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Abstract Social learning is thought to be advantageous as it allows an animal to gather information quickly without engaging in costly trial-and-error learning. However, animals should be selective about when and whom they learn from. Familiarity is predicted to positively influence an animal's reliance on social learning; yet, few studies have empirically tested this theory. We used a lizard (*Liopholis whitii*) that forms long-term monogamous pair bonds to examine the effects of partner familiarity on social learning in two novel foraging tasks, an association and reversal task. We allowed female lizards to observe trained conspecifics that were either familiar (social mate) or unfamiliar execute these tasks and compared these two groups with control females that did not receive social information. Lizards preferentially relied on trial-and-error learning in the association task. In the reversal task, lizards that were demonstrated by familiar partners learnt in fewer trials compared to control lizards and made more correct choices. Our results provide some evidence for context-dependent learning with lizards differentiating between when they utilize social learning, and, to a limited degree, whom they learnt from. Understanding the role of the social context in which learning occurs provides important insight into the benefits of social learning and sociality more generally.

Keywords (separated by '-') Cognition - Social learning - Familiarity - Reptiles - *Egernia*

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We provide novel evidence that individual characteristics, such as familiarity, mediate the propensity to utilize social information and in more nuanced ways than theory would predict.
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Mate familiarity and social learning in a monogamous lizard

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Abstract

Social learning is thought to be advantageous as it allows an animal to gather information quickly without engaging in costly trial-and-error learning. However, animals should be selective about when and whom they learn from. Familiarity is predicted to positively influence an animal's reliance on social learning; yet, few studies have empirically tested this theory. We used a lizard (*Liopholis whitii*) that forms long-term monogamous pair bonds to examine the effects of partner familiarity on social learning in two novel foraging tasks, an association and reversal task. We allowed female lizards to observe trained conspecifics that were either familiar (social mate) or unfamiliar execute these tasks and compared these two groups with control females that did not receive social information. Lizards preferentially relied on trial-and-error learning in the association task. In the reversal task, lizards that were demonstrated by familiar partners learnt in fewer trials compared to control lizards and made more correct choices. Our results provide some evidence for context-dependent learning with lizards differentiating between when they utilize social learning, and, to a limited degree, whom they learnt from. Understanding the role of the social context in which learning occurs provides important insight into the benefits of social learning and sociality more generally.

Keywords Cognition · Social learning · Familiarity · Reptiles · *Egernia*

Introduction

The ability of animals to acquire, process and act on information in their environment is fundamental to their fitness (Dayananda and Webb 2017). There are a multitude of ways in which an animal can acquire this information. For example, an individual can rely on personal information via

trial-and-error learning (e.g., asocial learning) or alternatively an individual can rely on information acquired through the observation of and/or interaction with others (e.g., social learning). While social learning was once considered largely restricted to animals living in groups, it is now recognized that a wide range of organisms, not generally thought to be social, utilize social learning strategies (Duffy et al. 2009; Wilkinson et al. 2010a; Noble et al. 2014; Trompf and Brown 2014). Indeed, social learning is predicted to be highly advantageous, allowing individuals to avoid the costs of trial-and-error learning (such as increased effort and risk) (Heyes 1994; Shettleworth 2010; Hoppitt and Laland 2013). Utilizing conspecifics as an information source is thought to be particularly advantageous when the cost of asocial learning is high, especially if there is overlap in resource requirements (such as mate choice decisions and food acquisition) and/or shared predators (Galef and White 1998; Brown and Laland 2003; Lonsdorf and Bonnie 2010).

Theoretical work suggests that, despite its broad benefits, social learning should not be used indiscriminately; instead individuals should adopt strategies that dictate the circumstances under which they copy others, and from whom they learn (Laland 2004; Galef and Laland 2005; Heyes 2016;

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49 Leris and Reader 2016). Coussi-Korbel and Fragaszy (1995)
 50 argue that certain characteristics of the individual conveying
 51 information (e.g., the demonstrator), such as age, sex, domi-
 52 nance status, level of success (i.e., mating/foraging), or the
 53 relationship to the focal individual, should affect the likeli-
 54 hood of social learning occurring (referred to as ‘directed
 55 social learning’). Such context dependent social learning
 56 has fundamental implications for the way in which infor-
 57 mation is transferred through animal populations (Kawai
 58 1965; van de Waal et al. 2010; Aplin et al. 2015; Dubosq
 59 et al. 2016). Despite this, relatively few studies have experi-
 60 mentally tested the extent to which individuals discriminate
 61 between social information sources (see Nicol and Pope
 62 1994; Swaney et al. 2001; Schwab et al. 2008; Noble et al.
 63 2014; Kar et al. 2017).

64 Familiarity is one aspect of the social environment that
 65 is likely to be particularly important in the context of social
 66 learning. Familiar demonstrators are likely to impact focal
 67 individual decisions in a number of different ways. First,
 68 familiar individuals are more likely to occur in the same
 69 temporal and spatial environment; thus, they should convey
 70 more accurate information specific to dealing with that par-
 71 ticular environment. An individual would therefore benefit
 72 more by copying behaviours of familiar demonstrators com-
 73 pared to unfamiliar individuals (Boyd and Richerson 1988;
 74 Galef and Giraldeau 2001; Laland 2004). Secondly, famili-
 75 arity between the focal individual and the demonstrator
 76 means that focal individuals will have previous experience
 77 regarding the accuracy of the information conveyed (Heyes
 78 and Pearce 2015). Indeed, familiarity with a demonstrator
 79 results in more effective acquisition of information in a vari-
 80 ety of species including fishes (foraging decisions: Lachlan
 81 et al. 1998; Swaney et al. 2001; shoaling decision: Griffiths
 82 2003), rodents (predator response: Kavaliers et al. 2005),
 83 and birds (foraging decisions: Scheid et al. 2007; Benskin
 84 et al. 2002; nest building: Guillette et al. 2016). Despite such
 85 studies providing valuable insights into the complexity of
 86 social learning and the extent to which social information is
 87 conveyed differentially through animal populations, studies
 88 that explicitly test the causal role of familiarity in mediating
 social information transfer are still uncommon.

