



# The gullible genius: fast learners fall for fake news

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Received: 5 October 2021 / Revised: 16 December 2021 / Accepted: 20 December 2021  
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## Abstract

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

## Significance statement

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

**Keywords** Cognition · Social learning · Lizards · Decision-making

## Introduction

Learning involves the perception, acquisition, storage and use of information collected from the environment (Dukas and Ratcliffe 2009; Buchanan et al. 2013). An animal's learning ability can offer an adaptive advantage by influencing ecologically relevant behaviours (Dukas and Ratcliffe

2009; Buchanan et al. 2013). In social learning, information is acquired through the observation of (or interaction with) other individuals (Hoppitt and Laland 2013). Much like humans, other animals often rely on social learning to cope with social and environmental challenges (Galef and Heyes 2004; Borenstein et al. 2008). For example, there is now ample evidence that decisions regarding what to eat (Galef and Giraldeau 2001), who to mate (White 2004) or fight with (Peake and McGregor 2004) and how to avoid being eaten (Griffin 2004) can all be influenced by social learning. Honeybees, for instance, learn the direction, distance and quality of food sources from the waggle dances performed by conspecifics (von Frisch 1967); female Trinidadian guppies (*Poecilia reticulata*) imitate the mate choice of other

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Communicated by T. Madsen.

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females (Dugatkin 1992), and male red-winged blackbirds (*Agelaius phoeniceus*) adjust their aggressive behaviour based on information obtained by watching contests (Freeman 1987). Juvenile rhesus monkeys (*Macaca mulata*) copy the alarm behaviours displayed by more experienced conspecifics (Mineka et al. 1984).

Copying the behaviour of others (i.e. imitating or observational learning) constitutes an important way by which animals acquire valuable life skills and ecological knowledge (Zentall 2012; Hoppitt and Laland 2013). By copying behavioural choices of “demonstrators”, individuals are thought to acquire relevant information rapidly, without suffering the costs of sampling and trial-and-error associated with personal learning (Kendal et al. 2005; Rendell et al. 2010). However, occasionally, social learning may also lack benefits or even bear substantial costs. Social or public information can be risky to acquire, since it raises the prospect of copying and learning useless or even improper behaviours and skills (Boyd and Richerson 1985; Johnstone et al. 2002; Kendal et al. 2005; van Schaik 2010). A dilemma presents itself when socially obtained information conflicts with personal experience, and the both types of information steer decisions in opposite directions. In such cases, individuals are confronted with a trade-off between the use of accurate, but potentially costly, personal information or cheap, but potentially unreliable, inaccurate or irrelevant social information (Boyd and Richerson 1985; Dunlap et al. 2016).

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

Intriguingly, some individuals within a population are more prone to use social information than others (Mesoudi et al. 2016). For instance, individual barnacle geese (*Branta leucopsis*), depending on their personality, differ consistently

in their attention towards conspecifics, with bolder individuals relying less on socially and more on personally acquired information (Kürvers et al. 2010). Pigeons (*Columba livia*) that perform better in individual learning tasks seem to rely more on social knowledge (Bouchard et al. 2007), whilst the opposite holds true for house sparrows (*Passer domesticus*) (Katsnelson et al. 2011) and common marmosets (*Callithrix jacchus*) (Burkart et al. 2009). These findings suggest that the relative weighting of socially and personally learned information depends on different aspects of personality or cognitive performance (Heyes 2012).

In this study, we were interested in how individual Italian wall lizards (*Podarcis siculus*) differ in their tendency to copy conspecific behaviour. We tested the hypothesis that an individual’s willingness to accept and use new, albeit conflicting, social information depends on its cognitive profile. To do so, we tested whether previously trained lizards that have reliable personal information on a food location can be influenced by observing conspecifics making opposite foraging choices. We also investigated whether an individual’s tendency to copy false information correlated with aspects of its cognitive profile.

