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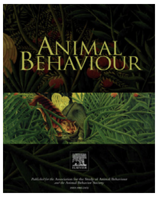

# Precocial juvenile lizards show adult level learning and behavioural flexibility

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

Species vary in the degree to which offspring are independent and cognitively developed at birth or hatching. Altricial young are born at an early developmental stage dependent on parental care, whereas precocial young are more advanced and need little or no parental care (Charvet & Striedter, 2011; Grand, 1992). These differences in developmental trajectory also directly affect brain maturation and size. For example, while adult altricial birds have a greater relative brain volume than adults of precocial species, the opposite can be seen in juveniles. Altricial bird species experience most neural growth posthatching, while in precocial species most brain maturation occurs before hatching (Charvet & Striedter, 2011; Iwaniuk & Nelson, 2003). Similar trends can be seen in mammals (Grand, 1992). Consequently, developmental mode is expected to affect cognitive ability at an early age.

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

Behavioural flexibility can be measured in different ways, including reversal learning and intradimensional (ID)/extradimensional (ED) attentional set shifting (Brown & Tait, 2015). In tests of reversal learning, animals first learn a discrimination between at least two stimuli of which only one is rewarded. After this discrimination is acquired, the reward contingencies change to one of the formerly nonrewarded stimuli. Reversal learning is affected

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by the inability to inhibit responding to the previously rewarded stimulus. When testing set shifting, multiple discrimination stages are used to develop a perceptual attentional set which is later challenged by a shift to a novel set (e.g. a second dimension). More specifically, a comparison is made between learning performance in an ID acquisition, a discrimination between novel stimuli of an already learned set (e.g. colour dimension) and an ED shift during which reinforcement is moved to stimuli of a novel set (e.g. shape dimension; Dias, Robbins, & Roberts, 1996; Roberts, Robbins, & Everitt, 1988). Learning during a shift is slowed by attentional perseveration to the formerly relevant dimension, as the subject learns the newly relevant aspect of the stimuli that predicts the rewarded outcome. The skill with which the challenges of reversal and shifting are overcome indicate a subject's level of behavioural flexibility (Brown & Tait, 2015; Garner, Thogerson, Wurbel, Murray, & Mench, 2006).

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

To the best of our knowledge, no direct comparison of juvenile and adult behavioural flexibility has been made in a precocial animal species in which adults show no parental care. Previous studies have shown that lizards have an ability to perform a visual choice reversal (e.g. Burghardt, 1978; Clark, Amiel, Shine, Noble, & Whiting, 2014; Day, Crews, & Wilczynski, 1999; Day, Ismail, & Wilczynski, 2003; Gaalema, 2007, 2011; Leal & Powell, 2012), successfully learn in an ID/ED attentional set-shifting task (Szabo, Noble, Byrne, Tait, & Whiting, 2018) and solve novel problems (e.g. Manrod, Hartdegen, & Burghardt, 2008), all indicative of behavioural flexibility (Auersperg, Gajdon, & von Bayern, 2014). However, no data are available to compare behavioural flexibility between different age classes of the same lizard species (but see Noble, Byrne, & Whiting, 2014). Our aim was to investigate whether and how behavioural flexibility differs between juvenile and adult individuals in the precocial eastern blue-tongue lizard, *Tiliqua scincoides scincoides*. This species is a large, diurnal, omnivorous, viviparous skink that gives birth to well-developed offspring (Koenig, Shine, & Shea, 2001; Phillips, Roffey, Hall, & Johnson, 2016; Shea, 1981). Its generalist feeding habits and relatively slow developing young make it an excellent candidate to investigate age-related learning and behavioural flexibility in a multistage discrimination task. Because precocial species are born with a more advanced and developed brain, we predicted similar levels of behavioural flexibility in both juvenile and adult lizards.

## METHODS

### *Study Animals*

We acquired 12 wild-caught and two captive-bred adult (Appendix Table A1) eastern blue-tongue lizards between November 2016 and February 2017 from the suburban Sydney area, New South Wales, Australia, where the species is relatively abundant, to participate in the set-shifting experiment (Koenig et al., 2001; Phillips et al., 2016; Shea, 1981). During December/January 2017 and 2018, seven wild-caught and one captive female gave birth in captivity (litter size range 7–19, mean ± SD = 12.13 ± 4.36). We randomly selected 16 juveniles to participate in this study; two each from two females and one each from four females ($N = 8$) in 2017 and four each from two females ($N = 8$) in 2018 (Appendix Table A2). Snout–vent length (SVL), total length (TL), head width (HW), head height (HH), head length (HL) and weight of all lizards were determined on the day of arrival/birth, 1 week before the start of the experiment; to monitor growth rate, juveniles were measured every 5 weeks. All animals (except for two males and eight juveniles) were individually identified using passive integrated transponders (PITs; HPT8, 8.4 mm long × 1.4 mm in diameter, 33 ± 5 mg, less than 0.02% of total body weight; Biomark, Boise, ID, U.S.A.); the other 10 individuals were identified by individual markings and coloration. We sexed lizards based on morphological measurements (Phillips et al., 2016) and/or by everting the hemipenes of males. All subjects were experimentally naïve.

