

1 **Precocial juvenile lizards show adult level learning and behavioural flexibility**

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26 In altricial species, young rely on parental care and brain maturation mainly occurs after
27 birth. In precocial species, young are born in a more advanced developmental stage in need of
28 less or no parental care and brain development is mostly completed at the time of birth. We
29 therefore predicted early maturation of learning ability in precocial species. We used a series
30 of visual discrimination and reversal stages to investigate the ability of the precocial eastern
31 blue-tongue lizard, *Tiliqua scincoides scincoides*, a long-lived Australian lizard species with
32 slow-developing young, to respond to changes in stimulus relevance and test for behavioural
33 flexibility. To test whether age affects learning in this species, we compared juveniles (23–56
34 days) with adults (sexually mature, at least 2 years). In accordance with our expectations,
35 adults and juveniles performed similarly well in all stages, suggesting that juveniles of this
36 precocial species learn at adult levels from an early age. Both age classes performed well
37 during reversals showing good behavioural flexibility. This is the first study in lizards to
38 directly compare juvenile and adult behavioural flexibility. Importantly, we demonstrate that
39 precocial lizards can begin life with an advanced cognitive ability already in place.

40

41 *Keywords:* age difference, altricial–precocial, cognition, ID/ED attentional set shifting,
42 squamates

43

44 Species vary in the degree to which offspring are independent and cognitively developed at
45 birth or hatching. Altricial young are born at an early developmental stage dependent on
46 parental care, whereas precocial young are more advanced and need little or no parental care
47 (Charvet & Striedter, 2011; Grand, 1992). These differences in developmental trajectory also
48 directly affect brain maturation and size. For example, while adult altricial birds have a
49 greater relative brain volume than adults of precocial species, the opposite can be seen in
50 juveniles. Altricial bird species experience most neural growth posthatching, while in

51 precocial species most brain maturation occurs before hatching (Charvet & Striedter, 2011;
52 Iwaniuk & Nelson, 2003). Similar trends can be seen in mammals (Grand, 1992).

53 Consequently, developmental mode is expected to affect cognitive ability at an early age.

54 With low or no parental investment, young of precocial species experience many
55 early life challenges. For example, relatively small body size and the absence of parental
56 protection makes juveniles vulnerable to predation (Genovart et al, 2010). Young precocial
57 vertebrates show adult-like locomotor skills in coping with predation and competing with
58 conspecifics for resources (Herrel & Gibb, 2005). Rapid and flexible learning might similarly
59 improve competitive capability and survival. In precocial red junglefowl, *Gallus gallus*, for
60 example, juveniles outperform adults on reversal learning (Zidar et al., 2018). However, the
61 extent to which juveniles can problem-solve and show behavioural flexibility has largely
62 been studied in a few altricial species (e.g. Newman & McGaughy, 2011; Weed, Bryant, &
63 Perry, 2008).

64 Behavioural flexibility can be measured in different ways, including reversal learning
65 and intradimensional (ID)/extradimensional (ED) attentional set shifting (Brown & Tait,
66 2015). In tests of reversal learning, animals first learn a discrimination between at least two
67 stimuli of which only one is rewarded. After this discrimination is acquired, the reward
68 contingencies change to one of the formerly nonrewarded stimuli. Reversal learning is
69 affected by the inability to inhibit responding to the previously rewarded stimulus. When
70 testing set shifting, multiple discrimination stages are used to develop a perceptual attentional
71 set which is later challenged by a shift to a novel set (e.g. a second dimension). More
72 specifically, a comparison is made between learning performance in an ID acquisition, a
73 discrimination between novel stimuli of an already learned set (e.g. colour dimension) and an
74 ED shift during which reinforcement is moved to stimuli of a novel set (e.g. shape dimension;
75 Dias, Robbins, & Roberts, 1996; Roberts, Robbins, & Everitt, 1988). Learning during a shift

76 is slowed by attentional perseveration to the formerly relevant dimension, as the subject
77 learns the newly relevant aspect of the stimuli that predicts the rewarded outcome. The skill
78 with which the challenges of reversal and shifting are overcome indicate a subject's level of
79 behavioural flexibility (Brown & Tait, 2015; Garner, Thogerson, Wurbel, Murray, & Mench,
80 2006).

81 Set shifting and reversal learning are mediated by different subregions of the
82 mammalian prefrontal cortex and underlying abilities including attention, inhibition and
83 working memory develop slowly until adolescence (Brown & Tait, 2015; McAlonan &
84 Brown, 2003; Moriguchi & Hiraki, 2013; Newman & McGaughy, 2011). For example,
85 children find performing an ED shift extremely challenging at 3 years of age; at the age of 5,
86 however, children shift with no difficulty (e.g. Romine & Reynolds, 2005; Zelazo & Frye,
87 1998). Similar results have been obtained in monkeys. Young monkeys make more errors
88 during reversal and shift learning compared to adults (e.g. Weed et al., 2008). In rodents, the
89 results are less clear. While some studies indicate the same trend as found in humans and
90 monkeys (adolescent rats, *Rattus norvegicus*, took longer to learn during reversals and a shift;
91 e.g. Newman & McGaughy, 2011), others found no such difference (juvenile mice, *Mus*
92 *musculus*, learnt at similar levels to adults; e.g. Johnson & Wilbrecht, 2011).

93 To the best of our knowledge, no direct comparison of juvenile and adult behavioural
94 flexibility has been made in a precocial animal species in which adults show no parental care.
95 Previous studies have shown that lizards have an ability to perform a visual choice reversal
96 (e.g. Burghardt, 1978; Clark, Amiel, Shine, Noble, & Whiting, 2014; Day, Crews, &
97 Wilczynski, 1999; Day, Ismail, & Wilczynski, 2003; Gaalema, 2007; 2011; Leal & Powell,
98 2012), successfully learn in an ID/ED attentional set-shifting task (Szabo, Noble, Byrne, Tait,
99 & Whiting) and solve novel problems (e.g. Manrod, Hartdegen, & Burghardt, 2008), all
100 indicative of behavioural flexibility (Auersperg et al., 2014). However, no data are available

101 to compare behavioural flexibility between different age classes of the same lizard species
102 (but see Noble, Byrne, & Whiting, 2014). Our aim was to investigate whether and how
103 behavioural flexibility differs between juvenile and adult individuals in the precocial eastern
104 blue-tongue lizard, *Tiliqua scincoides scincoides*. This species is a large, diurnal,
105 omnivorous, viviparous skink that gives birth to well-developed offspring (Koenig, Shine, &
106 Shea, 2001; Phillips, Roffey, Hall, & Johnson, 2016; Shea, 1981). Its generalist feeding
107 habits and relatively slow developing young make it an excellent candidate to investigate
108 age-related learning and behavioural flexibility in a multistage discrimination task. Because
109 precocial species are born with a more advanced and developed brain, we predicted similar
110 levels of behavioural flexibility in both juvenile and adult lizards.

