

## **Age-dependent social learning in a lizard**

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## 1 **Summary**

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

17

## 18 **1. Introduction**

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

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

35           Learning ability is influenced by a host of factors including sex, relatedness,  
36 familiarity and age [1,2]. The relationship between age and learning ability in animals  
37 is not well understood, although there is some suggestion that younger individuals are  
38 more likely to benefit from copying. Examples in support of this idea occur in guppies  
39 (age-biased mate choice copying), foraging decisions in nine-spined sticklebacks and  
40 foraging innovation in blue tits (juvenile females learn fastest) [2].

41           Among reptiles, social learning has only been tested in a tortoise, *Geochelone*  
42 *carbonaria* [5] and an aquatic turtle, *Pseudemys nelsoni* [6]. Lizards are likely to be  
43 good candidates for testing social learning because they show behavioural flexibility  
44 and rapid learning [7-9]. We tested for age-related social learning in a non-group-  
45 living lizard (*Eulamprus quoyii*) known for relatively rapid spatial learning ability  
46 [8,9].

47

## 48 **2. Materials and methods**

49

50 We used *E. quoyii* from our captive colony housed in outdoor enclosures on  
51 Macquarie University campus. To remove sex-effects we used only male lizards for  
52 our experiments: n = 18 ‘old’ (~ 5+ years) and n = 18 ‘young’ lizards (~ 1.5-2 years;  
53 *E. quoyii* live for up to 8 years). In addition, we used n = 12 ‘old’ male lizards as  
54 ‘demonstrators’ in social demonstration experiments. Cognition trials were conducted  
55 in the lizards’ home enclosure in the lab in opaque enclosures [678 (L) x 483 (W) x  
56 418 (H) mm] divided in half with both fixed transparent Perspex® and a removable  
57 opaque wooden divider.

58

59 *(a) Social demonstration experiments*

60

61 Our social demonstration experiments were modified versions of an instrumental and  
62 association-based foraging task previously used with lizards [7,10]. We first  
63 accustomed all lizards (n = 48) to eating mealworms (*Tenebrio molitor*) from an open  
64 dish. During the two tasks the opaque divider and the experimental lizard’s refuge and  
65 water bowl were removed to provide an unobstructed view of the demonstrating  
66 lizard. After 1 hour of viewing, the opaque divider was replaced to separate lizards  
67 and give the experimental lizard the opportunity to attempt the task. We set up two  
68 treatments: 1) social demonstration (hereafter social), where the experimental lizard  
69 viewed the demonstrator executing the task; and 2) social control, where the  
70 experimental lizard only viewed the demonstrator (hereafter control). Prior to the  
71 experiment, all lizards had a viewing phase in which they viewed the task (social  
72 treatment) or just the demonstrator lizard (control) for six trials (figure 1).

73

74 *(b) Instrumental task*

75

76 The first task required experimental lizards ( $n = 36$ ; 18 social and 18 control) to  
77 displace an opaque lid from a food-well by using their snout to lift the lid off the dish  
78 (figure 1a). Lizards were given a maximum of 16 trials to complete the task and were  
79 considered to have learnt this task when they successfully displaced the lid in 5/6  
80 trials. All lizards that achieved the learning criterion continued to correctly displace  
81 the lid on each subsequent trial. After 16 trials, all 36 lizards were successfully trained  
82 to displace lids and were able to commence the association task.

83

84 *(c) Association task*

85

86 Two dishes were placed on a wood block, one with a blue cover (reward) and the  
87 other with a white cover (figure 1b). To control for chemical and auditory cues, we  
88 placed mealworms in both the white and blue dishes. The food reward in the blue dish  
89 was accessible to the lizard, while cardboard blocked access to the mealworm in the  
90 white dish (figure 1b). We counter-balanced the location of the blue lid across  
91 treatments (right or left side of the approaching lizard); however, the position  
92 remained the same across trials. We therefore cannot be certain about the cue (spatial  
93 or colour) lizards used [See *Electronic Supplementary Materials (ESM)*]. In every  
94 trial we scored: 1) latency to choose the blue and white dish and 2) whether the lizard  
95 chose the blue dish or white dish first or only the blue or white. When a lizard  
96 displaced the blue lid first it was scored as a correct choice. Lizards were considered  
97 to have learnt the association task when they chose 5/6 trials correctly. We gave  
98 lizards a total of 24 trials (12 days) to learn this task. See ESM for more details.

99

100 (d) *Statistical analysis*

101

102 We analysed our data using generalized linear models (GLMs) and/or generalized

103 linear mixed models (GLMMs) with the appropriate error distribution for the data.

104 We tested for significant batch, age, treatment and age\*treatment effects using

105 likelihood ratio tests (LRTs). We included individual ID as a random effect in all

106 models. We also included a random slope (trial) in our models; however, this led to

107 poor model convergence. To test the robustness of our results, we re-ran our models

108 using generalized estimating equations (GEEs) and included an AR1 correlation

109 structure. This gave similar results to our GLMMs and thus we present results from

110 our random intercept model. We also tested the robustness of our learning criteria for

111 our association task and found that our criterion of ‘5/6 trials correct’ was sufficient.

