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Learning Simple and Compound Stimuli in a Social Lizard (*Egernia stokesii*)

Birgit Szabo[1, 2], Daniel W. A. Noble[3], and Martin J. Whiting[1]
[1] Department of Biological Sciences, Macquarie University
[2] Division of Behavioural Ecology, Institute of Ecology and Evolution, Department of Biology, Faculty of Science, University of Bern
[3] Division of Ecology and Evolution, Research School of Biology, The Australian National University

We tested learning and behavioral flexibility in family-living gidgee skinks (*Egernia stokesii*) using a multistage visual discrimination task that included acquisition and reversal stages using simple and compound stimuli composed of black shapes superimposed on a colored background. We evaluated how lizards learn compound cues through a probe test. Lizards showed behavioral flexibility through reversal learning using simple stimuli (only color or shape). Our lizards used compound stimuli to learn a discrimination but had problems reversing and generalizing across novel compound stimuli. In the probe test, lizards chose the correct stimulus in a novel pairing with a distractor feature even without previous experience with compound stimuli. Our results suggest that some lizards are likely able to attend selectively to the relevant features of our compound stimuli while ignoring irrelevant features instead of using the configuration of a cue card as a whole to learn to discriminate between compound stimuli. We hope that our work will spark interest in further studies looking at how lizards (and reptiles in general) learn to solve visual discrimination problems.

Keywords: cognition, executive functions, reptile, attentional set shifting, squamate

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Much discussion on how animals learn about stimuli and their value has focused around attention. Learning the solution to, for example, a discrimination problem involves learning to attend to the relevant stimulus features and learning which value of the feature predicts the reward (Pearce & Mackintosh, 2010). This is especially important if the stimulus presented is composed of multiple features, for example, different shapes and colors. Natural stimuli rarely vary across a single feature. For example, ripe fruit can typically be found only at specific times of the year, at a specific location; they have a distinct odor and often a distinct color. Not all of these cues, however, are of similar importance, meaning that some predict the ripeness of a fruit better than others. Selective attention ensures that the focus lies on the stimuli that are most important in a given situation (interference control; Diamond, 2013).

The traditional study of selective attention has generated different hypotheses about how animals acquire a discrimination. Animals might learn discontinuously, attending to only one feature at a time until they select a stimulus feature that is associated with reinforcement. Animals might learn continuously, being able to perceive all features of a stimulus simultaneously, but gradually paying more attention to the feature that predicts reward while learning to ignoring others (learnt irrelevance—learning that some stimulus features can be ignored; Castro & Wasserman, 2016). Furthermore, attention might not be given to the absolute properties of each stimulus but rather to distinguishing features (Mackintosh, 1965; Zentall, 2005; Zentall & Riley, 2000). Some animals do indeed gradually learn to pay attention to relevant features while ignoring irrelevant information in simultaneous discrimination problems with compound stimuli (Castro & Wasserman, 2016; Dopson et al., 2010; Lawrence, 1949), and they do learn

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Birgit Szabo https://orcid.org/0000-0002-3226-8621
Daniel W. A. Noble https://orcid.org/0000-0001-9460-8743
Martin J. Whiting https://orcid.org/0000-0002-4662-0227

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All datasets generated and the code used for analyses in the current study are available at the Open Science Framework (https://doi.org/10.17605/OSF.IO/Q2UF6).

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Correspondence concerning this article should be addressed to Birgit Szabo, Division of Behavioural Ecology, Institute of Ecology and Evolution, Department of Biology, Faculty of Science, University of Bern, Wohlenstrasse 50a, CH-3032 Bern, Switzerland. Email: birgit.szabo@gmx.at

something about the irrelevant features, although less so compared with features that are associated with a reward (Mackintosh, 1965). Pretraining of the relevant feature as a single stimulus, however, reduces the amount learnt about the irrelevant features in a compound cue (Mackintosh, 1965).