111

112 <H1>METHODS

113 <H2>*Study Animals*

114 We acquired 12 wild-caught and two captive-bred adult (Appendix Table A1) eastern blue-
115 tongue lizards between November 2016 and February 2017 from the suburban Sydney area,
116 New South Wales, Australia, where the species is relatively abundant, to participate in the
117 set-shifting experiment (Koenig et al., 2001; Phillips et al., 2016; Shea, 1981). During
118 December/January 2017 and 2018, seven wild-caught and one captive female gave birth in
119 captivity (litter size range 7–19, mean \pm SD = 12.13 \pm 4.36). We randomly selected 16
120 juveniles to participate in this study; two each from two females and one each from four
121 females ($N = 8$) in 2017 and four each from two females ($N = 8$) in 2018 (Appendix Table
122 A2). Snout–vent length (SVL), total length (TL), head width (HW), head height (HH), head
123 length (HL) and weight of all lizards were determined on the day of arrival/birth, 1 week
124 before the start of the experiment; to monitor growth rate juveniles were measured every 5
125 weeks. All animals (except for two males and eight juveniles) were individually identified

126 using passive integrated transponders (PITs; Biomark, HPT8, 8.4 mm long x 1.4 mm in
127 diameter, 33 ± 5 mg, less than 0.02% of total body weight; Biomark, Boise, ID, U.S.A.); the
128 other 10 individuals were identified by individual markings and coloration. We sexed lizards
129 based on morphological measurements (Phillips et al., 2016) and/or by everting the
130 hemipenes of males. All subjects were experimentally naïve.

131

132 <H2>*Captive Maintenance*

133 Adult lizards were transported to Macquarie University within 2 weeks of capture. They were
134 housed in a temperature-controlled (mean \pm SD = 25 ± 1 °C, depending on season) indoor
135 environment with a light cycle of 12 h and relative humidity of 30–60% (depending on
136 weather). After arrival adults were transferred into individual plastic tubs (800 x 600 mm and
137 450 mm high) and juveniles were housed together in tubs (sibling groups; 683 x 447 mm and
138 385 mm high) after birth. One week before the experiment each of the 16 selected juveniles
139 was transferred individually into a small tub (2017 cohort: 487 x 350 mm and 260 mm high;
140 2018 cohort: 683 x 447 mm and 385 mm high) and siblings were rehomed or released at their
141 mothers' capture site. After 7 weeks, juveniles from 2017 had become too big for the small
142 tubs and had to be transferred into bigger tubs (683 x 447 mm and 385 mm high). We
143 installed heat cord underneath the enclosures to increase temperature on one side to up to 33
144 ± 2 °C and iButtons (Thermochron iButton model DS1921; Thermochron, Baulkham Hills,
145 NSW, Australia) recorded temperature hourly within enclosures. We used newspaper as a
146 substrate and each enclosure was equipped with a hide, a water bowl and two wooden ramps.

147

148 <H2>*Husbandry*

149 Adult lizards were fed three times a week (Monday, Wednesday, Friday), twice with dog
150 food (Pedigree Adult, various flavours) and once with baby food (Heinz); all feedings

151 included an assortment of fruits and vegetables (powdered with URS Ultimate Calcium).
152 Juveniles were fed five times a week with a mixture of either dog food, dry cat food (Purina
153 Supercoat Adult chicken), baby food or mealworms (powdered with Aristopet Repti-vite and
154 URS Ultimate Calcium) accompanied by fruits and vegetables. During experiments, adults
155 were fed dog food (2 ± 0.3 g) daily as positive reinforcement and fruit and vegetables on
156 Fridays, while juveniles were tested using cat food (0.145 ± 0.001 g). All lizards had ad
157 libitum access to water. Diet adjustments were intended to accommodate differences in
158 energetic demands to ensure healthy growth of juveniles and to increase the likelihood of
159 similar motivation between adults and juveniles. Food fed outside the experiment was
160 presented in a different type of dish than during trials (adults: 150 mm diameter, brown plant
161 saucers; juveniles: 55 mm, transparent petri dish).

162

163 <H2>Learning experiment

164 <H3>Habituation and Pretraining

165 To prevent stress-induced learning impairment (Langkilde & Shine, 2006), the lizards were
166 kept and tested in their home enclosures throughout the experiment. Prior to the study, all
167 lizards were feeding consistently and had habituated to captivity over the course of 1–3
168 months (due to adults arriving at different times); overall, all lizards spent approximately the
169 same amount of time in captivity (balancing possible negative effects between age classes).
170 Pretraining was conducted 1 week prior to testing during which a baited food dish was
171 presented on top of a ramp once a day, for 1.5 h, five times a week (counterbalanced for
172 side). For adults, food dishes were 95 mm diameter and made of black, plastic food
173 containers with the sides cut down to 20 mm; larger dishes were necessary to accommodate
174 greater amounts of reward. For juveniles they were 55 mm diameter petri dishes, with the
175 outside covered in black insulation tape. The same dishes were used throughout the

176 experiment. One adult male responded on fewer than 50% of days during pretraining and was
177 subsequently replaced with another adult male lizard.

178

179 <H3>Set-up

180 Owing to large size differences between age classes (adults are about three times larger than
181 juveniles), equipment such as enclosures, ramps and food dishes were scaled to ensure that
182 relevant parameters including distance to the set-up, saliency of cues, accessibility of
183 dishes/reward and food motivation were the same between groups. To prevent subjects from
184 moving underneath the newspaper and out of sight during trials, the paper was secured to the
185 tub with masking tape. Enclosures contained two ramps with the water bowl in between at
186 one end of the tub opposite to the hide at the other end (Fig. 1). The ramps were switched
187 with each other once a week. During trials an opaque food dish was put on top of each ramp.
188 Both dishes were filled with a small quantity of dog food (2 ± 0.3 g) for adults or cat food
189 (0.145 ± 0.001 g) for juveniles (size of reward was adjusted to accommodate differences in
190 energetic demands). One dish was completely covered with a sheet of plastic mesh window
191 screen (preventing access to food but allowing even odour distribution), while the second
192 dish was only partly covered (a hole had been cut into the screen sheet) allowing access to the
193 food reward. We randomized the side (ramp) on which each food dish was presented. Lizards
194 could not see into the dishes from the start position, opposite the ramps. Allocation of adults
195 to groups was counterbalanced for sex and mean body size ($SVL \pm 0.1$ mm) and juveniles'
196 allocation was balanced for clutch. Individuals were randomly assigned to enclosures within
197 the experimental room.