90 Social monogamy is a particular form of familiarity
 91 whereby males and females pair up over multiple repro-
 92 ductive seasons. One hypothesis for the evolution of stable
 93 social monogamy is that it provides benefits in terms of the
 94 ability of individuals to produce and raise offspring (‘mate
 95 familiarity hypothesis’: Black 1996). This suggests some
 96 level of coordination between the social partners, mediated
 97 by information transfer (Sanchez-Macouzet et al. 2014; Leu
 98 et al. 2015). Here we examined the role that mate famili-
 99 arity plays in mediating the acquisition and use of social
 100 information in a monogamous family living lizard, *Liopholis*
 101 *whitii* (previously *Egernia whitii*). While social monogamy

is relatively rare in reptile systems, species from the Austral-
 ian *Egernia* group form long-term stable pair bonds (Bull
 2000) and vary in their social complexity from largely soli-
 tary species to those that live in large stable social groups
 (reviewed in Chapple 2003). Specifically, *L. whitii* form sta-
 ble nuclear family groups consisting of long-term socially
 monogamous pairs and their offspring (Chapple and Keogh
 2005; While et al. 2009b). Pairs remain together throughout
 the year sharing territories and shelter sites and fending off
 conspecific intruders, whereas offspring disperse within the
 first year or prior to reaching reproductive maturity (While
 et al. 2009a). Pair stability between years is high with some
 pairs remaining together for nine years (While et al. 2009b,
 GMW unpublished data). As a result of this pair stability,
 individuals within a population (i.e., the surrounding lizards
 outside the pair) vary in their degree of familiarity providing
 us with a unique opportunity to examine the effect of famili-
 arity on social learning in a natural lizard system.

We tested whether familiarity impacts social learning in
L. whitii using two social learning experiments. We com-
 pared the performance of female lizards that had access to
 trained demonstrators that were either their familiar pair-
 partner or an unknown male to females that had no dem-
 onstration. Based on the prolonged association between
 pairs in this species, and the potential benefits of relying
 on social information from closely affiliated individuals,
 we predicted that individuals with access to social learning
 would learn in fewer trials in both learning tasks, and indi-
 viduals with access to social demonstration from familiar
 partners should learn more readily than those with an unfa-
 miliar demonstrator.

Methods

Study species

Liopholis whitii is a medium sized [up to 100 mm snout-
 vent length (SVL)], viviparous lizard found throughout a
 broad altitudinal (0–1600 m) and habitat (coastal heaths,
 grasslands, and forests) range in south-eastern Australia
 (Chapple 2003; Wilson and Swan 2003). Males and females
 are sexually monomorphic and reach reproductive maturity
 at approximately 3 years and have an overall lifespan of
 10–15 years (GMW unpublished data).

Animal capture and husbandry

At the start of November 2015, we caught 124 *L. whitii* (62
 males, 62 females) from wild populations on the east coast
 of Tasmania (42°57'S, 147°88'E). We selectively targeted 20
 mating pairs ($n = 40$ individuals) that would remain together
 throughout the experiment. Mating pairs were determined

149 based on shared crevice site use, which is a defining fea- 200
 150 ture of *Egernia* mating pairs (Chapple 2003; While et al. 201
 151 2015) that has been used previously to define social mates 202
 152 (While et al. 2009a, b; Halliwell et al. 2017 for similar 203
 153 approaches). Once captured, sex was determined by eversion 204
 154 of the hemipenes, and lizards were individually marked with 205
 155 non-toxic metallic marker (Artline 990 XF Silver) before 206
 156 being transported in cool, damp cloth bags to the University 207
 157 of Tasmania (~1 h drive). At the University, lizards were 208
 158 weighed (± 1 mg) and measured for SVL and total length 209
 159 (± 0.5 mm). Lizards were then housed in opaque tubs [57 210
 160 (L) \times 38 (W) \times 32 (H) cm], provided with cat litter as a sub- 211
 161 strate (~5 thick) and a rock as a basking site and a refuge. 212
 162 Basking lights (25 W) and overhead UV lighting were set 213
 163 to 0800–1800 h night/day cycle to provide thermoregula- 214
 164 tory opportunities. Lizards had constant access to water and 215
 165 were fed twice daily with mealworms (*Tenebrio molitor*) 216
 166 as part of the experimental protocol, with the exception of 217
 167 demonstrators in the ‘control’ treatment who were provided 218
 168 with two mealworms every second day (see below). At the 219
 169 completion of the experiment, lizards were released back 220
 170 into the natural populations from which they were captured. 221

