

1 **Learning ability is unaffected by isolation rearing in a family-living lizard**

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26 **Abstract**

27 The social environment during development can affect learning; for example, raising
28 an obligate social mammal in isolation can hinder their learning ability. However, we
29 know little about how the social environment impacts learning in less-studied,
30 facultatively social taxa, like family-living lizards. We reared tree skinks (*Egernia*
31 *striolata*) in two treatments, either with a conspecific or in isolation. We used three
32 tasks to quantify skink learning ability (motor, discrimination, and reversal). Skinks
33 performed these tasks under two learning treatments: either after demonstration
34 (social learning) or without social information (individual learning). We did not find
35 any evidence that tree skinks used social information. The majority of skinks learnt
36 our motor (91%) and discrimination tasks (100%), and a third learnt our reversal task
37 (34%). Contrary to our predictions, and the majority of previous literature, we
38 detected no negative effect of rearing treatment on learning in any task. Our
39 surprising findings are likely due to this skink's variable social system, and we
40 suggest that birds and mammals with facultative sociality may not be affected by
41 isolation rearing in the same way as taxa with obligate sociality.

42

43 **Significance statement**

44 Survival can be impacted by an animal's ability to learn, but many factors can
45 influence this ability (i.e., age, sex, stress, developmental environment, etc.). In this
46 study we examined how social environment across ontogeny impacts the learning
47 ability of a facultatively family-living animal, the tree skink. Traditionally the
48 relationship between social environment and learning has been examined in obligate
49 social species. But, examining this relationship in species across all social systems
50 aids in our understanding of the evolution of sociality, and the consequences and

51 limitations of each social system. We found the social environment tree skinks were
52 raised in did not affect their social or individual learning abilities across three
53 foraging tasks. Our findings provide an initial examination of how social environment
54 impacts learning in a facultatively social species.

55

56 **Keywords:** aggregation, cognition, facultative sociality, individual learning, reptile,

57 social learning

58

59 **Introduction**

60 Learning ability is expected to impact survival; for instance, spatial learning ability
61 may benefit foraging, mating opportunities and predator avoidance, and innovation
62 may enhance survival in novel environments (Dukas 2004). An animal may learn by
63 trial-and-error from information coming directly from the environment (Shettleworth
64 2010); or, particularly within social species, an individual can utilize social
65 information through the observation of, or interaction with, a conspecific (aka. social
66 learning; Hoppitt and Laland 2013). In both cases, an individual's ability to learn may
67 be affected by a range of factors: for instance, age (Noble et al. 2014; Takahashi et al.
68 2014), stress level (Boogert et al. 2013; Crino et al. 2014), sex (Einon 1980; Carazo et
69 al. 2014), personality (Sih and Del Giudice 2012; Trompf and Brown 2014), and
70 developmental environment (i.e., abiotic factors: Clark et al. 2013, Dayananda and
71 Webb 2017; social factors: Thornton and Lukas 2012, Hoppitt and Laland 2013, etc.).
72 Perhaps the most dramatic and best-known factor impacting cognitive development is
73 the social environment during ontogeny.

74 The effect of early social environment was first demonstrated in 1965, in the
75 impaired learning abilities of socially-isolated juvenile rhesus macaques (*Macaca*
76 *mulatta*; Harlow et al. 1965). Subsequently, many studies have confirmed a negative
77 relationship between isolation rearing and individual learning in social mammals and
78 birds. Yet, this relationship is not always consistent and a variable/positive effect of
79 isolation on learning has also been found (Greenough et al. 1972; Morgan et al. 1975;
80 Einon 1980; Juraska et al. 1984; Wongwitdecha and Marsden 1996; Frisone et al.
81 2002; Apelfelbeck and Raess 2008; Cacioppo and Hawley 2009; Goerlich et al.
82 2012). Isolation rearing has the potential to also affect an individual's social learning
83 ability, because it can reduce an individual's ability to associate with conspecifics,

84 and hinder their comprehension of social cues and behavior (e.g., facial signalling,
85 dominance hierarchies; Harlow et al. 1965; Taborsky and Oliveira 2012;
86 Schausberger et al. 2017). This may limit an individual's exposure to social
87 information and/or their ability to use, process, and comprehend social information
88 from conspecifics. Thus, isolation rearing may impact both individual and social
89 learning ability.