198

199 <H3>Protocol

200 Before each trial, the hide was placed over each animal and both were slowly moved to the
201 start position furthest from the ramps. Next, both cue cards were fixed (using Bostik Blu-
202 Tack reusable adhesive putty) to the inner wall of the tub at the end of each ramp and
203 immediately afterwards dishes were placed directly in front of them on the ramps. The trial
204 started after about 1 min for acclimation, by removing the hide and exposing the lizard to the
205 set-up. A trial lasted for 1.5 h, after which the hide was replaced, and dishes and cards were
206 removed. We cleaned and baited both dishes between trials, making sure both were touched
207 in the same manner, to control for any chemical cues. The lizards' set-up order was alternated
208 during the study (to avoid order effects) and items were never interchanged between
209 individuals. Trials ran from March to October 2017 (14 adults and eight juveniles) and from
210 March to August 2018 (eight juveniles) twice a day, between 0800 and 1230 hours, 5 days a
211 week, with an intertrial interval of 40 min and were videotaped (H.264 Digital Video
212 Recorder, 3-Axis Day & Night Dome Cameras) with no experimenter present (to minimize
213 stress and distraction). Videos were scored by B.S. and a subset (20%) by three independent
214 observers unfamiliar with the objectives of the study (interobserver reliability coefficient,
215 Cohen's kappa: B.S. and M.L. = 0.964; B.S. and P.Y. = 0.969, B.S. and H.N. = 0.981;
216 Falissard, 2012). We scored the first food dish on which a subject placed its snout (choice:
217 correct/incorrect) and the time from the start of the trials as well as from first movement
218 (directed, uninterrupted forward movement of the whole body ending in a choice; an
219 interruption was defined as no movement for 20 s or more) to choice (trial latency and choice
220 latency). Lizards were able to correct their own mistakes by visiting both food dishes during
221 a single trial. The learning criterion was defined as either six consecutive correct trials, or
222 seven correct out of eight trials. Each lizard received a maximum of 60 trials in a stage (to
223 avoid trial fatigue); however, as soon as it reached criterion it moved on to the next stage. If a
224 subject did not reach criterion within 60 trials it was removed from the experiment

225 ('nonlearner'). Overall, 75% of lizards were removed as nonlearners by the end of the
226 experiment (i.e. seven stages; Appendix Table A3).

227

228 <H3>Set-shifting stages

229 A detailed description of cue cards and stimulus presentation can be found in Szabo et al.
230 (2018). However, minor changes were implemented: during the compound discrimination
231 (CD), we added blue as a background colour for stimulus group 1 to make the experience for
232 both stimulus groups as similar as possible (Fig. 2) and we did not test for an ED reversal.
233 Importantly, no UV was detectable by a spectrophotometer on the cue cards used. Lizards
234 were first presented with a simple discrimination followed by a reversal. During the CD and
235 CD reversal (CDR), we introduced a second dimension (irrelevant distractor), after which
236 they were presented with unfamiliar stimuli in the ID stage (followed by a reversal, IDR) as
237 well as the ED shift stage (Fig. 2).

238

239 <H2>Control of chemical cues

240 To test whether lizards were able to find the correct dish by chemical cues or any
241 uncontrolled stimulus, we administered 10 control trials to a subset ($N = 12$ randomly chosen
242 lizards from both learners and nonlearners) of animals after they had finished experimental
243 trials (Appendix Tables A1 and A2). Cue cards from the CD and CDR were used. We
244 randomized stimuli, dimensions, dishes and the side on which the open dish was presented.
245 Beforehand, cue cards and dishes were thoroughly cleaned with detergent (to remove odour
246 from other lizards and old food) and randomly redistributed among the lizards. Based on a
247 one-sample t test (comparing the number of correct choices with chance performance of 0.5)
248 none of the individuals tested used uncontrolled stimuli and selected dishes by chance ($t_{11} =$
249 2.152, $P = 0.055$).

250

251 <H2>*Statistical Analyses*

252 Modelling of the probability of making a correct choice (and performance within and across
253 stages) was based on Bayesian modelling methods. They were chosen because they provide a
254 powerful and flexible way to analyse non-Gaussian data (Hadfield, 2010). To test for
255 behavioural flexibility, we analysed learning performance during reversals and performance
256 during the ED shift stage using Bayesian generalized linear mixed-effects models (GLMM;
257 Hadfield, 2010) comparing data from specific stages of interest. We compared the probability
258 of a correct choice between the CD and CDR as well as between the ID and IDR (behavioural
259 flexibility through reversal learning). A positive effect would indicate better performance in
260 reversals compared to acquisition (flexible learning) and a negative effect better initial
261 learning (less flexible learning). To quantify set-shifting performance we compared the
262 probability of a correct choice between the ID and ED (behavioural flexibility through
263 attentional shifting).

264 To test our main prediction that juveniles would show adult level learning, we tested
265 whether the probability of making a correct choice (response variable) across consecutive
266 trials (*z*-transformed) was impacted by age (i.e. 'juvenile' versus 'adult') and the interaction
267 between stage and age (on the whole data set from both 2017 and 2018 cohorts) by applying
268 a Bayesian GLMM. At the start of the experiment, two lizards were too short to be classified
269 as adult (Appendix Table A1) but reached adult size within a few weeks of testing and were
270 therefore included as adult in the analyses. We ensured that juvenile learning performance
271 did not differ between years by testing whether the probability of making a correct choice
272 across trials differed across years (2017 versus 2018) using a Bayesian GLMM. To ensure
273 that no differences were caused by clutch identity, we applied a Bayesian GLMM with the
274 probability of making a correct choice as the response variable and scaled trial (scaling

275 variable) and clutch identity ($N = 8$ clutches) as the fixed effects. These analyses were based
276 on data from all animals that reached criterion in any given stage (excluding the stage at
277 which they were removed). Given the nature of the task (i.e. individuals needed to pass
278 previous stages to reach later stages), the number of individuals and statistical power changed
279 across stages (Appendix Table A3). As such, we were careful not to make inferences on
280 stages where sample sizes were low ($N < 4$). To ensure that motivation did not differ between
281 age classes, we compared their choice latency (response variable, log transformed and then z -
282 transformed) using a linear mixed-effects model (LME; Bates, Maechler, Bolker, & Walker,
283 2015) with age as the fixed effect and individual identity as the random factor. In all
284 Bayesian models, trial was z transformed and models included individual level random slopes
285 (trial) and intercepts (animal identity) to account for autocorrelation between successive
286 choices.

