

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

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3 Julia L. Riley¹, Daniel W.A. Noble², Richard W. Byrne³, and Martin J. Whiting¹

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5 ¹ Department of Biological Sciences, Macquarie University, Sydney, New South Wales,
6 Australia

7 ² Evolution & Ecology Research Centre, School of Biological, Earth and Environmental
8 Sciences, University of New South Wales, Kensington, New South Wales, Australia

9 ³School of Psychology & Neuroscience, University of St. Andrews, St. Andrews, Fife,
10 United Kingdom

11

12 Corresponding author: Julia L. Riley

13

14 Address: Department of Biological Sciences, Macquarie University, Sydney, New South
15 Wales 2109, Australia

16

17 Email address: julia.riley87@gmail.com, Phone: +61 0298504185

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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.

39

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 6th 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 1,000th 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 ($\text{learner} = 1$,
254 $\text{non-learner} = 0$) 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.

395

396

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399

400

401 **Compliance with ethical standards**

402

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409

410

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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421 REFERENCES

422 Ballen C, Shine R, Olsson M (2014) Effects of early social isolation on the behaviour and
423 performance of juvenile lizards, *Chamaeleo calyptratus*. *Anim Behav* 88:1–6. doi:
424 10.1016/j.anbehav.2013.11.010

425 Bonnett MP (1999) The ecology, behaviour and genetic relationships of a population of
426 *Egernia striolata*. Unpublished Honours Thesis: Flinders University of South Australia,
427 Adelaide, Australia.

428 Buchanan KL, Grindstaff JL, Pravosudov VV (2013) Condition dependence, developmental
429 plasticity, and cognition: implications for ecology and evolution. *Trends Ecol Evol*
430 28:290–296. doi: 10.1016/j.tree.2013.02.004

431 Burkart JM, van Schaik CP (2009) Cognitive consequences of cooperative breeding in
432 primates? *Anim Cogn* 13:1–19. doi: 10.1007/s10071-009-0263-7

433 Bustard HR (1970) A population study of the scincid lizard *Egernia striolata* in northern
434 New South Wales. *Proc K Ned Akad Wet C* 73: 202.

435 Cacioppo JT, Hawkley LC (2009) Perceived social isolation and cognition. *Trends Cogn Sci*
436 13:447–454. doi: 10.1016/j.tics.2009.06.005

437 Carazo P, Noble DWA, Chandrasoma D, Whiting MJ (2014) Sex and boldness explain
438 individual differences in spatial learning in a lizard. *Proc Biol Sci* 281:20133275–
439 20133275. doi: 10.1098/rspb.2013.3275

- 440 Cauchard L, Boogert NJ, Lefebvre L, Dubois F, Doligez, B(2013) Problem-solving
441 performance is correlated with reproductive success in a wild bird population. *Anim*
442 *Behav* 85:19–26. doi: 10.1016/j.anbehav.2012.10.005
- 443 Chapple DG (2003) Ecology, life-history, and behavior in the Australian Scincid genus
444 *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetol*
445 *Monogr* 17:145–180. doi: 10.1655/0733-1347(2003)017[0145:elabit]2.0.co;2
- 446 Clark BF, Amiel JJ, Shine R, Noble DWA, Whiting MJ (2013) Colour discrimination and
447 associative learning in hatchling lizards incubated at ‘hot’ and ‘cold’ temperatures.
448 *Behav Ecol Sociobiol* 68:239–247. doi: 10.1007/s00265-013-1639-x
- 449 Cogger HG (2014) *Reptiles and amphibians of Australia*, 7 edn. CSIRO Publishing, Clayton,
450 pp 549
- 451 Cunningham RB, Lindenmayer DB, Crane M, Michael D, MacGregor C (2007) Reptile and
452 arboreal marsupial response to replanted vegetation in agricultural landscapes. *Ecol Appl*
453 17:609–619. doi: 10.1890/05-1892
- 454 De Vosjoli P, Ferguson G (1995) Care and breeding of Panther, Jackson’s, Veiled, and
455 Parson’s chameleons. i5 Publishing, Los Angeles, pp 81-89
- 456 Dobson AJ, Barnett A (2008) *An introduction to generalized linear models*. CRC Press, Boca
457 Raton, pp. 45-66, 229-256
- 458 Doody JS, Burghardt GM, Dinets V (2012) Breaking the social-non-social dichotomy: a role
459 for reptiles in vertebrate social behavior research? *Ethology* 119:95–103. doi:
460 10.1111/eth.12047
- 461 Duckett PE, Morgan MH, Stow AJ (2012) Tree-dwelling populations of the skink *Egernia*