171 Social learning experiments 212

172 We established three treatment groups reflective of the 213
 173 nature of the relationship between the focal individual and 214
 174 their demonstrator that would occur naturally (While et al. 215
 175 2009b). In group one, social information was provided by 216
 176 the focal individual’s (familiar) partner ($n = 20$ mating pairs, 217
 177 hereafter ‘social familiar’). In group two, social information 218
 178 was provided by an unfamiliar individual to the focal indi- 219
 179 vidual ($n = 22$ pseudo-randomly paired males and females; 220
 180 males from this treatment were rotated every 14 days to 221
 181 maintain a level of unfamiliarity between the male and 222
 182 female pairings, hereafter ‘social unfamiliar’. While a pre- 223
 183 vious study has shown that individuals can become “famil- 224
 184 iar” with one another over relatively short periods of time 225
 185 (Wilkinson et al. 2010b), this familiarity is very different 226
 186 to the level of familiarity that individuals have as a result of the 227
 187 long-term pair bonding observed in this species. Group three 228
 188 was a control group in which the focal individual viewed 229
 189 a random conspecific but received no social information 230
 190 regarding the novel learning tasks [i.e., the control demon- 231
 191 strator did not perform the task ($n = 20$ pseudo-randomly 232
 192 paired males and females; males rotated between females 233
 193 every 14 days, hereafter ‘control’)]. To remove potential 234
 194 sex-effects, we used only females as ‘observers’ and males 235
 195 as ‘demonstrators’. Male–female pairs were housed together 236
 196 in the female home cage but were divided with both a fixed 237
 197 transparent Perspex and a removable opaque Perspex. Due 238
 198 to the placement of the fixed transparent barrier, recogni- 239
 199 tion of familiarity and unfamiliarity between the pairs was 240

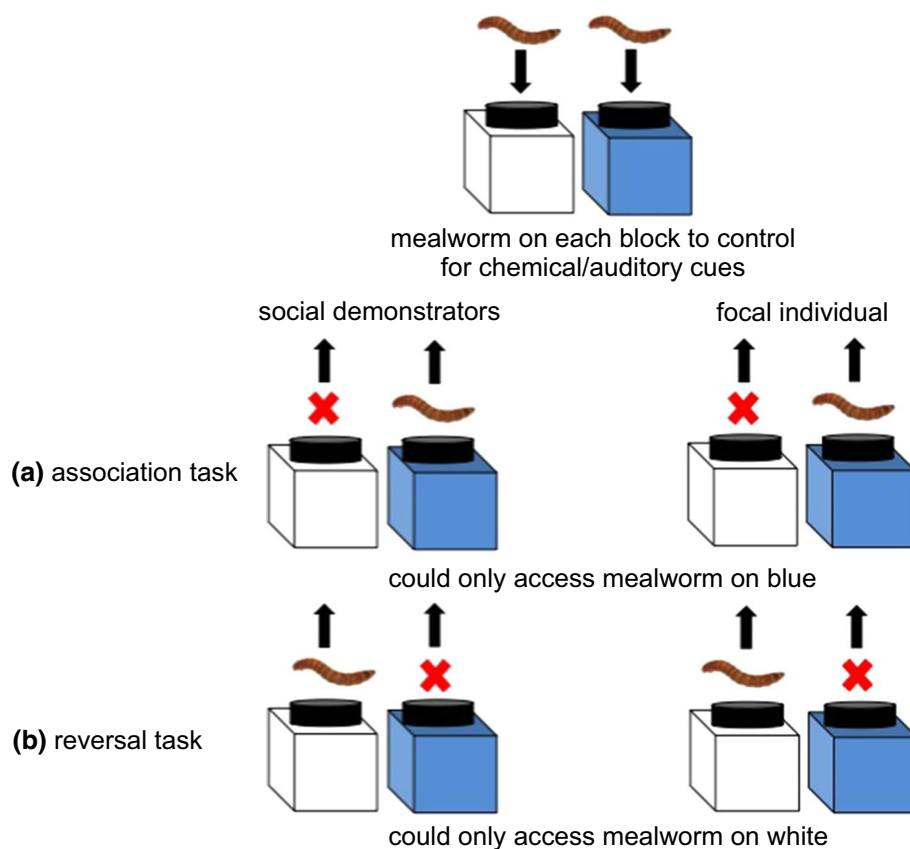
200 predominantly visual during the task. However, substrate 201
 202 exchange underneath both the fixed and the removable barri- 203
 204 ers allowed lizards access to chemical cues about their part- 204
 205 ner, and we often observed lizards exploring the boundary 205
 206 whilst tongue flicking excessively. All trials were conducted 206
 207 in home cages, and video recorded using a CCTV system 207
 208 (H.264 DVR with Sony 1/2" high resolution colour cam- 208
 209 eras). We conducted experiments twice-daily, in the morning 209
 210 (0900–1030 h) and afternoon (1300–1430 h) with a mini- 210
 211 mum interval between trials of 1.5 h. Trials were run daily, 211
 212 except every 14th day when demonstrators from the social 212
 213 unfamiliar and control treatment were rotated. 213