An individual's ability, or inability, to discriminate between multifeatured stimuli might depend on how they categorize stimuli. In the psychology literature, two systems are distinguished: implicit and explicit. In an implicit system of categorization, many features are recognized in parallel, and a stimulus is perceived holistically as a single entity; discriminations between stimuli are achieved through associative mechanisms. In an explicit system, attentional processes are focused on distinct stimulus features highlighting those features that are relevant for reinforcement and a rule might be derived to solve a discrimination problem. Humans, rhesus macaques (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*) are biased toward using the explicit system trying to find a single feature (or rule) that permits correct categorization even if, per the experimental design, no such single feature is available. Pigeons (*Columba livia*), in contrast, show no such bias (Smith et al., 2012). Rule transfer tests suggest that humans and macaques have, and use, both the explicit and implicit system of categorization (Casale et al., 2012; Smith et al., 2015). Pigeons, however, seem to use one system that is rule based and associative (Qadri et al., 2019).

Attention is an important process involved in the detection of change and in exerting behavioral flexibility (i.e., the ability to adapt behavior to changed conditions; Brown & Tait, 2015). In animals, behavioral flexibility is most often studied using discrimination reversal learning tasks (e.g., single reversal: Leal & Powell, 2012; Tebbich & Teschke, 2014; Tebbich et al., 2010; serial reversal: Liu et al., 2016) or attentional set-shifting tasks (Birrell & Brown, 2000; Bissonette et al., 2012; Dias et al., 1996; Roberts et al., 1988; Szabo et al., 2018, Szabo, Noble, Byrne, et al., 2019), among others (Nicolakakis et al., 2003; Sol & Lefebvre, 2000; Sol et al., 2002; Tebbich et al., 2010). To solve a reversal learning task, animals first need to recognize the change in a stimulus–reward relationship to stop responding to the formerly rewarded stimulus and shift behavior toward the formerly unrewarded stimulus (Dias et al., 1996). In set-shifting tasks (e.g., Wisconsin card sorting task in human children, Berg, 1948; or the intradimensional/extradimensional—ID/ED—attentional set-shifting task in animals, Mackintosh & Little, 1969; Roberts et al., 1988; Szabo et al., 2018, Szabo, Noble, Byrne, et al., 2019), individuals need to overcome an attentional bias toward one set of features (often referred to as belonging to the same dimension; e.g., lines) and shift attention toward stimuli from within another set of features (second dimension; e.g., shapes; Brown & Tait, 2015). Failure to do so might either be caused by an inability to shift attention away from previously relevant features (attentional perseveration) or the interference of learnt irrelevance (Castro & Wasserman, 2016). Furthermore, discrimination of compound stimuli (consisting of two or more features) might be impeded if stimuli within the same feature set (dimension) are distant (e.g., wavelength if color is used) or if stimulus features are spatially separated (e.g., one feature being intramaze cues and the other extramaze cues—cues outside the maze; Trobalon et al., 2003).

We have previously shown that reversal learning and intradimensional/extradimensional (ID/ED) attentional set-shifting tasks can be successfully applied in lizards (Szabo et al., 2018; Szabo, Noble, Byrne, et al., 2019; Szabo & Whiting, 2020). A growing body of literature is using reversal learning to quantify lizard behavioral flexibility in the visual (Leal & Powell, 2012) and spatial domain (Noble et al., 2012) and in relation to foraging ecology (Day et al., 1999), incubation temperature (Clark et al., 2014), or habitat features (Batabyal & Thaker, 2019) although a single reversal by itself might not be sufficient to demonstrate behavioral flexibility. Here, we investigated the visual discrimination learning ability of the Australian gidgee skink (*Egernia stokesii*), a family-living lizard. Gidgee skinks are a medium-sized species that inhabit arid or semiarid arboreal and rocky habitats in long-term, stable, kin-based, multigenerational family groups comprising of a monogamous mating pair and their offspring (Chapple, 2003; Cogger, 2014; Gardner et al., 2001). They are part of the Egernia group, a clade of Australian lizard species expressing varying degrees of sociality (Chapple, 2003; Whiting & While, 2017). Gidgee skinks are omnivorous with a large amount of plant material in their diet; they are active during the day, have a long life span of about 25 years, and take up to 5 years to reach sexual maturity (Chapple, 2003; Duffield & Bull, 1998, 2002).

