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The gullible genius : fast learners fall for fake news

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1 **Title:** The gullible genius: fast learners fall for fake news

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12 **Abstract:** In many animals, decision-making is influenced by social learning, i.e. the acquisition of  
13 insights through the observation of other individuals' behaviours. In cases where such socially obtained  
14 information conflicts with personally acquired knowledge, animals must weigh up one form of  
15 information against the other. Previous studies have found that individual animals differ consistently in  
16 how they trade-off socially versus personally acquired knowledge, but why this is so remains poorly  
17 understood. Here, we investigate whether an animal's cognitive profile affects its decision to use either  
18 prior personal or new, conflicting social information, using the Italian wall lizard (*Podarcis siculus*) as  
19 our model species. We trained lizards to associate one of two colour cues with food, and subsequently  
20 allowed them to observe a conspecific trained for the opposite colour. After social demonstrations, lizards  
21 overall tended to use the 'fake', non-rewarding social information, but some individuals were more likely  
22 to do so than others. Lizards that showed faster spatial learning were more likely to copy social  
23 information even in the presence of reliable previous knowledge. Our study highlights the existence of  
24 significant inter-individual variation in social learning in a lizard, possibly mirroring variation in  
25 cognitive abilities.

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28 **Keywords:** cognition, social learning, lizards, decision-making

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31 **Significance Statement:** Animals often use social information in daily decision-making. Whenever  
32 knowledge obtained through personal experience conflicts with observations of decisions made by  
33 conspecifics, individuals must weigh these two types of information against each other. Individuals tend  
34 to differ in whether they prioritize social versus private information, but why this is so, remains poorly  
35 understood. Using lizards, we tested whether an animal’s cognitive profile affects its decision to use  
36 either prior personal or new, conflicting social information. We found considerable variation among  
37 individuals in social information use and tendency to rely on personal or public knowledge. Specifically,  
38 faster spatial learners inclined to copy social information, even in the presence of reliable previous  
39 knowledge, suggesting that intrinsic, cognitive aspects influence how individuals trade-off public and  
40 private information.

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### 43 **1. Introduction**

44 Learning involves the perception, acquisition, storage, and use of information collected from the  
45 environment (Dukas and Ratcliffe 2009; Buchanan et al. 2013). An animal’s learning ability can offer an  
46 adaptive advantage by influencing ecologically relevant behaviours (Dukas and Ratcliffe 2009; Buchanan  
47 et al. 2013). In social learning, information is acquired through the observation of (or interaction with)  
48 other individuals (Hoppitt and Laland 2013). Much like humans, other animals often rely on social  
49 learning to cope with social and environmental challenges (Galef Jr and Heyes 2004; Borenstein et al.  
50 2008). For example, there is now ample evidence that decisions regarding what to eat (Galef Jr and  
51 Giraldeau 2001), who to mate (White 2004) or fight with (Peake and McGregor 2004), and how to avoid  
52 being eaten (Griffin 2004) can all be influenced by social learning. Honeybees, for instance, learn the  
53 direction, distance, and quality of food sources from the waggle dances performed by conspecifics (Von  
54 Frisch 1967); female Trinidadian guppies (*Poecilia reticulata*) imitate the mate choice of other females  
55 (Dugatkin 1992) and male red-winged blackbirds (*Agelaius phoeniceus*) adjust their aggressive behaviour  
56 based on information obtained by watching contests (Freeman 1987). Juvenile rhesus monkeys (*Macaca*  
57 *mulata*) copy the alarm behaviours displayed by more experienced conspecifics (Mineka et al. 1984).

58 Copying the behaviour of others (i.e. imitating or observational learning) constitutes an important way by  
59 which animals acquire valuable life skills and ecological knowledge (Zentall 2012; Hoppitt and Laland  
60 2013). By copying behavioural choices of “demonstrators”, individuals are thought to acquire relevant  
61 information rapidly, without suffering the costs of sampling and trial-and-error associated with personal  
62 learning (Kendal et al. 2005; Rendell et al. 2010). However, occasionally, social learning may also lack

63 benefits or even bear substantial costs. Social or public information can be risky to acquire, since it raises  
64 the prospect of copying and learning useless or even improper behaviours and skills (Boyd and Richerson  
65 1985; Johnstone et al. 2002; Kendal et al. 2005; van Schaik 2010). A dilemma presents itself when  
66 socially obtained information conflicts with personal experience, and the both types of information steer  
67 decisions in opposite directions. In such cases, individuals are confronted with a trade-off between the use  
68 of accurate, but potentially costly, personal information or cheap, but potentially unreliable, inaccurate or  
69 irrelevant social information (Boyd and Richerson 1985; Dunlap et al. 2016).