214 Our two social learning experiments consisted of an asso- 214
 215 ciation task with a reversal and were based on learning tasks 215
 216 previously used with lizards (Clark et al. 2013; Noble et al. 216
 217 2014). Each task consisted of two blocks of wood [7 (L) \times 7 217
 218 (W) \times 4 (H) cm] being placed in front of the lizard. A petri 218
 219 dish (6 cm diameter) was placed on top of each block using 219
 220 putty (Bluetak[®]) and was used as a food-well. In addition 220
 221 to dishes being elevated, we wrapped each dish in black, 221
 222 opaque tape to ensure that lizards could not use visual cues 222
 223 during the experiment. We placed a mealworm (~3 cm long) 223
 224 in each of the dishes for both the social demonstrators and 224
 225 the focal lizards to control for chemical and auditory cues, 225
 226 but the reward could only be accessed in one of the dishes. 226
 227 We used fiberglass window screening (601 mm mesh screen) 227
 228 to block access to the mealworm on the opposite block. The 228
 229 block placed on the right side was always blue, and the block 229
 230 placed on the left was always white. The position of the 230
 231 blocks did not change throughout the experiments. This was 231
 232 done deliberately to accelerate learning, as our goal was not 232
 233 to understand whether lizards were using colour or spatial 233
 234 cues to learn. Given sample size constraints, we were not 234
 235 able to counter balance the colour cues (i.e., when a sub- 235
 236 sample within each treatment and task were given either 236
 237 white or blue as the reward dish. While it is possible that 237
 238 lizards learnt one colour more easily than the other, there 238
 239 is no evidence that this occurs in this species (Munch et al. 239
 240 2018). Despite this, we checked individual choice data for 240
 241 any biases toward a colour or side prior to analysis and found 241
 242 no obvious biases (see “Statistical analysis”). 242

241 Demonstrator training 241

242 Before commencing either of the social learning experi- 242
 243 ments, we trained the demonstrators from the ‘social famil- 243
 244 iar’ and ‘social unfamiliar’ treatment ($n = 42$) to access a 244
 245 food reward from a specific coloured block. For the associa- 245
 246 tion task they had to access the food reward from the blue 246
 247 block, whereas for the reversal task, they had to access the 247
 248 reward from the white block (Fig. 1). To solve the task, the 248
 249 lizard had to climb the block and access the food reward 249
 250 hidden in the opaque food dish. The task was designed to 250

Fig. 1 Tasks presented to social demonstrators and focal (observer) lizards in both the **a** association task and **b** reversal task. (Online version in colour)



251 be relatively easy compared to those used in other learning
 252 studies on lizards (e.g., manipulation of lids; Clark et al.
 253 2013; Noble et al. 2014; Kar et al. 2017) as previous experi-
 254 ments with this species showed that they are unwilling to
 255 manipulate objects (KLM unpublished data). This most
 256 likely reflects the foraging behaviour of *L. whitii* where they
 257 are predominantly ambush predators (i.e., waiting for prey
 258 to pass their crevice site) rather than active foragers (GMW
 259 pers. obs.). We considered lizards to have learnt the task
 260 when they chose the correct block first in 7/8 sequential tri-
 261 als. We continued to give them the task after they achieved
 262 this learning criterion in order to assess the robustness of the
 263 learning criterion (only for the association task) but capped
 264 the number of trials at 75; this was not done for the reversal
 265 task due to time restrictions (see supplementary material).
 266 Lizards learnt the criterion within 7–75 trials in the associa-
 267 tion task (mean \pm standard errors (SE): 29.90 ± 3.54 ; $n = 42$)
 268 and within 10–161 trials in the reversal task (mean \pm SE:
 269 64.21 ± 7.06 ; $n = 29$). Other studies have previously reported
 270 that lizards often need more trials (up to twice as many) to
 271 learn a reversal task given the increased complexity of undo-
 272 ing previously associations (e.g., Clark et al. 2013; Kar et al.
 273 2017). We expected that demonstrators that learnt would
 274 make some incorrect choices during the experiment so we
 275 choose to control for this in our analysis (see “Statistical
 276 analysis”). In theory, however, incorrect choices might help

277 facilitate learning as it shows the observers which options
 278 are wrong (Beauchamp and Kacelnik 1991).
 279

Association task

280 Once we had trained the demonstrator lizards in the associa-
 281 tion task we then moved onto testing the focal lizard’s abil-
 282 ity to learn that specific task. The association task required
 283 focal lizards ($n = 62$, $n = 20$ ‘social familiar’, $n = 22$ ‘social
 284 unfamiliar’, $n = 20$ ‘control’) to associate a food-reward
 285 with the blue block (Fig. 1a). Each task consisted of two phases:
 286 1) a demonstration phase in which the focal individual was
 287 allowed to observe the demonstrator completing the task,
 288 and 2) a social learning phase in which the focal individual
 289 attempted to complete the task. During the demonstration
 290 phase, we removed the opaque Perspex (the fixed, transpar-
 291 ent Perspex still in place) between the demonstrating and
 292 focal lizards to provide an unobstructed view of the dem-
 293 onstrating lizard executing the task (social treatments) or
 294 just the conspecific lizard (control). After 30 min of view-
 295 ing, the trial entered the social learning phase in which we
 296 replaced the opaque divider, added the blocks to the focal
 297 lizard’s cage and allowed it to attempt the task. We gave
 298 the focal lizards a 30-min observation period, as we knew
 299 from the demonstrator training that this was roughly the
 300 time it took lizards with previous experience with the task

301 to choose correctly without allowing for multiple choices.
 302 The experimental setup was identical between demonstra-
 303 tor and focal lizards except that we capped the number of
 304 trials at 75 (based on the demonstrator training). We used
 305 a two-step learning criteria to assess whether lizards had
 306 learnt the task. First, they had to successfully chose the blue
 307 block as their first choice in 7/8 sequential trials. We then
 308 ensured that they were 'true' learners by checking that they
 309 maintained their learning for a further 7 trials (i.e., 70%
 310 correct choices). Those that did not maintain their learning
 311 were not classified as having learnt the task. See supple-
 312 mentary material for robustness of the learning criterion.
 313 Focal lizards were allowed to continue with the task even if
 314 incorrect choice were initially made; however, these trials
 315 did not count towards the learning criterion. Focal lizards
 316 reached the learning criterion within 7–58 trials (mean \pm SE:
 317 19.57 ± 1.94 ; $n = 40$). Not all lizards learnt the task ($n = 22$);
 318 these were excluded from the subsequent reversal task.

