

Behavioural Processes



journal homepage: www.elsevier.com/locate/behavproc

Do lizards have enhanced inhibition? A test in two species differing in ecology and sociobiology



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ARTICLE INFO	A B S T R A C T			
A R T I C L E I N F O Keywords: Cognition Inhibitory control Reptile Shingleback skink Squamate	Waiting for the right moment to strike, avoiding the ingestion of harmful foods, or ignoring stimuli associated with ephemeral or depleted resources requires the inhibition of prepotent responses. Good response inhibition facilities flexibility in behaviour which is associated with survival in unpredictable environments. To investigate differences in behavioural flexibility in lizards, we tested reversal learning in the sleepy lizard (<i>Tiliqua rugosa asper</i>) and compared its performance to the relatively closely related eastern blue-tongue skink (<i>Tiliqua scincoides scincoides</i>). We presented both species with a choice between either a light and dark blue stimulus or a triangle and X shape. Both species were able to learn to discriminate between these stimuli and showed similar learning ability during the acquisition of the discrimination. Sleepy lizards, however, demonstrated a higher probability of making a correct choice at the start of the reversal, hinting towards enhanced stimulus response inhibition. Sleepy lizards and blue-tongue skinks inhabit different environments and show differences in ecology and sociobiology, all of which could possibly lead to adaptive specialisation in cognitive ability. Although further research is required, we propose that selection might have led to a change in stimulus response inhibition in the arid-adapted sleepy lizard, because better response inhibition may help them avoid the costs of repeated choices towards stimuli which no longer predict a beneficial outcome.			

1. Introduction

Executive function comprises inhibition, working memory, and cognitive flexibility, all of which are necessary building blocks to execute more complex cognitive processes such as planning, reasoning, and self-control (Diamond, 2013). For example, inhibitory control is a necessary process enabling an individual to exercise control over its desire to delay gratification and obtain a more beneficial outcome at a later point in time (Diamond, 2013). Inhibitory control is generally subdivided into response inhibition or the inhibition of action, and cognitive inhibition-the inhibition of mental processes or attention. Controlling automatic responses towards tempting stimuli is an important part of self-control (Diamond, 2013) and exercised, for example, during foraging when it's important to strike at the appropriate time or avoid potentially harmful prey. In animals, different problemsolving tasks are used to test the different forms of inhibitory control. Attentional inhibition is often studied using attentional set-shifting tasks (e.g. Diamond, 2013; Dias et al., 1997; Roberts et al., 1988) while motor response inhibition can be investigated using the A-not-B task (e.g. Bray et al., 2014; Vernouillet et al., 2018) or object retrieval tasks (e.g. Marshall-Pescini et al., 2015; Santos et al., 1999), and stimulus response inhibition may be tested using a discrimination reversal learning task (e.g. Anderson et al., 2016; Boogert et al., 2011; Brucks et al., 2018; Ducatez et al., 2019).

In a standard reversal learning task, animals first learn to distinguish between two stimuli (e.g. two colours). Choosing one of these stimuli will result in a food reward (positive stimulus), while choosing the other will result in no reward (negative stimulus). After a stimulusreward association between the positive stimulus and the reward is established, individuals are presented with a reversal of this stimulusreward relationship. During the reversal the formerly negative stimulus becomes rewarded while the formerly positive stimulus becomes unrewarded. To accomplish a reversal, animals need to (1) stop responding to the formerly positive stimulus by exerting response inhibition and (2) form a new stimulus-reward association between the formerly negative stimulus and the reward (Dias et al., 1996). Animals are expected to take longer and make more errors during reversal learning compared to the acquisition of the discrimination. Furthermore, rapid learning during reversals is often seen as enhanced behavioural flexibility important for successfully adjusting when conditions change (Brown and Tait, 2015).

In lizards, reversal learning tasks are frequently used to test for

https://doi.org/10.1016/j.beproc.2020.104043 Received 12 September 2019; Received in revised form 13 January 2020; Accepted 13 January 2020 Available online 14 January 2020 0376-6357/ © 2020 Elsevier B.V. All rights reserved.

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flexible learning (e.g. Day et al., 1999; Gaalema, 2011; Leal and Powell, 2012; Szabo et al., 2018, 2019a); however, few studies have to date investigated how species differ in their reversal learning ability. The paucity of data therefore limits our ability to link reversal performance to ecological or social traits, and/or environmental conditions. In some lizard species, enhanced behavioural flexibility is associated with active foraging (Day et al., 1999) or invasive ability (Damas-Moreira, 2018), although this is not always true. For example, only one of seven invasive *Anolis cristatellus* learnt a reversal task. To do this, it needed more trials than two non-invasive, congeneric species, *A. pulchellus* and *A. evermanni* (Powell, 2012). We are just beginning to understand how reversal learning ability differs between species and how these differences relate to species' ecology and environmental conditions.

Here, our first aim was to quantify discrimination and reversal learning ability of sleepy lizards (T. r. asper) to deepen our understanding of lizard learning ability by collecting data on a novel species with an unusual social system. These lizards occur in arid or semi-arid habitats in the centre and south of Australia (Cogger, 2014). Their habitat is characterised by extreme variability and unpredictability in rainfall (< 20 days and < 300 mm per year; Bureau of Meteorology, Australian Government, 2019). Activity is greatly limited (September to December) and resource availability is highly dependent on these infrequent rainfall events. Sleepy lizards change their behaviour in line with these unexpected showers even outside their main activity period, where unexpected rainfall events can briefly increase lizard activity (Bull et al., 2017). Sleepy lizards are long-lived (> 50 years; Bull et al., 2017) and, depending on resource availability, can take between two to five years to reach sexual maturity (Bull, 1995). They show long-term (likely for their lifetime) monogamy, briefly pairing with their longterm partner at the beginning of each year's active season (Bull et al., 2017); however, individuals spend most of the year solitary and do not aggregate (Bull and Baghurst, 1998; Leu et al., 2010). They are considered mostly omnivorous with a large proportion (> 78 %) of plant material in their diet (Dubas and Bull, 1991) (Appendix Table A1).