287 To test for evidence of dimensional perseveration (a bias towards any stimulus within
288 the previously reinforced dimension) during the ED shift, we performed a binomial test (one-
289 tailed test of the probability of success being greater than 0.5) on the first 10 trials (first
290 week). We were particularly interested in assessing prevalence of responding to any given
291 exemplar within the previously reinforced dimension. If such a bias was present it would
292 indicate attentional set formation shown by the probability of choosing these stimuli
293 significantly above chance level ($5/10 = 0.5$). Owing to the order of presentation, each
294 stimulus (light pink, dark pink, H and star) appeared five times on the left ramp and five
295 times on the right; both dimensions (colour and shape) followed a different order.
296 Furthermore, the first week of testing was chosen because previous work has shown that
297 errors made towards the previously reinforced dimension are best analysed within the first
298 trials (first session used by Dias et al., 1996). Additionally, we performed a binomial test
299 (two-tailed) to investigate whether individuals showed a side bias during the same 10 trials.

300 We counted how many times a lizard responded to a specific stimulus/side. A random
301 response would amount to equal choice (five of 10) for all stimuli and indicates no
302 perseverance or bias.

303 Overall, 23 of 30 animals (14 juveniles, nine adults) were removed (in different
304 stages) as nonlearners. To ensure that no pre-existing differences caused this high dropout
305 rate, we compared body condition, sex, age and latency (proxy for motivation) between
306 learners and nonlearners. To investigate differences in body condition, we applied a linear
307 model (LM) with lizard weight as the response variable and SVL and success or failure to
308 complete all seven stages (categorical: 'yes' or 'no') as fixed effects (Bates et al., 2015). To
309 examine whether one sex or age class was more likely to fail to learn in any given stage or
310 whether latency was associated with bad performance (response variable = exclusion with
311 two levels 'yes' or 'no') we used a GLMM (Bates et al., 2015) that included animal
312 identification (PIT tag) as a random factor and sex, age and latency (choice) as fixed effects.
313 Finally, to determine the robustness of our learning criterion, we applied a generalized linear
314 mixed-effects multiresponse model (GLMM) and compared the errors made in each stage
315 (controlling for trial number by adding trials to criterion as a second response variable)
316 between learners and nonlearners (success or failure to complete all seven stages; categorical:
317 'yes' or 'no'). If nonlearners made significantly more errors, we deemed our learning
318 criterion robust enough to detect learning. All analyses were performed in R version 3.2.4
319 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) and
320 all reported *P* values are two tailed (if not otherwise specified). Raw data and code are
321 available at Zenodo (doi: 10.5281/zenodo.2548950). For further details on analyses and
322 results see the Appendix and Tables A4 and A5.

323

324 <H2>Ethical note

325 We followed the ASAB/ABS Guidelines for the Use of Animals in Research. All procedures
326 and protocols were approved by the Macquarie University Animal Ethics Committee (ARA
327 no. 2013/031) and collection of animals was approved by the New South Wales National
328 Parks and Wildlife Service, Office of Environment and Heritage (OEH; licence no.
329 SL101972). Lizards were hand captured and transported to Macquarie University by car in
330 cloth bags. At the end of the experiment they were rehomed following OEH guidelines.

331

332 <H1>RESULTS

333 Juveniles from 2017 and 2018 did not differ in their choice behaviour (GLMM: year = -0.17,
334 lower 95% confidence interval, CI = -0.53, upper 95% CI = 0.18, $P = 0.337$) and clutch
335 identity did not affect learning performance (GLMM: $P > 0.05$; Appendix Table A6). Data
336 from all juveniles (batch 2017 and 2018) were therefore analysed together. We found no
337 significant difference in learning performance between age classes in any stage (GLMM: $P >$
338 0.05; see Fig. 3 and Appendix Table A7); however, especially during the later stages (ID,
339 IDR and ED) sample sizes were small and differences might not have been detectable. No
340 difference was apparent in the response latency between age classes (LME: age = -0.05,
341 lower 95% CI = -0.55, upper 95% CI = 0.45, $df = 27.2$, $P = 0.846$) indicating no motivational
342 differences between adults and juveniles.

343 Our analysis revealed no effect (positive or negative) between the CD and CDR
344 (GLMM: $P > 0.05$) or the ID and IDR (GLMM: $P > 0.05$) indicating that lizards learnt the
345 reversals with the same proficiency as the initial acquisition (Appendix Table A7). We found
346 no shift cost between ID and ED (GLMM: $P > 0.05$; Appendix Table A8) and none of the
347 seven learners (successfully completed all seven stages) persevered on stimuli from the
348 formerly relevant dimension (binomial test: $P > 0.1$; Appendix Table A9) or showed a side

349 bias during the first 10 trials of the shift stage (binomial test: $P > 0.1$; Appendix Table A9)
350 indicating that no attentional set was formed.

351 Of the 23 nonlearners, seven did not learn during the SD (four juvenile, one adult
352 male and two adult females), five during the SDR (three juveniles, one adult male and one
353 female), one juvenile during the CD, six lizards during the CDR (four juveniles, one adult
354 male and one female), two juveniles during the ID, one adult female during the IDR and one
355 adult female during the ED (Appendix Table A3). Body condition did not differ between
356 learners and nonlearners (LM: estimate = 15.95, SE = 19.54, $t = 0.82$, $P = 0.421$).
357 Nonlearners made significantly more errors than learners (GLMM: $\text{excluded}_{\text{yes}} = 0.15$, SE =
358 0.06, $Z = 2.47$, $P = 0.013$). A nonlearner was defined as not reaching the learning criterion
359 within 60 trials in any stage. Our analysis showed that neither sex nor age class was more
360 likely to fail to reach our learning criterion and latency (choice) did not significantly correlate
361 with being excluded either (GLMM: $P > 0.05$: Appendix Table A10).