## Methods

### Study animals and housing

The Italian wall lizard (*P. siculus*) is a robust ground-dwelling and diurnal lizard species that occupies a variety of semi-open habitats in the Mediterranean basin. Probably thanks to its morphological, physiological and behavioural plasticity, the species has established new populations in localities well outside its native range, in Europe, Asia, Africa and North America (Vervust et al. 2007, 2010; Capula and Aloise 2011; Kapsalas et al. 2016; Damas-Moreira et al. 2019). The Italian wall lizard exhibits considerable cognitive flexibility and is capable of using social information from both conspecifics and heterospecifics (Damas-Moreira et al. 2018), making it a suitable species for this study.

In July 2020, we caught twenty-two adult male lizards (mean snout-to-vent length (SVL) = 67.75 mm, range = [61.21, 80.21]) near the city of Nin in Croatia, by noose or by hand. Individuals were transported in cloth bags to the animal facility of the University of Antwerp (Belgium), where they were housed individually in large plastic terraria (28 × 56 × 39 cm). Each terrarium contained a layer of sand, some plastic vegetation, and a rock. Between 6 a.m. and 6 p.m., a 45-Watt bulb suspended above one end of the terrarium provided light and heat so that lizards could maintain their body temperature within the preferred range. Lizards had access to fresh water at all times, and were fed

crickets (*Acheta domesticus*) and mealworms (*Tenebrio molitor*) dusted with multivitamin powder thrice a week.

### Cognitive traits

In order to construct broadly informative individual cognitive profiles, we tested several cognitive traits. In a situation where existing and new information must be weighed up against each other, inhibitory control (the cognitive process that allows individuals to overcome prepotent responses to reach a goal better; Diamond 2013) seemed a relevant function to test. Problem-solving (Bouchard et al. 2007; Burkart et al. 2009) and associative learning (Katsnelson et al. 2011) were also assessed, because they have been correlated with social information use in previous studies. Spatial learning ability was assessed because foraging in *P. siculus* requires navigational skills. And reversal learning performance was evaluated because it reflects an individual's cognitive flexibility (Reader 2003). The cognitive tests are presented in chronological order. All tests were conducted between August and December 2020. To minimize observer bias, blinded methods were used when all behavioural data were recorded and analysed.

### Inhibitory control

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

### Problem-solving

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

During the escape box trials, lizards were locked inside a transparent Plexiglass box (22 × 22 × 8 cm), which was placed inside a larger arena (55 × 38 × 27 cm). The box contained a small opening on top (which was used to introduce lizards into the box) and a slidable white opaque door (5.5 × 7.5 cm), which was already slightly opened (4 mm) and contained grooves to facilitate manipulation. Close to the escape box, we placed a pile of stones underneath a 45-W bulb, a promising opportunity to bask and hide (Noble et al. 2012; Carazo et al. 2014). After having been introduced into the box, a lizard received a maximum of 30 min to escape. An individual's escape time was calculated as the time between its first body movement and the moment that half of its body was outside the box. Lizards that failed to escape were assigned the maximum time of 1800s. Each lizard was tested once per day over three consecutive days. Average solving time was used as a proxy for individual problem-solving ability.

### Spatial and reversal learning

Spatial learning was tested using protocols similar to Noble et al. (2012), Carazo et al. (2014) and Dayananda and Webb (2017). Here, lizards first learned the location of a safe hiding spot within an experimental arena (60 × 60 × 30 cm). Two identical shelters (plastic cups covered in black insulation tape) were placed in opposite corners of the arena, and either the left or right—relative to the observer—shelter was designated as "safe" for a particular individual. Walls of the arena were blinded, but both intra- and extra-maze visual cues were provided to allow orientation and navigation. The position of these cues, as well as the location of the arena and the observer, remained constant throughout the experiment. Lizards received 15 trials to learn the location of the safe shelter. At the start of each trial, an individual was placed in the centre of the arena underneath a transparent cover. After 2 min, the cover was removed, and a predator attack

was simulated by a gentle poke at the base of the lizard's tail with a paintbrush. If the lizard fled underneath the safe shelter, it was allowed to rest for 2 min before being returned to its home enclosure. If the lizard chose the "unsafe" shelter, we lifted the shelter and continued chasing the lizard until it entered the safe shelter or until 120 s had passed (after which the lizard was caught and gently placed inside the safe shelter for 2 min).