Our second aim was to investigate if and how learning might differ between species by comparing performance of sleepy lizards with performance of a relatively closely related species, the eastern bluetongue skink (*T. s. scincoides*). Eastern blue-tongue skinks occur along the south-east coast of Australia (Cogger, 2014), in mesic environments with a higher abundance of critical resources and lower variability of annual rainfall (>75 days & >900 mm per year, Bureau of Meteorology, Australian Government, 2019) allowing for a much longer active season from September to April (Cogger, 2014). They are also a long-lived species (> 30 years; Koenig et al., 2001) and take approximately two years to reach sexual maturity (Shea, 1981). Eastern blue-tongue skinks are polygamous (Cogger, 2014) and occupy distinct home ranges throughout the year (Koenig et al., 2001). They feed on a large variety of food sources including plant material and invertebrates, opportunistically feeding on dog food and human food waste within



urban habitats (Cooper, 2000; Koenig et al., 2001) (Appendix Table A1).

We expected sleepy lizards to be able to learn the tasks we gave them because, previously, they relied on visual over spatial cues when selecting a refuge by using either brightness or shape stimuli (Zuri and Bull, 2000). When comparing performance between species, we did not expect to find a difference during the acquisition of the task because both species are terrestrial, omnivorous foragers. In this study, however, wild blue-tongue skinks were sourced from an urban population, while the wild-caught sleepy lizards were sourced from a rural, undeveloped area. Living in an urban habitat might have selected for enhanced learning ability in blue-tongue skinks (e.g. Batabyal and Thaker, 2019). Furthermore, we expected differences between species in their ability to learn a reversal. While being adapted to an arid environment might have made sleepy lizards better reversal learners (e.g. Kozlovsky et al., 2015; Tebbich and Teschke, 2014), again, urban bluetongue skinks might be more flexible learners as an adaptation to survive in an urban environment (e.g. Batabyal and Thaker, 2019). Overall, the aim of our study was to compare learning performance in two closely related species that differ in their ecology and sociobiology, to advance our understanding of how adaptive specialisations may lead to changes in cognitive ability.

2. Methods

2.1. Animal collection, housing and husbandry

Data for T. s. scincoides (N = 14 adult skinks) were available from a previous study and details on the study animals and testing procedures can be found in Szabo et al. (2019a). For the current study, we tested 17 adult Tiliqua rugosa asper (9 males and 8 females). During March 2018, five were hand-captured near Fowlers Gap Arid Zone Research Station (-31.086972 S, 141.704836 E) and two near Molong (-33.101416 S, 148.862219 E), New South Wales, Australia. Within two weeks of capture, wild skinks were transported to Macquarie University and transferred into individual plastic tubs (800 L \times 600 W \times 450 H mm). If possible, both animals in a pair were collected. The remaining lizards were on loan from private owners. Snout-vent-length (SVL), weight, head width and sex (based on measurements; Bull and Pamula, 1996) were determined at the time of acquisition (Appendix Table A2). As an arid species, lizards required low humidity and high temperatures and were therefore housed indoors, with room temperature set at 25 $\,\pm\,$ 1 $^{\circ}\text{C}$ (mean ± standard deviation, depending on season), relative humidity of 30-65 % and a 12:12 h light:dark cycle. We used heat cord underneath the tubs to increase temperature on one side to 33 $^{\circ}$ C (± 2 $^{\circ}$ C; room temperature was recorded hourly within enclosures using iButtons model DS1921). Lizards were kept on newspaper and enclosures contained a hide and two wooden ramps (Fig. 1A). During trials the newspaper substrate was taped down to ensure animals were visible

> **Fig. 1.** (A) Schematic experimental setup. Cues and dishes were presented on ramps to be visible from any point in the enclosure and prevent animals from seeing into the dishes. Lizards started each trial from the starting position and had to climb up a ramp to make a choice. (B) Order of stimulus presentation. First, animals were trained to discriminate between either of two shapes (stimulus group shape: X and triangle) or two colours (stimulus group colour: light and dark blue). Thereafter, they were presented with a reversal. Tick marks indicate the rewarded stimulus and Xs the unrewarded stimulus.

and prevent them from hiding underneath the paper. Animals were fed three times a week (Monday, Wednesday and Friday) with an assortment of small chopped fruit and vegetables powdered with calcium (URS Ultimate Calcium, at least once a week) in large (diameter of 175 mm), brown plant saucers. During experiments, skinks were fed small amounts of dog food (2 ± 0.3 g; various brands and flavours). To keep the humidity low and prevent animals from spilling their water, we introduced a water bowl twice a week for 40 min. All subjects were naïve and had never participated in any cognition experiments.