### *Captive Maintenance*

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

### *Husbandry*

Adult lizards were fed three times a week (Monday, Wednesday, Friday), twice with dog food (Pedigree Adult, various flavours) and once with baby food (Heinz); all feedings included an assortment of fruits and vegetables (powdered with URS Ultimate Calcium). Juveniles were fed five times a week with a mixture of either dog food, dry cat food (Purina Supercoat Adult chicken), baby food or mealworms (powdered with Aristopet Repti-vite and URS Ultimate Calcium) accompanied by fruits and vegetables. During experiments, adults were fed dog food (2 ± 0.3 g) daily as positive reinforcement and fruit and vegetables on Fridays, while juveniles were tested using cat food (0.145 ± 0.001 g). All lizards had ad libitum access to water. Diet adjustments were intended to accommodate differences in energetic demands to ensure healthy growth of juveniles and to increase the likelihood of similar motivation between adults and juveniles. Food fed outside the experiment was presented in a different type of dish than during trials (adults:

150 mm diameter, brown plant saucers; juveniles: 55 mm, transparent petri dish).

### *Learning Experiment*

#### *Habituation and pretraining*

To prevent stress-induced learning impairment (Langkilde & Shine, 2006), the lizards were kept and tested in their home enclosures throughout the experiment. Prior to the study, all lizards were feeding consistently and had habituated to captivity over the course of 1–3 months (due to adults arriving at different times); overall, all lizards spent approximately the same amount of time in captivity (balancing possible negative effects between age classes). Pretraining was conducted 1 week prior to testing during which a baited food dish was presented on top of a ramp once a day, for 1.5 h, five times a week (counterbalanced for side). For adults, food dishes were 95 mm diameter and made of black, plastic food containers with the sides cut down to 20 mm; larger dishes were necessary to accommodate greater amounts of reward. For juveniles they were 55 mm diameter petri dishes, with the outside covered in black insulation tape. The same dishes were used throughout the experiment. One adult male responded on fewer than 50% of days during pretraining and was subsequently replaced with another adult male lizard.

#### *Set-up*

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

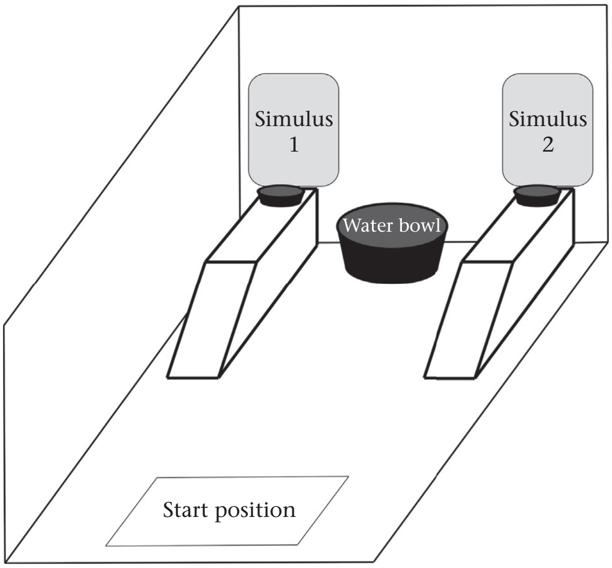

**Figure 1.** Schematic representation of the enclosure set-up used during the learning experiment. Set-up for juveniles: enclosures included two ramps and a hide on opposite ends. For small enclosures (487 × 350 mm and 260 mm high) ramps were 10 cm apart; for bigger enclosures (683 × 447 mm and 385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

