;  
331 Miyake et al., 2000). Discrepancies could also be explained by differences in motivation, which may  
332 have played a bigger role in the detour reach task as the food was visible, compared to the reversal

333 learning task, though we note that this is likely primarily an issue if rank order differences in  
334 motivation between individuals varies across tasks. Finally, although we acknowledge that the  
335 detour-reach task has been recently criticised as a measure of inhibitory control and is subject to  
336 various non-cognitive influences, including perception, stress, prior experience (Kabadayi et al.,  
337 2018; van Horik, Langley, Whiteside, Laker, Beardsworth, et al., 2018), this is likely true of all  
338 cognitive traits (Morand-Ferron & Quinn, 2015).

### 339 Conclusions

340 Our results across both task comparisons highlight that caution needs to be taken when making  
341 conclusions about learning speed or behavioural flexibility based on a single test, and that  
342 performance is highly sensitive to the context and type of task. On the one hand, if the lack of  
343 evidence for correlations reflects true cognitive differences related to either spatial learning or  
344 behavioural flexibility, then this would point towards greater complexity in the cognitive processes  
345 that drive animal navigation and behavioural plasticity. On the other hand, if the lack of correlation  
346 arises because of confounding effects which were not controlled for, or because one or both of the  
347 tasks within each domain does not measure learning or behavioural flexibility as expected, then this  
348 would point towards a common issue with experimental design used in cognitive tests. Either way,  
349 the context in which we measure cognition is therefore essential to consider, if we want to better  
350 understand causes and consequences of individual variation in cognition. Further investigation into  
351 the neurobiology related to performance in tasks which *a priori* measure the same cognitive  
352 processes may facilitate progress in validating cognitive tasks (van Horik, Langley, Whiteside, Laker,  
353 Beardsworth, et al., 2018), and distinguishing which of our interpretations are most valid. However,  
354 this approach may not often be feasible in non-model, wild animals. Pinning down the meaningful  
355 measures of individual differences in cognitive mechanisms remains a major challenge.  
356 Nevertheless, studies that aim to validate tasks, as we aimed to do here, are a step forward in  
357 understanding causes and consequences of individual variation in cognition.

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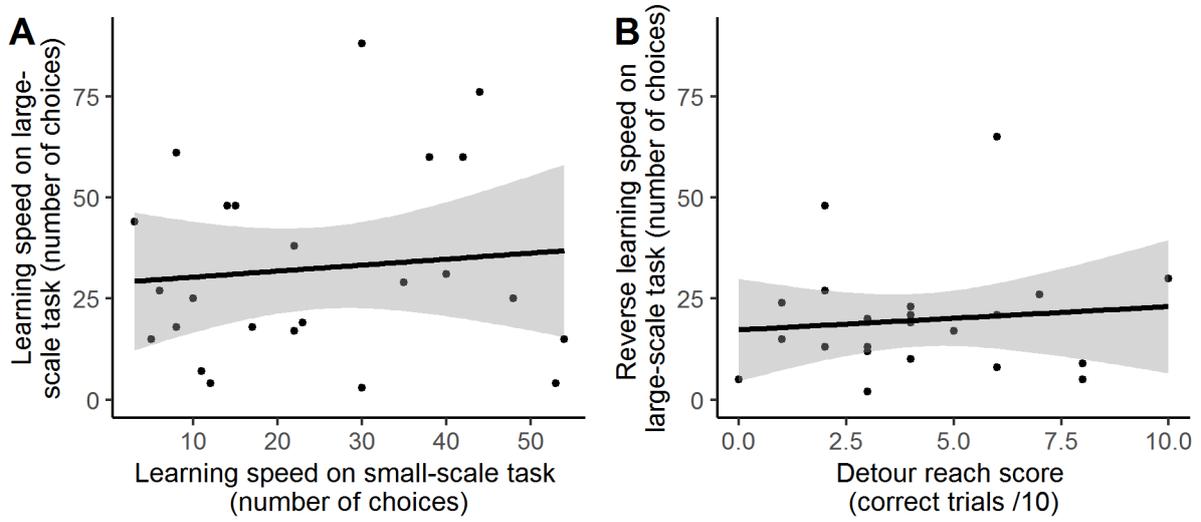
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586 **Figures**

587



588

589 Figure 1: Relationship between A) performance on small-scale and large-scale spatial learning tasks,

590 B) performance on detour reach and reversal learning tasks. The line is a fitted linear regression line

591 and the shaded grey area is the 95% confidence interval.

592 **Supplementary Information**

593 **All birds**

594 In the main text, the data description and analysis exclude birds that learn on their first choice, as we  
595 cannot say whether they learned or made a choice by chance (large-scale spatial learning task  $n = 1$ ;  
596 large-scale spatial reversal learning task  $n = 3$ ; small-scale spatial learning task  $n = 2$ ).

597 Here we report the same analysis on all birds, without exclusion:

598 On average, birds made 29.04 (SE = 4.44) choices before learning the large-scale spatial learning task  
599 (N=28), and 24.37 (SE = 3.11) choices before learning the small-scale spatial learning task (N=30).

600 Although birds needed to make more choices to learn the large-scale spatial learning task (model  
601 estimate = 0.29; C.I. = 0.18-0.39; p-value <0.001), they took slightly less time (seconds) to learn it

602 (model estimate = -0.04; C.I. = -0.04; -0.03; p-value <0.001), compared to the small-scale spatial

603 learning task. Birds took on average 129.06 (SE = 12.20) minutes to learn the large-scale spatial

604 learning task, while it took them 134.57 (SE = 19.11) minutes to learn the small-scale spatial learning

605 task. There was no evidence of a correlation between the two measures ( $z = 0.99$ ;  $\tau = 0.14$ ;  $p =$

606 0.320,  $n=26$ ).

607 On average, birds made 17.44 (SE = 2.97) choices before reverse learning (N=25), and made 3.81 (SE

608 = 0.41) correct choices in the detour reach task (N=32). There was no evidence of a correlation

609 between the detour reach and reversal learning ( $z = 0.59$ ;  $\tau = 0.00$ ;  $p = 0.554$ ,  $n=25$ ).

610

611 **Control birds**

612 A similar analysis was run on the control birds, and found similar results to the correlations with all

613 the birds included.

614 On average, birds assigned to the control condition made 22.11 (SE = 6.49) choices before learning  
615 the large-scale spatial learning task (N=9), and 22.44 (SE = 6.69) choices before learning the small-  
616 scale spatial learning task (N=9). There was no evidence of a correlation between the two measures  
617 ( $z = -1.82$ ;  $\tau = -0.59$ ;  $p = 0.068$ ,  $n=7$ ).

618 On average, birds assigned to the control condition made 18.37 (SE = 5.62) choices before reverse  
619 learning (N=8), and made 3.90 (SE = 0.74) correct choices in the detour reach task (N=10). There was  
620 no evidence of a correlation between the detour reach and reversal learning ( $z = -0.15$ ;  $\tau = -0.05$ ;  $p$   
621  $= 0.878$ ,  $n=7$ ).