Our aim was to investigate, for the first time, learning and behavioral flexibility in this social lizard. To this end, we tested lizards using a multistage visual two-choice discrimination task that included multiple reversal stages. We presented lizards with cards painted in different colors (background) containing different shapes superimposed on top (compound stimulus with multiple features). Reinforcement was associated with one feature set (e.g., one of two background colors), whereas the second set (e.g., two different shapes) was irrelevant for reinforcement. We also investigated what lizards attend to when learning compound stimuli. We hypothesized that lizards would either (a) use associative learning perceiving each compound stimulus holistically by combining all stimulus features (e.g., color and shape) and remembering which two out of four cards were associated with a reward, or (b) selectively attend to the stimulus features predicting reward (e.g., color) while learning to ignore irrelevant information (e.g., all shapes).

Method

Study Animals

We hand-captured 22 wild, adult *Egernia stokesii* (snout-vent-length >145 mm; Chapple, 2003), of undetermined sex, around Fowlers Gap Arid Zone Research Station (−31.086972 S, 141.704836 E), New South Wales, Australia. Three were captured during March 2018 and 19 during November 2018. Within 1 week of capture, individuals were transported to Macquarie University by car in cloth bags within a cooler box and transferred into individual plastic tubs (683 L × 447 W × 385 H mm).

Housing

Lizards were housed in a temperature-controlled environment (24 ± 2°C *SD*), relative humidity between 30 and 60%, and a light cycle of 12 h (06:00–18:00 h). Snout-vent-length (SVL), total length (TL), and head width (HW) of all lizards were determined on the day of capture and 1 week before the start of testing with the addition of lizard weight. We installed heat cords underneath the enclosures to increase temperature on one side to up to 33°C (±2 °C *SD*) and iButtons (Thermochron iButton model DS1921) recorded temperature hourly within enclosures. Each enclosure was lined with paper and equipped with a refuge for shelter, a water bowl (heavy, poly resin reptile water bowls made to look like rock, 130 L × 110 W × 40 H mm), and two wooden ramps.

Husbandry

When not being tested, lizards were fed three times a week. On Monday, Wednesday, and Friday, they were fed an assortment of small cut fruit and vegetables. Additionally, on Friday lizards were fed three to four adult crickets (powdered with aristopet Repti-vite and URS Ultimate Calcium). During experiments, lizards were fed only on Fridays because they were consuming fruit-based baby food (0.08 ± 0.01 g; Heinz, various flavors) as positive reinforcement during trials for the rest of the week. During regular feeding, vegetables and fruit were presented in green dishes (60 mm diameter), while within trials reinforcement was presented in 55-mm-diameter petri dishes, with the outside covered in black electrical tape. Lizards had ad libitum access to water.

Habituation and Pretraining

Before the study, all lizards were feeding consistently. They had habituated to captivity over the course of at least 1 month (three lizards had been in captivity for 9 months before testing began; Table S1 in the online supplemental materials).

Pretraining was conducted 1 week before testing and lasted for a maximum of 2 weeks (30 trials). During phase 1 ($N = 5$ trials), one baited food dish was presented in front of the water bowl for 1.5 h with the refuge removed. Individuals moved on to Phase 2 if they ate the reward in at least four of five (80%) trials. Phase 2 lasted at least 10 trials but a maximum of 25 trials. One baited food dish was presented on top of a ramp, for 1.5 h and the refuge was removed. An individual moved on to the first testing stage if it ate the reward in at least 80% of Phase 2 trials. For each lizard, two food dishes were available and used in a random order throughout pretraining to ensure that lizards had distributed their own scent evenly on both dishes before the first test stage. The side (ramp) on which a food dish was presented in Phase 2 was randomized but counterbalanced (each dish appeared an equal number of times on the left and right ramp).

To prevent stress-induced learning impairment (Langkilde & Shine, 2006), animals were kept and tested in their home enclosures throughout the experiment. Two lizards did not reach criterion in pretraining Phase 2 and were therefore removed from the experiment due to low food motivation (Table S1 in the online supplemental materials). The three lizards captured during March 2018 had preexperience with one cognitive assay testing their motor response inhibition (Szabo, Hoefer, et al., 2020), whereas the other 19 animals were experimentally naïve.

