

1 **Does social environment influence learning ability in a family-living lizard?**

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20

21 **ABSTRACT**

22 Early developmental environment can have profound effects on individual physiology,  
23 behaviour, and learning. In birds and mammals social isolation during development is known  
24 to negatively affect learning ability; yet in other taxa, like reptiles, the effect of social  
25 isolation during development on learning ability is unknown. We investigated how social  
26 environment affects learning ability in the family-living tree skink (*Egernia striolata*). We  
27 hypothesized that early social environment shapes cognitive development in skinks, and  
28 predicted that skinks raised in social isolation would have reduced learning ability compared  
29 to skinks raised socially. Offspring were separated at birth into two treatments: (1) raised  
30 alone, or (2) in a pair. After one year we quantified spatial learning ability of skinks in these  
31 treatments ( $N = 14$  solitary, 14 social). We found no effect of treatment on learning ability.  
32 The number of skinks to successfully learn the task, the number of trials taken to learn the  
33 task, the latency to perform the task, and the number of errors in each trial did not differ  
34 between isolated and socially-reared skinks. Our results were unexpected, yet the facultative  
35 nature of this species' social system may result in a reduced effect of social isolation on  
36 behaviour when compared to species with obligate sociality. Overall, our findings do not  
37 provide evidence that social environment affects development of spatial learning ability in  
38 this family-living lizard.

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40 **Keywords:** squamate, sociality, cognition, ontogeny, facultative sociality

41

## 42 INTRODUCTION

43 Animals learn by acquiring, processing, storing, and then acting on information collected  
44 from their environment (Dukas 2009; Shettleworth 2010; Buchanan et al. 2013). An  
45 individual's ability to learn can be adaptive by influencing behaviours with ecological  
46 significance, like foraging, competition, mating, anti-predatory behaviour, and dispersal  
47 (Dukas 2009; Buchanan et al. 2013). For example, American bird grasshoppers (*Schistocerca*  
48 *americana*) that readily learnt a foraging task exhibited a 20% higher growth rate than non-  
49 learners (Dukas and Bernays 2000); great tit (*Parus major*) parents that learnt a novel task  
50 had higher offspring survival and more offspring (Cauchard et al. 2013); and male satin  
51 bowerbird (*Ptilonorhynchus violaceus*) problem-solving performance relates positively to  
52 their mating success (Keagy et al. 2009; but see Isden et al. 2013 for contrasting results with  
53 spotted bowerbirds, *Chlamydera maculata*). These studies provide evidence of a link between  
54 animal learning and fitness (but see Thornton et al. 2014 for methodological concerns).

55 Although learning is a crucial trait for the survival and reproduction of some species, there  
56 are many factors that affect learning ability. Environmental severity (Shettleworth 2010; Roth  
57 et al. 2010), rapid environmental change as experienced during urbanisation (Sih et al. 2011;  
58 Sol et al. 2013), experimental methods (Noble et al. 2012), and sociality (Zuberbühler and  
59 Byrne 2006; Burkart and van Schaik 2009) are known to affect learning ability. In addition,  
60 individual-specific traits such as sex (Carazo et al. 2014), personality (Sih and Del Giudice  
61 2012; Carazo et al. 2014), age (Noble et al. 2014), as well as early developmental  
62 environment (Stamps and Groothuis 2010; Clark et al. 2013) are linked to learning ability.

63

64 The social environment during early development can influence an individual's learning  
65 ability throughout their lifetime (Cacioppo and Hawkley 2009). This relationship between  
66 social environment and learning ability was first demonstrated in the 1960s through Harlow's

67 research on rhesus macaques (*Macaca mulatta*). Rhesus macaques live in large, mixed-sex  
68 groups (~ 10 individuals; Melnick et al. 1984), and females care for their young from birth  
69 until the birth of their next offspring (Fooden 2000). Harlow's research isolated juvenile  
70 rhesus macaques from any social interaction; developing in social isolation debilitated these  
71 individuals in many ways, including significantly impairing learning ability (Harlow et al.  
72 1965). Subsequently, numerous studies have also demonstrated a negative relationship  
73 between social isolation and learning in rats (*Rattus norvegicus*; Greenough et al. 1972;  
74 Morgan et al. 1975; Einon 1980; Juraska et al. 1984; Holson 1986), although a few studies  
75 examining rats and chickens (*Gallus gallus domesticus*) have found variable and/or positive  
76 effects of isolation on learning (Wongwitdecha and Marsden 1996; Frisone et al. 2002;  
77 Goerlich et al. 2012). Overall it is well established that social environment, or lack thereof,  
78 can affect learning ability in mammal and birds. So far, studies have been taxonomically  
79 biased towards endotherms (e.g., birds and mammals) with obligate social systems. There has  
80 been little research on how social isolation affects learning in ectotherms (e.g., fish and  
81 reptiles).