90 To date, the relationship between social developmental environment and
91 learning ability has been predominately examined in obligate social species, limiting
92 its generality. Animal sociality varies from species that are mostly solitary (i.e.,
93 forming only temporary aggregations for the purposes of mating) to those that live in
94 complex societies (e.g., eusocial insects) or stable, long-term kin groups (e.g.,
95 primates). Restricting the examination of how social developmental environment
96 impacts learning ability to only obligate social species constrains our understanding to
97 only a particular suite of selective forces, and does not offer us a comparative
98 evolutionary perspective (Ward and Webster 2017). Animals with facultative sociality
99 are particularly promising systems for research on how social environment impacts
100 development. In species with facultative sociality, parental care is often not required,
101 which allows the social environment to be manipulated unlike in other animals where
102 parental care is obligate (Whiting and While 2017).

103 Here, we examine the effect of isolation rearing on a facultatively-social
104 lizard. Tree skinks (*Egernia striolata*) exhibit facultative, kin-based sociality
105 (Chapple 2003). *Egernia striolata* can be found alone or in groups of variable size (2-
106 10 skinks) mainly consisting of kin (Chapple 2003). Over 80% of aggregations
107 sampled for relatedness consist of parent-offspring relationships or sibling
108 relationships (Duckett et al. 2012). Thus, tree skink social groups are thought to be

109 formed by consecutive litters of offspring remaining with parents, which results in
110 groups with stable mating pairs and variously aged juveniles (Chapple 2003). Yet,
111 there is intra- and inter-population variation in their social behavior and organization.
112 Aggregation tendency depends on their age, sex, and relatedness (Bonnett 1999). For
113 instance, females are often more solitary than males, and sub-adults are more likely to
114 inhabit crevices with at least two other individuals (Bonnett 1999; Duckett et al.
115 2012). The social organization of within a tree skink population also varies over time
116 and space, suggesting that seasonal and environmental factors may also influence
117 their social organization (Bustard 1970; Duckett et al. 2012). Interestingly, tree skink
118 social rearing environment also affects their morphological and behavioural
119 development (Riley et al. 2017); a lack of social exposure (e.g., rearing in isolation)
120 and the type of social interactions experienced during development (e.g., competitive
121 or aggressive encounters) both impact juvenile growth and behavior (e.g., sociability,
122 aggression, and boldness; Riley et al. 2017).

123 Social structure of also varies between tree skink populations; for example,
124 within arboreal populations, skinks are manly found in small groups (maximum of 3
125 skinks) or alone (Bustard 1970; Cunningham et al. 2007) but in other arboreal and
126 saxicolous populations, tree skinks form social groups ranging up to a maximum of
127 10 individuals (Bonnett 1999; Michael and Cunningham 2010; Duckett et al. 2012).
128 The variable nature of tree skink sociality makes it a good model for studying the
129 generality of the relationships between early rearing and learning ability using an
130 experimental framework that manipulates the social rearing environment to mimic
131 what juveniles may experience in the wild. Furthermore, adult female tree skinks
132 socially-learn from conspecifics (MJW et al. unpubl. data), allowing us to examine
133 the effects of early rearing on social as well as individual learning ability.

134 We presented skinks from two rearing treatments (social or isolated) with
135 three learning tasks under two learning treatments (social or individual learning). Our
136 aim was to quantify the impact of social rearing environment on both individual and
137 social learning. We hypothesized that isolation rearing would hinder cognitive
138 development and reduce an individual's likelihood of using social information. We
139 predicted: 1) isolated skinks would be less likely and take longer to learn compared to
140 socially-reared skinks, 2) the social learning treatment would be more likely and be
141 faster to learn compared to the individual learning treatment, and 3) that isolated
142 skinks would be less likely to use social information compared to socially-reared
143 skinks.