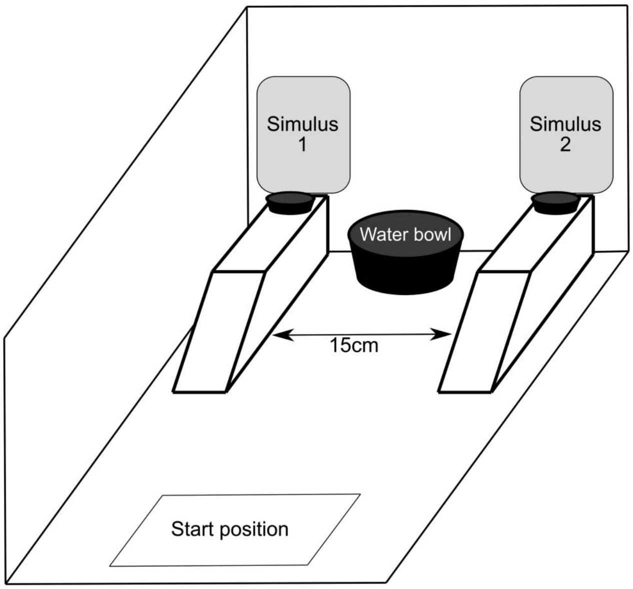
Setup and Procedure

The study was conducted from December 2018 to March 2019 (three trials per day, 5 days per week). Subjects were randomly divided into two groups: one group was tested on a shape discrimination (stimulus group shape, $N = 11$), and the other group was tested on a color discrimination (stimulus group color, $N = 9$). Average snout-vent-length (SVL; a commonly used measure for lizard size) of groups was equated as best as possible (mean $\mathrm{SVL}_{\mathrm{color}} = 179.2 \pm 17.0$ *SD*; mean $\mathrm{SVL}_{\mathrm{shape}} = 178.9 \pm 15.5$ *SD*).

To start a trial, the refuge was slowly placed on top of an animal and both were slowly moved to the start position at one end of the enclosure opposite to the ramps, stimuli, and dishes (see Figure 1). We ensured that the refuge was covering the head and most of the body to prevent the animals from seeing any unconsciously given cues from the experimenter while setting up a trial. Next, stimulus cards were fixed to the back wall of the enclosure on top of the ramps with Bostik Blu-Tack adhesive putty. This prevented cards from falling off the ramps during trials. Thereafter, the already-baited (2 ± 0.3 g of reward each) and closed (with fine PVC coated Polyester insect screen, Cyclone Screening Pet Mesh) food dishes were placed on top of the ramps directly in front of and as close as possible to the cue cards. The dish in front of the incorrect stimulus was completely covered with mesh blocking access to the reward. A hole in the mesh on the dish in front of the correct stimulus made the reward accessible. Using mesh allowed food odor to be detectable from both dishes controlling for the use of food chemicals to solve the tasks. By using ramps we ensured that the stimulus cards were visible from any location in the enclosure and that animals were unable to see into the dishes and determine which one provided food before making a choice (gidgee skinks are saxicolous and good climbers; Chapple, 2003). Each individual received the same refuge, ramps, cards, and dishes for the duration of the experiment.

Figure 1

Schematic Setup Used During Experiments



Note. Cards depicting stimuli were presented on top of wooden ramps at one end of the enclosure. Food dishes were presented right in front of the cards elevated on the ramps. The water bowl was present during trials between ramps that were approximately 15 cm apart. Lizards started each trial from the start position, on the warm side of the enclosure (heated by heat cord to 33 ± 2 °C *SD*) opposite the setup.

A trial started after about 1 minute of acclimation with the removal of the refuge exposing the lizard to the setup. The order in which the subjects received the setup and started each trial were alternated throughout the course of the study to prevent order effects. Trials lasted for 1.5 h each. Trial length was chosen 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 refuge to the enclosure and removed dishes and cards. Between trials, in the 40-min intertrial interval, both dishes were cleaned and refilled with fresh baby food (making sure that both dishes were touched to assure even odor distribution). Animals were tested between 07:30–13:30 hours. We left lizards undisturbed during trials to minimize stress and videotaped (H.264 Digital Video Recorder, 3-Axis Day & Night Dome Cameras) each trial to be scored later.