70 Theoretical models and experimental studies suggest that individuals and populations should adopt a  
71 mixture of both social and individual learning (Boyd and Richerson 1985; Johnstone et al. 2002; Kendal  
72 et al. 2005; Rieucou and Giraldeau 2011). However, once they have acquired information (personally or  
73 socially), animals typically become more reluctant to copy the behaviour of others. This even holds for  
74 species that rely heavily on social learning. Studies on social insects indicate that some ants and bees stop  
75 using social cues to find food sources, once they have learned the locations of renewable and high quality  
76 food sources (Ribbands 1949; Rosengren and Fortelius 1986; Grüter and Farina 2009). Chimpanzees that  
77 have socially learned a specific food retrieval tactic are reluctant to switch to alternative demonstrated  
78 tactics, even when those yield higher rewards (Hopper et al. 2011). Naïve guppies (*P. reticulata*), lacking  
79 prior personal information, copy the foraging behaviour of the demonstrator shoal, whereas experienced  
80 individuals rely upon their personal knowledge rather than upon social information (Kendal et al. 2004).  
81 Commitment to prior personal knowledge continues in the face of alternate social information in a  
82 number of species (Kendal et al. 2005).

83 Intriguingly, some individuals within a population are more prone to use social information than others  
84 (Mesoudi et al. 2016). For instance, individual barnacle geese (*Branta leucopsis*), depending on their  
85 personality, differ consistently in their attention towards conspecifics, with bolder individuals relying less  
86 on socially and more on personally acquired information (Kurvers et al. 2010). Pigeons (*Columba livia*)  
87 that perform better in individual learning tasks seem to rely more on social knowledge (Bouchard et al.  
88 2007), whilst the opposite holds true for house sparrows (*Passer domesticus*) (Katsnelson et al. 2011) and  
89 common marmosets (*Callithrix jacchus*) (Burkart et al. 2009). These findings suggest that the relative  
90 weighting of socially and personally learned information depends on different aspects of personality or  
91 cognitive performance (Heyes 2012).

92 In this study, we were interested in how individual Italian wall lizards (*Podarcis siculus*) differ in their  
93 tendency to copy conspecific behaviour. We tested the hypothesis that an individual's willingness to  
94 accept and use new, albeit conflicting, social information depends on its cognitive profile. To do so, we  
95 tested whether previously trained lizards, that have reliable personal information on a food location, can

96 be influenced by observing conspecifics making opposite foraging choices. We also investigated whether  
97 an individual's tendency to copy false information correlated with aspects of its cognitive profile.

98

99

## 100 **2. Methods**

### 101 *2. 1. Study animals and housing*

102 The Italian wall lizard (*P. siculus*) is a robust ground-dwelling and diurnal lizard species that occupies a  
103 variety of semi-open habitats in the Mediterranean basin. Probably thanks to its morphological,  
104 physiological, and behavioural plasticity, the species has established new populations in localities well  
105 outside its native range, in Europe, Asia, Africa and North America (Vervust et al. 2007, 2010; Capula  
106 and Aloise 2011; Kapsalas et al. 2016). The Italian wall lizard exhibits considerable cognitive flexibility  
107 and is capable of using social information from both conspecifics and heterospecifics (Damas-Moreira et  
108 al., 2018), making it a suitable species for this study.

109 In July 2020, we caught twenty-two adult male lizards (mean snout-to-vent length (SVL) = 67.75  
110 mm, range = [61.21, 80.21]) near the city of Nin in Croatia, by noose or by hand. Individuals were  
111 transported in cloth bags to the animal facility of the University of Antwerp (Belgium), where they were  
112 housed individually in large plastic terraria (28 x 56 x 39 cm). Each terrarium contained a layer of sand,  
113 some plastic vegetation, and a rock. Between 6am and 6pm, a 45-Watt bulb suspended above one end of  
114 the terrarium provided light and heat so that lizards could maintain their body temperature within the  
115 preferred range. Lizards had access to fresh-water at all times, and were fed crickets (*Acheta domesticus*)  
116 and mealworms (*Tenebrio molitor*) dusted with multivitamin powder thrice a week.

117

### 118 *2. 2. Cognitive traits*

119 In order to construct broadly informative individual cognitive profiles, we tested several cognitive traits.  
120 In a situation where existing and new information must be weighed up against each other, inhibitory  
121 control (the cognitive process that allows individuals to overcome prepotent responses to reach a goal  
122 better; Diamond 2013) seemed a relevant function to test. Problem-solving (Bouchard et al. 2007; Burkart  
123 et al. 2009) and associative learning (Katsnelson et al. 2011) were also assessed, because they have been  
124 correlated with social information use in previous studies. Spatial learning ability was assessed because  
125 foraging in *P. siculus* requires navigational skills. And reversal learning performance was evaluated

126 because it reflects an individual's cognitive flexibility (Reader 2003). The cognitive tests are presented in  
127 chronological order. All tests were conducted between August and December 2020.

### 128 *2. 2. 1. Inhibitory control*

129 The lizards' ability to exercise inhibitory control (Diamond 2013), was tested with a detour task  
130 (Kabadayi et al. 2017). Lizards were trained to eat from a transparent petri dish taped on top of a wooden  
131 platform (10 x 10 x 1.5 cm). To standardize motivation, lizards were only fed one worm per day (Amiel et  
132 al. 2014). At the beginning of a trial, a lizard was introduced into an experimental arena (30 x 30 x 28 cm)  
133 containing a sandy substrate and the platform. After a short acclimation period (2 min), a mealworm (0.10  
134 – 0.20 g) was placed in the petri dish and the lizard was allowed 15 minutes to find and consume it. In  
135 order to do so, the lizard had to demonstrate inhibitory control by suppressing its natural, but ineffective,  
136 response to attack the prey directly in favour of an alternative action, i.e. moving over the transparent wall  
137 of the petri dish (Kabadayi et al. 2017; Storks and Leal 2020). The time between first contact with the  
138 petri dish and obtaining the prey was recorded and labelled as 'solving time'. Lizards that failed to  
139 overcome the barrier were assigned a maximum time of 900 seconds. Each lizard was tested once per day,  
140 although a second attempt was allowed in case the lizard did not touch the dish during its first trial. All  
141 lizards were tested until they had successfully eaten from the dish in three out of four consecutive trials  
142 [following the criterion of Gomes et al. (2020)] or until they had completed ten valid trials (i.e. trials in  
143 which the lizard interacted with the petri dish). Average solving time was used as proxy for individual  
144 inhibitory control ability.