362

363 <H1>DISCUSSION

364 We found that blue-tongue lizards were able to inhibit responding to a previously established
365 stimulus–reward relationship, providing strong evidence for behavioural flexibility in this
366 species. Juvenile lizards showed adult levels of behavioural flexibility in our multistage
367 discrimination task. Importantly, both age classes learnt to discriminate between multiple
368 pairs of shapes and colours and showed flexibility in their responses by reversing multiple
369 learnt stimulus–reward relationships. The absence of age-related learning differences
370 supports our prediction that juvenile, precocial blue-tongue lizards may have more mature
371 brains, facilitating the same degree of learning abilities as sexually mature lizards. Our
372 findings contrast with those found in some altricial mammals (Newman & McGaughy, 2011;
373 Weed et al., 2008). Taken together, our findings suggest that precocial juvenile blue-tongue

374 lizards are well equipped to face the challenges of negotiating and learning novel
375 environments and relatively complex problems very early in life when parental guidance is
376 unavailable.

377 The juvenile precocial brain matures primarily before birth, which might benefit
378 young during the first months of life by enhancing cognitive ability (Grand, 1992; Iwaniuk &
379 Nelson, 2003). Successfully avoiding predators, finding food, outcompeting conspecifics and
380 adjusting to seasonal changes in temperature and food availability might give precocial
381 juveniles a better chance of survival. Behavioural flexibility may therefore be especially
382 important in juvenile reptiles. As mostly solitary animals, they experience only limited
383 opportunity for learning shortcuts such as social learning (Galef & Laland, 2005). Along with
384 seasonal change in temperature, reptiles face changes in food availability, basking time and
385 the need for appropriate shelter. Being inflexible might greatly impair a newborn lizard's
386 ability to learn about novel food sources or new basking sites, which in turn can impact
387 fitness (Genovart et al, 2010). Previously, hatchlings of only one species, the three-lined
388 skink, *Bassiana duperreyi*, incubated at two different temperatures, were tested on their
389 reversal learning ability (Clark et al., 2014). Unfortunately, no data are currently available on
390 adults of this species to compare performance. While we did not detect any statistically
391 significant difference between age groups, our power to detect such differences necessarily
392 dropped in later stages as lizards were unsuccessful. Nevertheless, if we only consider the
393 first few stages, in which sample sizes were sufficiently large, both juveniles and adults
394 demonstrated impressive discrimination abilities of one- and two-dimensional stimuli,
395 flexibility in learning during reversals and no age-related difference in performance. Our
396 study, therefore, provides the first evidence of adult-like reversal learning skills and
397 behavioural flexibility in juvenile blue-tongue lizards. In another precocial species, the red
398 junglefowl, juveniles show better learning than adults in a reversal task (Zidar et al., 2018).

399 Although all our lizards were held in captivity for approximately the same amount of time,
400 juveniles were captive raised from birth which might have affected their performance
401 compared to wild juveniles. Testing wild juveniles might reveal similar abilities to those of
402 the red junglefowl and give insights into how the environment shapes cognitive ability in the
403 wild. Increased brain growth before birth might give these juvenile reptiles a better start to
404 life.

405 We found no evidence that an attentional set was formed in the blue-tongue lizard,
406 with individuals being able to solve the ED shift stage without a performance decrement
407 relative to the ID stage. Tree skinks, *Egernia striolata*, a relatively closely related species,
408 also failed to show evidence of an attentional set (Szabo et al, 2018). Currently, we have no
409 knowledge about how lizards perceive and learn multidimensional cues. To understand what
410 lizards learn about the presented stimuli and whether their inability to generalize is due to
411 stimulus features not being salient for them (to be categorized into dimensions) needs to be
412 investigated. Additionally, our sample sizes were small (especially during the shift stage due
413 to high dropout rates during reversal stages) and more data might give more detailed insight
414 into how these lizards process information in the ID/ED attentional set-shifting task.

415 The high dropout rate might be explained by cognitive as well as noncognitive
416 factors. High failure rates at the beginning of the experiment might be due to issues directing
417 attention towards the relevant features of the set-up (slow learning). Later, most lizards failed
418 to reach criterion during the reversal stages, indicating a higher level of difficulty or even
419 issues with inhibitory control (Dias et al., 1996). Noncognitive factors might also include a
420 difficulty to properly motivate our lizards or other methodological parameters affecting the
421 saliency of the stimuli. However, we experienced similar numbers of nonlearners in both age
422 classes suggesting that both experienced conditions similarly. Research into lizard cognition
423 is still in its infancy and we need additional data on a wide range of species to further

424 investigate whether lizards are generally unable to form attentional sets or whether our
425 methodology is too weak to detect set formation in lizards and subsequently improve
426 experimental design in the future.

427 Overall, our results demonstrate that blue-tongue lizards are able to learn to respond
428 to different visual stimuli and to flexibly adjust their learning behaviour when conditions
429 change. Most importantly, juvenile and adults learnt during seven consecutive discrimination
430 stages including three reversals showing no differences in learning performance in any given
431 stage. For this species, the possibility of having an advanced brain at the time of birth may
432 enhance learning and behavioural flexibility such that it is comparable to adult level
433 performance. Our study is the first to test for age-related differences in behavioural flexibility
434 in a lizard, by directly comparing juvenile and adult performance, pointing towards a
435 developmental advantage in learning in these precocial juvenile lizards.

436

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547 **Appendix**

548 To further confirm that animals did learn during each stage, we used Bayesian GLMMs to
549 test whether choice performance (probability of choosing correctly) was positively correlated
550 with trial for each of the seven stages separately. However, the stage by stage analysis is less
551 powerful and only estimates are informative. The analysis revealed a positive correlation
552 between choice and trial (Table A4) for each stage, confirming the robustness of our learning
553 criteria.

554 Because no sex data were available for 2018 juveniles, we analysed sex effect only on
555 lizards tested during 2017. We applied a Bayesian GLMM to investigate whether choice was
556 influenced by sex and interaction between sex and stage as well as sex and stimulus group.
557 We found a significant impact of sex on choice. Females were more likely to make a correct
558 choice during ID, whereas males performed better during CDR (Table A5).

559 We applied a similar model to test for effects of stimulus group as well as interactions
560 between stage with stimulus group on data from all animals (2017 and 2018 cohorts). We
561 found a significant effect of stimulus group: animals initially trained on colour were more
562 likely to choose correctly in the CDR and set-shifting stage (Table A7).

