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Author for correspondence:

Martin J. Whiting e-mail: martin.whiting@mq.edu.au

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Animal behaviour

Age-dependent social learning in a lizard

Daniel W. A. Noble¹, Richard W. Byrne² and Martin J. Whiting¹

¹Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia ²School of Psychology and Neuroscience, University of St Andrews, St Andrews, Fife, UK

Evidence of social learning, whereby the actions of an animal facilitate the acquisition of new information by another, is taxonomically biased towards mammals, especially primates, and birds. However, social learning need not be limited to group-living animals because species with less interaction can still benefit from learning about potential predators, food sources, rivals and mates. We trained male skinks (*Eulamprus quoyii*), a mostly solitary lizard from eastern Australia, in a two-step foraging task. Lizards belonging to 'young' and 'old' age classes were presented with a novel instrumental task (displacing a lid) and an association task (reward under blue lid). We did not find evidence for age-dependent learning of the instrumental task; however, young males in the presence of a demonstrator learnt the association task faster than young males without a demonstrator, whereas old males in both treatments had similar success rates. We present the first evidence of age-dependent social learning in a lizard and suggest that the use of social information for learning may be more widespread than previously believed.

1. Introduction

The ability of an organism to learn information about its environment is thought to be adaptive because it pervades so many dimensions of behaviour and ecology [1]. In particular, animals that exploit conspecifics as an information source should be especially advantaged because of their obvious overlap in resource requirements and shared predators. This socially acquired information (social learning) is facilitated through the observation of, or interaction with, another individual [2].

Traditionally, social learning was thought to be the domain of primates and birds [3,4]. More recently, it has been documented for a wider range of organisms including arthropods, turtles, fishes and tadpoles [2]. This is not altogether surprising considering that learning from others is a shortcut to learning the location of a food source or a predator. Therefore, we can predict that social learning need not be restricted to species that exhibit higher frequencies of social interaction. For example, social learning has recently been demonstrated in the red-footed tortoise, a species with relatively low levels of social interaction, and which is able to learn a detour task only in the presence of a demonstrator [5].

The relationship between age and learning ability in animals is poorly understood, although there is some suggestion that younger individuals are more likely to benefit from copying. Examples in support of this idea occur in guppies (agebiased mate choice copying), foraging decisions in nine-spined sticklebacks and foraging innovation in blue tits (juvenile females learn fastest) [2].

Among reptiles, social learning has only been tested in a tortoise (*Geochelone carbonaria*) [5] and an aquatic turtle (*Pseudemys nelsoni*) [6]. Lizards are likely to be good candidates for testing social learning because they show behavioural flexibility and rapid learning [7–9]. We tested for age-related social learning in a non-group-living lizard (*Eulamprus quoyii*) known for relatively rapid spatial learning ability [8,9].

2. Material and methods

We used *E. quoyii* from our captive colony housed in outdoor enclosures. To remove sexeffects, we used only male lizards for our experiments: n = 18 'old' (approx. 5+ years)



Figure 1. Tasks presented to demonstrators and experimental lizards. (*a*) Instrumental task and (*b*) association task. 'exp.' = experimental and 'view trials' trials: experimental lizard only viewed demonstrator executing task (social demonstration treatment) or a conspecific (control). Large cross: lid could not be opened. Small cross: mealworm not accessible. (Online version in colour. See also online video of lizard attempting task.)

and n = 18 'young' lizards (approx. 1.5–2 years; *E. quoyii* live for up to 8 years). In addition, we used n = 12 old male lizards as 'demonstrators' in social demonstration experiments. Cognition trials were conducted in the lizards' home enclosure in the laboratory in opaque tubs (678 (L) × 483 (W) × 418 (H) mm) divided in half with both fixed transparent Perspex and a removable opaque wooden divider.