### 145 *2. 2. 2. Problem solving*

146 The problem-solving ability of the lizards was gauged by their performance on a lid-removal task (Leal  
147 and Powell 2012; Storks et al. 2020) and an escape box task [adjusted from Kis et al. (2015) and Mair et  
148 al. (2021)]. In the lid-removal task, lizards had to remove an opaque plastic disc (diameter = 6 cm) from a  
149 petri dish in order to gain access to a mealworm. As in the inhibitory control task, lizards were only fed  
150 one worm per day as to standardize motivation. A lizard successfully completed the task if it displaced the  
151 disc (e.g. by lifting or pushing it) and immediately grabbed the prey afterwards. Lizards were tested five  
152 times, and the average solving time was used as a proxy for individual problem-solving ability.

153 During the escape box trials, lizards were locked inside a transparent Plexiglass box (22 x 22 x 8 cm),  
154 which was placed inside a larger arena (55 x 38 x 27 cm). The box contained a small opening on top  
155 (which was used to introduce lizards into the box) and a slidable white opaque door (5.5 x 7.5 cm), which  
156 was already slightly opened (4 mm) and contained grooves to facilitate manipulation. Close to the escape  
157 box, we placed a pile of stones underneath a 45-watt bulb, a promising opportunity to bask and hide  
158 (Noble et al. 2012; Carazo et al. 2014). After having been introduced into the box, a lizard received a

159 maximum of 30 minutes to escape. An individual's escape time was calculated as the time between its  
160 first body movement and the moment that half of its body was outside the box. Lizards that failed to  
161 escape were assigned the maximum time of 1800 seconds. Each lizard was tested once per day over three  
162 consecutive days. Average solving time was used as a proxy for individual problem-solving ability.

163

### 164 2. 2. 3. *Spatial and reversal learning*

165 Spatial learning was tested using protocols similar to Noble et al. (2012), Carazo et al. (2014) and  
166 Dayananda and Webb (2017). Here, lizards first learned the location of a safe hiding spot within an  
167 experimental arena (60 x 60 x 30 cm). Two identical shelters (plastic cups covered in black insulation  
168 tape) were placed in opposite corners of the arena, and either the left or right —relative to the observer—  
169 shelter was designated as “safe” for a particular individual. Walls of the arena were blinded, but both  
170 intra- and extra-maze visual cues were provided to allow orientation and navigation. The position of these  
171 cues, as well as the location of the arena and the observer, remained constant throughout the experiment.  
172 Lizards received 15 trials to learn the location of the “safe” shelter. At the start of each trial, an individual  
173 was placed in the centre of the arena underneath a transparent cover. After two minutes, the cover was  
174 removed and a predator attack was simulated by a gently poke at the base of the lizard's tail with a  
175 paintbrush. If the lizard fled underneath the safe shelter, it was allowed to rest for two minutes before  
176 being returned to its home enclosure. If the lizard chose the “unsafe” shelter, we lifted the shelter and  
177 continued chasing the lizard until it entered the safe shelter or until 120 seconds had passed (after which  
178 the lizard was caught and gently placed inside the safe shelter for two minutes).

179 After five days, the reversal learning phase started, in which safe and unsafe shelters were switched, and  
180 lizards received an additional 15 trials in order to learn the new location of the safe shelter. Lizards were  
181 classified as “learners” if they made the correct choice in 5 out of 6 consecutive trials [as in Noble et al.  
182 (2014); Vardi et al. (2020); De Meester et al. (2021)]. For subsequent analyses, we used the number of  
183 trials required to reach the criterion as individual learning scores for both the spatial and reversal phase  
184 (with individuals that failed to learn receiving a score of 16 trials).

185

### 186 2. 2. 4. *Associative learning*

187 Lizards were tested for their ability to associate a colour cue with access to food. To ensure that all  
188 individuals were equally motivated to participate in the experiment, they remained 48 hours without food  
189 prior to the experiment. The experimental set-up consisted of two petri dishes (height: 1.5 cm, diameter:  
190 5.5 cm) fixed on wooden ramps with a colour cue card (orange or green; **Fig 1a**), similar to the set-up  
191 used in Szabo et al. (2018). At the start of each trial, the two petri dishes, each containing one mealworm  
192 of equal size (0.10 – 0.20 g), were introduced into the lizards' home enclosure. Food was accessible in