563 Additionally, to investigate whether a learning set (an individual's performance
564 increases based on extensive training) was established, we modelled the probability of
565 choosing correctly over the course of the experiment (trial as the fixed effect) accounting for
566 stage as an additional random effect. Our analysis revealed no formation of a learning set
567 (GLMM: posterior mean = 0.211, lower 95% CI = -0.121, upper 95% CI = 0.554, $P = 0.188$).

568 Model diagnostics were performed on all Bayesian models to ensure that no
569 autocorrelation between samples of the posterior distribution occurred (correlation between
570 lags < 0.1). We visually inspected plots of MCMC chains to check that sufficient mixing took
571 place and used a Heidelberg and Welch diagnostic test to ensure that the chain was long

572 enough. To verify that all linear models were applied appropriately, we visually inspected
573 whether residual distributions conformed to normality.

574 Food motivation was high throughout the experiment; most invalid trials (no choice
575 was made) occurred during SD, SDR, CD and CDR. However, invalid trials occurred a
576 maximum of four times during a given stage (mostly only once) for each individual, and one
577 lizard had 14 invalid trials within the stage in which it was classified as a nonlearner.

578

579 **Table A1.** Summary table of morphological measurements, life history data, stimulus group membership and test and control performance for

580 each tested adult individual

Sex	PIT tag no.	Capture order	Capture date	SVL start (mm)	SVL end (mm)	Weight start (g)	Learner	Origin	Stimulus group	Control	Location
Male	0110262	4	21 Nov 2016	283	294	304.6	Yes	Wild	Shape	6/10	-
Female	0107044	5	21 Nov 2016	301	309	458.8	No	Wild	Colour	6/10	-
Female	0110274	7	10 Dec 2016	312	314	455.5	Yes	Wild	Shape	-	Collaroy
Female	1469710	8	17 Dec 2016	303	307	379.2	No	Wild	Shape	4/10	Marsfield
Male	-	13	23 Dec 2016	285	279	327.0	Yes	Wild	Colour	7/10	Schofields
Female	0110310	10	23 Dec 2016	322	328	435.4	No	Wild	Shape	-	Thornleight
Female	0110347	11	23 Dec 2016	308	319	411.6	Yes	Wild	Colour	-	Glossodia
Male	0110304	12	23 Dec 2016	304	312	435.0	Yes	Wild	Colour	-	Baulkham Hills
Female	0110325	23	3 Feb 2017	251*	274	248.1	Yes	Wild	Colour	-	Guildford
Male	0110281	15	23 Dec 2016	283	298	319.6	Yes	Wild	Colour	4/10	Windsor
Female	1469673	16	23 Dec 2016	301	304	357.0	No	Wild	Shape	-	Windsor
Male	1469721	22	3 Feb 2017	249*	285	177.1	No	Wild	Shape	6/10	Yagoona
Male	3367544	0	30 Sep 2013	309	307	462.2	No	Captive	Colour	-	-
Male	-	24	23 Feb 2017	308	311	552.0	No	Captive	Shape	-	-

581 SVL: snout–vent length; start/end: start and end of the experiment; control: whether an individual participated in control trials and how many

582 times it chose the open dish out of 10 trials; location: suburb of Sydney where the individual was captured. –: no data available.

583 *Subadult at the start of the experiment.

584

585

586 **Table A2.** Summary table of morphological measurements, life history data, stimulus group membership and test and control performance for
 587 each tested juvenile individual

Sex	PIT tag/identity no.	Mother's PIT tag no.	Date of birth	SVL start (mm)	SVL end (mm)	Weight start (g)	Learner	Origin of mother	Stimulus group	Control
Male	0110299	0110310	1 Jan 2017	129	196	29.6	No	Wild	Shape	-
Male	1469694	0110310	1 Jan 2017	132	192	30.9	No	Wild	Colour	-
Male	1469732	0000006	4 Jan 2017	130	217	31.2	No	Wild	Shape	-
Female	0110255	0110347	6 Jan 2017	123	198	26.5	No	Wild	Shape	7/10
Female	1469217	0110093	20 Jan 2017	131	193	26.8	No	Captive	Shape	-
Male	0110339	0110093	20 Jan 2017	125	168	27.8	No	Captive	Colour	4/10
Female	0110285	1469673	18 Jan 2017	124	212	21.7	Yes	Wild	Colour	6/10
Female	0110288	1469710	8 Jan 2017	128	231	26.4	Yes	Wild	Colour	6/10
-	Ts41-4	Ts41	15 Jan 2018	142	231	46.0	No	Wild	Shape	-
-	Ts41-6	Ts41	15 Jan 2018	118	144	22.4	No	Wild	Shape	-
-	Ts41-7	Ts41	15 Jan 2018	124	164	28.9	No	Wild	Colour	-
-	Ts41-10	Ts41	15 Jan 2018	120	174	23.4	No	Wild	Colour	-
-	Ts44-4	Ts44	7 Feb 2018	124	159	33.7	No	Wild	Colour	6/10
-	Ts44-5	Ts44	7 Feb 2018	122	159	34.3	No	Wild	Colour	6/10
-	Ts44-17	Ts44	7 Feb 2018	112	134	25.9	No	Wild	Shape	-
-	Ts44-13	Ts44	7 Feb 2018	110	180	21.1	No	Wild	Shape	-

588 SVL: snout–vent length; start/end: start and end of the experiment; control: whether an individual participated in control trials and how many
 589 times it chose the open dish out of 10 trials. –: no data available.

590

591 **Table A3.** Trials to criterion for each of the 24 lizards that participated in the set-shifting experiment