2.2. Habituation and pre-training

To prevent stress-induced learning impairment (Langkilde and Shine, 2006), animals were kept and tested in their home enclosures throughout the experiment. Lizards were habituated for two weeks before pre-training to ensure they were feeding consistently. Pretraining enabled lizards to become familiar with the procedure and equipment. Trials were conducted three times/day (15 trials total) one week prior to testing. Pre-training was divided into two phases: during phase 1 (five trials), we introduced a randomly chosen dish (95 mm diameter black, plastic food container, sides cut down to 20 mm) with open mesh baited with dog food $(2 \pm 0.3 \text{ g})$ between the ramps for 1.5 h. An animal moved on to phase 2 if it ate the reward in at least four out of the five trials. During phase 2 (ten trials) one randomly chosen food dish was placed on top of one ramp. Again, lizards that ate in at least nine out of the ten trials moved on to testing. The hide was removed during trials to assure participation and the two dishes were used equally often in a random order. Three of 17 lizards showed low food motivation and were removed from the experiment (Appendix Table A2).

2.3. Setup and procedure

Learning trials were conducted from March to October 2018 (three trials/day, five days/week). Half of the subjects (N = 7) were tested first with shape as the relevant cue (stimulus group shape) and the other half (N = 7) with colour (stimulus group colour). All groups were counterbalanced for sex and mean SVL (± 2 mm).

At the start of a trial, the hide was placed on top of each animal and both were slowly moved to the start position (making sure to cover the head to prevent the animal from watching the trial-setup) opposite the ramps (Fig. 1A). Stimulus cards (for a detailed description of the cue cards see Szabo et al., 2018) and dishes were placed on top of each ramp (they were never interchanged between individuals) and, after about one minute of acclimation, the trial began following the removal of the hide. The order in which the subjects received the setup and started each trial was alternated throughout the course of the study to prevent order effects. Animals were not able to see into the dishes and had to climb up a ramp to gain access. Cue cards were attached (with Bostik Blu-Tack adhesive putty) directly behind the dishes and were visible from any point in the enclosure (none of the lizards had problems climbing ramps and accessing the food reward). Both dishes contained a piece of dog food (2 \pm 0.3 g) and were covered with fine screen mesh. The reward was accessible through a hole cut in the screen of one of the dishes. Trials lasted for 1.5 h. Trial length was set to give lizards ample opportunity to make a choice (individuals can take over an hour to start moving). At the end of the trial we returned the hide and removed dishes and cards. Between trials both dishes were cleaned and refilled with fresh dog food (making sure that both dishes were touched to assure even odour distribution). Animals were tested between 07:30-13:30 h, with 40 min between trials (ITI). We left lizards undisturbed during trials to minimise stress and videotaped (H.264 Digital Video Recorder, 3-Axis Day & Night Dome Cameras) each trial to be scored later.

Choice (correct/incorrect) was scored based on the first food dish an animal's head passed over. Lizards needed to climb up the full length of

a ramp and lift their head above the rim of the dish to be able to see inside. Trial latency was scored as the time from removal of the hide to choice and choice latency was scored from first movement (directed, uninterrupted forward movement of the whole body ending in the examination of a food bowl; an interruption is defined as no movement for 20 s or more) to choice. Animals were not actively corrected when making a wrong choice and had ample opportunity to correct their own mistakes by visiting both stimuli and dishes within a single trial. To determine when a lizard moved on to the next stage we used a learning criterion of 7/7 or 8/9 correct choices in consecutive trials. This method was chosen because it is a good indicator of successful learning (Szabo et al., 2018, 2019a). To prevent trial fatigue (decreased motivation to participate), a lizard was only allowed 60 trials to show criterion performance otherwise it was removed from the experiment ('non-learner', N = 9). A subset (about 30 % = 357) of trials were rated by an independent observer and inter-observer reliability was calculated based on Cohen's kappa (inter-observer reliability was high both between BS & LW: 0.95 and SH & LW: 0.87; Falissard, 2012).

First, skinks were trained to discriminate between two colour/shape stimuli (acquisition). Then, they were presented with a reversal during which the previously rewarded stimulus became unrewarded and the previously unrewarded stimulus became rewarded (Fig. 1B). The colour pair (light and dark blue; Fig. 1) was chosen to be easily discriminable based on lizards' perception (Fleishman et al., 2011) and shapes were made up of lines or were solid and drawn with a black marker onto the coloured cards. During experiments, presentation of stimuli and food dishes was counterbalanced for side and followed a predetermined random order (each stimulus/dish was never on the same side more than twice in a row).

2.4. Preparations for species comparison

To investigate possible differences in learning performance between species we compared data collected from sleepy lizards to data collected during a previous study investigating differences in behavioural flexibility between two age classes in eastern blue-tongue skinks (see Szabo et al., 2019a). Overall, both species were tested at the same time of the year (blue-tongue skinks between March to October 2017 and sleepy lizards from March to October 2018) using the same procedure and equipment; some details, however, were changed in the current study. First, three trials were conducted per day (sleepy lizards) instead of two trials per day (blue-tongue skinks), for logistical reasons. Second, to quantify the point of learning, we used a slightly more stringent learning criterion of 7/7 or 8/9 for sleepy lizards. While we used 6/6 or 7/8 consecutive trials correct for blue-tongue skinks, in this study we wanted to make sure that sleepy lizards had learnt the given stage more reliably. Similar to previous work, we ensured that the minor differences in methodology had as little effect as possible on our analysis comparing the two species (Tebbich et al., 2010). Before comparing learning performance between species, we removed the last correct trial performed by each individual sleepy lizard during acquisition and reversal from the raw dataset to account for the difference in learning criterion. After removal, instead of 7/7 or 8/9 correct trials, our raw data displayed 6/6 or 7/8 correct trials (the same as for blue-tongue skinks). Additionally, although no differences in learning between age classes could be identified in blue-tongue skinks (Szabo et al., 2019a), we only used data from adult lizards to reduce the number of dependent variables in our statistical analyses. Last, pre-training was divided into two phases and we increased the number of trials (three trials per day) to increase the amount of data collected for each individual to better evaluate food motivation.