A choice was scored as correct if the lizard approached the dish in front of the correct stimulus first and passed over it with its head. We assumed that if the head passed over the dish the lizard was able to see into the chosen dish. A choice was scored as incorrect if the lizard first approached the dish in front of the incorrect stimulus. We scored trial latency (time from removal of the refuge to when the head passed over a dish for the first time) and choice latency (from the first directed, uninterrupted forward movement of the whole body to choice; an interruption is defined as no movement for 20 s or more). Animals were able to visit both dishes multiple times within a trial being able to correct wrong choices in each trial (self-correction). To determine the point of task acquisition, we used a predetermined criterion of 6/6 or 7/8 correct choices in consecutive trials (based on Szabo et al., 2018; Szabo, Noble, Byrne, et al., 2019). To prevent decreased motivation to participate due to prolonged exposure to the same task, a maximum number of trials was given in each task. In Stage 1, we allowed 70 trials and in all subsequent stages (2 to 6), we allowed only 60 trials. If acquisition was not reached within the maximum number of trials, a lizard was removed from the experiment ("non-learner"). To ensure unbiased scoring of a lizard's choice behavior, a random subset of trials (14%) was scored by an independent observer. Cohen's kappa interobserver reliability was calculated at 0.903 (high; Falissard, 2012).

Stimulus Cards

Cards were made of pressed wood (rectangle coaster, Boyle Industries Pty Ltd, 113 L × 93 W × 3 H mm), sprayed with spray paint and finally, shapes were drawn onto the sprayed cards (see Figure 2). Color pairs were chosen to be easily discriminable based on the lizard perceptual system (Fleishman et al., 2011). During experiments, each stimulus (and dish) was never presented more than twice in a row on the same side and the left/right position of each feature within compound stimuli varied independently of each other. For more details on spray paint brand and color as well as shape measurements, see Szabo et al., 2018.

Test Stages

In Stage 1, simple discrimination (SD), lizards were trained to discriminate between two color/shape stimuli (single feature) and thereafter on a simple discrimination reversal (SDR) of the same stimuli (see Figure 2). Next, a second set of features was added to the cards: For lizards trained on shape, background colors were added to the cards and for lizards trained to discriminate between colors, shapes were superimposed on the background color (see Figure 2). These irrelevant features were intended as a distractor. A compound discrimination acquisition (CD) and a reversal (CDR) were tested. Lastly, lizards that learnt to discriminate between these compound cues were presented with an intradimensional shift (see Figure 2). We presented lizards with novel stimuli (novel colors and shapes) for all features in an acquisition (ID) and reversal stage (IDR). We had planned to also test our lizards on an extradimensional shift (similar to Szabo et al., 2018, Szabo, Noble, Byrne, et al., 2019); however, none made it this far.

After lizards had finished the test stages, they were tested using a probe test to investigate if they had the ability to separate cards into distinct stimulus features when learning to discriminate compound cues. Only lizards that had successfully reached the learning criterion in at least one stage were tested on the probe test. The probe test was similar to an intradimensional shift. We again introduced a novel set of shape and color stimuli (see Figure 2); however, the positive stimulus feature was paired with only one of the distractor features (Phase 1). For example, the reinforced shape "Z" was paired with a light brown background only, whereas the nonreinforced heart shape was paired with both a light and dark brown background (see Figure 2). Similar to the previous test stages, in Phase 1, lizards had to learn the discrimination. They could either learn the configuration of the whole reinforced card (e.g., Z with a light brown background) or learn the distinct feature (e.g., shape Z) predicting reward. If a lizard reached the learning criterion (6/6 or 7/8) within 30 trials, it was given 15 additional trials (Phase 2). In Trials 1, 3, 7, 13, and 15 of Phase 2, we presented the missing compound stimulus (e.g., "Z" with the dark brown background). We predicted that, if lizards had learnt to choose based on the configuration of cards, then the introduced compound card would be novel and lizards would chose at random in Trials 1, 3, 7, 13, and 15. Conversely, if they had learnt to choose based on the reward predicting feature, the new distractor would have no effect on performance and lizards would choose correctly in Trials 1, 3, 7, 13, and 15.