193 only one of the dishes, via a large hole cut through the centre of the transparent lid. The other dish was  
194 covered with a lid perforated by small holes, allowing the lizard to smell but not access the mealworm.  
195 For half of the lizards, the accessible dish was indicated by an orange card, and the non-accessible dish  
196 with a green card. For the other half of the lizards, colour cues were opposite. Individuals were subjected  
197 to a total of 24 trials, two per day, to complete the associative learning task. The side of the rewarding  
198 colour (left or right) was randomised between trials, to ensure that lizards will learn the colour and not the  
199 position of the rewarding dish. A trial was considered successful if the lizard investigated and captured  
200 the mealworm from the accessible dish first. The lizards were considered to have successfully learned the  
201 rewarding colour cue once they reached the same success criterion as in spatial and reversal learning (i.e.  
202 made the correct choice in 5 out of 6 consecutive trials). The number of trials it took an individual to  
203 reach the criterion was used as a proxy for its associative learning ability. Two individuals did not reach  
204 the criterion and were assigned the maximum value of 25 trials.

### 205 *2. 3. Social experiment*

206 In order to test whether previously trained lizards copy the foraging decisions made by others, we paired  
207 lizards that were assigned the opposite rewarding colours during the associative learning task. One of the  
208 lizards was assigned the role of observer and the other acted as the demonstrator. Lizards were transferred  
209 into adjacent transparent glass terraria (50 x 30 x 30 cm) with a removable cardboard barrier in-between  
210 them to control the visual contact between the observer and the demonstrator of each pair (**Fig 1a**). The  
211 terraria were equipped as in the associative-learning test. The experiment consisted of a “training phase”  
212 (independent learning) and a “demonstration phase” (social learning).

213 To reinforce and reassure that lizards had learned the location (or colour cue) of the food reward, we  
214 subjected them to a short training period until they re-reached the criterion. During training, the  
215 removable opaque barrier was in place to ensure that observers had no visual contact with demonstrators,  
216 and *vice versa* (**Fig 1b**). Lizards were allowed sufficient trials (two trials per day between 9:00h and  
217 16:00h), to reach the learning criterion. The side of the colours (left or right) was randomized between  
218 pairs, but kept constant within the pairs to facilitate learning. Each observer always had the same  
219 arrangement of dishes as its demonstrator. Therefore, the correct site choice and rewarding colour for the  
220 observers were always opposite to the one for the demonstrator. After all lizards reached the learning  
221 criterion (the last 5 or 6 consecutive correct trials were used for further analysis), the demonstration phase  
222 was initiated.

223 Demonstration trials began by removing the opaque barrier between a pair, leaving only the transparent  
224 glass barrier. The experimental set-ups were placed in the demonstrator’s terrarium facing the observer  
225 (**Fig 1c**). The demonstrator was allowed 10 minutes to eat the mealworm, which was deemed sufficient



226 based on the average latency of the last successful trial of each individual in the associative learning  
227 experiment (mean latency = 2.02 min, SD = 4.06). When the demonstrator performed the task  
228 successfully, the barrier was reinserted and the platforms were placed in the observer's area, mirroring the  
229 arrangement in the demonstrator's area (**Fig 1d**). Individual decisions were scored as 1 or 0 depending on  
230 whether the lizard went to the rewarding or non-rewarding petri dish, respectively. The same procedure  
231 was repeated in 6 trials.

232 All trials were filmed and the researchers left the room prior to the start of each trial. The researchers  
233 were blind in respect to individual cognitive profiles when performing the social experiments.

#### 234 2. 4. *Statistical analysis*

235 All analyses were conducted in R (version 4.0.4).

236 To reduce the number of cognitive variables and take into account any potential interrelation of cognitive  
237 traits for subsequent analyses, we ran principal component (PC) analysis (*stats* package) on the  
238 correlation matrix of the individual scores obtained for inhibitory control (average learning time),  
239 problem solving (lid removal time, escape time), spatial, reversal and associative learning (number of  
240 trials required to reach criterion). The first two VARIMAX-rotated axes had eigenvalues above one and  
241 were used to summarize cognitive profiles.

242 To test the effect of social exposure on decision-making, and to test for associations between an  
243 individual's cognitive profile and its confidence in social information, we used Bayesian generalised  
244 mixed effect models (BGLMMs) with the *brms* package (Bürkner 2017). Default (weakly informative)  
245 prior distributions were used for each parameter of interest in each model ('get\_prior' function). Effects  
246 were considered "significant" when credible intervals (CrI) of posterior distributions did not overlap zero.

247 First, in order to investigate the effect of demonstration on the decision-making of individuals, a BGLMM  
248 (Bernoulli distribution; logit function) was fitted with success ("0": lizard went immediately to rewarding  
249 dish; or "1": lizard was misled by social information and went to the other dish) over 6 consecutive trials  
250 as dependent variable and "learning phase" (two-level factor: independent vs. demonstration) as the main  
251 predictor. To incorporate the inter-individual variability in copying, a random slope and intercept for  
252 learning phase in lizard ID was included.

253 Next, we tested whether lizards with particular cognitive profiles were more likely to use social  
254 information. To do so, we calculated the copying propensity, i.e. the difference in the number of correct  
255 choices before and after exposure to demonstrators for each individual. These scores (values were  
256 transformed by adding 1 to meet model assumptions) were then used as the response variable in

257 subsequent BGLMM (Poisson distribution; log function) with the two principal components as predictive  
258 variables. Additional models were run with raw scores for spatial learning ability and associative learning  
259 ability as predictor variables, because these scores dominated the second PC-axes.