82

83 There is increasing evidence that reptiles exhibit diverse social systems that can be kin-based  
84 (Doody et al. 2012; Gardner et al. 2015). For example, Australian skinks in the *Egernia*  
85 group exist in stable social aggregations, some with kin, some exhibiting long-term  
86 monogamy, and even parental care of offspring (Chapple 2003; Gardner et al. 2015; While et  
87 al. 2015). *Egernia striolata* (the Australian tree skink) is known to aggregate in social groups  
88 consisting of mating adult pairs, parents with offspring, and juveniles (Bonnett 1999; Duckett  
89 et al. 2012). Yet, interestingly, the social structure of *E. striolata* is highly variable both  
90 within and between populations. Within populations, skinks can be either found alone or in  
91 groups of variable size (2-10 skinks; Bustard 1970; Bonnett 1999). Across the tree skink's

92 range, different social systems have been described between arboreal  
93 populations, tree skinks have been found in small groups (maximum of 3 individuals) and  
94 most often found alone (Bustard 1970; Cunningham et al. 2007). Yet, in other arboreal and in  
95 saxicolous populations, tree skinks were most often in larger social groups (< 10 lizards) of  
96 closely related individuals (Swanson 1976; Ehmann 1992; Bonnett 1999; Michael and  
97 Cunningham 2010; Duckett et al. 2012). In the wild, groups consisting of parents and  
98 offspring are the most common, yet groups of only juveniles do exist (Bonnett 1999; Duckett  
99 et al. 2012, Riley unpubl. data). These juvenile-only groups vary in size, ranging from pairs  
100 to 4 individuals; often juveniles are also observed on their own (Bonnett 1999; Michael and  
101 Cunningham 2010; Duckett et al. 2012). This social nature of *E. striolata* makes it a good  
102 model for studying the influence of social environment on learning ability. We examined the  
103 effect of developing in social isolation versus within a social group, and hypothesized that  
104 developing in social isolation would affect the learning ability of *E. striolata*. As the *Egernia*  
105 group of skinks exhibit similar social behaviours to birds and mammals, we expected that  
106 social environment would similarly affect development of reptile behaviour. Thus, we  
107 predicted that (1) fewer skinks raised in social isolation would learn a spatial maze task, and  
108 (2) it would take longer for skinks raised in isolation to learn the task compared to skinks  
109 raised socially.

110

111

## 112 **METHODS**

### 113 *Study species, collection and husbandry*

114 Tree Skinks are a viviparous skink found across southeastern Australia (Cogger 2014). They  
115 inhabit hollow limbs of, and cracks under the bark of, standing trees or within fallen timber,  
116 as well as crevices on rock outcrops (Cogger 2014).

117

118 We collected 20 gravid female *E. striolata* from near Albury, New South Wales (-35.98°S,  
119 146.97°E), and held them at Macquarie University until parturition. Parturition occurred from  
120 10 February to 12 March 2014. Offspring were separated from females and randomly  
121 allocated into two treatments, social and isolated, on 14 April 2014 (after baseline  
122 behavioural trait assays occurred; Riley unpublished data). The social treatment consisted of  
123 two unrelated juveniles housed together ( $N = 14$  lizards within 7 pairs; 4 males and 10  
124 females); in the isolated treatment lizards were housed alone ( $N = 14$  lizards; 8 males and 6  
125 females). Juvenile social groupings of similar sizes have been reported for wild populations  
126 of *E. striolata* (Chapple 2003), although social groups most often consist of parent(s) and  
127 offspring (Chapple 2003). Including parents in our social treatment was logistically not  
128 feasible because adult *Egernia*, particularly females, are known to be highly aggressive  
129 towards juveniles (O'Connor and Shine 2004; Sinn et al. 2008). In fact, infanticide is  
130 common in multiple *Egernia* group spp. (Lanham and Bull 2000; Post 2000; O'Connor and  
131 Shine 2004), and there are even instances wherein females eat their own offspring (*E.*  
132 *stokesii*, Lanham and Bull 2000; *E. striolata*, Riley pers. obs. 2015). We housed juveniles  
133 within their social treatments for approximately one year before we conducted our learning  
134 assay (17 May to 4 June 2015).

135

### 136 *Learning assay*

137 We quantified the learning ability of juvenile *E. striolata* ( $N = 28$ ) with a spatial learning  
138 task. During the assay, we housed juveniles in a paper-lined, 100 litre rectangular arena (690  
139 mm W x 470 mm L x 455 mm H) containing a water dish and a refuge (120 mm W x 175  
140 mm L x 38 mm H). A 100W heat lamp directed at the refuge, which allowed lizards to  
141 thermoregulate, lighted each arena. We did not feed lizards during the assay; the only food

142 they received was the food reward (1.25 ml of puréed fruit; Heinz® apple and mango, apple,  
143 and pear) offered twice daily, and eaten only if the trial was completed successfully. Prior to  
144 trials commencing we gave lizards 24 hours to acclimate to their novel housing area.