Odor Control

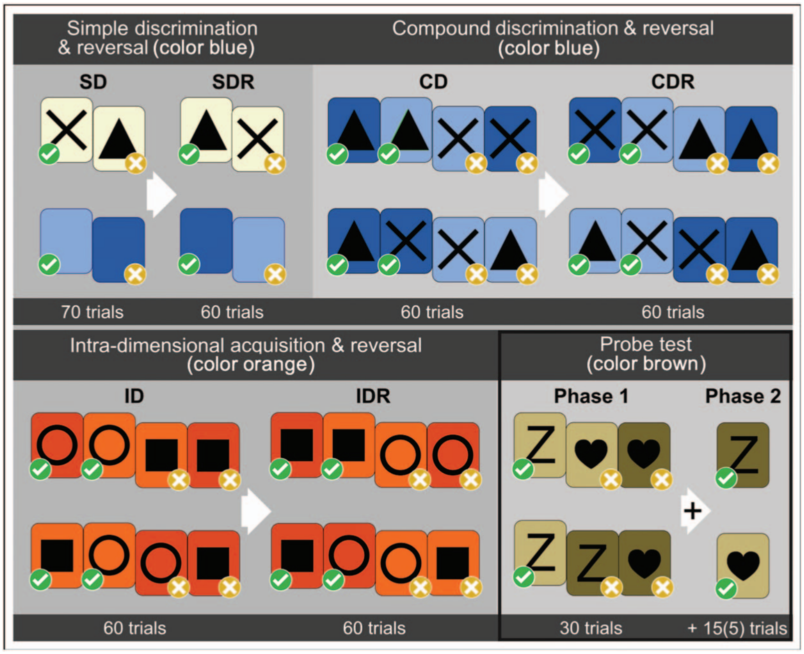
Because we had cut a hole into only one of the mesh sheets covering the food dishes (which might have changed food odor diffusion), we tested 10 randomly chosen lizards in an odor control task (Table S1 in the online supplemental materials). We administered 10 trials each after lizards had finished test trials. We used compound stimuli (stages CD and CDR) but neither of the color or shape features, dish or side of stimulus/dish presentation predicted reinforcement. Dishes and cards were thoroughly cleaned with detergent before testing. We used a one-sample Wilcoxon's test to compare lizards number of correct choices (approaching the open dish) out of 10 trials to chance performance (= 5/10 trials). The lizards choice did not deviate from chance (one-sample Wilcox test, $V = 8.5$, median = 5; $p = .746$).

Statistical Analyses

We analyzed general learning performance within each stage using Bayesian generalized linear mixed effects models (GLMM;

Figure 2

Sequence in Which Stimuli Were Presented



Note. Half of the lizards were assigned to stimulus Group 1 (top row) and learned to discriminate between shapes (shape as the relevant feature). The other half were assigned to stimulus Group 2 (bottom row) and started learning to discriminate between colors (color as the relevant feature). The first couple of stages are called simple discrimination (SD) and reversal (SDR) in which cards were made up of only one feature (e.g., either sprayed in one color or a black shape on beige background). One stimulus was associated with a reward (tick mark), whereas the other was not associated with a reward (X). This was followed by two stages (compound discrimination—CD, and reversal—CDR) in which a second, but irrelevant feature was added to the cue cards (either a background color other than beige or a shape superimposed over the colored background). Next, novel colors and shapes were used in the intradimensional acquisition (ID) and reversal (IDR). Finally, in the probe test, again novel colors and shapes were introduced, but only three possible combinations of stimuli were presented during Phase 1. After lizards reached the predetermined learning criterion, the fourth and novel combination was introduced five times out of 15 in Phase 2 to test if lizards had learnt to use compound stimuli or had separated stimuli into feature sets (or dimensions) to make a successful discrimination. Except for SD and the probe test, lizards received a maximum of 60 trials to reach the learning criterion. See the online article for the color version of this figure.