(a) Social demonstration experiments

Our social demonstration experiments were modified versions of an instrumental and association-based foraging task previously used with lizards [7,10]. We first accustomed all lizards (*n* = 48) to eating mealworms (*Tenebrio molitor*) from an open dish. During the two tasks, the opaque divider and the experimental lizard's refuge and water bowl were removed to provide an unobstructed view of the demonstrating lizard. After 1 h of viewing, the opaque divider was replaced to separate lizards and give the experimental lizard the opportunity to attempt the task. We set up two treatments: (i) social demonstration (hereafter social), where the experimental lizard viewed the demonstrator executing the task, and (ii) social control, where the experimental lizard only viewed the demonstrator (hereafter control). Prior to the experiment, all lizards had a viewing phase in which they viewed the task (social treatment) or just the demonstrator lizard (control) for six trials (figure 1).

(b) Instrumental task

The first task required experimental lizards (n = 36; 18 social and 18 control) to displace an opaque lid from a food-well by using their snout to lift the lid off the dish (figure 1*a*). Lizards were given a maximum of 16 trials to complete the task and were considered to have learnt this task when they successfully displaced the lid in 5/6 trials. All lizards that achieved the learning criterion continued to correctly displace the lid on each subsequent trial. Not all lizards learnt and all were trained to remove the lid before commencing the association task (see the electronic supplementary material).

(c) Association task

Two dishes were placed on a wooden block, one with a blue cover (reward) and the other with a white cover (figure 1*b*). To

control for chemical and auditory cues, we placed mealworms in both the white and blue dishes. The food reward in the blue dish was accessible to the lizard, while cardboard blocked access to the mealworm in the white dish (figure 1b). We counter-balanced the location of the blue lid across treatments (right or left side of the approaching lizard); however, the position remained the same across trials. We therefore cannot be certain about the cue (spatial or colour) lizards used (see the electronic supplementary material). In every trial, we scored: (i) latency to choose the blue and white dish and (ii) whether the lizard chose the blue dish or white dish first or only the blue or white. When a lizard displaced the blue lid first, it was scored as a correct choice. Lizards were considered to have learnt the association task when they chose 5/6 trials correctly. We gave lizards a total of 24 trials (12 days) to learn this task. See the electronic supplementary material for more details.

(d) Statistical analysis

We analysed our data using generalized linear models (GLMs) and/ or generalized linear mixed models (GLMMs) with the appropriate error distribution for the data. We tested for significant batch, age, treatment and age × treatment effects using likelihood ratio tests. We included individual ID as a random effect in all models. We also included a random slope (trial) in our models; however, this led to poor model convergence. To test the robustness of our results, we re-ran our models using generalized estimating equations and included an AR1 correlation structure. This gave similar results to our GLMMs and thus we present results from our random intercept model. We also tested the robustness of our learning criteria for our association task and found that our criterion of '5/6 trials correct' was sufficient. See the electronic supplementary material for full details on analyses and data availability.

3. Results

(a) Instrumental task

Of 23/36 (64%) lizards that learnt the instrumental task, 11 were old (48%) and 12 young (52%). Seven old lizards and five young lizards that learnt the task were in the social treatment (12/23, 52% total learners). Young lizards in the social treatment had

a lower probability of learning (age × treatment interaction: $\chi^2 = 3.97$, p = 0.046); however, this effect was marginally significant and became non-significant when accounting for over-dispersion (GLM—quasi-binomial: age × treatment: F = 3.37, p = 0.08). The probability of learning did not depend on treatment (F = 0.12, p = 0.73) or age (F = 0.12, p = 0.73), but was marginally dependent on batch (F = 2.99, p = 0.07).