144

145 **Material and methods**

146 We used 32 tree skinks that were offspring from 19 females collected near Albury,
147 New South Wales (35.98'S, 146.97'E; see supplementary materials for details about
148 parturition, husbandry, and measurements). After all juveniles were born, we
149 randomly allocated juveniles into two rearing treatments: either isolated or social.

150 We used a total of 16 isolated (housed alone), and 16 socially raised (housed
151 within 8 unrelated pairs) juveniles within our experiment. Our captive rearing
152 treatments reflect juvenile social behaviour that has been reported in wild tree skink
153 populations; juvenile groups range in size from pairs to 4 individuals, and juveniles
154 have also been observed on their own (Bonnett 1999; Michael and Cunningham 2010;
155 Duckett et al. 2012, JLR unpubl. data). Including parents in the social treatment was
156 not logistically feasible because adult *Egernia* are known to be highly aggressive
157 towards juveniles. Infanticide has been reported in several *Egernia* group spp.
158 (Lanham and Bull 2000; Post 2000; O'Connor and Shine 2004); there are even

159 instances, within captivity, where females eat their own offspring (*E. stokesii*,
160 Lanham and Bull 2000; *E. striolata*, JLR pers. obs. 2015). Thus, due to ethical and
161 logistical considerations, our study was restricted to social groups consisting of
162 juveniles, although wild social groups often consist of parent(s) and offspring
163 (Chapple 2003). Skinks resided within rearing treatments for approximately 1.5 years
164 before we quantified their learning ability (see experimental design below). During
165 development, both isolated and socially reared skinks had limited visual exposure to
166 adult conspecifics during a separate study (details in supplementary materials).

167 During the learning trials, we housed juveniles in newspaper-lined, opaque
168 plastic tubs (390 mm W x 580 mm L x 390 mm H) divided in half by a fixed
169 transparent Perspex[®] divider covered by a removable opaque wooden cover. This
170 allowed us to keep skinks physically separated while also controlling when they
171 viewed each other. The tubs contained a water dish and a refuge (120 mm W x 175
172 mm L x 38 mm H). A 100 W heat lamp was directed at the refuge, which allowed
173 skinks to thermoregulate and illuminated each tub. We fed skinks 3 house crickets
174 (*Acheta domesticus*; adults for adult skinks and nymphs for juveniles) dusted with
175 calcium and vitamins once a week after assays were completed. Other than that, the
176 only food the skinks received was the food reward (1.25 ml of puréed fruit; Heinz[®]
177 apple and pear) that was offered twice daily, and eaten only if the learning task was
178 completed successfully.

179

180 ***Learning trial design***

181 Our learning trial was modified from Noble et al. (2014) by altering the food reward
182 from mealworms to 1.25 ml of puréed fruit (Heinz[®] baby food: apple, and pear). The
183 experiment consisted of motor, discrimination, and reversal learning tasks.

184 There were two learning treatments: social learning, where skinks observed a
185 conspecific demonstrator correctly executing the task, and individual learning, where
186 skinks simply observed a non-demonstrating conspecific. We allocated an equal
187 number of isolated and socially reared skinks to each learning treatment (Table S1).
188 We randomly paired an unrelated, adult female skink with each experimental skink
189 for a total of 16 ‘demonstrators’ and 16 ‘non-demonstrating’ conspecifics. The same
190 individuals were paired with each focal skink across all three learning tasks.
191 Demonstrators were trained prior to the experiment with the focal skinks (details in
192 supplementary materials) and performed tasks correctly in all experimental trials,
193 which ensured that focal skinks received the correct social information.