145

146 We tested spatial learning ability using a vertical maze. This is a biologically relevant task,  
147 because in the wild *E. striolata* forage within their rock and tree habitats by vertically  
148 climbing from one crevice to another (Riley pers. obs. 2015). In our spatial learning task, the  
149 lizards had to navigate a set of five ladders and three ledges to access a food reward (see  
150 Supplementary Video 1). In stage one of the task, lizards had to choose between one of three  
151 mesh ladders running from the ground to one of two wooden ledges (Fig.1). If done correctly,  
152 in stage two, lizards then had a choice between one of two ladders running from these  
153 wooden ledges to a third ledge that held the food reward (Fig. 1). Incorrect ladders at all  
154 stages were partially covered with clear tape, so the lizard could not completely climb them  
155 but otherwise they looked identical to the correct ladder. The slippery, clear tape covered the  
156 mesh ladders starting at 50 mm above the ground (50 mm is approximately half the body  
157 length of our skinks; Fig. 1). So, unless the lizard attempted the climb the ladder, it could not  
158 feel or see a difference between the ladders at ground level. We randomized the position of  
159 the correct first ladder to control for lateralization bias (Fig. 1). In other words, either the first  
160 left-most ladder and then the second right ladder were climbable, or vice versa. We randomly  
161 assigned an equal number of lizards to each set-up. This task was attached to a laminated  
162 plywood board (390 x 300 mm), and during trials it was placed along the side of the trial tub  
163 opposite to the refuge (Fig. 1). The task had both intra-maze spatial cues (e.g., black circle on  
164 right and diagonal stripes on left), as well as extra-maze spatial cues (e.g., the location of  
165 items outside the trial bin) that the lizards could have used to navigate the task (Fig. 1).

166

167 At the beginning of each trial we first removed the water dish, and placed the lizard within its  
168 refuge at the opposite end of the arena to the task (Fig. 1). We would then place the task-  
169 board within the housing bin, and then, marking the start of the trial, remove the refuge. The  
170 trial was remotely video-recorded using CCTV cameras for 1 hour. We conducted two trials  
171 per day, in the morning (09:00-10:00 h) and the afternoon (12:00-14:00 h) with a minimum  
172 of 2 hours between trials. All lizards were given a maximum of 30 trials to attempt the task;  
173 nevertheless, due to variability in lizard behaviour, the total number of trials completed  
174 varied between individuals. Most skinks attempted the first stage of the task for 30 trials, but  
175 one skink only interacted with the first stage of the task for 25 trials. Similarly, most lizards  
176 attempted the full task for 30 trials ( $N = 24$ ), but one skink interacted with the task for 25  
177 trials, one skink interacted with the task for 26 trials, and another two skinks interacted with  
178 the task for 28 trials.

179

180 From the videos we scored: 1) successful completion of task, 2) latency to perform the task  
181 successfully, and 3) number of errors made during each trial. Successful completion of the  
182 task was considered in two stages (Fig. 1). First, the lizard had to climb the correct first  
183 ladder and reach the ledge. If the lizard attempted to climb (had a minimum of both forelimbs  
184 on a ladder) any of the incorrect ladders, the task was marked as unsuccessful. Second, once  
185 on the first ledge, the lizards had to move across the gap between the two ledges, climb the  
186 second correct ladder, gain access to the final ledge, and access the food reward (see  
187 Supplementary Video 1). When lizards were situated on the first ledge, we observed that they  
188 preferred to grip onto the exposed portion of the incorrect ladder's mesh with one, or more,  
189 limbs to allow stability while they were attempted to move across the ledges. So, we marked  
190 the second stage of the task as successful if the lizard (1) moved horizontally, or diagonally  
191 across the first ledge and did not encounter the tape-covered portion of the incorrect ladder,



192 and then (2) climbed the correct second ladder. If, instead, the lizard moved vertically up the  
193 incorrect ladder and encountered the tape-covered portion of the ladder, it was marked as  
194 unsuccessful. We separately assessed if each lizard correctly performed the first stage of the  
195 task (e.g., climbed the correct first ladder; Fig. 1), and the full task (e.g., climbed both the  
196 correct first and second ladders). We then classified each lizard as a ‘learner’ or a ‘non-  
197 learner’ by examining the tally of correct/incorrect choices (Tables S1 and S2). We  
198 considered a lizard to be a ‘learner’ if it successfully performed the task a minimum of 5/6  
199 consecutive times (Noble et al. 2014). We scored latency to perform the task by recording the  
200 time (s) from the start of the trial (as marked by lifting the refuge from the arena) until the  
201 lizard placed its head in the food dish. We scored latency for the full task only, and for each  
202 trial regardless of whether the task was initially completed successfully. For example, if a  
203 lizard initially climbed an incorrect ladder but then completed the task, it would have been  
204 unsuccessful at the task but we would still measure latency until it accessed the food reward.  
205 For the full task only, we also tallied how many times a lizard climbed incorrect ladders  
206 before it performed the full task correctly or the trial ended. For all behaviours (task success  
207 for the first stage and full task, latency, number of errors) there were high levels of  
208 congruence in our scoring (see Supplementary Materials).