(b) Association task

In total, 33/36 (92%) lizards learnt the association task in 24 (or fewer) trials. All young lizards (n = 18) learnt the task, whereas 15 (83%) old lizards (seven social and eight control) learnt. The latency to displace the blue lid did not differ between treatment, age or batch (GLM: age \times treatment: *F* = 2.07, *p* = 0.16; age: F = 0.06, p = 0.80, treatment: F = 0.12, p = 0.73, batch: F = 0.76, p = 0.48). However, the number of trials it took to learn the association task depended on both age and treatment (GLM: age × treatment: $\chi^2 = 17.40$, p < 0.001; batch: $\chi^2 = 7.36$, p = 0.03). Young lizards in the social treatment required significantly fewer trials to learn the association task compared with young control lizards (figure 2*a*; t = -3.35, d.f. = 14, p = 0.005), whereas old lizards in the social and control treatment were not significantly different (figure 2*a*; t = 1.28, d.f. = 15, p = 0.22). The probability of correctly choosing the blue dish across trials was also dependent on age and treatment (age × treatment: $\chi^2 = 6.1$, p = 0.01; batch: $\chi^2 = 4.8$, p = 0.09; trial: $\chi^2 = 99.5$, p < 0.001). Importantly, the probability of choosing only the blue dish (ignoring the white) across all trials also depended on age and treatment (GLMM: age \times treatment: $\chi^2 = 9.2$, p < 0.003; batch: $\chi^2 = 8.8$, p = 0.01, trial: $\chi^2 = 72.3$, p < 0.001). Young lizards in the social treatment had more than twice the probability of choosing only the blue dish and not the white compared with young control lizards (figure 2b). Young social lizards also had a higher probability of choosing only the blue lid on Trial 1 and this probability appeared to increase more steeply with successive trials (figure 2b; electronic supplementary material, S1). By contrast, the probability of choosing only the blue dish did not differ between old lizards in the social and control treatment (figure 2c; electronic supplementary material, S1) and lizards in both treatments had similar predicted probability curves across trials (figure 2c; electronic supplementary material, S1).

4. Discussion

Social learning is traditionally considered to be associated with animals exhibiting complex social behaviour [2]. While *E. quoyii* is not considered a species with social affinity (i.e. group living), individuals are frequently in view of each other in the wild, raising the possibility of social transmission of information. In an instrumental task, we found that lizards in both the social control and social learning treatment learnt to displace the lid from the well containing a food reward but success was unrelated to age or treatment. However, in the association task, only young males used social information to learn which of two differently coloured lids signalled food.

Our current understanding of cognition in lizards is in its infancy [11,12] despite growing appreciation of their cognitive abilities [8–12]. As such, it is currently difficult to make predictions about differences in learning styles and rates between juvenile and adult lizards. Here, younger male



Figure 2. (*a*) Mean (\pm s.e.) number of trials to learn association task for 'old' and 'young' lizards in the social demonstration treatment (social) and control treatment (control). (*b*,*c*) Predicted probabilities of choosing only the blue dish within a trial for each lizard in the social demonstration and control treatments: (*b*) young lizards and (*c*) old lizards. Each individual's learning trials are plotted up to point of learning; hence, not all individuals are computed for all 24 trials. Black and grey dots are averaged predicted probabilities and 95% prediction interval in Trial 1 averaged across all individuals in social demonstration and control treatments. **Differences significant at $\alpha < 0.05$.

lizards used social information to solve an association task, whereas older males did not—perhaps as a result of local enhancement given that we did not observe the same effect in the instrumental task that required lizards to open the food-well. Given that adult males are more likely to exclude male rivals than juveniles from their territories, there may be more opportunity for social learning by juveniles.

4

Furthermore, during this early phase of their life, juvenile lizards may be more likely to benefit from social information through enhanced foraging opportunities and as a result, may be more attentive to the actions of others.

This result is particularly significant given the dearth of studies examining age-dependent effects on social learning. Furthermore, our study is, to the best of our knowledge, the first case of social learning in a lizard and provides compelling evidence that social learning in water skinks is age-dependent.

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3

4 Extended Materials and Methods

5 *Study animal and husbandry*

6 The Eastern Water Skink (Eulamprus quovii) is a ground-dwelling lizard found throughout 7 much of southeastern Australia. Males of this species defend territories and adopt alternative 8 reproductive tactics and have been suggested to form dominance hierarchies [1, 2]. As such, 9 males tend to be visible to one another in the landscape but do not form groups. They are 10 capable of rapid spatial learning and do well in captivity [3]. We used E. quovii from our 11 captive colony that was originally maintained in large semi-natural enclosures as part of a 12 mating experiment conducted in 2010 [2, 4]; young lizards were born in 2011. Heat cable 13 was placed under part of each lizard's enclosure to provide a thermal gradient. Enclosures 14 were lined with mulch substrate and each lizard was provided with a single refuge, a water 15 bowl, and thermoregulatory opportunities. Lizards were housed in these enclosures two days 16 prior to the beginning of the habituation stage and remained there for the duration of the 17 experiment (except for a few demonstrators; see below).