260 In a final BGLMM (Bernoulli distribution; logit function), we considered the success rate of lizards (“1”  
261 if they went to the rewarding dish; “0” if they headed for the unrewarding one) in both learning phases,  
262 testing for effects of learning phase (individual versus social), of spatial learning ability, and of their  
263 interaction.

264

265

## 266 **Results**

267 We observed that individual decision-making was strongly influenced by exposure to demonstrators (**Fig**  
268 **2, 3b**). Lizards visited the inaccessible (unrewarding) petri dish more often (and therefore did more  
269 mistakes), after having been exposed to demonstrators (**Fig 2**), than during the independent learning phase  
270 ( $\beta=-1.52$ ,  $SE=0.42$ , 95% CrI=[-2.38, -0.70]) (**Table 3**). The percentage of correct decisions (i.e.  
271 rewarding dish visited first) fell from 90% when alone to 68% after demonstration, implying that  
272 observers copied, to a large extent, the opposite foraging behaviour of the demonstrators. The degree to  
273 which individuals were influenced by the behaviours of others, however, showed substantial  
274 interindividual variation (random effect of individual:  $\beta=0.60$ ,  $SE=0.41$ , 95% CrI=[0.03, 1.55]), meaning  
275 that some individuals copied the demonstrated choices more than others (**Fig 2**).

276 Part of this observed variation in copying behaviour was contingent on the lizards’ cognitive profile.  
277 **Table 1** provides a summary of the scores that the lizards obtained in the respective cognitive tests.  
278 Roughly 96% of the lizards exhibited some degree of inhibitory control, requiring on average 146 seconds  
279 to surmount the transparent wall of the petri dish and eat the worm. In the two problem solving tasks,  
280 namely lid removal and escape box, the success rates of participants were 43% and 55% respectively.  
281 Lizards needed on average 706 seconds to remove the lid and 1095 seconds to escape from the box. The  
282 success rates in the spatial learning and in the reversal learning task were 50% and 68% respectively.  
283 Lizards required on average 12 trials to complete the tasks successfully. Lastly, approximately 91% of the  
284 participant lizards completed the associative learning tasks, requiring on average 12 trials. However, only  
285 5% of the lizards succeeded in all cognitive tasks. Correlations between performance in the different  
286 cognitive tasks are presented in **Fig 4**.

287 A PCA on all scaled and centred cognitive variables yielded two principal component axes that jointly  
288 explained 60% of the variation (**Table 2**). An individual's propensity to imitate conspecifics correlated  
289 positively with its score on PC2 axis of the cognitive profile ( $\beta=-0.38$ ,  $SE=0.17$ , 95% CrI=[-0.70, -0.06])  
290 (**Table 3**). This second axis (28%) showed strong loadings of  $\geq 0.7$ , namely for associative (-0.79) and  
291 spatial learning (0.70) (**Table 2**). Additional models that specifically tested for the role of a lizard's  
292 spatial and associative learning skills on its copying behaviour indicated a significant effect of spatial  
293 learning (but not associative learning;  $\beta= 0.03$ ,  $SE= 0.03$ , 95% CrI=[- 0.03, 0.08]) (**Table 3**). In specific,  
294 lizards that required a higher number of trails to reach the spatial learning criterion had lower propensity  
295 to copy the behaviour of others ( $\beta=-0.09$ ,  $SE=0.03$ , 95% CrI=[-0.16, -0.02]) and higher success rates  
296 during demonstration (interaction effect:  $\beta=0.32$ ,  $SE=0.14$ , 95% CrI=[0.09, 0.62]) (**Table 3, Fig 3a, b**). In  
297 other words, slow spatial learners copied their demonstrators less and had higher success rates in the  
298 social learning phase.

299

300

## 301 **Discussion**

302 Our results show that Italian wall lizards copy foraging decisions of conspecifics, even if that means  
303 changing decision patterns developed by personal experience. However, individuals exhibited  
304 considerable variation in the trust they place in social versus prior private information. Certain individuals  
305 relied exclusively on their personally acquired knowledge while others relied more on the information  
306 provided by their demonstrators. How much individuals valued personally acquired relative to socially  
307 obtained information was associated with spatial learning speed. Relative to slow learners, fast spatial  
308 learners were more willing to disregard accurate prior personal knowledge and copy faulty social  
309 information provided by the demonstrators. Performance in associative and reversal learning as well as  
310 inhibitory control and problem solving tasks did not affect the outcome of the social learning experiment.

311 The ability of Italian wall lizards to use social information contradicts the widely held notion that only  
312 group-living animals are capable of social learning (Klopfer 1959, 1961). Consisting primarily of solitary  
313 species with little or no parental care, reptiles in particular have long been considered poor social learners.  
314 However, there is now growing evidence that non-group living animals, including many reptile species,  
315 copy conspecific behaviour and use social information (e.g. Lefebvre 1995; Pérez-Cembranos and Pérez-  
316 Mellado 2015; Kar et al. 2017; Vila Pouca et al. 2020). Damas-Moreira et al. (2018) demonstrated that  
317 individuals from an invasive population of Italian wall lizards (*P. siculus*), successfully imitate  
318 conspecifics and members of a local congeneric species. This ability might be linked to the species'

319 opportunistic nature (Capula and Aloise 2011; Mačát et al. 2015), ecological flexibility (Vervust et al.  
320 2010; Kapsalas et al. 2016; Wehrle et al. 2020) and invasive success (Silva-Rocha et al. 2014).  
321 ‘Opportunistically’ foraging species are more likely to exhibit social learning (Klopfer, 1959, 1961). For  
322 example, insular Lilford’s wall lizards (*Podarcis lilfordi*) prefer to forage in food patches chosen by  
323 conspecifics, which may be a beneficial strategy in unpredictable and resource-constrained insular  
324 environments (Pérez-Cembranos and Pérez-Mellado 2015).