209

#### 210 *Assessment of learning criteria*

211 We assessed robustness of our learning criteria by tallying the number of correct/incorrect  
212 choices from the last trial in the learning criterion to the lizard’s last trial (e.g., if a lizard  
213 performed 5/6 trials correctly we started the tally at the 6<sup>th</sup> trial; Table S1 and S2). We only  
214 tested the learning criteria for a subset of lizards that had six or more trials after the trial in  
215 which they learnt. We tested whether this tally of correct/incorrect choices was significant  
216 according to an exact binomial choice test. For the first stage of the task, 21/23 (91%) of

217 lizards performed the task correctly significantly more than expected by chance. For the full  
218 learning task, 16/17 (94%) of the skinks performed the task correctly significantly more than  
219 expected by chance. These results suggest our learning criterion was sufficient in  
220 categorizing lizards that learnt from those that did not.

221

### 222 *Statistical analyses*

223 We analysed our data using generalized linear mixed effects models (GLMM) with a  
224 Bayesian Markov chain Monte Carlo (MCMC) sampling approach. We used mixed effect  
225 models (GLMMs) to incorporate the dependency among observations of lizards from the  
226 same litter, as well as repeated observations of the same individual into our analyses (Dobson  
227 and Barnett 2008). MCMC is a simulation technique that we used to obtain the distribution of  
228 each parameter in our GLMMs, and this technique requires specification of a probability  
229 distribution (prior) for the analysis (Masson 2011; Zuur et al. 2013; Gelman et al. 2014;  
230 Krushke 2014). We preliminarily ran our GLMMs with multiple priors, but there was  
231 negligible difference between model results with varying priors. So, we used default diffuse  
232 uniform priors for our fixed effects, and for the random effect variance-covariance matrix our  
233 prior specification was  $V = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$  and  $nu = 0.002$  (Hadfield, 2010). In brief, diffuse priors  
234 assign equal probabilities to all possibilities, and typically yield parameter estimates that are  
235 not too different from Frequentist statistical analyses (Zurr et al. 2013; Krushke 2014).  
236 Analyses were performed in R v 3.0.3 using the *MCMCglmm* package (Hadfield 2010; R  
237 Core Team 2016).

238

239 In each model, we estimated model parameters 2,000,000 times (iterations), discarded the  
240 first 10,000 estimations (burn-in), and only sampled the parameter every 1,000<sup>th</sup> estimate  
241 (thinning interval). We repeated this procedure three separate times (chains) to reduce the

242 autocorrelation of successive samples from one chain (Zurr et al. 2013). We verified  
243 convergence of chains using the Gelman-Rubin test in the R package *coda* (Plummer et al.  
244 2015). We also visually inspected all plots of our chains to ensure they were well mixed (i.e.,  
245 were sampling randomly). Autocorrelation of the chains for both fixed and random effects  
246 was assessed to ensure levels were low ( $\text{lag} < 0.1$ ) using the *autocorr* function in R, and we  
247 also performed Geweke and Heidelberg auto-correlation diagnostics (all from the R package  
248 *coda*; Plummer et al. 2015).

249

250 Data from the first stage of the task and the full task were analysed separately, but the  
251 variables included in each of the models (1-3) were the same (see Table 1 for details):

252

253 (1) This binomial MCMC-GLMM examined if the probability of learning a task (learner = 1,  
254 non-learner = 0) was influenced by social treatment (isolated or social). We also controlled  
255 for sex (fixed effect) and mother identity (random effect).

256

257 (2) This Poisson MCMC-GLMM examined if the number of trials taken to learn the task was  
258 influenced by social treatment, while controlling for lizard sex and mother identity.

259

260 (3) This binomial MCMC-GLMM examined if the probability of task success during each  
261 trial was influenced by social treatment. The model also included the fixed effects of sex, trial  
262 number, and an interaction between treatment and trial number. It also included lizard and  
263 mother identity as random effects.

264

265 (4) This Gaussian MCMC-GLMM examined if latency to successfully complete the task  
266 (transformed with a square-root transformation to ensure normality of residuals) was

267 influenced by social treatment. The model also included the fixed effects of sex, trial number,  
268 and an interaction between treatment and trial number, as well as the random effects of lizard  
269 and mother identity.

270

271 (5) This Poisson MCMC-GLMM examined if the number errors made during each trial was  
272 affected by social treatment. The model also included the fixed effects of sex, trial number,  
273 and an interaction between treatment and trial number, as well as the random effects of lizard  
274 and mother identity.