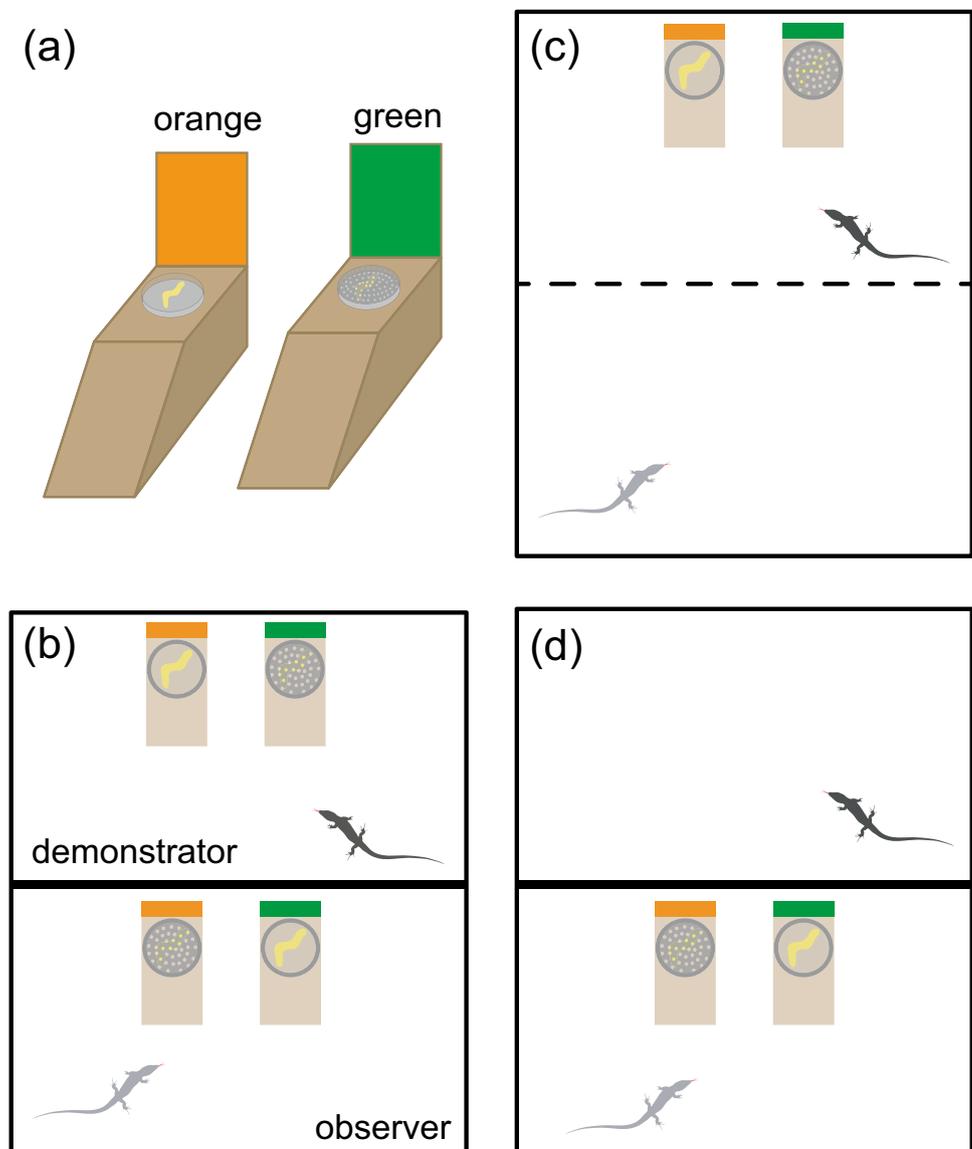
After 5 days, the reversal learning phase started, in which safe and unsafe shelters were switched, and lizards received an additional 15 trials in order to learn the new location of the safe shelter. Lizards were classified as "learners" if they made the correct choice in 5 out of 6 consecutive trials (as in Noble et al. (2014); Vardi et al. (2020); De Meester et al. (2021)). For subsequent analyses, we used the number of trials required to reach the criterion as individual learning

scores for both the spatial and reversal phase (with individuals that failed to learn receiving a score of 16 trials).