194 Prior to trials commencing, we gave skinks 48 hours to acclimate to the novel
195 trial housing. At the beginning of all trials the opaque wooden cover was removed to
196 allow the experimental skink and adult female to view each other’s portion of the
197 enclosure through the transparent Perspex[®] divider. The experimental skink’s water
198 dish and refuge were also removed to ensure an unobstructed view. After 20 min of
199 the experimental skink viewing the conspecific, the wooden cover was replaced, the
200 task apparatus was placed within the experimental skink’s enclosure, and the
201 experimental skink attempted each task for 1 hour. Trials were remotely video-
202 recorded for behavioral scoring. We conducted two trials each weekday, in the
203 morning (0900-1130 h) and the afternoon (1330-1600 h).

204

205 *(a) Motor task (lid removal)*

206 This task required skinks (N = 32; Table 1) to remove an opaque, yellow lid from a
207 dish to gain a food reward (Video S1). Skinks were given 24 trials to complete this

208 task, and were classified as learners if they performed 5/6 trials correctly (Table S2).

209 Twenty-nine skinks (91%) learnt this task, and moved on to the discrimination task.

210

211 *(b) Discrimination task*

212 This task required skinks (Table 1) to learn that a blue lid was a reliable cue for a

213 reward, when presented with two dishes on a wooden block (blue vs. white lid; Video

214 S1). Tree skinks do not show any significant difference in preference for blue or white

215 (MJW et al. unpubl. data). To control for chemical cues, we placed puréed fruit in

216 both dishes but the reward in the dish with the white lid was inaccessible because of

217 mesh covering under the lid (Fig. S1). Both lids were removable from both dishes,

218 and this task was scored as being performed correctly if a skink removed the blue lid

219 first (Video S1). A skink could investigate both lids (e.g., via tongue-flicking or visual

220 investigation), but if it removed the white lid first the task was scored as incorrect. We

221 randomly counter-balanced the blue lid's location across rearing and learning

222 treatments. Skinks were given this task for 24 trials, and were classified as learners if

223 they performed 7/8 trials correctly (Table S3). All skinks learnt this task, and moved

224 on to the reversal task.

225

226 *(c) Reversal of discrimination task (hereafter, reversal)*

227 This task was identical to the discrimination task with two exceptions: 1) skinks

228 needed to learn that the white lid now cued reward, instead of the blue lid (Video S1),

229 and 2) skinks were given this task for 34 trials as it was more challenging. Ten skinks

230 (34%) met the reversal task's learning criterion (7/8 trials correct; Table S4).

231

232 ***Behavioral Scoring***

233 From video recordings we scored successful task performance during each trial (either
234 removing the yellow lid, or the correctly colored lid first). Behavioral scorers marked
235 videos blind to skink rearing treatment.

236 Prior to statistical analysis, we investigated potential inter-observer bias
237 between scorers. JLR and AK scored task success (removing the dish lid) from motor
238 task videos, and JLR, AK and TD scored task success (removing the correctly colored
239 lid) in discrimination and reversal tasks. Inter-observer reliability statistics were run
240 from data for 21% of the trials for the motor task (N = 160), as well as the
241 discrimination and reversal task combined (N = 145) using Cohen’s Kappa (using the
242 function *cohen.kappa* from the R package *psych* in R v 3.0.3; Kaufman and Rosenthal
243 2009; R Core Team 2016). For all tasks, inter-observer agreement scores were high
244 (motor task $k = 0.96$; discrimination and reversal task ranged from $k = 0.98$ to 1), and
245 coincided with what are considered “excellent” ($k \geq 0.75$; Kaufman and Rosenthal
246 2009).

247

248 ***Assessment of learning criteria***

249 Prior to statistical analyses we also needed to assess if our learning criteria were
250 appropriate in categorizing skinks that learnt from those that did not. For this
251 assessment we used the subset of skinks that had a minimum of six trials after the trial
252 in which they reached the task’s learning criterion (Table S2, S3, S4). Unfortunately,
253 our sample size of skinks that met the learning criterion for the reversal task was too
254 low to perform the assessment. But for the motor and discrimination tasks, we
255 assessed the robustness of our learning criteria by tallying the number of
256 correct/incorrect choices made by each skink from its final trial needed to reach
257 learning criterion to its very last trial (e.g., if a skink performed 5/6 trials correctly