275

276 We report the mode of the MCMC sample and 95% credible intervals for our parameter  
277 estimates. Parameter estimates were considered significant when the credible intervals did  
278 not include 0, and the  $p_{MCMC}$  values calculated by *MCMCglmm* were less than 0.05  
279 (Hadfield 2010). When we predicted fitted lines from the models for visualization of  
280 differences in response variables between developmental treatments, we set sex, our  
281 secondary fixed factor, to the intercept-level value. Data for this study is available from  
282 <https://dx.doi.org/10.6084/m9.figshare.3984111.v1>

283

284

## 285 **RESULTS**

### 286 *First stage of learning task (3 ladder choice)*

287 Twenty-five of 28 (89%) of the lizards met our learning criterion for choosing the correct  
288 first stage ladder (out of 3 possibilities). Whether a lizard learnt or did not learn the first stage  
289 of the task did not depend on social treatment (Table 1): 12/14 (86%) socially-reared and  
290 13/14 (93%) isolated lizards were categorized as learners. Social treatment also did not affect  
291 the number of trials taken to learn stage one of the task. Socially-reared skinks took on

292 average 15 trials (*95% CI* 10-19) to learn stage one of the task, and isolated skinks took on  
293 average 14 trials (*95% CI* 11-17). Males were less likely to learn the first stage of the task  
294 than females, but there was no sex-effect on the number of trials taken to learn the task and  
295 this observed sex-effect was not consistent when we examined the full task (Table 1).

296

297 Social treatment did not affect probability of task success during each trial (Table 1; Fig. 2A).

298 There also was no sex-effect on the probability of task success during each trial (Table 1).

299 Yet, probability of task success during each trial increased over time (as trial number

300 increased), which indicates that, regardless of social treatment, tree skinks were learning

301 stage one of the task (Table 1; Fig. 2A).

302

303 *Full learning task (3 ladder choice then a two ladder choice)*

304 When we considered the learning task in its entirety (3 ladder choice followed by a 2 ladder  
305 choice), 19/28 (68%) of skinks met our learning criterion. Whether a lizard learnt the full task

306 or not did not depend on social treatment (Table 1): 9/14 (64%) socially-reared and 10/14

307 (71%) isolated lizards were categorized as learners. Social treatment did not affect number of

308 trials taken to learn the full task (Table 1): socially-reared skinks took an average of 16 trials

309 (*95% CI* 11-21) to learn the task, and isolated skinks took an average of 17 trials (*95% CI* 14-

310 19). The probability of learning the full task, and the number of trials taken to learn the task

311 were not significantly affected by sex (Table 1).

312

313 Similarly, social treatment did not affect probability of task success, latency, or number of

314 errors made during each trial (Table 1; Fig. 2B). Socially-reared skinks took an average of

315 1269 s to complete the task (*95% CI* 1261-1278), and made on average 0.90 incorrect choices

316 during a trial (*95% CI* 0.83 - 0.97). Isolated skinks took on average 1321 s to complete the

317 task (95% CI 1313-1328), and made on average 1.26 incorrect choices during a trial (95% CI  
318 1.20 – 1.32). There were no sex-effects on probability of task success during each trial,  
319 latency or number of errors made during each trial (Table 1). Probability of task success  
320 during each trial increased over time (as trial number increased; Fig. 2B), and latency to  
321 complete the task (Fig. S1) and number of errors (Fig. S2) during a trial both decreased over  
322 time (Table 1). These results are evidence that tree skinks were learning the full task.

323

324

## 325 **DISCUSSION**

326 Our prediction that social isolation during development would negatively affect learning  
327 ability in *E. striolata* was not supported. An almost equivalent number of skinks in our two  
328 treatments (social vs. isolated developmental environment) were categorized as ‘learners’ in  
329 our spatial learning task. Moreover, the number of trials it took skinks to learn the task did  
330 not differ between social treatments. We found no effect of social treatment on probability of  
331 task success during each trial, latency until task success, and number of errors made during  
332 the trial. All our findings, across analyses for both the first stage of the task and the full task,  
333 consistently demonstrate no evidence for an effect of social isolation on learning ability of a  
334 social skink.

335

336 The key to why we found this unexpected result may lie in the tree skink’s variable social  
337 system. As noted above, the social structure of *E. striolata* is quite variable; within one  
338 population, individuals can vary from being solitary to highly aggregative with kin (Bustard  
339 1970; Bonnett 1999; Duckett et al. 2012). This natural flexibility in group size and variation  
340 in individual sociability may simply mean that developing in isolation is simply a normal  
341 option in the wild, as such social isolation is possibly less stressful for this species. Thus,

342 there are limited negative consequences to this social state. For example, in domestic  
343 chickens stress (or lack of it) has been suggested as a mechanism that regulates learning  
344 ability (Goerlich et al. 2012). In this study, isolated chicks actually made more correct  
345 choices in an associative learning task. These chicks had a reduced stress response, which  
346 likely resulted in a higher coping ability and an enhanced learning ability (Goerlich et al.  
347 2012). It would be beneficial to follow-up our study on *E. striolata* by measuring stress levels  
348 in both our isolated and socially-reared treatments to examine if stress may be the mechanism  
349 that explains our unexpected findings. All in all, the plastic social nature of *E. striolata* may  
350 buffer these lizards from the extreme negative effects of social isolation previously observed  
351 in studies on mammals and birds. These previous studies often examined the effects of social  
352 isolation on species with more complex, more rigid, and obligate social structure.