### Associative learning

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

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



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

## Social experiment

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

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

Demonstration trials began by removing the opaque barrier between a pair, leaving only the transparent glass barrier. The experimental set-ups were placed in the demonstrator’s terrarium facing the observer (Fig. 1c). The demonstrator was allowed 10 min to eat the mealworm, which was deemed sufficient based on the average latency of the last successful trial of each individual in the associative learning experiment (mean latency = 2.02 min, SD = 4.06). When the demonstrator performed the task successfully, the barrier was reinserted, and the platforms were placed in the observer’s area, mirroring the arrangement in the demonstrator’s area (Fig. 1d). Individual decisions were scored as 1 or 0 depending on whether the lizard went to the rewarding or non-rewarding petri dish, respectively. The same procedure was repeated in 6 trials.

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

## Statistical analysis

All analyses were conducted in R (version 4.0.4; R Development Core Team 2021).

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

To test the effect of social exposure on decision-making, and to test for associations between an individual’s cognitive profile and its confidence in social information, we used Bayesian generalised mixed effect models (BGLMMs) with the *brms* package (Bürkner 2017). Default (weakly informative) prior distributions were used for each variable of interest in each model (`get_prior` function). Effects were considered “significant” when credible intervals (CrI) of posterior distributions did not overlap zero.

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

Next, we tested whether lizards with particular cognitive profiles were more likely to use social information. To do so, we calculated the copying propensity, i.e. the difference in the number of correct choices before and after exposure to demonstrators for each individual. These scores (values were transformed by adding 1 to meet model assumptions) were then used as the response variable in subsequent BGLMM (Poisson distribution; log function) with the two principal components as predictive variables. Additional models were run with raw scores for spatial learning ability and associative learning ability as predictor variables, because these scores dominated the second PC-axes.

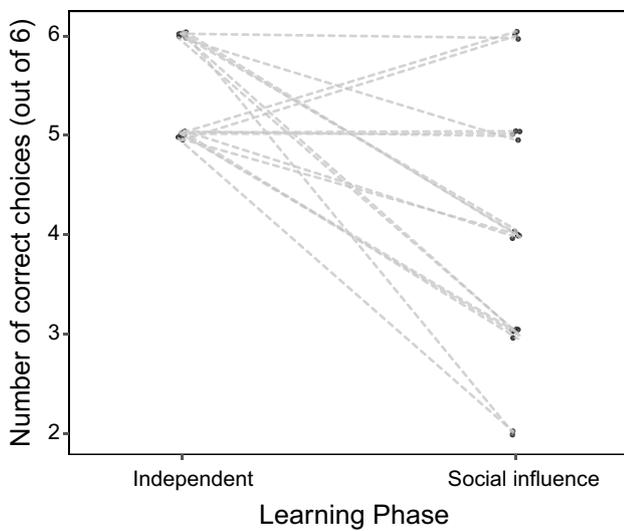
In a final BGLMM (Bernoulli distribution; logit function), we considered the success rate of lizards (“1” if they went to the rewarding dish; “0” if they headed for the

unrewarding one) in both learning phases, testing for effects of learning phase (individual versus social), of spatial learning ability and of their interaction.