2.5. Statistical analyses

First, we analysed if sleepy lizards' probability of making a correct choice differed between acquisition and reversal. Initially, we

performed a generalised linear mixed effects model (GLMM; Bates et al., 2015); however, due to the small sample size, models were over-parameterised which led to singularity (variance of at least one effect of zero or close to zero). To deal with singularity, we instead used Bayesian modelling (McElreath, 2015) because it is robust to non-Gaussian data (Hadfield, 2010). We applied a Bayesian GLMM (Hadfield, 2010) with choice (Bernoulli: correct = 1 or incorrect = 0) as the response variable and stage and trial (scaled and centred), and an interaction between stage and trial as the fixed effects. The model included a random effect of trial nested in animal identity to account for individual differences in intercept and slope. For the Bayesian model, we confirmed that no autocorrelation (correlation between lags < 0.1; Hadfield, 2010) and sufficient mixing (by visually inspecting plots of MCMC chains) occurred and that the Markov chain was run for long enough (Heidelberg and Welch diagnostic tests). Importantly, we did not compare learning performance between males and females or between captive and wild individuals due to small sample sizes and associated low statistical power to detect differences.

Between species, we compared learning (measured as the probability of making a correct choice) on both acquisition and reversal applying a generalised linear model (GLM; Bates et al., 2015) for each stage with choice (Bernoulli: correct = 1 or incorrect = 0) as the response variable and species, trial (scaled and centred) and an interaction between species and trial as fixed effects (to investigate possible differences in learning rate between species). To make sure that the number of daily trials did not affect general learning performance between species, we also analysed choice against test day (blue-tongue skinks received 2 trials = 1 block, and sleepy lizards received 3 trials = 1 block). We applied a GLM for each stage with choice (Bernoulli: correct = 1 or incorrect = 0) as the response variable and species, block (scaled and centred) and an interaction between species and block as fixed effects. To further confirm that the difference in the number of trials conducted per day did not cause differences in choice behaviour, we analysed if the probability of a correct choice differed between species when only looking at trials within a day using a GLM for acquisition and reversal separately. Choice (Bernoulli: correct = 1or incorrect = 0) was used as the response variable and trial number per day (scaled and centred; 1 and 2 for blue-tongue skinks and 1, 2, or 3 for sleepy lizards), species, and an interaction between trial number per day and species as fixed effects.

Lastly, to confirm the robustness of our learning criterion, we applied a generalised linear multi-response mixed model (GLMM) with the number of errors and trials given as response variables and excluded (categorical: 'yes' or 'no') as the fixed effect (Bates et al., 2015) to test if lizards that were excluded from the experiment made more errors than learners. Second, because only 50 % of sleepy lizards learnt during acquisition, we investigated the reason behind the high dropout rate by comparing body condition and latency (both choice and trial) between learners and non-learners. We used a linear model (LM; Bates et al., 2015) with weight as the response variable and SVL as the fixed effect to generate a body condition index (BCI; residual values from the model). Then, we applied a LM with the BCI as the response variable and if a lizard was excluded (categorical: 'yes' or 'no') as the fixed effect (McElreath, 2015). For latency, we applied a linear mixed model (LMM; Bates et al., 2015) each for trial and choice latency (log transformed) used as response variable and, again, excluded as the fixed effect. We also included temperature (average temperatures for each trial measured by iButtons within enclosures hourly) as a fixed effect because temperature might affect motivation to move. In all mixed effects models we included both animal identity and stage as random effects and to verify that all linear models were applied appropriately, we made sure that residual distributions conformed to normality by visual inspection of plots. Moreover, to ensure that base motivation to participate was not the cause of the poor learning performance we counted the number of times each non-learner failed to finish a trial (did not make a choice within 1.5 h). Additionally, we investigated if a side bias hindered learning in non-learners by calculating an overall bias index (BI; Szabo et al., 2019b) for each animal; a BI between -0.2 and 0.2 was regarded as no bias (too weak to affect learning, based on Szabo et al., 2019b). All statistical analyses were run in R v. 3.5.3 (R Development Core Team, 2008) and raw data files and R code are available online (Open Science Framework, https://doi.org/10.17605/OSF.IO/GN4UP).

2.6. Ethical note

Our study involved non-invasive observations of behaviour which were approved by the Macquarie University Animal Ethics Committee (ARA # 2013/031) and followed guidelines laid out by the Association for the Study of Animal Behaviour/Animal Behaviour Society for the use of animals in research (Guidelines for the treatment of animals in behavioural research and teaching, 2018). Wild lizards were captured by hand and transported to Macquarie University by car in cloth bags within cooler boxes. Collection of skinks was approved by the New South Wales National Parks and Wildlife Service (OEH; License #SL101972). At the end of the experiment animals were rehomed following OEH guidelines.