353

354 An alternative hypothesis could be that the presence or absence of a parent during  
355 development may affect tree skink behaviour. As both of our experimental treatments did not  
356 include parents due to logistical constraints (see Methods), any potential effects of removing  
357 a parent were not quantified. In the wild, the most common tree skink social group does  
358 consist of parents and offspring (Bonnett 1999; Duckett et al. 2012). Although both juveniles  
359 and adults can be found alone, social groups can also consist of adults only, juveniles only, or  
360 parents and offspring (Bonnett 1999; Duckett et al. 2012, Riley pers obs 2016). In fact, in  
361 multiple *Egernia* group sp., offspring benefit from the presence of parents and gain added  
362 protection, closer to optimal thermoregulation, and increased access to prey (O'Connor and  
363 Shine 2004; Langkilde et al. 2007; Sinn et al. 2008). Thus, as offspring benefit from the  
364 presence of parents in *Egernia* group sp., one might expect there could be parental effects on  
365 offspring behaviour. It is still unknown if juveniles benefit from the presence of parents in *E.*  
366 *striolata*, yet it is an aspect to consider in the early development of behaviour of this species.

367

368 Although our study did not find any evidence that social isolation negatively affects spatial  
369 learning in tree skinks, there are other lizard behaviours that could be affected by social  
370 isolation. Personality traits and an individual's ability to interact with conspecifics are known  
371 to be altered by social environment during development in mammals and birds (Harlow et al.  
372 1965; Naguib et al. 2011). Hatchling veiled chameleons (*Chameleo calyptratus*) raised in  
373 isolation were more submissive when interacting with conspecifics, and took longer to attack  
374 prey in a foraging task (Ballen et al. 2014). However, adult *C. calyptratus* are largely  
375 intolerant of conspecifics (De Vosjoli and Ferguson 1995), so our understanding of social  
376 environment on lizard behaviour would benefit from further research on a known social  
377 species. Social isolation may also hinder the ability an individual has to process and interpret  
378 social cues and information. Thus, isolation may affect social learning ability because lack of  
379 social cues during development may obstruct information transfer between conspecifics.  
380 While we found no effect of social isolation on individual learning ability, the same may not  
381 be true of social learning and warrants further investigation.

382

383 As the sociality of reptiles is becoming increasingly recognized (Doody et al. 2012; Gardner  
384 et al. 2015), it is crucial to also study the consequences and impact that being social has on  
385 reptilian behaviour, ecology, and evolution. Understanding the consequences of sociality for  
386 reptiles is practically important for captive research, breeding programs, and conservation.  
387 Management, conservation, and research programs may need to implement group housing of  
388 social species to reduce potential negative impacts of isolation on these animals'  
389 development. Our study did not find any evidence that social isolation negatively affects  
390 spatial learning ability in the social tree skink. However, more research is required to better  
391 understand the negative effects of social isolation on other behavioural and learning traits of



392 this species. Because lizards have relatively rudimentary parental care and many species are  
393 solitary, they may represent a unique opportunity to easily manipulate early social  
394 environment and examine how behavioural development can be shaped by sociality.

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396

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400

401 **Compliance with ethical standards**

402

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411 **Ethical approval:** We followed guidelines for the care and use of animals as laid out by the  
412 Association for the Study of Animal Behaviour. Experimental protocols were approved by  
413 the Macquarie University Animal Ethics Committee (ARA # 2013/039). Collection of skinks  
414 was approved by the New South Wales National Parks and Wildlife Service, Office of  
415 Environment and Heritage (License # SL101264). Female skinks were captured either by  
416 hand, noosing or Eliot trap and were placed in cloth bags until they could be transported by

417 vehicle to Macquarie University from Albury, New South Wales in an insulated box. We  
418 observed no injuries resulting from our cognition experiment.