### Results

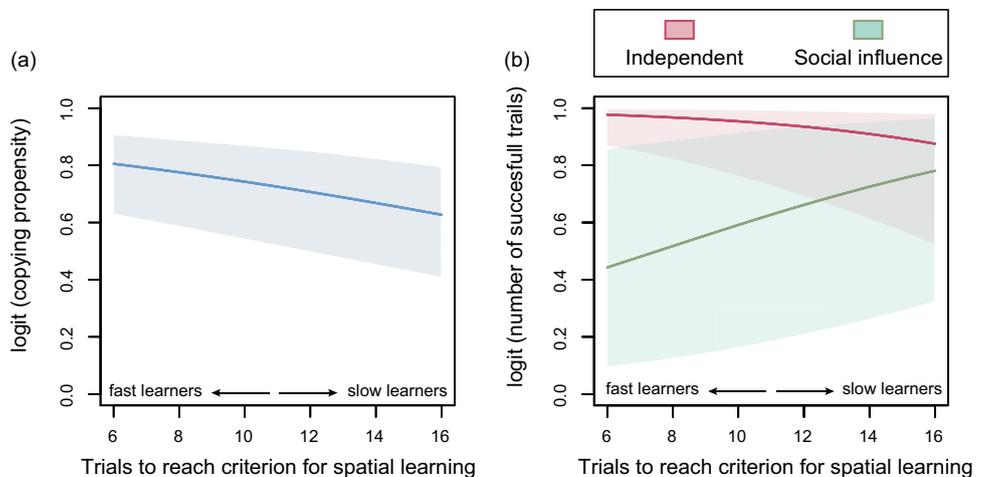
We observed that individual decision-making was strongly influenced by exposure to demonstrators (Figs. 2 and 3b). Lizards visited the inaccessible (unrewarding) petri dish more often (and therefore did more mistakes) after having been exposed to demonstrators (Fig. 2) than during the independent learning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

Part of this observed variation in copying behaviour was contingent on the lizards’ cognitive profile. Table 1 provides a summary of the scores that the lizards obtained in the respective cognitive tests. Roughly 96% of the lizards exhibited some degree of inhibitory control, requiring on average 146 s to surmount the transparent wall of the petri dish and eat the worm. In the two problem-solving tasks, namely lid removal and escape box, the success rates of participants were 43% and 55% respectively. Lizards needed on average 706 s to remove the lid and 1095 s to escape from the box. The success rates in the spatial learning and in the reversal learning task were 50% and 68% respectively. Lizards required on average 12 trials to complete the tasks successfully. Lastly, approximately 91% of the participant



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

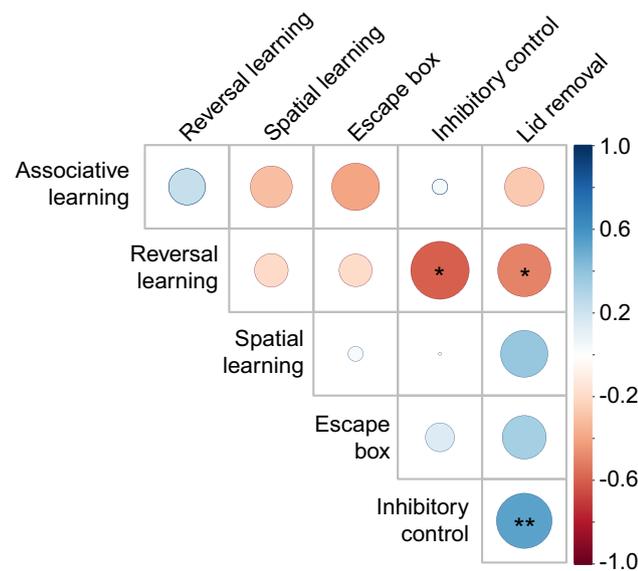
**Fig. 3** Relationship between spatial learning and social information use. In comparison to lizards that process spatial information quickly (“fast learners”), lizards that process spatial information slowly (“slow learners”) have (a) a lower propensity to copy the behaviour of others and (b) a higher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



**Table 1** Summary of the results for each cognitive trait. The average performance along with the standard deviation ( $\pm$ SD) for all individuals participating in a cognitive task and only the ones considered

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

successful (complete the learning criterion or solving the task at least once) is shown. The range of values (square brackets) as well as the number of individuals per category (round brackets) is given as well