#### *Protocol*

Before each trial, the hide was placed over each animal and both were slowly moved to the start position furthest from the ramps. Next, both cue cards were fixed (using Bostik Blu-Tack reusable adhesive putty) to the inner wall of the tub at the end of each ramp and immediately afterwards dishes were placed directly in front of them on the ramps. The trial started after about 1 min for acclimation, by removing the hide and exposing the lizard to the set-up. A trial lasted for 1.5 h, after which the hide was replaced, and dishes and cards were removed. We cleaned and baited both dishes between trials, making sure both were touched in the same manner, to control for any chemical cues. The lizards' set-up order was alternated during the study (to avoid order effects) and items were never interchanged between individuals. Trials ran from March to October 2017 (14 adults and eight juveniles) and from March to August 2018 (eight juveniles) twice a day, between 0800 and 1230 hours, 5 days a week, with an intertrial interval of 40 min and were videotaped (H.264 Digital Video Recorder, 3-Axis Day & Night Dome Cameras) with no experimenter present (to minimize stress and distraction). Videos were scored by B.S. and a subset (20%) by three independent observers unfamiliar with the objectives of the study (interobserver reliability coefficient, Cohen's kappa: B.S. and M.L. = 0.964; B.S. and P.Y. = 0.969, B.S. and H.N. = 0.981; Falissard, 2012). We scored the first food dish on which a subject placed its snout (choice: correct/incorrect) and the time from the start of the trials as well as from first movement (directed, uninterrupted forward movement of the whole body ending in a choice; an interruption was defined as no movement for 20 s or more) to choice (trial latency and choice latency). Lizards were able to correct their own mistakes by visiting both food dishes during a single trial. The learning criterion was defined as either six consecutive correct trials, or seven correct out of eight trials. Each lizard received a maximum of 60 trials in a stage (to avoid trial fatigue); however, as soon as it reached criterion it moved on to the next stage. If a subject did not reach criterion within 60 trials it was removed from the experiment ('nonlearner'). Overall, 75% of lizards were removed as nonlearners by the end of the experiment (i.e. seven stages; Appendix Table A3).

#### *Set-shifting stages*

A detailed description of cue cards and stimulus presentation can be found in Szabo, Noble, Byrne, Tait, and Whiting (2018). However, minor changes were implemented: during the compound discrimination (CD), we added blue as a background colour for stimulus group 1 to make the experience for both stimulus groups

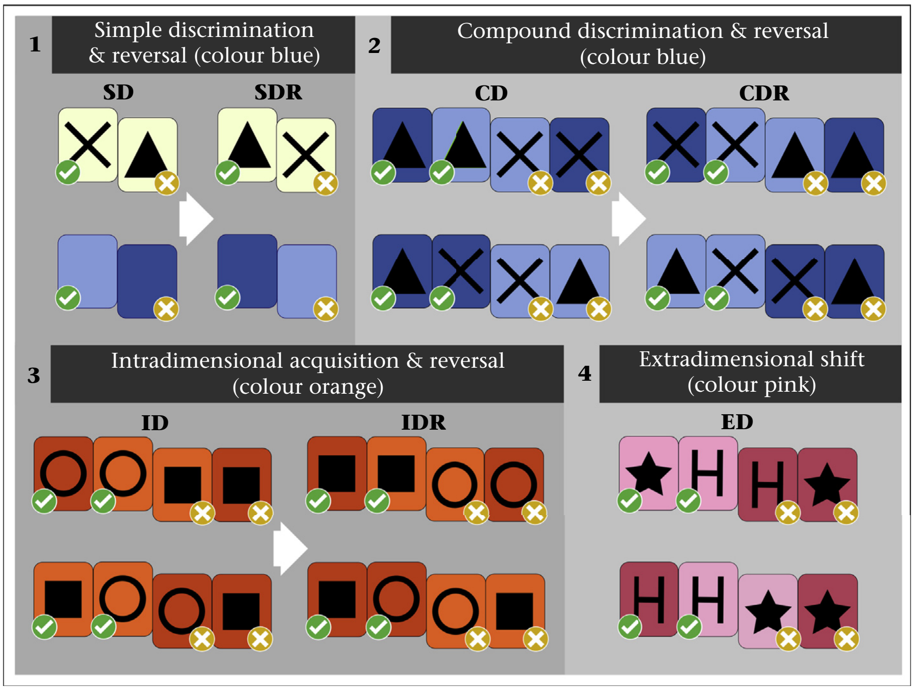

**Figure 2.** Order of stimulus presentation during the seven stages of the set-shifting task. Stimulus group 1 (SG1; top row within each set of stages) started with shape as the relevant dimension and stimulus group 2 (SG2) with colour (bottom row within each set of stages). During the simple discrimination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

as similar as possible (Fig. 2) and we did not test for an ED reversal. Importantly, no UV was detectable by a spectrophotometer on the cue cards used. Lizards were first presented with a simple discrimination followed by a reversal. During the CD and CD reversal (CDR), we introduced a second dimension (irrelevant distractor), after which they were presented with unfamiliar stimuli in the ID stage (followed by a reversal, IDR) as well as the ED shift stage (Fig. 2).