3. Results

3.1. Learning performance of sleepy lizards

A total of seven (out of 14) sleepy lizards reached the learning criterion in the acquisition stage and 70 % (5/7) of these learners also learnt the subsequent reversal. When comparing sleepy lizards' probability of making a correct choice between acquisition and reversal, neither the probability of a correct choice (GLMM, reversal = 0.268, $CI_{low} = -0.400$, $CI_{up} = 0.839$, p = 0.418) nor its increase over trials (learning rate; GLMM, reversal = -0.417, $CI_{low} = -1.031$, $CI_{up} = 0.227$, p = 0.207) differed significantly (Fig. 2). Although results were not significant, sleepy lizards were more likely to make a correct choice (positive probability of the intercept) during the reversal.

When investigating the high dropout rate, none of the predicted variables could explain why 50 % of our lizards did not reach the



Fig. 2. Change in the probability of a correct choice from trial 1–60 in acquisition (solid line) and reversal (dashed line) for sleepy lizards (*T. rugosa asper*; $N_{\text{acquisition}} = 7$, $N_{\text{reversal}} = 5$). Performance based on the learning criterion 7/7 or 8/9 consecutive correct trials. 95 % confidence intervals are plotted in grey. Sleepy lizard outline in Fig. 2 and 3 from http://www.phylopic.org/ (license: https://creativecommons.org/licenses/by-nc-sa/3.0/).

Table 1

Bias index and number of failed trials for non-learners. Failed trials correspond to trials during which no choice was made and were counted in the stage the exclusion criterion was met (*N* out of 60 trials). Additional information on the animal identity (PIT), sex and stimulus group (SG) are given.

PIT	Sex	SG	Overall BI	Failed trials
4	Female	Shape	0.017	1
1	Female	Colour	-0.200	0
5	Female	Shape	0.100	0
17	Female	Colour	0.000	0
15	Male	Colour	0.167	0
20	Male	Shape	-0.088	6
6	Male	Shape	0.167	0
10	Female	Shape	0.254	2
14	Male	Shape	0.133	1

learning criterion during acquisition. Body condition (LM, excluded_{ves} $= -0.004, 95 \% \text{ CI}_{\text{low}} = -0.072, 95 \% \text{ CI}_{\text{up}} = 0.064, t\text{-value} =$ -0.117, p = 0.909) and latency (trial: LMM, excluded_{ves} = -0.378, 95 % CI_{low} = -0.795, CI_{up} = 0.023, t-value = -1.863, p = 0.063; choice: LMM, excluded_{yes} = -0.335, 95 % CI_{low} = -0.699, CI_{up} = 0.018, t-value = -1.889, p = 0.060) did not differ between learners and non-learners. Furthermore, neither choice nor trial latency were correlated with temperature (trial: LMM, temperature = -0.070, 95% $CI_{low} = -0.150$, $CI_{up} = 0.013$, *t*-value = -1.707, p = 0.088; choice: LMM, temperature = -0.026, 95 % CI_{low} = -0.099, CI_{up} = 0.049, tvalue = -0.721, p = 0.471). Non-learners did not show high numbers of failed trials or a bias preventing them from learning the discrimination except for one female whose BI was 0.254, marginally above 0.2 (Table 1). Additionally, non-learners made significantly more errors than learners (GLMM, excluded_{ves} = $0.419, 95 \% CI_{low} = 0.188$, $CI_{up} = 0.653$, *z*-value = 3.535, *p* = 0.0004) confirming the robustness of our learning criterion.

3.2. Species comparison

During reversals, species differed significantly in their probability of making a correct choice (measured from trial 1 to n as well as day 1 to n). Sleepy lizards showed a higher probability of making a correct choice compared to blue-tongue skinks (trial: GLM. species_{SleepyLizards} = 0.443, N_{SleepyLizards} = 5, N_{Blue-tongueSkins} = 9, 95 % CI_{low} = 0.043, CI_{up} = 0.851, *z*-value = 2.154, *p* = 0.031; day/block: GLM, species_{SleepyLizards} = 0.487, 95 % CI_{low} = 0.084, CI_{up} = 0.900, zvalue = 2.344, p = 0.019; Fig. 3B) but both species learnt at a similar rate (trial: GLM, species_{SleepyLizards} = -0.002, 95 % CI_{low} = -0.324, $CI_{up} = 0.324$, z-value = -0.012, p = 0.991; day/block: GLM, spe $cies_{SleepyLizards} = -0.057, 95 \% CI_{low} = -0.479, CI_{up} = 0.371, z-value$ = -0.265, p = 0.791; Fig. 3B). During acquisition, no difference was apparent in the probability of making a correct choice (trial: GLM, species_{SleepyLizards} = 0.128, N_{SleepyLizards} = 7, N_{Blue-tongueSkins} = 11, 95 % $CI_{low} = -0.188$, $CI_{up} = 0.466$, z-value = 0.828, p = 0.408; day/ block: GLM, species_SleepyLizards = 0.299, 95 % CI_{low} = -0.053, CI_{up} = 0.659, z-value = 1.647, p = 0.100) or learning rate (GLM, spe $cies_{SleepyLizards} = -0.082, 95 \% CI_{low} = -0.469, CI_{up} = 0.307, z-value$ $= -0.416, p = 0.678; day/block: GLM, species_{SleepyLizards} = 0.093, 95$ % $CI_{low} = -0.293$, $CI_{up} = 0.486$, z-value = 0.467, p = 0.641; Fig. 3A) with the latter confirming that the number of trials given per day had no strong effect on learning performance. Furthermore, no differences in choice behaviour could be identified between species when looking at the number of trials given within a day neither during acquisition (probability of making a correct choice: GLM, species_{SleepyLizards} = -0.220, CI_{low} = -1.129, CI_{up} = 0.690, p = 0.636; learning rate:

GLM, species_{SleepyLizards} = 0.191, CI_{low} = -0.314, CI_{up} = 0.697, p = 0.460; Fig. 3C) nor reversal (probability of making a correct choice: GLM, species_{SleepyLizards} = 0.545, CI_{low} = -0.581, CI_{up} = 1.692, p = 0.346; learning rate: GLM, species_{SleepyLizards} = -0.023, CI_{low} = -0.635, CI_{up} = 0.588, p = 0.941; Fig. 3D). Together, it is unlikely that the number of trials given per day affected learning performance strong enough to lead to the difference we found in reversal learning between species.