**Fig. 4** Correlation matrix presenting the relationship among performance in the different cognitive tasks, namely associative, spatial and reversal learning, inhibitory control and problem-solving tasks (lid removal and escape box). Asterisks denote level of statistical significance (\*\* < 0.01; \* < 0.05). Positive correlations are displayed in blue and negative correlations in red colour. The size and colour intensity of the circles are proportional to the correlation coefficient values

lizards completed the associative learning tasks, requiring on average 12 trials. However, only 5% of the lizards succeeded in all cognitive tasks. Correlations between performance in the different cognitive tasks are presented in Fig. 4.

A PCA on all scaled and centred cognitive variables yielded two principal component axes that jointly explained 60% of the variation (Table 2). An individual’s propensity to imitate conspecifics correlated positively with its score on PC2 axis of the cognitive profile ( $\beta = -0.38$ ,  $SE = 0.17$ , 95% CrI = [-0.70, -0.06]) (Table 3). This second axis (28%) showed strong loadings of  $\geq 0.7$ , namely for associative (-0.79) and spatial learning (0.70) (Table 2). Additional models that specifically tested for the role of a lizard’s spatial and associative learning skills on its copying behaviour

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

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

indicated a significant effect of spatial learning (but not associative learning;  $\beta = 0.03$ ,  $SE = 0.03$ , 95% CrI = [-0.03, 0.08]) (Table 3). In specific, lizards that required a higher number of trails to reach the spatial learning criterion had lower propensity to copy the behaviour of others ( $\beta = -0.09$ ,  $SE = 0.03$ , 95% CrI = [-0.16, -0.02]) and higher success rates during demonstration (interaction effect:  $\beta = 0.32$ ,  $SE = 0.14$ , 95% CrI = [0.09, 0.62]) (Table 3; Fig. 3a, b). In other words, slow spatial learners copied their demonstrators less and had higher success rates in the social learning phase.

### Discussion

Our results show that Italian wall lizards copy foraging decisions of conspecifics, even if that means changing decision patterns developed by personal experience. However, individuals exhibited considerable variation in the trust they place in social versus prior private information. Certain individuals relied exclusively on their personally acquired knowledge while others relied more on the information provided by their demonstrators. How much individuals valued

**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 variable as well as the sample size ( $N$ ) for each model.  $R_{hat}$  diagnostic for convergence was equal to 1 for all variables

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

personally acquired relative to socially obtained information was associated with spatial learning speed. Relative to slow learners, fast spatial learners were more willing to disregard accurate prior personal knowledge and copy faulty social information provided by the demonstrators. Performance in associative and reversal learning as well as inhibitory control and problem-solving tasks did not affect the outcome of the social learning experiment.

The ability of Italian wall lizards to use social information contradicts the widely held notion that only group-living animals are capable of social learning (Klopfer 1959, 1961). Consisting primarily of solitary species with little or no parental care, reptiles in particular have long been considered poor social learners. However, there is now growing evidence that non-group living animals, including many reptile species, copy conspecific behaviour and use social information (e.g. Lefebvre 1995; Pérez-Cembranos and Pérez-Mellado 2015; Kar et al. 2017; Vila Pouca et al. 2020). Damas-Moreira et al. (2018) demonstrated that individuals from an invasive population of Italian wall lizards (*P. siculus*) successfully imitate conspecifics and members of a local congeneric species. This ability might be linked to the species' opportunistic nature (Capula and Aloise 2011; Mačát et al. 2015), ecological flexibility (Vervust et al. 2010; Kapsalas et al. 2016; Wehrle et al. 2020) and invasive success (Silva-Rocha et al. 2014). 'Opportunistically' foraging species are more likely to exhibit social learning (Klopfer 1959, 1961). For example, insular Lilford's wall lizards (*Podarcis lilfordi*) prefer to forage in food patches chosen by conspecifics, which may be a beneficial strategy in unpredictable and resource-constrained insular environments (Pérez-Cembranos and Pérez-Mellado 2015).