PIT tag/identity no.	Age	Sex	SG	SD	SDR	CD	CDR	ID	IDR	ED	Sum
24	Adult	Male	Shape	60	-	-	-	-	-	-	60
274	Adult	Female	Shape	45	41	44	23	21	21	16	211
339	Juvenile	Male	Colour	60	-	-	-	-	-	-	60
255	Juvenile	Female	Shape	17	40	33	60	-	-	-	150
732	Juvenile	Male	Shape	49	20	60	-	-	-	-	129
694	Juvenile	Male	Colour	23	60	-	-	-	-	-	83
347	Adult	Female	Colour	54	40	36	8	6	60	-	204
281	Adult	Male	Colour	57	8	22	19	49	11	37	203
262	Adult	Male	Shape	8	45	9	6	32	32	51	183
13	Adult	Male	Colour	43	10	41	22	11	14	8	149
710	Adult	Female	Shape	46	33	14	63	-	-	-	156
721	Adult	Male	Shape	26	48	26	60	-	-	-	160
673	Adult	Female	Shape	60	-	-	-	-	-	-	60
217	Juvenile	Female	Shape	33	60	-	-	-	-	-	93
288	Juvenile	Female	Colour	25	52	10	46	31	17	15	196
285	Juvenile	Female	Colour	38	40	31	12	12	24	18	175
299	Juvenile	Male	Shape	10	13	51	60	-	-	-	134
044	Adult	Female	Colour	19	60	-	-	-	-	-	79
544	Adult	Male	Colour	38	60	-	-	-	-	-	98
325	Adult	Female	Colour	45	48	58	54	40	34	60	339
304	Adult	Male	Colour	52	24	9	13	61	10	37	206
310	Adult	Female	Shape	60	-	-	-	-	-	-	60
Ts41-4	Juvenile	-	Shape	52	27	39	33	60	-	-	211
Ts41-6	Juvenile	-	Shape	60	-	-	-	-	-	-	60
Ts41-7	Juvenile	-	Colour	13	33	7	60	-	-	-	113

Ts41-10	Juvenile	-	Colour	45	16	24	60	-	-	-	145
Ts44-17	Juvenile	-	Shape	19	60	-	-	-	-	-	79
Ts44-13	Juvenile	-	Shape	17	25	23	50	60	-	-	175
Ts44-5	Juvenile	-	Colour	60	-	-	-	-	-	-	60
Ts44-4	Juvenile	-	Colour	60	-	-	-	-	-	-	60

592 Values in bold indicate when the exclusion criterion (no learning within 60 trials) was met. -: no data available. SG: stimulus group; SD: simple

593 discrimination; SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound discrimination reversal; ID:

594 intradimensional acquisition; IDR: intradimensional reversal; ED: extradimensional shift; sum: sum of trials received overall.

595

596 **Table A4.** Summary of parameter estimates and test statistics calculated to investigate learning for each stage

Parameter	Posterior mean	Lower 95% CI	Upper 95% CI	<i>P</i>
Simple discrimination				
Intercept	0.523	0.218	0.858	0.001
Trial	0.439	0.152	0.739	0.001
Simple discrimination reversal				
Intercept	0.488	0.163	0.828	0.003
Trial	0.361	0.058	0.678	0.018
Compound discrimination				
Intercept	0.761	0.310	1.239	<0.001
Trial	0.359	-0.077	0.802	0.079
Compound discrimination reversal				
Intercept	1.144	0.045	2.495	0.021
Trial	0.615	-0.518	1.823	0.225
Intradimensional discrimination				
Intercept	0.807	-0.211	2.002	0.071
Trial	0.375	-0.481	1.422	0.376
Intradimensional discrimination reversal				
Intercept	1.026	-0.219	2.452	0.085
Trial	0.731	-0.211	1.800	0.105
Extradimensional shift				

Intercept	1.223	-0.155	2.844	0.050
Trial	0.745	-0.449	2.167	0.178

597 We estimated the probability of choosing correctly as a function of trial for each of the seven stages of the set-shifting task separately. Owing to
598 the lower power (small sample size) of the single-stage analysis fixed effects appear nonsignificant. Significant parameters are indicated in bold.
599

600

601 **Table A5.** Summary table of parameter estimates and test statistics calculated to test for sex and effects

Parameter	Posterior mean	Lower 95% CI	Upper 95% CI	<i>P</i>
Intercept	0.284	-0.116	0.680	0.170
Scaled trial	0.222	0.053	0.395	0.011
Sex	0.161	-0.382	0.728	0.566
Female*SDR	-0.065	-0.471	0.334	0.754
Male*SDR	0.311	-0.166	0.783	0.201
Female*CD	0.234	-0.196	0.673	0.292
Male*CD	0.182	-0.348	0.700	0.506
Female*CDR	0.234	-0.286	0.748	0.378
Male*CDR	0.994	0.216	1.733	0.009
Female*ID	0.645	0.080	1.214	0.023
Male*ID	-0.303	-0.797	0.224	0.242
Female*IDR	0.491	-0.105	1.077	0.103
Male*IDR	0.080	-0.590	0.762	0.817
Male*ED	0.722	-0.072	1.495	0.071
Female*ED	0.235	-0.312	0.778	0.400
Female*SG	0.025	-0.461	0.471	0.910
Male*SG	-0.174	-0.631	0.317	0.467

602 Estimates (probability of choosing correctly) were calculated overall (all stages) as well as for interactions between sex and stage and sex and
603 stimulus group to investigate sex differences between stages and groups. To make estimate values interpretable, we included trial (scaled and
604 centred) in the model. CI: confidence interval. *P*: significance of parameter based on Bayesian modelling. Significant parameters are indicated in

605 bold. SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound discrimination reversal; ID: intradimensional

606 acquisition; IDR: intradimensional reversal; ED: extradimensional shift; SG: stimulus group.

607

608

609 **Table A6.** Summary table of parameter estimates and test statistics calculated to investigate whether clutch identity affects learning performance
 610 in juveniles

Parameter	Posterior mean	Lower 95% CI	Upper 95% CI	<i>P</i>
Intercept	0.474	-0.913	1.960	0.477
Scaled trial	0.423	-0.174	1.010	0.121
Clutch 8	0.129	-1.475	1.742	0.852
Clutch 10	0.455	-1.141	1.979	0.508
Clutch 11	0.281	-1.399	1.999	0.706
Clutch 16	0.494	-1.121	2.123	0.478
Clutch 41	0.210	-1.170	1.598	0.742
Clutch 44	0.235	-1.317	1.777	0.740
Clutch 110093	-0.237	-2.117	1.631	0.783

611 The model included parameters to test for possible clutch effects controlling for animal identity and stage as random effects. CI: confidence
 612 interval. *P*: significance of parameter based on Bayesian modelling.