18

19 Social demonstration experiments

For logistical reasons we tested six 'old' and six 'young' lizards at a time (i.e. a single batch) for a total of three batches. We randomly allocated lizards to treatments and balanced the number of young and old lizards. In all experiments we conducted two trials per day, in the morning (0900-1100h) and the afternoon (1300-1500h) with a minimum interval between trials of 1.5 h (1.5-3 h). Trials were run every day for the duration of the experiment. Before commencing experiments demonstrators were trained to remove the lid independently of experimental lizards and we ensured that demonstrators were consistently removing lids before commencing experiments. During this period, experimental lizards continued the habituation stage I. If, during the experiment, the demonstrator lizard was not motivated to do the task, we did not count the trial and we switched this demonstrator with a demonstrator from a lizard in the control treatment (n = 3).

31

32 Stage I. Habituation – feeding from a dish

We placed a single petri dish on a block of wood and secured it in place using putty
(Bluetak®). Black, opaque electrical tape was wrapped around the sides of the dish so that
lizards could not use visual cues during the experiment. A single mealworm was placed in an
uncovered dish during each trial. Lizards had to eat from the open dish at least 6 times in a
row to move to the next stage. Mealworms were approximately 3 cm in length.

38

39 Stage II. Instrumental task

40 All trials were video recorded using a CCTV system (Avermedia with Sony 1/3" high 41 resolution color cameras) that enabled us to record the latency until the lid was displaced. 42 Lizards could either learn how to manipulate this lid from demonstrators in order to gain 43 access to the food reward, or learn by themselves. All trial videos were scored by a single 44 observer, however, it was not possible to score trials 'blind' because the camera captured 45 multiple lizards in the same frame. Given the lack of ambiguity of our variables (lizards 46 either displaced the lid or not) and because all trials were conducted without observer 47 interference, we doubt this confounded the results in any way.

48

49 Stage III. Training – experimental lizards trained to manipulate lid

50 Not all lizards learnt to displace the lid in the instrumental task. Therefore, prior to the

association task, lizards were trained to open the lid covering the dish in the instrumental

task. We used the same habituation procedures demonstrators experienced, except that we switched to a two-dish habituation procedure, where one of the two dishes was three-quarters covered and the second dish was fully covered. This expedited training of the instrumental task, particularly for those lizards that were unsuccessful. One mealworm was placed in each of the two dishes. A lizard was considered to have learnt how to shift the lid when it ate from both dishes 5/6 times.

58

59 Stage IV. Association task

60 The association task required that lizards (n = 36) learnt to associate the food reward with a 61 dish covered by a blue lid. We randomized and counter-balanced the position of the blue dish 62 (right or left placement) to account for possible lateralization biases and then kept it in the 63 same position for every trial. We were therefore not able to test whether lizards used spatial 64 or colour cues to learn the task. We did this deliberately to expedite learning since our goal 65 was not to understand what cues lizards were using to learn tasks, but to determine whether 66 lizards were capable of social learning. To ensure that demonstrators were presenting unambiguous information to experimental lizards in the social treatment we firmly attached 67 68 the white lid to prevent removal.

To test whether our learning criteria correctly categorized learners, we ran a subset of lizards (n = 21) for five or more trials beyond their learning trial. We then tallied their overall learning score to see whether it was significant according to a binomial choice test. In total 20/21 (95%) lizards with five or more trials beyond their learning trial (11-32 trials in total per lizard; mean = 19.81 ± 1.40) retained a significant tally of choosing the blue lid in the first try, strongly suggesting that our learning criterion was sufficient.