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

Both 'external' and 'internal' factors can influence individual decisions whether to rely on private or public information. Most studies have focused on the former. The reliability of the information source seems to play an important role in individual decision-making (van Bergen et al. 2004; Fraser et al. 2006; King and Cowlshaw 2007). For

example, nine-spined sticklebacks (*Pungitius pungitius*) ignored social information when the private information they held was reliable, or recently acquired, but not when the private information was unreliable or dated (van Bergen et al. 2004). In addition, the detail of the information might affect individual decisions to rely on one source or the other. Ants that previously ignored less detailed social information, which provided good directional information about the food source but poor information about food quality, quickly changed their decision when social information became more detailed (Czaczkes et al. 2019). The costs associated with acquiring either type of information (e.g. in terms of predation risk, or the amount of time or energy spent) may also be a factor. Minnows (*Phoxinus phoxinus*) (Webster and Laland 2008) and guppies (Kendal et al. 2004) also switched to public information, when the costs of obtaining private knowledge were high. Moreover, the difficulty of the demonstrated behaviour has also been found to affect decision-making. Bumblebees (*Bombus terrestris*) prioritized social over personal information mostly when the foraging task (i.e. flower discrimination) was difficult and therefore with a higher probability of making errors (Baracchi et al. 2018). Social information is also used more often if it derives from a larger number of conspecifics ('conformist social learning'; Grove 2019). Lastly, the characteristics of the demonstrator might also affect the decision of observers to rely on demonstrated social or personal information. Generally, observers tend to copy more competent (Kuzyk et al. 2020), experienced (Rauber and Manser 2018) and familiar (Munch et al. 2018) individuals, or base their decisions on a series of other characteristics, such as the condition, status and success of the demonstrator (reviewed in Laland 2004).

Recently, the interest has shifted towards internal factors and why individuals within populations differ in their reliance on social versus private information when taking decisions. Individual characteristics might play a crucial role in such trade-offs. In the few species that have been studied in this respect, there are systematic differences among conspecifics in social information use and reliance on social over individual learning (reviewed in Mesoudi et al. 2016), and our results suggest *P. siculus* is no exception. Reliance on private versus social information may vary with age or between sexes (Choleris and Kavaliers 1999; Noble et al. 2014). Individual personalities also underpin the propensity for social information use (Mesoudi et al. 2016). For example, bolder and more anxious chacma baboons (*Papio ursinus*) (Carter et al. 2014), but shyer barnacle geese (*B. leucopsis*) (Kurvers et al. 2010), were more likely to use social information. In flycatchers (*Fidicula albicollis*), bolder and more aggressive individuals are more likely to use heterospecific social information (Morinay et al. 2020). A small number of studies have tried to link individual variation in the propensity to use social information to aspects

of cognition (reviewed in Mesoudi et al. 2016). Bouchard et al. (2007) found that pigeons (*Columba livia*) with good problem-solving abilities were more likely to use social information, but Burkart et al. (2009) reported the reverse in common marmosets (*Callithrix jacchus*). In house sparrows (*Passer domesticus*), fast associative learners make more use of social information (Katsnelson et al. 2011).

In our study, we found that lizards that performed relatively well in a spatial learning task were more likely to use public information that contradicted prior private knowledge. Individual cognitive abilities and overall cognitive style (*sensu* Yarkoni and Braver 2010; Sih and Del Giudice 2012) might explain the outcome of our social experiment. Fast spatial learners, typically capable of rapid spatial information processing, can quickly use spatial cues to guide their decisions. Along these lines, fast spatial learner lizards in the social experiment might be able to quickly memorize and recall spatial information (here side of platform) on the demonstrated food locations. Consequently, they are able to copy to a larger extent the foraging choices of the demonstrators. On the other hand, slow spatial learners may be incapable of remembering the choice of the demonstrator and therefore based their decisions on their previous knowledge. Alternatively, slow learners might differ in the speed by which they acquire social information and copy demonstrated behaviours. Unfortunately, our experimental design does not allow testing this hypothesis, since the demonstration phase consisted of only 6 trials. Fast learners are also thought to retain information for a shortterm (Carere and Locurto 2011; Sih and Del Giudice 2012), and therefore are expected to act more on recently acquired information (in this case, the most recent information on food location was the demonstrated one) rather than long-term memory. In contrast to slow lizards, fast lizards might also be more observant to the demonstrator's actions and therefore be able to copy them to a larger degree. However, it contradicts both theoretical (Sih and Del Giudice 2012) and experimental studies (e.g. Nácarová et al. 2018) that view fast individuals as less attentive to environmental cues and with shorter attention spans.