### *Control of Chemical Cues*

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

### *Statistical Analyses*

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

To test our main prediction that juveniles would show adult level learning, we tested whether the probability of making a correct choice (response variable) across consecutive trials (*z*-transformed) was impacted by age (i.e. ‘juvenile’ versus ‘adult’) and the interaction between stage and age (on the whole data set from both 2017 and 2018 cohorts) by applying a Bayesian GLMM. At the start of the experiment, two lizards were too short to be classified as adults (Appendix Table A1) but reached adult size within a few weeks of testing and were therefore included as adults in the analyses. We ensured that juvenile learning performance did not differ between years by testing whether the probability of making a correct choice across trials differed across years (2017 versus 2018). To ensure that no differences were caused by clutch identity, we applied a Bayesian GLMM with the probability of making a correct choice as the response variable and scaled trial (scaling variable) and clutch identity ($N = 8$ clutches) as the fixed effects. These analyses were based on data from all animals that reached criterion in any given stage (excluding the stage at which they were removed). Given the nature of the task (i.e. individuals needed to pass previous stages to reach later stages), the number of individuals and statistical power changed across stages (Appendix Table A3). As such, we were careful not to make inferences on stages where sample sizes were low ($N < 4$). To ensure that motivation did not differ between age classes, we compared their choice latency (response variable, log transformed and then $z$-transformed) using a linear mixed-effects model (LME; Bates, Maechler, Bolker, & Walker, 2015) with age as the fixed effect and individual identity as the random factor. In all Bayesian models, trial was $z$ transformed and models included individual level random slopes (trial) and intercepts (animal identity) to account for autocorrelation between successive choices.

To test for evidence of dimensional perseveration (a bias towards any stimulus within the previously reinforced dimension) during the ED shift, we performed a binomial test (one-tailed test of the probability of success being greater than 0.5) on the first 10 trials (first week). We were particularly interested in assessing prevalence of responding to any given exemplar within the previously reinforced dimension. If such a bias was present it would indicate attentional set formation shown by the probability of choosing these stimuli significantly above chance level ($5/10 = 0.5$). Owing to the order of presentation, each stimulus (light pink, dark pink, H and star) appeared five times on the left ramp and five times on the right; both dimensions (colour and shape) followed a different order. Furthermore, the first week of testing was chosen because previous work has shown that errors made towards the previously reinforced dimension are best analysed within the first trials (first session used by Dias et al., 1996). Additionally, we performed a binomial test (two-tailed) to investigate whether individuals showed a side bias during the same 10 trials. We counted how many times a lizard responded to a specific stimulus/side. A random response would amount to equal choice (five of 10) for all stimuli and indicates no perseverance or bias.

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

### *Ethical Note*

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

## RESULTS

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

Our analysis revealed no effect (positive or negative) between the CD and CDR (GLMM: $P > 0.05$) or the ID and IDR (GLMM: $P > 0.05$) indicating that lizards learnt the reversals with the same proficiency as the initial acquisition (Appendix Table A7). We found no shift cost between ID and ED (GLMM: $P > 0.05$; Appendix Table A8) and none of the seven learners (successfully completed all seven stages) persevered on stimuli from the formerly relevant dimension (binomial test: $P > 0.1$; Appendix Table A9) or showed a side bias during the first 10 trials of the shift stage (binomial test: $P > 0.1$; Appendix Table A9) indicating that no attentional set was formed.

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

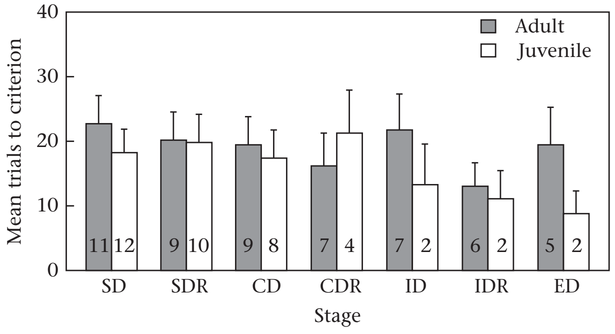

**Figure 3.** Mean trials to criterion + SE of adults and juveniles. SD: simple discrimination; SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound discrimination reversal; ID: intradimensional acquisition; IDR: intradimensional reversal; ED: extradimensional shift. Sample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

not significantly correlate with being excluded either (GLMM: $P >$ 0.05: Appendix Table A10).