325 Social information use might be adaptive under particular ecological conditions. In spatio-temporally  
326 variable environments, social information will occasionally conflict with prior personal knowledge. In  
327 new or spatio-temporally heterogeneous environments, personally learned information may have a limited  
328 validity period: previously known food sources can become depleted, shelters may stop to exist, familiar  
329 predators may no longer be around or may have been replaced by new ones. Adjusting to changing  
330 ecological settings requires continuous effort to reduce uncertainty by gathering and updating information  
331 whenever it becomes available (Dall and Johnstone 2002), including information derived from the  
332 behaviour of conspecifics. However, relying heavily on social information may also have its downside.  
333 Individuals that tend to subordinate personal knowledge and choose to copy the decisions of others might  
334 be vulnerable to tactical deception (Bugnyar and Heinrich 2006; Hall et al. 2017), misinformation (if the  
335 sources are not reliable or out of date) and copying suboptimal behaviours, all of which can have  
336 important consequences, both at individual and population level (Beauchamp et al. 1997; Laland and  
337 Williams 1998; Luncz et al. 2018). Therefore, animals are faced with trade-offs between acquiring costly  
338 but accurate personal information via sampling and trial-and-error or using cheap but potentially  
339 unreliable, inaccurate or irrelevant social information (Boyd and Richerson 1985).

340 Both ‘external’ and ‘internal’ factors can influence individual decisions whether to rely on private or  
341 public information. Most studies have focused on the former. The reliability of the information source  
342 seems to play an important role in individual decision-making (Van Bergen et al. 2004; Fraser et al. 2006;  
343 King and Cowlshaw 2007). For example, nine-spined sticklebacks (*Pungitius pungitius*) ignored social  
344 information when the private information they held was reliable, or recently acquired, but not when the  
345 private information was unreliable or dated (Van Bergen et al. 2004). In addition, the detail of the  
346 information might affect individual decisions to rely on one source or the other. Ants that previously  
347 ignored less detailed social information, which provided good directional information about the food  
348 source but poor information about food quality, quickly changed their decision when social information  
349 became more detailed (Czaczkes et al. 2019). The costs associated with acquiring either type of  
350 information (e.g. in terms of predation risk, or the amount of time or energy spent) may also be a factor.  
351 Minnows (*Phoxinus phoxinus*) (Webster and Laland 2008) and guppies (Kendal et al. 2004) also

352 switched to public information, when the costs of obtaining private knowledge were high. Moreover, the  
353 difficulty of the demonstrated behaviour has also been found to affect decision-making. Bumblebees  
354 (*Bombus terrestris*) prioritized social over personal information mostly when the foraging task (i.e. flower  
355 discrimination) was difficult and therefore with a higher probability of making errors (Baracchi et al.  
356 2018). Social information is also used more often if it derives from a larger number of conspecifics  
357 ('conformist social learning'; Grove 2019). Lastly, the characteristics of the demonstrator might also  
358 affect the decision of observers to rely on demonstrated social or personal information. Generally,  
359 observers tend to copy more competent (Kuzyk et al. 2020), experienced (Rauber and Manser 2018), and  
360 familiar (Munch et al. 2018) individuals, or base their decisions on a series of other characteristics, such  
361 as the condition, status, and success of the demonstrator (reviewed in Laland 2004).

362 Recently, the interest has shifted towards 'internal' factors and why individuals within populations differ  
363 in their reliance on social versus private information when taking decisions. Individual characteristics  
364 might play a crucial role in such trade-offs. In the few species that have been studied in this respect, there  
365 are systematic differences among conspecifics in social information use and reliance on social over  
366 individual learning (reviewed in Mesoudi et al. 2016), and our results suggest *P. siculus* is no exception.  
367 Reliance on private versus social information may vary with age or between sexes (Choleris and  
368 Kavaliers 1999; Noble et al. 2014). Individual personalities also underpin the propensity for social  
369 information use (Mesoudi et al. 2016). For example, bolder and more anxious chacma baboons (*Papio*  
370 *ursinus*) (Carter et al. 2014), but shyer barnacle geese (*B. leucopsis*) (Kurvers et al. 2010) were more likely  
371 to use social information. In flycatchers (*Ficedula albicollis*), bolder and more aggressive individuals are  
372 more likely to use heterospecific social information (Morinay et al. 2020). A small number of studies  
373 have tried to link individual variation in the propensity to use social information to aspects of cognition  
374 (reviewed in Mesoudi et al. 2016). Bouchard et al. (2007) found that pigeons (*Columba livia*) with good  
375 problem solving abilities were more likely to use social information, but Burkart et al. (2009) reported the  
376 reverse in common marmosets (*Callithrix jacchus*). In house sparrows (*Passer domesticus*), fast  
377 associative learners make more use of social information (Katsnelson et al. 2011).