112 See ESM for full details on analyses.

113

### 114 **3. Results**

115

116 (a) *Instrumental task*

117 Of 23/36 (64%) lizards that learnt the instrumental task, 11 were old (61%) and 12

118 young (67%). Seven old lizards and five young lizards that learnt the task were in the

119 social treatment (12/23, 52% total learners). Young lizards in the social treatment had

120 a lower probability of learning (Age\*Treat interaction:  $\chi^2 = 3.97$ ,  $p = 0.046$ ); however,

121 this effect was marginally significant and became non-significant when accounting for

122 over-dispersion (GLM – quasibinomial: Age\*Treat:  $F = 3.37$ ,  $p = 0.08$ ). The

123 probability of learning did not depend on treatment ( $F = 0.12$ ,  $p = 0.73$ ) or age ( $F =$

124  $0.12$ ,  $p = 0.73$ ), but was marginally dependent on batch ( $F = 2.99$ ,  $p = 0.07$ ).

125

126 (b) Association task

127 In total, 33/36 (92%) lizards learnt the association task in 24 (or fewer) trials. All  
128 young lizards ( $n = 18$ ) learnt the task whereas 15 (83%) old lizards (7 social and 8  
129 control) learnt. The latency to displace the blue lid did not differ between treatment,  
130 age or batch (GLM: Age\*Treatment:  $F = 2.07$ ,  $p = 0.16$ ; Age:  $F = 0.06$ ,  $p = 0.80$ ,  
131 Treatment:  $F = 0.12$ ,  $p = 0.73$ , Batch:  $F = 0.76$ ,  $P = 0.48$ ). However, the number of  
132 trials it took to learn the association task depended on both age and treatment (GLM:  
133 Age\*Treatment:  $\chi^2 = 17.40$ ,  $P < 0.001$ ; Batch:  $\chi^2 = 7.36$ ,  $P = 0.03$ ). Young lizards in  
134 the social treatment required significantly fewer trials to learn the association task  
135 compared to young control lizards (figure 2a;  $t = -3.35$ ,  $df = 14$ ,  $p = 0.005$ ), whereas  
136 old lizards in the social and control treatment were not significantly different (figure  
137 2a;  $t = 1.27$ ,  $df = 15$ ,  $p = 0.22$ ). The probability of correctly choosing the blue dish  
138 across trials was also dependent on age and treatment (Age\*Treatment:  $\chi^2 = 6.1$ ,  $p =$   
139  $0.01$ ; Batch:  $\chi^2 = 4.8$ ,  $p = 0.09$ ; Trial:  $\chi^2 = 99.5$ ,  $p < 0.001$ ). Importantly, the  
140 probability of choosing only the blue dish (ignoring the white) across all trials also  
141 depended on age and treatment (GLMM: Age\*Treatment:  $\chi^2 = 9.2$ ,  $p < 0.003$ ; Batch:  
142  $\chi^2 = 8.8$ ,  $p = 0.01$ , Trial:  $\chi^2 = 72.3$ ,  $p < 0.001$ ). Young lizards in the social treatment  
143 had more than twice the probability of choosing only the blue dish and not the white  
144 compared to young control lizards (figure 2b; social: 36% probability, control: 16%).  
145 Young social lizards also had a higher probability of choosing only the blue lid on  
146 trial 1 and this probability appeared to increase more steeply with successive trials  
147 (figure 2b). In contrast, the probability of choosing only the blue dish did not differ  
148 between old lizards in the social and control treatment (figure 2c; 21% for control and

149 20% for social) and lizards in both treatments had similar predicted probability curves  
150 across trials (figure 2c).

151

#### 152 **4. Discussion**

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

161         Our current understanding of cognition in lizards is in its infancy [11,12]  
162 despite growing appreciation of their cognitive abilities [8-10]. As such, it is currently  
163 difficult to make predictions about differences in learning styles and rates between  
164 juvenile and adult lizards. Younger male lizards used social information to solve a  
165 novel association task whereas older males did not. This may have been a result of  
166 local enhancement given that we did not observe the same effect in an instrumental  
167 task that required lizards to learn to open a lid. Given that adult males are more likely  
168 to exclude male rivals than juveniles from their territories, there may be more  
169 opportunity for social learning by juveniles. Furthermore, during this early phase of  
170 their life, juvenile lizards may be more likely to benefit from social information  
171 through enhanced foraging opportunities and as a result, may be more attentive to the  
172 actions of others.

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

177

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185

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224 **Figure legends**

225

226 **Figure 1** – Tasks presented to demonstrators and experimental lizards. *a)* instrumental  
227 task; *b)* association task. ‘exp.’ = experimental and ‘view trials’ are trials where  
228 experimental lizard only viewed demonstrator executing task (social demonstration  
229 treatment) or a conspecific (control).

230

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

240