613

614 **Table A7.** Summary table of parameter estimates and test statistics calculated to test for effects of age or stimulus group (SG)

Parameter	Posterior mean	Lower 95% CI	Upper 95% CI	<i>P</i>
Intercept	0.381	-0.037	0.816	0.078
Scaled trial	0.247	0.099	0.391	0.001
SG	-0.017	-0.450	0.420	0.939
Age	0.027	-0.418	0.456	0.905
SG1*SDR	0.077	-0.431	0.577	0.762
SG2*SDR	0.109	-0.345	0.567	0.637
SG1*CD	0.032	-0.524	0.604	0.911
SG2*CD	0.379	-0.062	0.831	0.100
SG1*CDR	0.577	-0.223	1.357	0.154
SG2*CDR	0.633	0.117	1.161	0.017
SG1: ID	-0.228	-0.582	1.007	0.575
SG2*ID	-0.010	-0.468	0.473	0.967
SG1*IDR	-0.340	-1.146	0.422	0.398
SG2*IDR	-0.427	-0.238	1.090	0.205
SG1*ED	-0.286	-1.054	0.495	0.463
SG2*ED	0.712	0.105	1.364	0.025
Age*SDR	-0.156	-0.726	0.404	0.589
Age*CD	0.060	-0.552	0.693	0.849
Age*CDR	-0.768	-1.528	-0.034	0.054
Age*ID	0.493	-0.484	1.446	0.317
Age*IDR	0.523	-0.576	1.622	0.353
Age*ED	0.096	-1.031	1.248	0.875

615 Estimates (probability of choosing correctly) were calculated overall (all stages) as well as for interactions between stage with SG and age. To
 616 make estimate values interpretable, we included trial (scaled and centred) in the model. *P*: significance of parameter based on Bayesian
 617 modelling. Significant parameters are indicated in bold. SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound
 618 discrimination reversal; ID: intradimensional acquisition; IDR: intradimensional reversal; ED: extradimensional shift; SG1: stimulus group
 619 initially trained on shapes; SG2: stimulus group initially trained on colour.

620

621 **Table A8.** Summary table of parameter estimates and test statistics calculated to investigate set shifting and reversal learning performance

Parameter	Posterior mean	Lower 95% CI	Upper 95% CI	<i>P</i>
Shift performance				
Intercept	0.815	-0.158	1.968	0.064
Stage	0.359	-0.148	0.870	0.166
Trial	0.440	-0.369	1.354	0.236
Reversal learning in compound stages				
Intercept	0.675	0.297	1.068	0.001
Stage	0.061	-0.337	0.472	0.773
Trial	0.275	-0.046	0.628	0.087
Reversal learning in intradimensional stages				
Intercept	0.765	-0.075	1.717	0.056
Stage	0.021	-0.523	0.562	0.938
Trial	0.319	-0.376	1.064	0.320

622 Estimates (probability of choosing correctly) were calculated for difference between respective stages. To make estimate values interpretable, we
623 included trial (scaled and centred) in the model. CI: confidence interval. *P*: significance of parameter based on Bayesian modelling. Significant
624 parameter is indicated in bold.
625

626

627 **Table A9.** Perseverative errors during the first 10 trials of the extradimensional shift stage

PIT tag no.	Sex	Stimulus group	Perseverative trials	Binomial P_{persev}	Side chosen	Binomial P_{side}
304	Male	Colour	8/10	0.055	4/10	0.754
285	Female	Colour	5/10	0.623	5/10	> 0.99
288	Female	Colour	5/10	0.623	4/10	0.754
262	Male	Shape	6/10	0.377	5/10	> 0.99
281	Male	Colour	5/10	0.623	5/10	> 0.99
13	Female	Colour	3/8	0.856	4/8	> 0.99
274	Female	Shape	6/10	0.377	5/10	> 0.99

628 Only seven individuals were tested in this stage. PIT 13 reached the learning criterion after only eight trials. Perseverative trials: number of

629 errors to the previously reinforced dimension; side chosen: number of times each animal went to the left cue card; binomial P : significance based

630 on a two-tailed binomial test.

631

632 **Table A10.** Summary table of parameter estimates and test statistics calculated to investigate composition of learners and nonlearners

Parameter	Estimate	SE	<i>z</i>	<i>P</i>
Intercept	18.484	4.183	4.418	<0.001
Sex	-1.055	5.610	-0.188	0.851
Age	0.653	6.780	0.096	0.923
Latency	0.002	0.030	0.049	0.961

633 The model included parameters to test for possible sex, age and latency (choice) effects. *P*: significance of parameter based on Bayesian

634 modelling. Significant parameter is indicated in bold.

635

636
637 **Figure 1.** Schematic representation of the enclosure set-up used during the learning
638 experiment. Set-up for juveniles: enclosures included two ramps and a hide on opposite ends.
639 For small enclosures (487 x 350 mm and 260 mm high) ramps were 10 cm apart; for bigger
640 enclosures (683 x 447 mm and 385 mm high) ramps were 15 cm apart. The same ramps (175
641 x 70 mm and 45 mm high) were used. Set-up for adults: enclosures (800 x 600 mm and 450
642 mm high) included two ramps, 25 cm apart, and a hide on opposite ends. Bigger ramps (365
643 x 140 mm and 70 mm high) were used for adults (small ramps were too low to prevent
644 animals from seeing into the dishes from the start position). Enclosure size was adjusted to
645 body length to standardize the distance between starting position and dishes/stimuli.
646 Independent of age class, animals had to cross a distance of, on average, 1.5 times their body
647 length to make a choice. None of the animals had difficulties climbing ramps in any trial.

648

649 **Figure 2.**
650 Order of stimulus presentation during the seven stages of the set-shifting task. Stimulus group
651 1 (SG1; top row within each set of stages) started with shape as the relevant dimension and
652 stimulus group 2 (SG2) with colour (bottom row within each set of stages). During the simple
653 discrimination (SD) and reversal (SDR) lizards were presented with two one-dimensional
654 stimuli of either two shapes or two colours (1) of which only one was rewarded (correct; tick
655 marks indicate the rewarded choice during each stage). During the compound discrimination
656 (CD) and reversal (CDR) a second dimension was added (SG1: a background colour; SG2:
657 superimposed shapes) but the former relevant stimuli (from SD) stayed relevant (2). In the
658 intradimensional acquisition (ID) and reversal (IDR) novel stimuli of both colours and shapes
659 were introduced (3). This order of presentation was designed to facilitate the formation of an
660 attentional set (either colours or shapes are important for reinforcement). Finally, during the
661 extradimensional shift (ED) new stimuli were again introduced (4) and the learnt set was
662 challenged by moving the reinforcement to the formerly irrelevant dimension (SG1: to the
663 colour dimension; SG2: to the shape dimension).

664

665 **Figure 3.** Mean trials to criterion + SE of adults and juveniles. SD: simple discrimination;
666 SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound
667 discrimination reversal; ID: intradimensional acquisition; IDR: intradimensional reversal;
668 ED: extradimensional shift. Sample sizes are given within bars.