462 *striolata* aggregate in groups of close kin. *Copeia* 2012:130–134. doi: 10.1643/ce-10-183

463 Dukas R (2009) Learning: mechanisms, ecology and evolution. In: Dukas R, Ratcliffe JM
464 (eds) *Cognitive ecology II*. The University of Chicago Press, Chicago, pp 7–26

465 Dukas R, Bernays EA (2000) Learning improves growth rate in grasshoppers. *P Natl Acad*
466 *Sci USA* 97:2637–2640. doi: 10.1073/pnas.050461497

467 Ehmann H (1992) *Encyclopedia of Australian Animals: Reptiles*. Angus and Robertson,
468 Sydney, pp 242

469 Einon D (1980) Spatial memory and response strategies in rats: age, sex and rearing
470 differences in performance. *Q J Exp Psychol* 32:473–489. doi:
471 10.1080/14640748008401840

472 Fooden J (2000) Systematic review of the rhesus macaque, *Macaca mulatta* (Zimmermann,
473 1780). *Field Zool* 96:1–180. doi: 10.5962/bhl.title.7192

474 Frisone DF, Frye CA, Zimmerberg B (2002) Social isolation stress during the third week of
475 life has age-dependent effects on spatial learning in rats. *Behav Brain Res* 128:153–160.
476 doi:10.1016/S0166-4328(01)00315-1

477 Gardner MG, Pearson SK, Johnston GR, Schwarz MP (2015) Group living in squamate
478 reptiles: a review of evidence for stable aggregations. *Biol Rev Camb Philos Soc*. doi:
479 10.1111/brv.12201

480 Gelman A, Carlin JB, Stern HS, Rubin DB (2014) *Bayesian data analysis*. Volume 3.
481 Chapman and Hall/CRC Press, Boca Raton, pp 3-27

482 Goerlich VC, Nätt D, Elfving M, Macdonald B, Jensen P (2012) Transgenerational effects of

483 early experience on behavioral, hormonal and gene expression responses to acute stress
484 in the precocial chicken. *Horm Behav* 61:711–718. doi: 10.1016/j.yhbeh.2012.03.006

485 Greenough WT, Madden TC, Fleischmann TB (1972) Effects of isolation, daily handling,
486 and enriched rearing on maze learning. *Psychon Sci* 27:279–280. doi:
487 10.3758/bf03328961

488 Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the
489 MCMCglmm R package. *J Stat Softw* 33:1–22. doi: 10.18637/jss.v033.i02

490 Harlow HF, Dodsworth RO, Harlow MK (1965) Total social isolation in monkeys. *P Natl*
491 *Acad Sci USA* 54:90–97. doi: 10.1073/pnas.54.1.90

492 Holson RR (1986) Feeding neophobia: a possible explanation for the differential maze
493 performance of rats reared in enriched or isolated environments. *Physiol Behav* 38:191–
494 201. doi:10.1016/0031-9384(86)90154-X

495 Isden J, Panavi C, Dingle C, Madden J (2013) Performance in cognitive and problem-solving
496 tasks in male spotted bowerbirds does not correlate with mating success. *Anim Behav*
497 86:829-838. doi: 10.1016/j.anbehav.2013.07.024

498 Juraska JM, Henderson C, Müller J (1984) Differential rearing experience, gender, and radial
499 maze performance. *Dev Psychobiol* 17:209–215. doi: 10.1002/dev.420170302

500 Keagy J, Savard, JF, Borgia G (2009) Male satin bowerbird problem-solving ability predicts
501 mating success. *Anim Behav* 78:809-817. doi: 10.1016/j.anbehav.2009.07.011

502 Kruschke, J (2014) *Doing Bayesian data analysis: a tutorial with R, JAGS and Stan.*
503 Academic Press, Cambridge, pp 7-59