4. Discussion

Sleepy lizards showed evidence of behavioural flexibility during reversal learning and although differences between stages were not significant, sleepy lizards were more likely to make a correct choice during the reversal compared to acquisition. Importantly, sleepy lizards showed a higher probability of making a correct choice at the start of the reversal compared to eastern blue-tongue skinks suggesting better stimulus response inhibition in the sleepy lizard. These results remain the same even after accounting for differences in methodology between species. During acquisition both species performed similarly, both in the initial probability of making a correct choice and its increase over trials (learning rate), whereas, sleepy lizards were more likely to make a correct choice at the beginning of the reversal but both species showed similar associative learning ability throughout the task.

Half of our sleepy lizards did not reach criterion during the acquisition, however, neither body condition, motivation, or a side bias could explain the cause of this high drop-out rate. In blue-tongue skinks, only about 25 % of lizards did not learn during acquisition (Szabo et al., 2019a; Appendix Table A2). It is likely that differences in motivation might have caused the difference in drop-out rate between species. We were unable to collect a large enough sample of wild sleepy lizards and resorted to including a large proportion of captive individuals to reach a large enough sample size for testing. Although we do not know if these captive lizards were captive bred or originally sourced from the wild, we cannot rule out that prolonged captivity decreased motivation to participate in our food rewarded discrimination task. Of the wild caught lizards, five (out of seven) did not learn during the acquisition stage while only two (out of seven) of the captive animals were removed (Table A1). With the data available it was not possible to draw clear conclusions on how captivity affected cognitive ability in sleepy lizards. Furthermore, we still have little knowledge on how captivity affects cognitive ability in lizards in general, a promising future research avenue.

To improve our previously used methodology for testing lizards, we made some minor changes in the current study. First, sleepy lizards were tested to a more stringent learning criterion. This could have led to an increase in the number of trials taken to learn in sleepy lizards, however, we compared choice behaviour until the criterion was reached and not the number of trials taken to reach the criterion. In the acquisition, both species took the same average number of trials to reach criterion, both species started out choosing randomly (portability of 0.5) and their probability of making a correct choice increased at a similar rate. The small difference in learning criterion seems not to have caused a detectable difference in learning between species. During reversals, blue-tongue skinks took, on average, fewer trials to learn, which could be a result of the lower learning criterion. This is, however, not reflected in their probability of making a correct choice. Sleepy lizards started the reversal with a higher probability of making a correct choice indicating that they were more flexible in their choice while blue-tongue skinks performance dropped back down towards chance. If the criterion affected learning performance we would expect sleepy lizards which were tested to a more stringent criterion to show



Fig. 3. A) Change in the probability of a correct choice from trial 1-60 in acquisition for sleepy lizards (T. r. asper; N = 7; dashed line; performance after removal of the last correct trial) and for blue-tongue skinks (T. s. scincoides; N = 11, solid line). B) Change in the probability of a correct choice from trial 1-60 in the reversal for sleepy lizards (T. rugosa asper; N = 5; dashed line; performance after removal of the last correct trial) and for bluetongue skinks (T. s. scincoides; N = 9, solid line). C) Change in the probability of a correct choice during acquisition of both sleepy lizards (dashed line) and blue-tongue skinks (solid line) within testing days. Blue-tongue skinks received two trials per day while sleepy lizards received three trials a day. D) Change in the probability of a correct choice during the reversal of both sleepy lizards (dashed line) and blue-tongue skinks (solid line) within testing days. 95 % confidence intervals are plotted in grey. Sleepy lizard outline in Fig. 2 and 3 from http://www.phylopic.org/ (license: https:// creativecommons.org/licenses/by-nc-sa/3.0/).

impaired reversal learning not an improvement similar to an overtraining effect (e.g. Ishida and Papini, 1997). Second, sleepy lizards received three trials a day while blue-tongue skinks were only tested twice a day. If learning was facilitated by one more trial per day, we would expect sleepy lizards' learning performance to already be higher during acquisition, when both species first experienced our task. Despite differences in the number of trials given per day, species exhibited no differences in the initial probability of making a correct choice or rate of learning over trials or days during acquisition. Differences could only be found when looking at reversal performance, in which sleepy lizards showed a higher probability of a correct choice, indicative of better inhibitory skill (Dias et al., 1997), compared to blue-tongue skinks. Importantly, learning rates, both when looking at trial to trial and day to day, were the same during reversals, further confirming that the number of trials per day did not facilitate learning in sleepy lizards otherwise we would see a steeper learning rate in sleepy lizards. Furthermore, our analysis did not indicate any difference in learning within a day between animals experiencing two trials or three trials a day, neither during acquisition nor reversal. Taken together, the minor differences in methodology are unlikely to have caused the difference in reversal learning between the tested species.