378 In our study, we found that lizards that performed relatively well in a spatial learning task were more  
379 likely to use, public information that contradicted prior private knowledge. Individual cognitive abilities  
380 and overall cognitive style (*sensu* Gruszka et al. 2010; Sih and Del Giudice 2012) might explain the  
381 outcome of our social experiment. Fast spatial learners, typically capable of rapid spatial information  
382 processing, can quickly use spatial cues to guide their decisions. Along these lines, fast spatial learner  
383 lizards in the social experiment might be able to quickly memorize and recall spatial information (here  
384 side of platform) on the demonstrated food locations. Consequently they are able to copy to a larger

385 extent the foraging choices of the demonstrators. On the other hand, slow spatial learners may be  
386 incapable of remembering the choice of the demonstrator and therefore based their decisions on their  
387 previous knowledge. Alternatively, slow learners might differ in the speed by which they acquire social  
388 information and copy demonstrated behaviours. Unfortunately, our experimental design does not allow  
389 testing this hypothesis, since the demonstration phase consisted of only 6 trials. Fast learners are also  
390 thought to retain information for a short-term (Carere and Locurto 2011; Sih and Del Giudice 2012), and  
391 therefore are expected to act more on recently acquired information (in this case the most recent  
392 information on food location was the demonstrated one) rather than long-term memory. In contrast to  
393 slow lizards, fast lizards might also be more observant to the demonstrator's actions and therefore be able  
394 to copy them to a larger degree. However, it contradicts both theoretical (Sih and Del Giudice 2012) and  
395 experimental studies (e.g. Nácarová et al. 2018), that view fast individuals as less attentive to  
396 environmental cues and with shorter attention spans.

397 Social information use did not correlate with performance in the other cognitive abilities, namely  
398 associative learning, reversal learning, inhibitory control and problem solving. Performance in spatial  
399 learning tasks did not correlate with performance in any other cognitive tasks. Given the nature of the task  
400 (i.e. location of the rewarding dish and colour were kept constant), lizards might primarily use spatial  
401 cues to guide their decisions. Previous research also demonstrated that whiptail lizards (*Cnemidophorus*  
402 *inornatus*) learn faster based on positional cues than colour/pattern cues (Day et al. 2003), which would  
403 explain why spatial but not associative learning predicted copying propensity in our study. Since lizards  
404 were already familiarised with the process of obtaining the mealworm from the petri dish, no learning of  
405 novel motor skills or innovative foraging tactics was involved.

406 According to the cognitive style hypothesis, faster, proactive individuals tend to be asocial and relatively  
407 insensitive to novel social information (Sih and Del Giudice 2012). In our study, fast spatial learners used  
408 social information more frequently than slow learners. The willingness of fast learners to readily exploit  
409 novel social information presented by the demonstrators, might be related to certain personality aspects,  
410 such as exploration, boldness, and risk-taking. Although we did not test for personality, boldness and  
411 exploration are typically associated with fast cognitive styles (Sih and Del Giudice 2012) and spatial  
412 learning speed (Trompf and Brown 2014; Kareklas et al. 2017). Bolder and more exploratory individuals  
413 have been shown to quickly exploit social information (Marchetti and Drent 2000; Nomakuchi et al.  
414 2009; Trompf and Brown 2014, but see Kurvers et al. 2010). For example, bolder female guppies (*P.*  
415 *reticulata*) based their foraging decisions more on social information to avoid competition and/or  
416 potential patch depletion (Trompf and Brown 2014). Bolder individuals might also engage more in risky  
417 decision-making behaviour (Sih and Del Giudice 2012). Therefore, risk prone individuals, by copying the

418 demonstrated choice, could potentially maximize the rewards and gain resources from both food locations  
419 (the new demonstrated one in case there is access now and the safe one that they had previous knowledge  
420 on). Contrarily, risk-averse individuals relied on previously learned reliable locations of food sources for  
421 which there is no risk of losing access. In this study, however, wrong choices did not bear substantial  
422 costs, since lizards could still access their assigned rewarding petri dish, even if initially they made the  
423 wrong choice. In contrast, under natural conditions, making a wrong choice comes with associated risks  
424 and potential costs, e.g. energy loss, missed foraging opportunities, or increased predation risk.

425 Our study adds to a growing body of evidence that animals of different provenance are capable of using  
426 social information and are willing to do so even if that information contradicts personal learning  
427 experiences. Our data suggest that intrinsic, cognitive characteristics influence how individuals trade-off  
428 public and private information.

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443 **Table 1** — Summary of the results for each cognitive trait. The average performance along with the  
 444 standard deviation ( $\pm$ SD) for all individuals participating in a cognitive task and only the ones considered  
 445 successful (complete the learning criterion or solving the task at least once) is shown. The range of values  
 446 (square brackets) as well as the number of individuals per category (round brackets) are given as well.