Social information use did not correlate with performance in the other cognitive abilities, namely associative learning, reversal learning, inhibitory control and problem-solving. Performance in spatial learning tasks did not correlate with performance in any other cognitive tasks. Given the nature of the task (i.e. location of the rewarding dish and colour were kept constant), lizards might primarily use spatial cues to guide their decisions. Previous research also demonstrated that whiptail lizards (*Cnemidophorus inornatus*) learn faster based on positional cues than colour/pattern cues (Day et al. 2003), which would explain why spatial but not associative learning predicted copying propensity in our study. Since lizards were already

familiarised with the process of obtaining the mealworm from the petri dish, no learning of novel motor skills or innovative foraging tactics was involved.

According to the cognitive style hypothesis, faster, proactive individuals tend to be asocial and relatively insensitive to novel social information (Sih and Del Giudice 2012). In our study, fast spatial learners used social information more frequently than slow learners. The willingness of fast learners to readily exploit novel social information presented by the demonstrators might be related to certain personality aspects, such as exploration, boldness and risk-taking. Although we did not test for personality, boldness and exploration are typically associated with fast cognitive styles (Sih and Del Giudice 2012) and spatial learning speed (Trompf and Brown 2014; Kareklas et al. 2017). Bolder and more exploratory individuals have been shown to quickly exploit social information (Marchetti and Drent 2000; Nomakuchi et al. 2009; Trompf and Brown 2014; but see Kurvers et al. 2010). For example, bolder female guppies (*P. reticulata*) based their foraging decisions more on social information to avoid competition and/or potential patch depletion (Trompf and Brown 2014). Bolder individuals might also engage more in risky decision-making behaviour (Sih and Del Giudice 2012). Therefore, risk-prone individuals, by copying the demonstrated choice, could potentially maximize the rewards and gain resources from both food locations (the new demonstrated one in case there is access now and the safe one that they had previous knowledge on). Contrarily, risk-averse individuals relied on previously learned reliable locations of food sources for which there is no risk of losing access. In this study, however, wrong choices did not bear substantial costs, since lizards could still access their assigned rewarding petri dish, even if initially they made the wrong choice. In contrast, under natural conditions, making a wrong choice comes with associated risks and potential costs, e.g. energy loss, missed foraging opportunities or increased predation risk.

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

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00265-021-03122-0>.

**Acknowledgements** We thank Jan Scholliers and Jorrit Mertens for the technical support, Reyes Salas for assistance during experiments, and an anonymous reviewer for providing valuable and constructive feedback on a previous version of the manuscript.

**Funding** Financial support was given by the University of Antwerp (LVL, RVD) and the Research Foundation-Flanders (FWO) (IG: 1105122 N; GDM: 1144118 N; SB: 1218822N).

**Data availability** Data available within the article or its [supplementary materials](#).

## Declarations

**Ethics approval** Experiments approved by the Ethical Committee from the University of Antwerp (file: 2017–67) and the Flemish Government (Department of Environment, file nr: DWZ/KF/20/1.15/41). Permits for animal collection for 2020 (517–05-1–1-20–4) for 2021 (517–10-1–1-21–4) provided by the Croatian Ministry of Nature Protection and Energetics. All applicable national, and institutional guidelines for the use of animals were followed.

**Conflict of interest** The authors declare no competing interests.

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