During the reversal, most of the lizards that learnt the initial discrimination (acquisition) succeeded in the following reversal. Both species performed well during the reversal; some lizards made correct choices right from the start of the reversal which is contrary to what is expected (Brown and Tait, 2015). We propose three possible underlying

causes for this finding. First, using a predetermined learning criterion might have been insufficient to quantify the point of learning, leaving lizards with a weak association between the reward and stimulus after acquisition, resulting in some lizards making correct choices in the first reversal trial. This might have made it more likely that lizards made correct choices in future trials. Second, during trials, lizards had the opportunity to visit each stimulus and food dish multiple times giving them the opportunity to form a positive association with the formerly incorrect stimulus and collecting information about the changes in conditions on every trial, contrary to procedures in which the reward is removed after an incorrect choice is made. Together with the previous point, this might have facilitated learning early during the reversal. Lastly, sleepy lizards seem to differ from blue-tongue skinks in how they collect and process information. The higher probability of making a correct choice of sleepy lizards at the start of the reversal could reflect greater flexibility in the use of information through improved inhibition after new information is available. Generally, flexible behaviour seems to be a beneficial trait in both species, however, sleepy lizards process the provided information differently, possibly contributing to the difference we found in reversal learning.

Based on previous work (e.g. Batabyal and Thaker, 2019; Kozlovsky et al., 2015; Tebbich and Teschke, 2014), we propose a number of ecological and social traits that could explain the difference between species in reversal performance. First, habitat or resource predictability might affect reversal learning ability. In woodpecker finches (*Cactospiza pallida*) and Indian rock agamas (*Psammophilus dorsalis*), individuals adapted to an unpredictable habitat (more arid or urbanised, respectively), were faster reversal learners (Batabyal and Thaker, 2019; Tebbich and Teschke, 2014). Results are, however, not always supportive of this relationship. In delicate skinks (Lampropholis delicata), lizards from urban and rural habitats both showed similar learning ability when solving a Y-maze (Kang et al., 2018). Behavioural shifts occur rapidly, which is especially important in unpredictable environments. Inhibiting responses towards stimuli which are no longer beneficial can facilitate flexible learning (Tebbich et al., 2010) and a higher degree of behavioural flexibility helps animals cope with resource unpredictability, allowing an organism to successfully adapt to changing conditions (Leal and Powell, 2012; Lefebyre et al., 2004; Wright et al., 2010). The arid adapted sleepy lizard might benefit from greater behavioural flexibility compared to eastern blue-tongue skinks by improving sleepy lizards' ability to find new food sources in times when harsher conditions make resources scarce. Furthermore, a more pronounced difference between species might be present comparing lizards sourced from the same habitat (rural or urban). Second, differences in sociobiology might explain some of the variance in the patterns we observed. Social complexity can select for enhanced reversal learning ability (Bond et al., 2007; Lefebvre et al., 2004). Our two focus species mainly differ in their mating system: life-long monogamy in the sleepy lizards while blue-tongue skinks mate multiply (Bull, 1988; Cogger, 2014; Whiting and While, 2017). Due to intense competition for females, blue-tongue skinks might have greater social complexity and be much better at tracking individuals in their neighbourhood. As of yet, it is unclear if sleepy lizards track more individuals beyond their mating partner (Bull et al., 2017). Therefore, mating system may have an inverse relationship with social complexity in that monogamous species may have lower social complexity. It is, however, unlikely that differences in sociobiology entirely explain our result. Lastly, rather than ecological and sociobiological factors, the suitability of the methods might have differed between species. Overall, our methodology could be improved upon by reducing the quantity of the reward to increase trials given per day or removing the dish that was not chosen. Additionally, comparing only two species allows only limited conclusions. We encourage researchers to sample more species to allow comparative and meta-analytic studies (e.g. Cauchoix et al., 2018; Dougherty and

Appendix A

Table A1

Comparison of ecology, sociobiology and life history traits between sleepy lizards (*T. rugosa asper*) and eastern blue-tongue skinks (*T. s. scincoides*). SVL – Snout Vent Length.

Trait	Sleepy lizard	Blue-tongue skink	Reference
Distribution	Centre and south of Australia	South-east coast of Australia	Cogger, 2014
Habitat type	Arid or semi-arid	Mesic	Cogger, 2014
Activity period	September to December	September to April	Cogger, 2014; Bull et al., 2017
Preferred temperature range	33 – 35 °C	30 – 35 °C	Firth and Belan, 1998; Koenig et al.,
			2001
Activity cycle	Diurnal	Diurnal	Cogger, 2014; Firth and Belan, 1998
Foraging mode	Terrestrial, active foraging	Terrestrial, active foraging	Dubas and Bull, 1991; Cooper, 2000
Diet	Omnivorous	Omnivorous	Cogger, 2014; Dubas and Bull, 1991;
			Cooper, 2000
Body size (SVL)	Male: 18–34 cm	Male: 25-33 cm	Bull and Pamula, 1996; Phillips et al.,
	Female: 19–35 cm	Female: 27–35 cm	2016
Body shape	Large, terrestrial with short limbs and little	Large, terrestrial with short limbs and little	Bull and Pamula, 1996; Phillips et al.,
	sexual dimorphism	sexual dimorphism	2016
Life span	> 50 years	> 30 years	Bull et al., 2017; Koenig et al., 2001
Reproductive mode	Viviparous	Viviparous	Cogger, 2014; Shea, 1981; Bull, 1987
Mating system	Monogamous	Polygamous	Cogger, 2014; Bull, 1988
Litter size	Average of 2	Up to 18	Shea, 1981; Bull et al., 1993
Minimum age at sexual maturity	2 years	2 years	Bull, 1995; Shea, 1981

Guillette, 2018; Szabo et al., 2019c) in the future, thereby adding to the growing body of data on the learning ability of lizards and how ecology and sociobiology interact with the environment to affect cognition.