319 Reversal task

320 The reversal task required the focal lizards (total $n = 38$;
 321 $n = 10$ 'social familiar', $n = 14$ 'social unfamiliar', $n = 14$
 322 'control') to reverse their previous learning and associate
 323 the food reward with the white rather than the blue block
 324 (Fig. 1b). Two pairs were excluded due to the escape or
 325 death of one of the pair members [$n = 2$; $n = 1$ 'social famil-
 326 iar', $n = 1$ 'unfamiliar']. We first trained the demonstrator
 327 lizards in the reversal task and then moved onto testing the
 328 focal lizards. As with the previous task, we gave focal lizards
 329 a 30-min viewing phase of the demonstrating lizard execut-
 330 ing the task (social treatments) or just the demonstrator liz-
 331 ard (control), before allowing them to attempt the task. Focal
 332 lizards received more trials (a maximum of $n = 145$ trials)
 333 in total for the reversal task as it took some of them longer
 334 to reach the learning criterion (range 7–117; mean \pm SE:
 335 51.52 ± 5.94 ; $n = 21$). As with the previous task, we always
 336 ensured that they were 'true' learners by checking that they
 337 maintained their learning for a further 7 trials (i.e., 70% cor-
 338 rect choices). Not all lizards learnt the task ($n = 17$).

339 Statistical analysis

340 An observer scored all trials for each of the two tasks; the
 341 observer was blind to the treatments for the social groups
 342 (i.e., the social familiar and unfamiliar treatment) but not
 343 to the control treatment, as the 'demonstrator' in this group
 344 did not perform the trials in any of the tasks. For each trial,
 345 the behaviour scored for both the demonstrator and focal
 346 lizard was the lizard's first choice (i.e., whether it chose the
 347 correct dish first). A lizard was considered to have made a
 348 choice when it placed its front claws on the top edge of the
 349 block. To ensure that there were no unconscious biases, a

research assistant re-scored a random selection of 10% of
 our trials ($n = 365$ trials), while being blind to the hypoth-
 esis, original score and the treatment. We assessed score
 agreement between the two observers using Cohen's Kappa
 (using the 'psyche' package in R v 3.2.2; Revelle 2017).
 Cohen's Kappa agreement scores are considered 'excel-
 lent' when $k \geq 0.75$ (Kaufman and Rosenthal 2009). Scores
 agreed 100% of the time ($k = 1$) indicating that our scores
 were accurate and unbiased. We analysed our data in three
 different ways. Lizards that did not reach the learning cri-
 terion during a task were excluded from all analyses (asso-
 ciation task, total $n = 22$; reversal task, total $n = 17$). First,
 we compared the number of lizards that learnt (i.e., those
 achieving the 7/8 correct) in the association and in the rever-
 sal tasks using a Fisher's exact test to examine whether our
 treatments impacted the total number of lizards learning.
 Second, to compare how quickly lizards learnt in each of the
 three treatments for both the association and reversal tasks,
 we compared the mean number of trials taken to reach our
 learning criteria using a generalised linear model (GLM)
 with a negative binomial error distribution. Given the logis-
 tical constraints in obtaining large samples sizes, which can
 impact P values, we also calculated Hedge's g to estimate
 the effect size between the treatment groups (Hedges et al.
 1999). We compared the effect sizes for the mean number of
 trials taken to learn the tasks between: (a) 'social familiar'
 and 'control' lizards, (b) 'social familiar' and 'social unfa-
 miliar' lizards and (c) 'social unfamiliar' and 'control'. We
 used Cohen's (1988) benchmarks of small (0.2), medium
 (0.5) and large (0.8) effects as a guide to interpreting the
 magnitude of effect size.

Third, to test for differences in the rates of learning (i.e.,
 how cognitive performance changed across trials) in our
 treatments we retained all individual choice data. We then
 modelled the probability of focal lizards choosing the correct
 dish first ('1' = yes; '0' = no) as a function of the independent
 variables, lizard treatment (i.e., 'control', 'social unfamiliar'
 and 'social familiar'), trial and the interaction between treat-
 ment and trial to test for differences in learning rate. We also
 included a quadratic parameter of trial in the models to test
 for the possibility that trial number was not necessarily lin-
 early related to the probability of choosing correct. We used
 generalised linear mixed effects models (GLMMs) with a
 Bernoulli probability distribution ('logit' link). Lizard treat-
 ment (i.e., 'control', 'social unfamiliar' and 'social famil-
 iar') was included as an independent variable in our model.
 This approach explicitly allows us to incorporate both
 between- and within-individual variation in choices, improv-
 ing power, whilst still allowing us to estimate group-level
 changes in probability of making correct choices (increases
 of which provide evidence for learning) in the different
 treatments (see Kar et al. 2017; Riley et al. 2016 for similar
 approaches). While mass did not differ significantly between

403 the treatment groups (ANOVA: $F_{2,58} = 1.89, P = 0.16$), body
 404 size (SVL) did (ANOVA: $F_{2,59} = 4.04, P = 0.02$). However,
 405 this was only the case for ‘control’ and ‘unfamiliar social’
 406 treatments. Nonetheless, we included body size to account
 407 for the possible effects of SVL on learning (Amiel et al.
 408 2014). To control for non-independence of lizard choices, we
 409 estimated a random slope (i.e., trial) and intercept for each
 410 lizard (i.e., a random regression model). In all models, we
 411 also included an observation-level random effect to account
 412 for over-dispersion; this did not impact results, and so, we
 413 present models without this variance estimate throughout.