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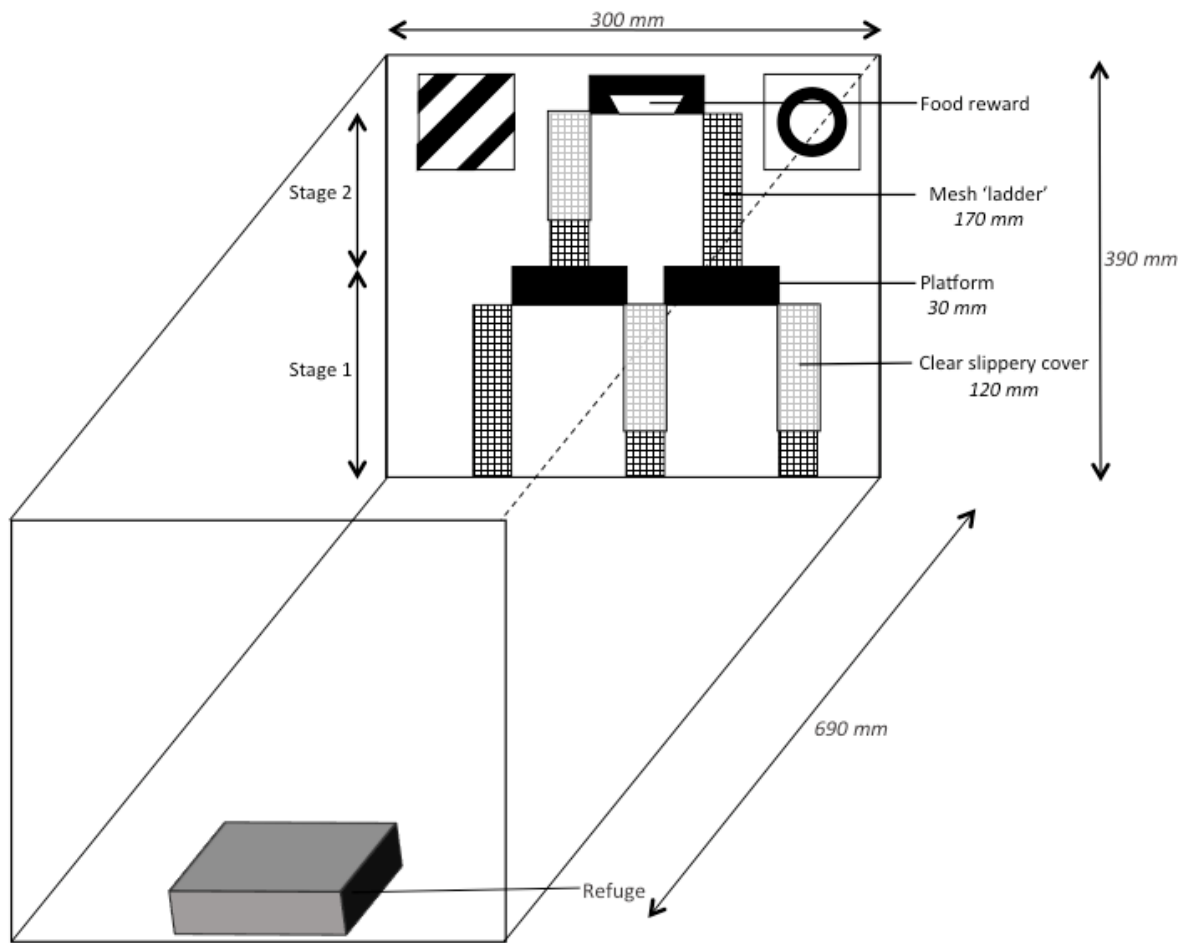
566 **Table 1.** Pooled posterior modes and highest posterior density intervals from Bayesian Markov chain Monte Carlo generalized linear mixed  
567 effect models (MCMC-GLMM) that examine the effect of a lizard's social environment (ISOLATED or SOCIAL) on (1) the probability of  
568 learning the task, (2) number of trials until learnt the task, (3) probability of task success, (4) latency (s; transformed using a square root  
569 transformation), and (5) number of errors made during each trial. These models were used to examine effects for (a) the first stage of the task (3  
570 ladder choice;  $N_{obs} = 835$ ,  $N_{lizards} = 28$ ), and (b) the full learning task (3 ladder choice then a 2 ladder choice;  $N_{obs} = 827$ ,  $N_{lizards} = 28$ ). Models  
571 also included additional fixed factors of sex (MALE or FEMALE), trial number, and an interaction between trial and treatment when  
572 appropriate. Parameter estimates for binomial models are on the *log odds* link scale, Poisson models are on the *log* link scale, and Gaussian  
573 models are on the *identity* link scale. Bolded estimates are significant (95% credible intervals do not include 0).

(a) First stage (3 ladder choice)