- 504 Langkilde T, O'Connor D, Shine R (2007) Benefits of parental care: Do juvenile lizards
505 obtain better-quality habitat by remaining with their parents? *Austral Ecol* 32:950–954.
506 doi: 10.1111/j.1442-9993.2007.01783.x
- 507 Lanham EJ, Bull CM (2000) Maternal care and infanticide in the Australian skink, *Egernia*
508 *stokesii*. *Herpetol Rev* 31:151–152. doi: 10.1016/j.anbehav.2004.02.014
- 509 Masson ME (2011) A tutorial on a practical Bayesian alternative to null-hypothesis
510 significance testing. *Behav Res Methods* 43:679-690. doi: 10.3758/s13428-010-0049-5
- 511 Melnick DJ, Pearl MC, Richard AF (1984) Male migration and inbreeding avoidance in wild
512 rhesus monkeys. *Am J Primatol* 7:229–243. doi: 10.1002/ajp.1350070303
- 513 Michael DR, Cunningham RB (2010) The social elite: habitat heterogeneity, complexity and
514 quality in granite inselbergs influence patterns of aggregation in *Egernia striolata*
515 (Lygosominae: Scincidae). *Austral Ecol* 35:862–870. doi: 10.1111/j.1442-
516 9993.2009.02092.x
- 517 Morgan MJ, Einon DF, Nicholas D (1975) The effects of isolation rearing on behavioural
518 inhibition in the rat. *Q J Exp Psychol* 27:615–634. doi: 10.1080/14640747508400524
- 519 Naguib M, Flörcke C, van Oers K (2011) Effects of social conditions during early
520 development on stress response and personality traits in great tits (*Parus major*). *Dev*
521 *Psychobiol* 53:592–600. doi: 10.1002/dev.20533
- 522 Noble DWA, Carazo P, Whiting MJ (2012) Learning outdoors: male lizards show flexible
523 spatial learning under semi-natural conditions. *Biol Letters* 8:946-948. doi:
524 10.1098/rsbl.2012.0813
- 525 Noble DWA, Byrne RW, Whiting MJ (2014) Age-dependent social learning in a lizard. *Biol*

526 Letters 10:20140430–20140430. doi: 10.1098/rsbl.2014.0430

527 O'Connor DE, Shine R (2004) Parental care protects against infanticide in the lizard *Egernia*
528 *saxatilis* (Scincidae). Anim Behav 68:1361–1369. doi: 10.1016/j.anbehav.2004.02.014

529 Plummer M, Best N, Cowles K, Vines K (2015) coda: Output analysis and diagnostics for
530 MCMC. R package version 0.13-3, URL <http://CRAN.R-project.org/package=coda>.

531 Post MJ (2000) The captive husbandry and reproduction of the Hosmer's Skink *Egernia*
532 *hosmeri*. Herpetofauna 30:2–6.

533 R Core Team (2016) A language and environment for statistical computing. R Foundation for
534 Statistical Computing, Vienna, Austria, URL <https://www.R-project.org/>.

535 Roth TC, LaDage LD, Pravosudov VV (2010) Learning capabilities enhanced in harsh
536 environments: a common garden approach. P Roy Soc B: Biol 277:3187–3193. doi:
537 10.1098/rspb.2010.0630

538 Shettleworth SJ (2010) Cognition, evolution, and behavior. Second edition. Oxford
539 University Press, New York, New York, pp 371-394

540 Sih A, Del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural
541 ecology perspective. Philos Trans R Soc Lond B 367:2762–2772. doi:
542 10.1098/rstb.2012.0216

543 Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-
544 induced rapid environmental change. Evol Appl 4:367–387. doi: 10.1111/j.1752-
545 4571.2010.00166.x

546 Sinn DL, While GM, Wapstra E (2008) Maternal care in a social lizard: links between female

547 aggression and offspring fitness. *Anim Behav* 76:1249–1257. doi:
548 10.1016/j.anbehav.2008.06.009

549 Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city.
550 *Anim Behav* 85:1101–1112. doi: 10.1016/j.anbehav.2013.01.023

551 Stamps JA, Groothuis TGG (2010) Developmental perspectives on personality: implications
552 for ecological and evolutionary studies of individual differences. *Philos Trans R Soc*
553 *Lond B* 365:4029–4041. doi: 10.1098/rstb.2010.0218

554 Swanson S (1976) *Lizards of Australia*. Angus and Robertson, Sydney, pp 43

555 Thorton A, Isden J, Madden JR (2014) Toward wild psychometrics: linking individual
556 cognitive differences to fitness. *Behav Ecol* 25:1299-1301. doi: 10.1093/beheco/aru095

557 While GM, Chapple DG, Gardner MG, et al (2015) *Egernia* lizards. *Curr Biol* 25:R593–
558 R595. doi: 10.1016/j.cub.2015.02.070

559 Wongwitdecha N, Marsden CA (1996) Effects of social isolation rearing on learning in the
560 Morris water maze. *Brain Res* 715:119–124. doi: 10.1016/0006-8993(95)01578-7