414 We carried out a number of additional analyses that
 415 allowed us to assess the robustness of our results to compo-
 416 nents of our experimental design. First, we tested whether
 417 the choices made by focal lizards in social treatments were
 418 impacted by the choices made by the demonstrators. Such
 419 effects might be predicted to differ between treatments as
 420 lizards in familiar treatments might pay more attention to
 421 the choices of the familiar demonstrator compared to lizards
 422 in with unfamiliar demonstrators. To test for this possibility,
 423 we re-ran the above models while including an interaction
 424 parameter between the treatment and the choice made by
 425 demonstrators in each trial. This was only run for the social
 426 familiar and unfamiliar treatment groups as ‘control’ groups
 427 did not have demonstrators for the task. Second, we tested
 428 for inherent colour/side bias in individuals. We expected
 429 that individuals that choose randomly without any colour/
 430 side preferences would have approximately 50:50 correct/
 431 incorrect choices within a task before they learnt, and that
 432 the number of trials expected to learn would be shorter for
 433 the association task, than for the reversal task (Noble et al.
 434 2012; Kar et al. 2017). None of the lizards that learnt in
 435 either of the tasks displayed any obvious bias, and we there-
 436 fore included all lizards that learnt our analyses.

437 Parameters in all models were estimated using a likeli-
 438 hood framework in R version 3.3.2 (R Core Team 2016).
 439 GLMMs were modelled with the *glmer* function in the
 440 ‘lme4’ package (Bates et al. 2015), whereas GLMs were

run using ‘stats’ package (R Core Team 2016). We z-trans-
 441 formed all continuous variables (i.e., SVL and trial) prior
 442 to analysis by mean centring and dividing by their standard
 443 deviation to improve model interpretation (Schielzeth 2010).
 444 Nested models were compared using likelihood ratio tests
 445 assuming the likelihood ratio followed a Chi square distri-
 446 bution with the degrees of freedom equal to the number of
 447 parameters that differed between the models.
 448

Results

Association task

449
 450
 451 Forty of 62 (67%) lizards were categorized as learners
 452 [social familiar, $n = 11$ of 18 (61%); social unfamiliar, $n = 15$
 453 of 22 (68%); control, $n = 14$ of 20 (70%)]. There was no
 454 significant difference between treatments in the number of
 455 learners (Fisher’s exact test: $P = 0.83$), or between treatment
 456 groups in the mean number of trials it took the lizards to
 457 learn (Likelihood ratio test (*LRT*): $df = 2, \chi^2 = 1.00, P = 0.61$;
 458 Fig. 2a). Effect sizes were small between the treatment
 459 groups (‘social familiar’ vs. ‘control’, Hedge’s $g = 0.18$,
 460 $SE = 0.39$; ‘social familiar’ vs. ‘social unfamiliar’, Hedge’s
 461 $g = 0.39, SE = 0.39$; ‘social unfamiliar’ vs. ‘control’, Hedge’s
 462 $g = -0.16, SE = 0.36$).

463 The probability of correctly choosing the reward
 464 dish increased nonlinearly across trials (*LRT*: $df = 1$,
 465 $\chi^2 = -0.20, P < 0.001$; Table 1; Fig. S1a). That is, focal
 466 lizards initially increased their probability of choosing
 467 correct, only to decrease their number of correct choices
 468 in the second half of the task. This suggests that over-
 469 training may have occurred in this task (see Carazo et al.
 470 2014). This pattern did not differ between treatments
 471 (Trial² × treatment interaction, *LRT*: $df = 2, \chi^2 = 0.25$
 472 $P = 0.88$). Demonstrators made a number of incorrect
 473 choices during trials. However, controlling for the demon-
 474 strator’s choice in analyses of the two social treatments did

Fig. 2 Number of trials (mean ± SE) until an individual reached the learning criterion (7/8 trials) for **a** the association task and **b** the reversal task. ** $P < 0.05$, N.S. not significant for treatment difference. (Online version in colour)

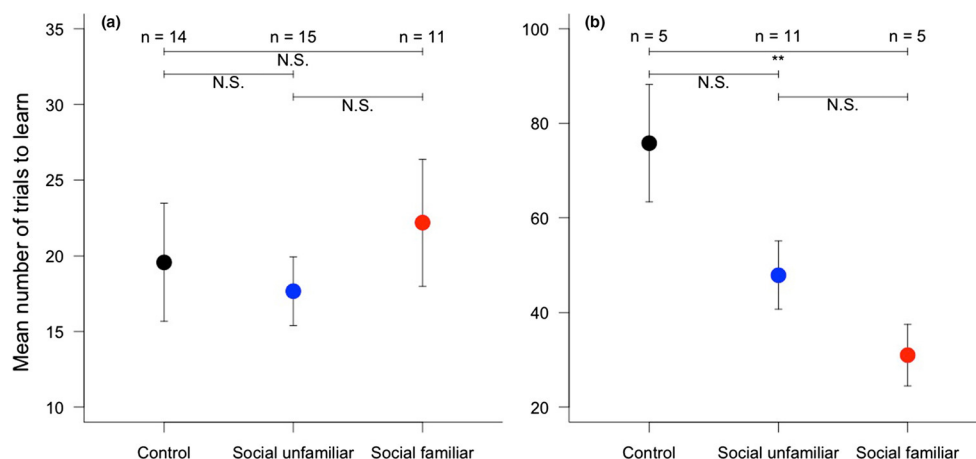


Table 1 Parameter estimates and 95% confidence intervals for generalized linear mixed effects models (GLMMs) examining the effect of familiarity (control, social familiar and social unfamiliar) on social learning in an association and a reversal task with trial modelled as non-linear