258 during the motor task we started the tally at the 6th trial; Noble et al. 2012, 2014;
259 Riley et al. 2016; Table S2, S3, S4). We tested whether this tally of correct/incorrect
260 choices was significant according to an exact binomial choice test (Carazo et al. 2014;
261 Noble et al. 2014). For the motor and discrimination tasks respectively, 25/27 (93%)
262 and 25/28 (89%) of skinks performed the task correctly significantly more than
263 expected by chance after meeting the learning criteria. Our findings suggest that our
264 learning criterion for the motor and discrimination tasks was sufficient in categorizing
265 individuals that learnt from those that did not.

266

267 ***Statistical Analysis***

268 First, we explored the data to ensure it fitted the assumptions of our analyses (Zuur et
269 al. 2009). During this process we removed missing values where applicable, thus
270 there are a variable number of observations and individuals within each model
271 (sample sizes are provided in all results tables; Table S5, S6, S7).

272 To fit all our generalized linear mixed effect models (GLMMs) we used the
273 function *glmer* in the *lme4* R package (Bates et al. 2015). For all models, we opted to
274 use the simplest possible model to avoid over-parameterization and issues with model
275 convergence (see details below). The potential confounding factors of skink sex and
276 size were experimentally balanced across rearing and learning treatments to minimize
277 any impact on the data (Table S1). Also, we have previously found that sex does not
278 significantly affect tree skink learning (Riley et al. 2016). For all models, α was set at
279 0.05. When we predicted fitted lines from the models for visualization, we set the
280 factorial fixed factors to intercept-level values.

281 Data from motor, discrimination, and reversal tasks were analyzed separately, but
282 the variables included in each of the models were consistent (see Tables S5, S6, and
283 S7 for finalized models):

284 (1) This binomial GLMM examined if the *probability of learning a task* (learner = 1,
285 non-learner = 0) was influenced by the *rearing treatment* (isolated or social) or
286 *learning treatment* (social or individual). We also included the additional fixed
287 effect of an interaction between *rearing treatment* x *learning treatment*, but
288 removed this effect and re-ran the model if it was not significant. We accounted
289 for dependency between observations of multiple skinks from each clutch by
290 including a random intercept for *mother identity*. We also included a random
291 intercept for *housing tub* to incorporate dependency among observations of
292 skinks from the same captive environment (e.g., social pairings). We did not
293 analyze the probability of learning the discrimination task because all skinks were
294 successful; this analysis was only performed for the motor and reversal task.

295 (2) This Poisson GLMM examined if the *number of trials taken to learn the task* was
296 influenced by the *rearing treatment* (isolated or social) or *learning treatment*
297 (social or individual). If significant, the model also included an interaction
298 between *rearing treatment* x *learning treatment*. This model also included the
299 random intercepts of *mother identity* and *housing tub*.

300 (3) This binomial GLMM examined if *probability of task success during each trial*
301 (either removing the lid or correctly choosing lid color = 1) was influenced by
302 *trial number* (aka. time), *rearing treatment* (isolated or social) or *learning*
303 *treatment* (social or individual). This model also included the random intercepts
304 of *mother identity* and *housing tub*, as well as a random intercept and slope for
305 *juvenile identity* across trial number to incorporate the dependency among

306 repeated observations of the same individual. If their effect was significant, we
307 also included the additional fixed effects of interactions between *rearing*
308 *treatment* x *learning treatment*, *trial number* x *rearing treatment*, and *trial*
309 *number* x *learning treatment*.

310 We also calculated unconditional means and corresponding 95% CIs (corrected
311 for non-independence) using the function *Effect* in the R package *effect* (Fox 2003;
312 Fox and Hong 2009). Unconditional means of all response variables in each task
313 (*probability to learn*, *number of trials until learnt a task*, and *probability of task*
314 *success*) were calculated for each rearing and learning treatment. Assessment of
315 unconditional means and the magnitude of their differences (i.e., effects) places more
316 emphasis on biological significance, rather than just statistical significance (which can
317 be affected by sample size) of differences between our treatments (Nakagawa and
318 Cuthill 2007; Gerstner et al. 2017).