561 Zuberbühler K, Byrne RW (2006) Social cognition. *Curr Biol* 16:R786–R790. doi:
562 10.1016/j.cub.2006.08.046

563 Zurr AF, Hilbe JM, Ieno EN (2013) A beginner's guide to GLM and GLMM with R: a
564 frequentist and Bayesian perspective for ecologists. Highland Statistics, Ltd., Newburgh,
565 pp 66-72

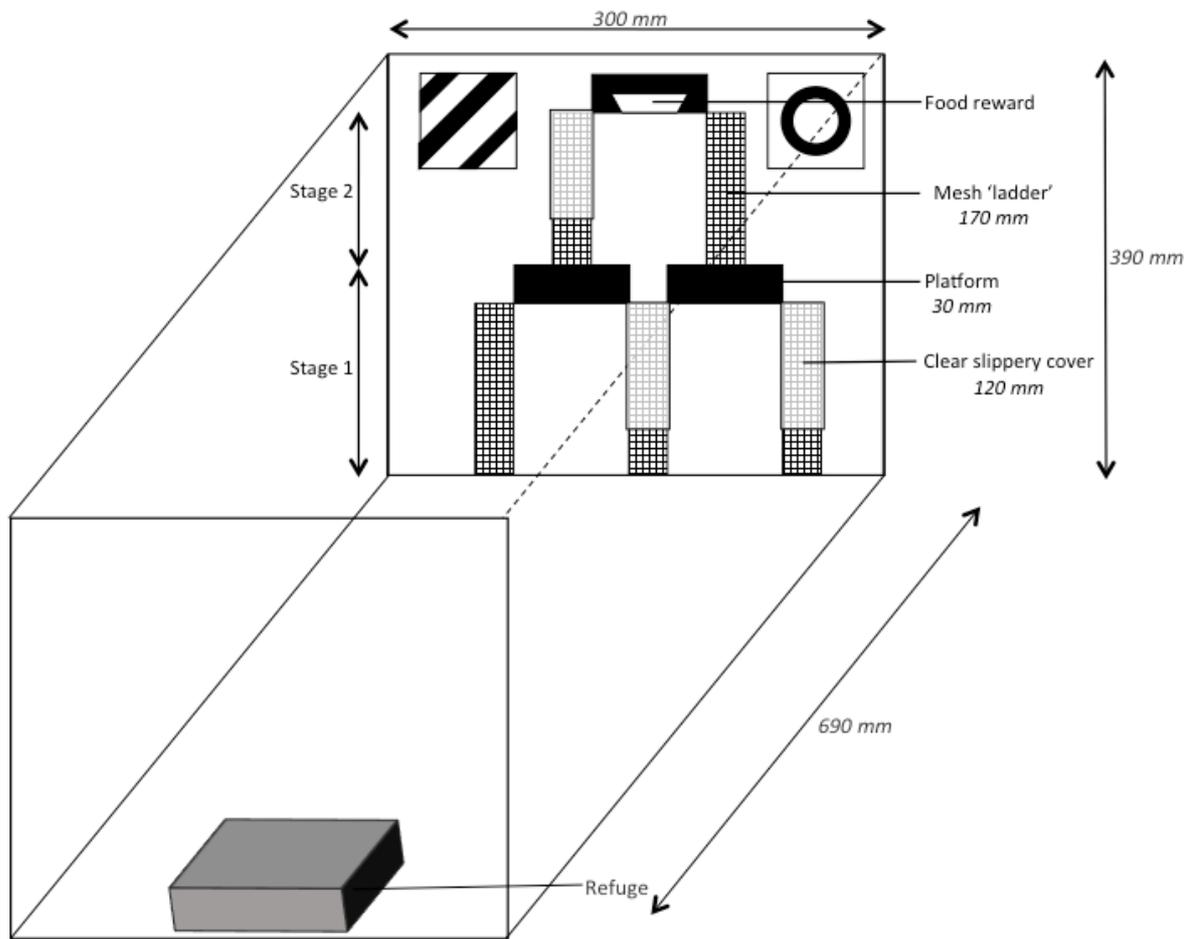
566 **Table 1.** Pooled posterior modes and highest posterior density intervals from Bayesian Markov chain Monte Carlo generalized linear mixed
567 effect models (MCMC-GLMM) that examine the effect of a lizard's social environment (ISOLATED or SOCIAL) on (1) the probability of
568 learning the task, (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)