	Association task				Reversal task			
	Estimate	Lower	Upper	<i>P</i>	Estimate	Lower	Upper	<i>P</i>
Intercept	1.40	1.06	1.76	< 0.001	0.07	-0.52	0.54	0.98
Body size (SVL)	0.12	-0.09	0.32	0.25	-0.27	-0.56	0.03	0.07
Trial number	0.18	0.02	0.35	0.03	0.79	0.48	1.17	< 0.001
Trial number ²	-0.20	-0.31	-0.09	< 0.001	0.11	-0.05	0.28	0.17
Treatment social unfamiliar	-0.07	-0.55	0.40	0.78	0.57	-0.08	1.28	0.08
Treatment social familiar	-0.27	-0.77	0.23	0.30	0.86	0.05	1.72	0.03

The models examine the probability for observers of making correct choices (association task: $N_{\text{obs}} = 2463$, $N_{\text{observer lizards}} = 40$, $N_{\text{demonstrator}} = 53$; reversal task: $N_{\text{obs}} = 1193$, $N_{\text{observer lizards}} = 21$, $N_{\text{demonstrator}} = 26$). Statistically significant results are shown in bold

475 not affect the probability of the observer choosing correct
476 ($LRT: \chi^2 = 0.62$, $P = 0.43$) and this did not differ between
477 the two social treatments (demonstrator's choice \times treat-
478 ment interaction, $LRT: \chi^2 = 1.29$, $P = 0.26$; Table S1).

479 Reversal task

480 Twenty-one of the 38 (55%) lizards were categorized as
481 learners [social familiar, $n = 5$ of 10 (50%); social unfam-
482 ilar, $n = 11$ of 14 (79%); control, $n = 5$ of 14 (36%)].
483 There was no statistically significant difference between
484 the treatments in the number of learners (Fisher's exact
485 test: $P = 0.08$). However, there was a significant differ-
486 ence between the treatment groups in the mean number
487 of trials it took lizards to learn ($LRT: df = 2$, $\chi^2 = 7.62$,
488 $P = 0.02$; Fig. 2b) with lizards in the 'social familiar'
489 treatment learning the reversal task in significantly fewer
490 trials compared to 'control' lizards (Hedges' $g = -1.82$,
491 $se = 0.70$). While this effect was weaker when compar-
492 ing the 'social familiar' to 'social unfamiliar' treatment
493 (Hedges' $g = -0.74$, $SE = 0.53$) and 'social unfamiliar' to
494 'control' (Hedges' $g = -1.05$, $SE = 0.54$), all were moder-
495 ate to strong effects.

496 The probability of choosing the correct dish significantly
497 increased across trials in the reversal task ($LRT: \chi^2 = 19.01$,
498 $p < 0.001$; Table 1). While the increased probability in
499 choosing the correct dish across trials did not differ signifi-
500 cantly between treatment groups (trial \times treatment interac-
501 tion, $LRT: df = 2$, $\chi^2 = 2.87$, $P = 0.24$), on average, lizards in
502 'social familiar' treatment made more correct choices than
503 'control' lizards ($P = 0.04$; Table 1). We found no evidence
504 that the relationship between the probability of choosing cor-
505 rect and trial was nonlinear (Trial², $LRT: \chi^2 = 1.89$, $P = 0.17$;
506 Table 1; Fig. S1b). Demonstrator choice did not affect the
507 choice made by the focal (observer) lizard ($LRT: \chi^2 = 0.43$,
508 $P = 0.51$) and this did not differ between the two social treat-
509 ments (demonstrator's choice \times treatment interaction: LRT :
510 $\chi^2 = 0.12$, $P = 0.73$; Table S1).

Discussion

We found that *L. whitii* learning from familiar demonstrators use social information to reverse previously learnt associations – learning the reversal task in fewer trials and making more correct choices compared to the control group. This fits with our predictions, namely that individuals with access to social learning would learn in fewer trials, and that lizards with familiar demonstrators would learn more readily. This was not the case for the association task where individuals preferentially relied on trial-and-error learning, suggesting that social learning might not be used indiscriminately. Below we discuss these results in the context of *L. whitii* social system and findings from other species along with the broader implications of our results for our understanding social learning.