319

320 **Results**

321 *(a) Motor task*

322 Rearing treatment did not affect whether a skink learnt the motor task ($z = -0.60$, $p =$
323 0.55 ; Table 1). Isolated skinks learnt the motor task in, on average, three fewer trials
324 than socially reared skinks ($z = -2.09$, $p = 0.04$; Table 2). The probability of removing
325 the lid during a trial was only an average of 9% higher for isolated skinks, and this
326 difference was non-significant ($z = 1.73$, $p = 0.08$; Table 2).

327 Learning treatment did not affect whether a skink learnt this task ($z = -0.60$, p
328 $= 0.55$), the number of trials to learn the task ($z = -0.15$, $p = 0.88$; Table 1), or the
329 probability of removing the lid during a trial ($z = 0.86$, $p = 0.39$).

330 Across trials, the probability of removing the lid increased as trials progressed
331 ($z = 6.95, p < 0.01$; Fig. 1A).

332

333 *(b) Discrimination task*

334 Skinks from all rearing and learning treatments successfully learnt this task. Neither
335 rearing nor learning treatment affected the number of trials necessary to learn the
336 discrimination task (rearing treatment: $z = -0.38, p = 0.70$; learning treatment: $z =$
337 $0.28, p = 0.78$; Table 1), or the probability of making a correct choice (rearing
338 treatment: $z = -1.01, p = 0.31$; learning treatment: $z = -0.62, p = 0.53$). Across trials,
339 the probability of removing the correct lid increased as trials progressed ($z = 3.67, p <$
340 0.01 ; Fig. 1B).

341

342 *(c) Reversal task*

343 Neither rearing nor learning treatment affected whether a skink learnt the task (rearing
344 treatment: $z = 0.84, p = 0.40$; learning treatment: $z = 0.16, p = 0.88$), the number of
345 trials needed to learn the task (rearing treatment: $z = 0.14, p = 0.89$; learning
346 treatment: $z = 0.06, p = 0.95$; Table 1), or the probability of making a correct choice
347 (rearing treatment: $z = 0.32, p = 0.75$; learning treatment: $z = -0.22, p = 0.83$). Across
348 trials, the probability of removing the correct lid increased as trials progressed ($z =$
349 $5.29, p < 0.01$; Fig. 1C).

350

351 **Discussion**

352 Our hypothesis that isolation would hinder tree skink cognitive development
353 was not supported; in most cases we found no effect of rearing treatment on tree skink
354 performance for any of our three cognitive tasks. Indeed, isolated skinks learnt the

355 motor task faster than socially reared skinks – a finding opposite to our prediction.
356 However, the effect of rearing treatment on learning speed was weak, as reflected in
357 the conditional means (Table 2). We did not find strong evidence that social
358 environment during tree skink ontogeny affects their learning ability.

359 Our results contrast with the harmful effects of isolation rearing on cognitive
360 ability that have previously been found in obligate social mammals and birds.
361 Potentially, alternative cognitive tasks may have revealed a negative impact of rearing
362 treatment (Harlow et al. 1965; Thornton and Lukas 2012); but we also failed to find
363 any effect of rearing environment on tree skink individual learning in a previous
364 study, where they were presented with a vertical, spatial maze (Riley et al. 2017). Our
365 findings therefore corroborate previous results on this species, and suggest that tree
366 skink learning ability is not negatively affected by developing in social isolation. This
367 finding may be due to the facultative nature of tree skink sociality and parental care
368 (Chapple 2003). Conversely, in mammals and birds where sociality and parental care
369 is largely obligate, the requirements of social exposure for behavioral development
370 may be more fixed. Perhaps a mammal or bird with facultative sociality (e.g., the
371 African striped mouse; Schradin et al. 2011) would show the same, unexpected lack
372 of relationship between isolation and learning ability.