## DISCUSSION

We found that blue-tongue lizards were able to inhibit responding to a previously established stimulus–reward relationship, providing strong evidence for behavioural flexibility in this species. Juvenile lizards showed adult level behavioural flexibility in our multistage discrimination task. Importantly, both age classes learnt to discriminate between multiple pairs of shapes and colours and showed flexibility in their responses by reversing multiple learnt stimulus–reward relationships. The absence of age-related learning differences supports our prediction that juvenile, precocial blue-tongue lizards may have more mature brains, facilitating the same degree of learning abilities as sexually mature lizards. Our findings contrast with those found in some altricial mammals (Newman & McGaughy, 2011; Weed et al., 2008). Taken together, our findings suggest that precocial juvenile blue-tongue lizards are well equipped to face the challenges of negotiating and learning relatively complex problems very early in life when parental guidance is unavailable.

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

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

The high dropout rate might be explained by cognitive as well as noncognitive factors. High failure rates at the beginning of the experiment might be due to difficulties directing attention towards the relevant features of the set-up (slow learning). Later, most lizards failed to reach criterion during the reversal stages, indicating a higher level of difficulty or even issues with inhibitory control (Dias et al., 1996). Noncognitive factors might also include a difficulty to properly motivate our lizards or other methodological parameters affecting the saliency of the stimuli. However, we experienced similar numbers of nonlearners in both age classes suggesting that both experienced conditions similarly. Research into lizard cognition is still in its infancy and we need additional data on a wide range of species to further investigate whether lizards are generally unable to form attentional sets or whether our methodology is too weak to detect set formation in lizards and subsequently improve experimental design in the future.

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

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## Appendix

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

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

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

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

Model diagnostics were performed on all Bayesian models to ensure that no autocorrelation between samples of the posterior distribution occurred (correlation between lags $< 0.1$). We visually inspected plots of MCMC chains to check that sufficient mixing took place and used a Heidelberg and Welch diagnostic test to ensure that the chain was long enough. To verify that all linear models were applied appropriately, we visually inspected whether residual distributions conformed to normality.

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

**Table A1**

Summary table of morphological measurements, life history data, stimulus group membership and test and control performance for 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 | – | – |

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

[*] Subadult at the start of the experiment.

**Table A2**

Summary table of morphological measurements, life history data, stimulus group membership and test and control performance for each tested juvenile individual

| Sex | PIT tag/identity no. | Mother's PIT tag/identity 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 | – |

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

**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 |

**Table A3** (*continued*)

| PIT tag/identity no. | Age | Sex | SG | SD | SDR | CD | CDR | ID | IDR | ED | Sum |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 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 |

Values in bold indicate when the exclusion criterion (no learning within 60 trials) was met. –: no data available. SG: stimulus group; SD: simple discrimination; SDR: simple discrimination reversal: CD: compound discrimination; CDR: compound discrimination reversal; ID: intradimensional acquisition; IDR: intradimensional reversal; ED: extradimensional shift; sum: sum of trials received overall.

**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 | *P* |
|---|---|---|---|---|
| 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 |

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 the lower power (small sample size) of the single-stage analysis fixed effects appear nonsignificant. Significant parameters are indicated in bold.

**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 | *P* |
|---|---|---|---|---|
| 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 |

Estimates (probability of choosing correctly) were calculated overall (all stages) as well as for interactions between sex and stage and sex and stimulus group to investigate sex differences between stages and groups. To make estimate values interpretable, we included trial (scaled and centred) in the model. CI: confidence interval. *P*: significance of parameter based on Bayesian modelling. Significant parameters are indicated in bold. SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound discrimination reversal; ID: intradimensional acquisition: IDR: intradimensional reversal: ED: extradimensional shift; SG: stimulus group.

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

| Parameter | Posterior mean | Lower 95% CI | Upper 95% CI | *P* |
|---|---|---|---|---|
| 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 |

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

**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 | *P* |
|---|---|---|---|---|
| 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 |

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

**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 | *P* |
|---|---|---|---|---|
| **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 |

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

**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 |

Only seven individuals were tested in this stage. PIT 13 reached the learning criterion after only eight trials. Perseverative trials: number of errors to the previously reinforced dimension; side chosen: number of times each animal went to the left cue card; binomial *P*: significance based on a one-tailed test ($P_{persev}$) and a two-tailed binomial test ($P_{side}$).

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

| Parameter | Estimate | SE | *z* | *P* |
|---|---|---|---|---|
| **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 |

The model included parameters to test for possible sex, age and latency (choice) effects. *P*: significance of parameter based on Bayesian modelling. Significant parameter is indicated in bold.