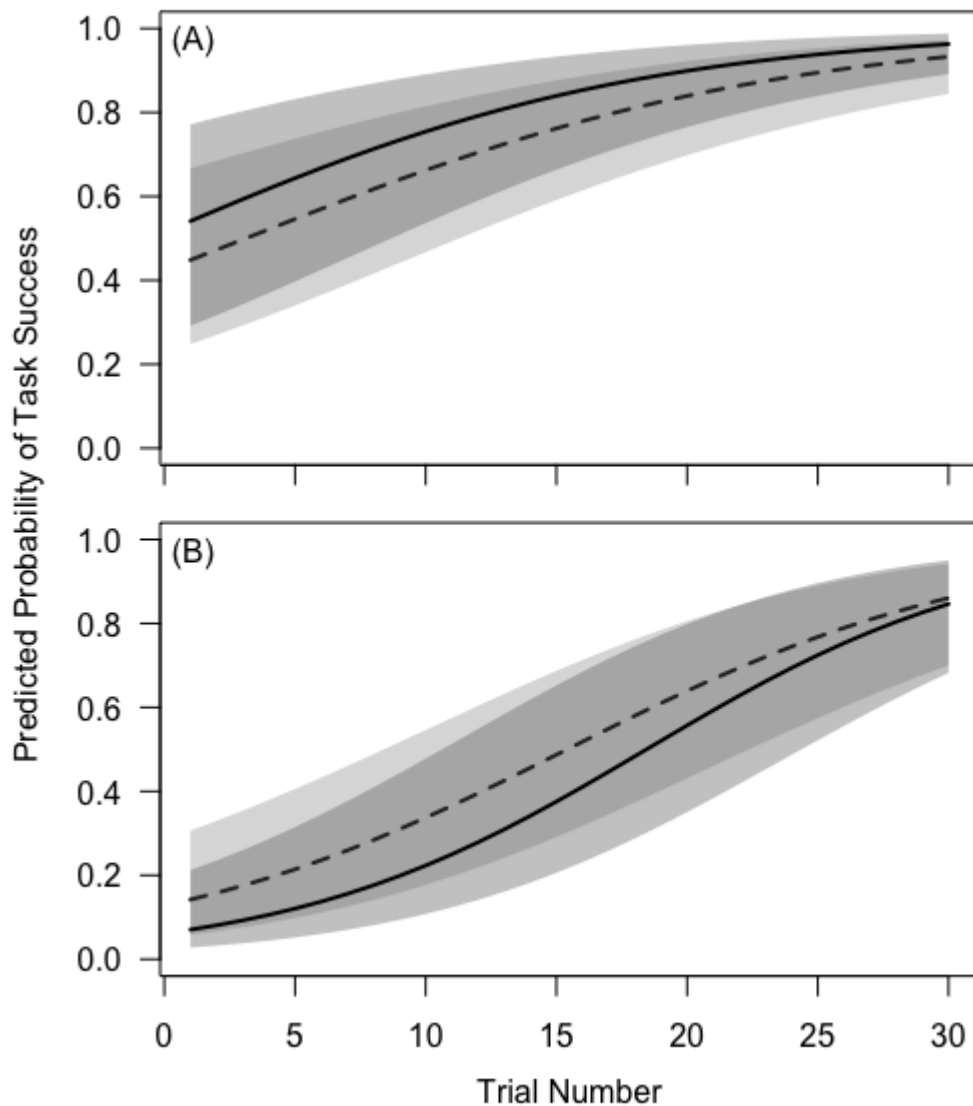
	Probability of learning the task			Number of trials until learnt the task			Probability of task success			Latency to access the food reward			Number of errors		
	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper
Intercept	<b>34.70</b>	<b>1.67</b>	<b>331.06</b>	<b>2.53</b>	<b>2.22</b>	<b>2.90</b>	-0.37	-1.24	0.58	-	-	-	-	-	-
Treatment ISOLATED	5.62	-22.02	183.90	-0.014	-0.47	0.41	0.34	-0.72	1.47	-	-	-	-	-	-
Sex MALE	<b>-31.54</b>	<b>-242.16</b>	<b>-3.03</b>	0.033	-0.43	0.53	-0.90	-1.92	0.40	-	-	-	-	-	-
Trial number	-	-	-	-	-	-	<b>0.098</b>	<b>0.066</b>	<b>0.13</b>	-	-	-	-	-	-
Trial x Treatment	-	-	-	-	-	-	0.01	-0.039	0.055	-	-	-	-	-	-

(c) The full learning task (3 ladder choice then a two ladder choice)

Intercept	1.07	-0.98	9.40	<b>2.74</b>	<b>2.42</b>	<b>3.01</b>	<b>-2.04</b>	<b>-2.91</b>	<b>-0.92</b>	<b>41.64</b>	<b>34.40</b>	<b>47.47</b>	0.44	-0.024	1.05
Treatment ISOLATED	0.66	-2.53	3.75	0.09	-0.27	0.40	-0.66	-1.89	0.71	-1.72	-10.30	6.68	0.37	-0.36	0.92
Sex MALE	-1.48	-5.54	2.26	0.014	-0.36	0.42	-0.25	-1.44	0.78	2.21	-3.96	9.24	-0.076	-0.58	0.51
Trial number	-	-	-	-	-	-	<b>0.12</b>	<b>0.090</b>	<b>0.16</b>	<b>-0.38</b>	<b>-0.59</b>	<b>-0.17</b>	<b>-0.071</b>	<b>-0.094</b>	<b>-0.046</b>
Trial x Treatment	-	-	-	-	-	-	0.027	-0.026	0.071	0.097	-0.16	0.44	0.014	-0.013	0.046



574 **Fig. 1** Schematic diagram of our spatial learning assay arena as set-up at the beginning of our  
 575 trials. The clear tape covering the incorrect mesh 'ladders' was not visible, but is included in  
 576 the diagram for clarity. The task, the vertical spatial learning maze, was insertable and was  
 577 only within the arena during the trial.



578 **Fig. 2** Predicted probabilities of task success during each trial did not differ between  
 579 developmental treatments (social: light grey shading and dashed line; isolated: dark grey  
 580 shading and solid line) for either (a) stage one or the (b) full spatial learning task. The darkest  
 581 shade of grey is where the 95% predicted credible intervals, which are represent by shaded  
 582 polygons around predicted probabilities, overlap.