373 An alternative hypothesis is that the presence or absence of parents, siblings
374 and/or kin during development may affect tree skink cognition, whereas the presence
375 of an unrelated individual does not. Our rearing treatments did not include parents due
376 to logistical constraints (see above) so these potential effects could not be quantified.
377 Offspring of *Egernia* spp. benefit from the presence of parents by gaining protection,
378 enhanced thermoregulation, and increased access to prey (O'Connor and Shine 2004;
379 Langkilde et al. 2007). Litters of *E. whitii* form size-based dominance hierarchies in

380 which competition reduces growth and increases mortality in the youngest siblings
381 (While and Wapstra 2008); so the social environment can also be costly for *Egernia*
382 spp. Benefits and costs of living with kin still need to be considered in the cognitive
383 development of *E. striolata*. Furthermore, cognitive development in natural
384 populations may differ from that of our captive-reared individuals; thus, an
385 investigation into the cognitive abilities within natural tree skink populations would
386 be beneficial.

387 Nonetheless, the social rearing environments within our study were
388 comparable to the social environments found in natural tree skink populations (Riley,
389 2017; JLR unpublished data). Simply because tree skink social pairs were unrelated in
390 this study does not mean that our subjects detected lack of genetic kinship. The
391 mechanism behind kin recognition in *E. striolata* remains unknown, and may either
392 be based on phenotypic matching or on cues learnt from developing in proximity to
393 their natal, family social group (i.e., familiarity; Bull et al. 2001). Although unrelated
394 juveniles were paired within our social rearing treatment, these individuals lacked
395 exposure to related skinks post-birth, so we would expect that individuals would
396 determine their social group based on proximity and familiarity (similar to what may
397 happen via crevice-sharing in the wild; Bull et al. 2001). During development, we
398 observed similar social interactions within our social pairs as have been observed in
399 litters of the closely-related *Egernia whitii* (While and Wapstra 2008). Aggressive
400 encounters are common in *E. whitii* litters, which can impact juvenile survival and
401 growth rates (While and Wapstra 2008). We similarly documented antagonistic
402 encounters within social pairs of tree skinks in our study, which increased the
403 incidence of tail loss and affected their growth rates (Riley et al. 2017). Thus, it would
404 be interesting to repeat our study and manipulate relatedness within the social group

405 to investigate if this impacts tree skink cognitive development in a different manner
406 than our findings.

407 Contrary to our predictions, we also found no evidence that sub-adult tree
408 skinks used social information. Social learning propensity may develop as individuals
409 age (Leris and Reader 2016), or may not be present at particular life-stages (Noble et
410 al. 2014). In the context of our study, sub-adults may avoid unfamiliar adults because
411 they can be lethally aggressive (Chapple 2003; O'Connor and Shine 2004). We are
412 therefore hesitant to conclude that tree skinks cannot use social information. Instead
413 we suggest that sub-adults may not be motivated to use social information from
414 unfamiliar, potentially aggressive, adults. There is prior research that suggests that
415 competition, aggressive interactions, and dominance hierarchies may influence an
416 individual's use of social information (Laland 2004; Kendal 2014; Leris and Reader
417 2016). For example young guppies (*Poecilia reticulata*) do not use social information
418 from adults likely because they are not motivated to visit locations where larger adult
419 guppies were present due to the potential for aggression interactions (Leris and
420 Reader 2016). Yet, a guppy's use of social information changed once they reached
421 adulthood, and the size difference between the observer and demonstrator was
422 reduced (Leris and Reader 2016). Future research, focusing on social learning
423 between individuals matched in age or between individuals within the same social
424 group (i.e., familiar and/or related) may still find evidence that tree skinks learn
425 socially.

426 In summary, we did not find that isolation rearing hindered tree skink learning
427 ability. Our study is an initial examination of how social environment impacts
428 individual and social learning in a facultatively social species that is from a
429 taxonomic group (squamate reptiles) underappreciated for their degree of sociality.