75

77 Statistical analysis

78 Data used for all analyses are located in the Dryad Digital Repository,

79 http://datadryad.org/resource/doi:10.5061/dryad.6rj28 [5]. We analyzed the probability of 80 learning the instrumental task using generalized linear models (GLMs) with a binomial error distribution ('logit' link). We included treatment and age as two-level categorical variables 81 82 along with an interaction between age and treatment because we hypothesized that there may be differences in the use of social information between young and old lizards. We included 83 84 'batch' in our models to control for batch effects. Latency to open the dish and choose the 85 blue dish was first log transformed prior to analysis to ensure normality of residuals and 86 modeled using a Gaussian error distribution (identity link) using a GLM. To supplement 87 these analyses we also ran generalized linear mixed models (GLMMs) using all available trial 88 data for each individual. We treated correct and incorrect choices ('1' or '0') as coming from 89 a binomial probability distribution (i.e. binomial error – logit link) and included treatment, 90 age and a treatment by age interaction in the model. We also estimated a fixed effect for trial 91 to account for the fact that the probability of making a correct choice should increase across 92 trials for individual lizards because lizards were not rewarded for opening the white dish. In 93 all models we controlled for batch effects and included lizard ID as a random effect to 94 account for non-independence in measurements from the same lizard. To better account for 95 the correlation between residuals across trials within lizards, given the difficulty in estimating 96 random slopes, we re-ran our model using generalized estimating equations (GEEs) and 97 included an AR1 correlation structure to test whether temporal correlation affected our 98 estimates. This gave similar results to our GLMMs and thus we present results from our 99 random intercept model. Latency to choose the correct dish was modeled using a GLMM 100 with a Gaussian error distribution. In all cases models were simplified using likelihood ratio tests by dropping each term from the full model and computing the χ^2 test statistics (binomial 101

102 or Poisson models) or F- statistics (Gaussian and quasipoisson/binomial) and their 103 corresponding p-values are presented for each predictor variable dropped from the final 104 model. Interactions were dropped first and then models were refitted and each term excluded 105 one at a time from the main effects model. In Poisson and binomial GLMs and GLMMs we 106 tested whether inferences were affected by over-dispersion (variance estimate deviates from 107 the mean) by re-running our top-supported models using either a quasipoisson/binomial error 108 distributions (GLMs) or including an observation level random effect (GLMMs). All 109 analyses were run using 'lme4' in R [6].

110

111 Assessing motivation

112 We considered whether lizards from the different treatments might have differed in their 113 levels of motivation because of a range of factors including age, mass and body size. First, 114 animals were completely randomized to each of the groups. Age is strongly related to both 115 mass and body size, as is the case in most lizards, and thus these variables were not included 116 in the final models. Although younger animals were smaller and lighter than older males, we 117 are confident that this did not lead to differences in motivation between groups. In the 118 association task, lizards did not eat in 9/797 (1.13%) trials based on all the lizards (young and 119 old) in the study. Furthermore, these 'no eat' trials were spread out across the groups (young-120 social: 2; old-social: 5; young-control: 1; old-control: 1) and were not counted towards the 121 learning tally or in the models. In the instrumental task, which was much more difficult to 122 learn, we are also confident that motivation was not a driver in whether lizards removed the 123 lid or not. In the 12 trials prior to the start of the instrumental task (habituation to eating from 124 the dish and the 6 trials viewing prior to start of the task) only 3/36 lizards did not eat during 125 all of their trials. These lizards (1 young and 2 old) did achieve the learning criterion and also 126 ate very consistently in the association task. This is not what we would predict if there were

- 127 differences in motivation driving our effects, but rather we would expect to see older lizards
- 128 having far more trials where they did not eat, which was not the case. Based on these data we

are convinced that motivation was not an issue for our tasks.

- 130
- 131 Results
- 132 Given the age*treatment interaction, we have further analysed our data and tested for
- 133 significant differences between old lizards and young lizards in the control and social
- demonstration experiments. As expected, old lizards in the social treatment were significantly
- 135 different (took more trials to learn) compared to young lizards in the social treatment (t = -
- 136 2.8, df = 11.2, p = 0.02), while old lizards in the control treatment and young lizards in the
- 137 social treatment were not significantly (t = -1.64, df = 13, p = 0.13) different.
- 138



Fig S1 – Predicted probability of choosing only the blue lid (solid lines) and 95% confidence
intervals (dashed lines) for a) 'Old' lizards in the social demonstration ('black') and control
('gray') treatments; b) 'Young' lizards in the social demonstration ('black') and control
('gray') treatments.

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