In summary, our results point towards enhanced response inhibition in the arid-adapted sleepy lizard compared to the eastern blue-tongue skink. Both species performed similarly during acquisition but sleepy lizards showed a higher probability of making a correct choice during reversal learning. Our results also suggest that sleepy lizards might be uniquely equipped to survive in their natural habitat — these lizards find sufficient food to survive and reproduce during a relatively brief period of the year (Bull et al., 2017). Errors caused by revisits to ephemeral resources due to lack of inhibition especially when activity is only possible during a short period of time might be highly costly. However, we acknowledge the limitation of a two-species comparison and that other explanations are, at this point, similarly likely. Our results provide an important avenue for future research while helping to fill an existing void in comparative cognition.

CRediT authorship contribution statement

Birgit Szabo: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing - original draft, Writing - review & editing. **Martin J. Whiting:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Resources, Writing original draft, Writing - review & editing.

Declaration of Competing Interest

None.

Acknowledgements

We thank Anthony Stimson for providing lizards, Isabel Damas and Bruno Pleno for their help catching skinks, Sebastian Hoefer for helping to collect data, Daniel Noble for his advice on statistical analysis and Levin Wiedenroth for blind coding. This project was funded by the Australian Society of Herpetologists and Macquarie University.

Table A2

Identity and trials to criterion for each of the 17 sleepy lizards (*T. rugosa asper*) and 14 blue-tongue skinks (*T. s. scincoides*) tested on their discrimination and reversal learning ability. Morphological measurements (length and weight measured at the start of the experiment), place of origin and trials to criterion are given for each individual (criterion for sleepy lizards was 7/7 or 8/9 and for blue-tongue skinks was 6/6 or 7/8). Only data from individuals that reached the learning criterion in both acquisition (ACQ) and reversal (REV) stages were compared in our analysis. – no data available. ID/PIT – animal identity, SVL – snout vent length, SG – stimulus group, Wild – lizard collected from the wild, Captive – private owned lizard with unknown origin (captive bred or initially wild caught). * did not reach the learning criterion and was not included in the analyses.

Species	ID/PIT	Sex	SVL (cm)	Weight (g)	Origin	Location	SG	ACQ	REV
T. rugosa asper	1	Female	310	541.6	Wild	Fowlers Gap	Colour	60*	-
T. rugosa asper	3	Male	314	583.8	Wild	Fowlers Gap	Colour	17	27
T. rugosa asper	4	Female	332	595.2	Wild	Fowlers Gap	Shape	60*	-
T. rugosa asper	5	Female	324	487.1	Wild	Fowlers Gap	Colour	60*	-
T. rugosa asper	6	Male	280	563.7	Wild	Fowlers Gap	Shape	60*	-
T. rugosa asper	9	Male	288	794.6	Captive	-	-	-	-
T. rugosa asper	10	Female	334	897.4	Captive	-	Shape	60	60*
T. rugosa asper	11	Female	276	459.6	Captive	-	-	-	-
T. rugosa asper	12	Male	309	681.0	Captive	-	-	-	-
T. rugosa asper	13	Male	321	699.0	Captive	-	Shape	29	61
T. rugosa asper	14	Male	320	704.9	Captive	-	Shape	18	60*
T. rugosa asper	15	Male	300	538.2	Captive	-	Colour	60*	-
T. rugosa asper	16	Female	321	620.8	Captive	-	Colour	59	9
T. rugosa asper	17	Female	300	552.7	Captive	-	Shape	60*	-
T. rugosa asper	18	Female	306	514.9	Captive	-	Colour	12	18
T. rugosa asper	19	Male	263	401.2	Wild	Molong	Colour	53	59
T. rugosa asper	20	Male	259	412.2	Wild	Molong	Shape	60*	-
T. s. scincoides	262	Male	283	304.6	Wild	-	Shape	8	45
T. s. scincoides	044	Female	301	458.8	Wild	-	Colour	19	60*
T. s. scincoides	274	Female	312	455.5	Wild	Collaroy	Shape	45	41
T. s. scincoides	710	Female	303	379.2	Wild	Marsfield	Shape	46	33
T. s. scincoides	13	Male	285	327.0	Wild	Schofields	Colour	43	10
T. s. scincoides	310	Female	322	435.4	Wild	Thornleight	Shape	60*	-
T. s. scincoides	347	Female	308	411.6	Wild	Glossodia	Colour	54	40
T. s. scincoides	304	Male	304	435.0	Wild	Baulkham Hills	Colour	52	24
T. s. scincoides	325	Female	251	248.1	Wild	Guildford	Colour	45	48
T. s. scincoides	281	Male	283	319.6	Wild	Windsor	Colour	57	8
T. s. scincoides	673	Female	301	357.0	Wild	Windsor	Shape	60*	-
T. s. scincoides	721	Male	249	177.1	Wild	Yagoona	Shape	26	48
T. s. scincoides	544	Male	309	462.2	Captive	-	Colour	38	60*
T. s. scincoides	24	Male	308	552.0	Captive	-	Shape	60*	-

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