430 Our results contrast with the majority of findings in obligate social mammals and
431 birds, and this difference may stem from this species' variable social system, and
432 suggests that other facultatively social taxa may also be unaffected by isolation
433 rearing.

434

435 **Compliance with ethical standards**

436 **Ethical approval** Experimental protocols were approved by the Macquarie
437 University Animal Ethics Committee (ARA no. 2013/039). Our research was
438 approved by the New South Wales National Parks and Wildlife Service, Office of
439 Environment and Heritage (License no. SL101264).

440

441 **Conflict of interest** The authors declare that they have no conflict of interest.

442

443 **Data accessibility** All data and R code from this study can be accessed from the
444 Bitbucket repository at https://bitbucket.org/julia_riley/social-learning-analysis

445

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576

577 **TABLES**

578

579 **Table 1** Sample sizes (N), number of skinks that learnt each task, and the average number of trials it took to learn all tasks (with 95% CIs
 580 calculated from raw data) for each rearing and learning treatment

Rearing Treatment	Learning Treatment	<i>(a) Motor Task</i>			<i>(b) Discrimination Task</i>			<i>(c) Reversal Task</i>		
		N	Number of Learners	Number of Trials Taken to Learn	N	Number of Learners	Number of Trials Taken to Learn	N	Number of Learners	Number of Trials Taken to Learn
Social	Social	8	7	12 (9 to 15)	7	7	10 (7 to 13)	7	1	30
Social	Individual	8	8	13 (9 to 17)	8	8	12 (7 to 16)	8	3	22 (14 to 31)
Isolated	Social	8	7	10 (4 to 15)	7	7	12 (9 to 14)	7	2	24 (14 to 33)
Isolated	Individual	8	7	9 (5 to 13)	7	7	9 (7 to 11)	7	4	28 (17 to 38)

581

582

	<i>(a) Motor Task</i>			<i>(b) Discrimination Task</i>		<i>(c) Reversal Task</i>		
	Probability of Learning the Task	Number Trials Taken to Learn	Probability of Trial Success	Number Trials Taken to Learn	Probability of Trial Success	Probability of Learning the Task	Number Trials Taken to Learn	Probability of Trial Success
<i>Rearing Treatment</i>								
Social	0.94 (0.67, 0.99)	12.32 (9.84, 15.42)	0.84 (0.68, 0.93)	10.73 (8.95, 12.87)	0.90 (0.85, 0.94)	0.21 (0.03, 0.68)	24.30 (19.69, 29.99)	0.39 (0.30, 0.48)
Isolated	0.88 (0.61, 0.97)	9.18 (7.29, 11.55)	0.93 (0.84, 0.97)	10.24 (8.55, 12.27)	0.87 (0.81, 0.92)	0.41 (0.15, 0.73)	24.80 (20.98, 29.31)	0.41 (0.32, 0.50)
<i>Learning Treatment</i>								
Social	0.88 (0.61, 0.97)	10.58 (8.43, 13.28)	0.91 (0.80, 0.96)	10.68 (8.85, 12.88)	0.88 (0.82, 0.92)	0.31 (0.09, 0.69)	24.70 (20.53, 29.72)	0.40 (0.32, 0.49)
Individual	0.94 (0.67, 0.99)	10.79 (8.70, 13.38)	0.87 (0.73, 0.94)	10.32 (8.68, 12.28)	0.90 (0.84, 0.93)	0.28 (0.06, 0.70)	24.50 (20.35, 29.50)	0.39 (0.30, 0.48)

583 **Table 2** Unconditional means and 95% CIs for each rearing and learning treatment

584

585

586 **FIGURE CAPTIONS**

587

588 **Fig. 1** Probability of removing the correct lid during each trial of the **(a)** motor, **(b)**
589 discrimination, and **(c)** reversal task for isolated skinks (grey 95% CI polygon and
590 solid fitted line) and socially-reared skinks (black dotted 95% CI lines and dashed
591 fitted line)