We found evidence that lizards expedited learning by making use of social information in the reversal task, but not the association task. Specifically, lizards with access to familiar social information performed better (i.e., learnt quicker and made more correct choices) in the reversal task, learning in nearly half the time compared to the control lizards. The reason why social learning would be utilized to learn a reversal, but not an association task is not entirely clear. One explanation may be that social information is more useful when personal information becomes unreliable as a result of encountering a more complex problem. Indeed, Boyd and Richerson (1988) suggest that individuals will take advantage of relatively cheap information provided by others when personal information becomes costly or difficult to acquire ('costly information hypothesis'). While the costs associated with learning in our foraging tasks are likely minimal, the association task may have been simple enough that trial-and-error learning was a sufficient learning strategy. Our finding of a non-linear relationship between trial and probability of correct choice in this task further supports the idea that the task was simple, as lizards appear to have lost their motivation to engage with the task halfway through the trial process due to over-training (see Carazo

549 et al. 2014). In contrast, in the reversal task, where the com-
 550 plexity increased, previous foraging knowledge became out-
 551 dated and it became advantageous to use social information.
 552 While we cannot confirm this without additional experimen-
 553 tal work (e.g., subjecting different groups of lizards to tasks
 554 of varying complexity and measuring their relative use of
 555 social vs. asocial learning), previous research has shown that
 556 task difficulty influences the particular learning strategy that
 557 an individual undertakes (Laland 2004; Kendal et al. 2005).
 558 For example, captive *callitrichid* monkeys switch learning
 559 strategies when presented with a series of novel puzzle box
 560 tasks that varied in difficulty, only relying on social learning
 561 to solve the more difficult puzzle boxes (Day et al. 2003). An
 562 alternative explanation for our findings may be that lizards
 563 were more habituated to the experimental design during the
 564 reversal task, allowing them to pay more attention to the
 565 demonstrators.

566 Learning from socially familiar individuals elicited a
 567 faster rate of learning compared to lizards without social
 568 information, whereas learning from unfamiliar lizards did
 569 not elicit as strong of an effect. This provides some sup-
 570 port for the suggestion that individuals not only rely on
 571 social information but they may do so more from familiar
 572 individuals compared to unfamiliar ones. It is possible that
 573 by allowing lizard in the 'social unfamiliar' treatments to
 574 interact with their demonstrators for 14 days we may have
 575 dampened the differences between the two social treatment
 576 groups, as the lizards would have become more familiar
 577 with their demonstrator over time. While additional work
 578 is required to confirm the importance of familiarity, given
 579 that a limited number of lizards learnt the reversal task
 580 overall (dropping power), these results are in line with
 581 previous research showing that the identity of the demon-
 582 strator can have important implications for the extent to
 583 which individuals rely on social vs. asocial information
 584 (Nicol and Pope 1994; Swaney et al. 2001; Schwab et al.
 585 2008; Noble et al. 2014). These results also provide some
 586 evidence for the 'mate familiarity hypothesis' in *L. whittii*
 587 (Black 1996), which predicts that social monogamy should
 588 select for greater information transfer between long-term
 589 partners in order to coordinate reproductive behavior
 590 (Sanchez-Macouzet et al. 2014; Leu et al. 2015). Further
 591 work, which focus on the length of the pair bond may
 592 provide further insights into the nature of effect of pair
 593 familiarity on social learning within this system. Indeed,
 594 the actual length of the familiar pair bonds were unknown
 595 for our animals and could have varied quite significantly
 596 (e.g., pair bond lengths vary from 1 to 9 years in this sys-
 597 tem; GMW unpublished data) and may mean our result of
 598 familiarity-effect on social learning were relatively con-
 599 servative. Repeating this experiment with lizards of known
 600 pair length provides an exciting potential avenue for future
 601 research. It would also be interesting to examine whether

602 there are differences between males and females in their
 603 use of social learning and how that related to the identity
 604 of the demonstrator, as previous studies have reported sex
 605 differences in both brain structure and learning ability in
 606 lizards (LaDage et al. 2009; Carazo et al. 2014).

607 Despite evidence of social information use, the accu-
 608 racy of the choices made by demonstrators did not appear
 609 to influence the performance of the focal lizards. It is gen-
 610 erally assumed that individuals should preferentially learn
 611 from successful demonstrators (Laland 2004), however,
 612 empirical studies have found that this might not always be
 613 the case (Beauchamp and Kacelnik 1991; Nicol and Pope
 614 1999; Swaney et al. 2001). Furthermore, any wrong initial
 615 choices by the demonstrators may help served to reinforce
 616 correct choices later on (Beauchamp and Kacelnik 1991;
 617 Templeton 1998).

618 In summary, we show that individuals that learnt the
 619 association task relied on trial-and-error learning but
 620 switched learning strategies to make use of social infor-
 621 mation for the reversal task. Furthermore, we show that in
 622 those circumstances, individuals learnt to solve the task in
 623 fewer trials and made more correct choices when demon-
 624 strated to by familiar demonstrators. While further work
 625 is required to confirm these results, our study adds to the
 626 growing evidence that individual characteristics, such as
 627 familiarity, may mediate the propensity to utilize social
 628 information in more nuanced ways than theory would pre-
 629 dict (Kendal et al. 2005). Social learning can be affected
 630 not only by the social dynamics that exist among indi-
 631 viduals, but also by the social setting in which individuals
 632 find themselves. We argue that a greater appreciation for
 633 the social contexts in which learning is expressed, and
 634 explicitly examining not only when but also whom animals
 635 learn from, will provide important insight into the fitness
 636 benefits of social learning and sociality more generally. **AQ3**

637 **Data availability** All data generated and analysed during this
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 648 GMW. KLM wrote the paper with assistance from all authors.

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655 Compliance with ethical standards

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

658 **Ethical approval** All applicable institutional and national guidelines for
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660 here was conducted with the approval of the University of Tasmania's
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