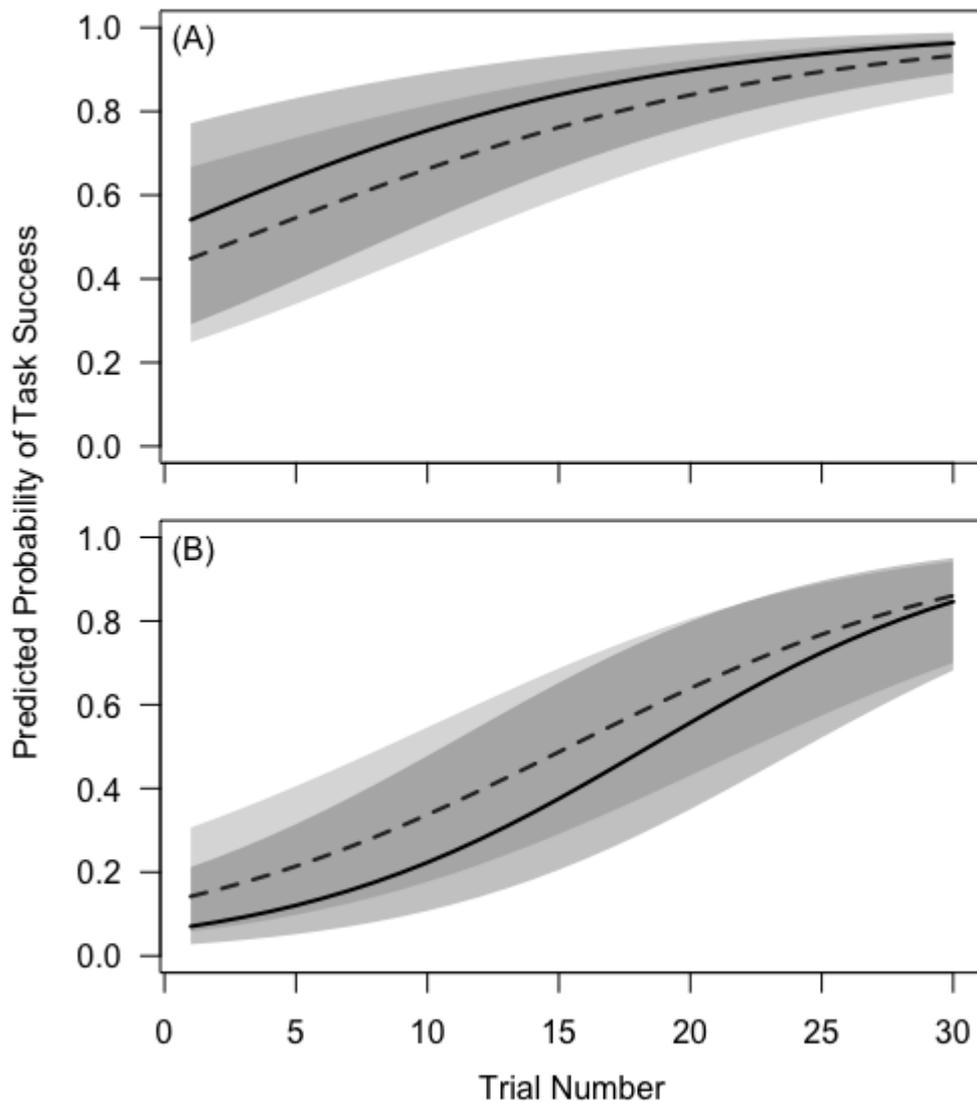
	Probability of learning the task			Number of trials until learnt the task			Probability of task success			Latency to access the food reward			Number of errors		
	<u>Estimate</u>	<u>Lower</u>	<u>Upper</u>	<u>Estimate</u>	<u>Lower</u>	<u>Upper</u>	<u>Estimate</u>	<u>Lower</u>	<u>Upper</u>	<u>Estimate</u>	<u>Lower</u>	<u>Upper</u>	<u>Estimate</u>	<u>Lower</u>	<u>Upper</u>
Intercept	34.70	1.67	331.06	2.53	2.22	2.90	-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	-31.54	-242.16	-3.03	0.033	-0.43	0.53	-0.90	-1.92	0.40	-	-	-	-	-	-
Trial number	-	-	-	-	-	-	0.098	0.066	0.13	-	-	-	-	-	-
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	2.74	2.42	3.01	-2.04	-2.91	-0.92	41.64	34.40	47.47	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	-	-	-	-	-	-	0.12	0.090	0.16	-0.38	-0.59	-0.17	-0.071	-0.094	-0.046
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.