<b>Cognitive trait</b>	<b>Average performance (all individuals)</b>	<b>Average performance (successful individuals)</b>
<i>Associative learning (number of trials to reach criterion)</i>	12.2 $\pm$ 6.1 [6, 25] (21)	10.9 $\pm$ 4.6 [6, 20] (19)
<i>Spatial learning (number of trials to reach criterion)</i>	12.2 $\pm$ 4.4 [6, 16] (22)	8.5 $\pm$ 3.0 [6, 15] (10)
<i>Reversal learning (number of trials to reach criterion)</i>	11.5 $\pm$ 4.1 [6, 16] (22)	9.4 $\pm$ 3.3 [6, 15] (15)
<i>Inhibitory control (mean solving time in seconds)</i>	146.0 $\pm$ 195.4 [2, 671] (22)	121.0 $\pm$ 160.2 [2, 573] (21)
<i>Problem solving – lid removal (mean solving time in seconds)</i>	706.0 $\pm$ 249.2 [218, 900] (21)	447.0 $\pm$ 152.8 [218, 700] (9)
<i>Problem solving – escape box (mean solving time in seconds)</i>	1095.0 $\pm$ 721.2 [76, 1800] (22)	508 $\pm$ 406.1 [76, 1600] (12)

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**Table 2** — Output of the VARIMAX-rotated principal component analysis (PCA) on all six cognitive parameters showing the first two principal components and their respective loadings for each cognitive parameter. Only individuals with complete set of values for each cognitive trait were used (N = 20).

	<b>PC1</b>	<b>PC2</b>
<i>Eigenvalues</i>	1.92	1.70
<i>Proportion of variance</i>	0.32	0.28
<i>Loadings for:</i>		
<i>Associative learning</i>	-0.15	-0.79
<i>Spatial learning</i>	-0.02	0.70
<i>Reversal learning</i>	-0.83	-0.12
<i>Inhibitory control</i>	0.88	0.04
<i>Problem solving – lid removal</i>	0.62	0.46
<i>Problem solving – escape box</i>	0.23	0.59

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**Table 3** — Summary output of the models. Estimates for fixed ( $\beta$ ) and random ( $\sigma^2$ ) with 95% credible intervals (CrI) and standard errors ( $\pm$ SE) are shown for each parameter as well as the sample size (N) for each model.  $R_{\text{hat}}$  diagnostic for convergence was equal to 1 for all parameters.

Response variable	Success	Copying propensity	Copying propensity	Success
<i>Fixed effects</i>	$\beta \pm$ SE [95% CrI]	$\beta \pm$ SE [95% CrI]	$\beta \pm$ SE [95% CrI]	$\beta \pm$ SE [95% CrI]
<b>Intercept</b>	2.32 $\pm$ 0.35 [1.69, 3.03]	0.72 $\pm$ 0.17 [0.36, 1.04]	1.96 $\pm$ 0.43 [1.08, 2.79]	4.81 $\pm$ 1.83 [1.79, 8.89]
<b>Learning phase</b>	-1.52 $\pm$ 0.42 [-2.38, -0.70]			-5.92 $\pm$ 1.98 [-10.29, -2.49]
<b>RC1</b>		0.08 $\pm$ 0.17 [-0.26, 0.41]		
<b>RC2</b>		-0.38 $\pm$ 0.17 [-0.70, -0.06]		
<b>Spatial learning</b>			-0.09 $\pm$ 0.03 [-0.16, -0.02]	-0.18 $\pm$ 0.12 [-0.44, 0.03]
<b>Spatial learning*Learning phase</b>				0.32 $\pm$ 0.14 [0.09, 0.62]
<i>Random effects</i>				
<b>ID/Learning phase</b>	0.60 $\pm$ 0.41 [0.03, 1.55]			0.43 $\pm$ 0.34 [0.02, 1.24]
<b>N</b>	19	17	19	19

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479 **Fig 1** — Illustration of the experimental set up for the social experiment. (a) Two petri dishes (one  
480 accessible and one covered with a perforated transparent lid) fixed on wooden ramps with a colour cue  
481 card (orange or green); (b) individual learning phase (training period) with the removable opaque barrier  
482 in place to block visual contact between demonstrators and observers; (c) the barrier is removed during  
483 the demonstration period to allow visual contact between observers and demonstrators; (d) after the  
484 successful completion of the task by the demonstrators, the barrier was reinserted and the platforms were  
485 placed in the observer’s area, mirroring the arrangement in the demonstrator’s area.

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487 **Fig 2** — Number of correct choices (the rewarding petri dish was visited first) for each individual  
488 (N=19) when alone (independent learning phase) and after observing the demonstrator (social influence  
489 learning phase).

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491 **Fig 3** — Relationship between spatial learning and social information use. In comparison to lizards that  
492 process spatial information quickly (“fast learners”), lizards that process spatial information slowly  
493 (“slow learners”) have (a) a lower propensity to copy the behaviour of others and (b) a higher success rate  
494 during the social learning phase. Full lines show the estimate ( $\beta$ ) regression models from the statistical  
495 tests (see Results) and the shaded areas denote standard errors (SE).

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497 **Fig 4** — Correlation matrix presenting the relationship among performance in the different cognitive  
498 tasks, namely associative, spatial and reversal learning, inhibitory control and problem solving tasks (lid  
499 removal and escape box). Asterisks denote level of statistical significance (\*\* < 0.01; \* < 0.05)

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525 **Data availability:** Data available within the article or its supplementary materials.

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