Hadfield, 2010). We only looked at the first three stages because our sample sizes were too low in later stages ($N = 1$ in CDR and ID, none of the lizards learnt during IDR). Criterion trials (last six to eight trials in which the learning criterion of 6/6 or 7/8 consecutive correct choices was reached) were included in the analyses. We were also interested in comparing learning performance between stimulus groups and capture locations. Because gidgee skinks live in multigenerational family groups, we used capture location as a proxy for group identity to investigate if groups differed in their learning ability. We compared groups only if data on a minimum sample of three animals were available in each group (Forstmeier et al., 2017). Therefore, we allocated lizards captured within the same rock outcrop into the same group to increase sample size. This was warranted because gidgee skinks live in large, stable, kin-based family groups composed of a monogamous pair and multiple generations of offspring that exhibit low rates of dispersal (Duffield & Bull, 2002; Gardner et al., 2001, 2002) and high site fidelity (Gardner et al., 2007; Pearson et al., 2016). Due to small sample sizes, stimulus groups were compared only within the first stage and certain capture locations had to be excluded from the analysis (due to low sample size); location was, therefore, only compared in the first two stages.

To investigate possible differences in learning in Stage 1 (*SD*), our model included choice (1—correct, 0—incorrect) as the response variable and trial, stimulus group, and their interaction as the fixed effects. Because certain capture locations had to be excluded because of low sample size, we ran an extra model to compare performance between capture locations to avoid limiting our analysis of general learning performance and stimulus group due to removing data. We did not correct alpha levels but instead present estimates and confidence intervals generated from our models (Nakagawa, 2004). The model investigating differences between capture locations included choice (1—correct, 0—incorrect) as the response variable and trial, capture location, and their interaction as the fixed effects. Similarly, in Stage 2 (SDR), we ran a model to look at general learning performance (sample size for stimulus groups was too small to run an analysis) with choice (1—correct, 0—incorrect) as the response variable and trial as the fixed effect and a second model for capture location (same as above). Finally, sample sizes were too small to compare stimulus groups or capture locations in Stage 3(CD). Therefore, we only ran a model to look at general learning performance using choice (1—correct, 0—incorrect) as the response variable and trial as the only fixed effect.

We also made two comparisons between stages: (a) to compare acquisition (SD) to reversal (SDR) performance and (b) to compare learning between stages in which simple stimuli (SD) were used to when distractor features (CD) were added (compound stimuli). No further comparisons were made due to limitations in sample size. We focused only on data from the respective stages of interest and used Bayesian GLMMs with choice (1—correct, 0—incorrect) as the response variable and trial, stage, and their interaction as the fixed effects. Furthermore, we compared the number of correct/incorrect choices performed in the last 10 trials of Stage 2 (SDR) to the number of correct/incorrect choices made in the first 10 trials of Stage 3 (CD) using the Fisher's exact test of independence to further investigate how the addition of an irrelevant feature affected lizard performance. Additionally, we used a Bayesian GLMM to investigate if lizards showed a training effect (improvement across stages) after being repeatedly tested on similar problems. The model was based on the whole data set and choice (1—correct, 0—incorrect) was used as the response variable and trial, stage, and their interactions as the fixed effects. To account for changes in performance across stages, we used a random effect of trial, stage, and their interaction, nested in animal identity. Due to our limited data set, we did not estimate all covariates (compared with all other Bayesian models for which all covariates were estimated) and z-transformed trial to ensure good model conversion. All other Bayesian models included a random effect of trial nested in individual identity to account for differences in intercepts and slopes (respectively) and to account for autocorrelation between successive choices. Furthermore, for all models, we confirmed that no auto-correlation (correlation between lags <0.1; Hadfield, 2010) occurred, that sufficient mixing (by visually inspecting plots of Markov chain Monte Carlo (MCMC) chains; Hadfield, 2010) took place, and that the Markov chain was run for long enough (Heidelberg and Welch diagnostic tests; Hadfield, 2010). All statistical analyses were run in R Version 3.5.3 (R Development Core Team, 2008).

We also investigated if errors, food motivation during test trials, a side bias, or body condition differed between successful learners and nonlearners (removed due to not reaching the learning criterion). For details on these analyses, see the online supplemental materials. No statistical analyses were conducted on the data collected from the probe test because only two lizards reached the learning criterion in Phase 1 and were tested in Phase 2 of the probe test. All data sets generated and the code used for analyses in the current study are available at the Open Science Framework (https://doi.org/10.17605/OSF.IO/Q2UF6).

Ethics

The experiments performed in this study were strictly noninvasive observations of behavior and followed the guidelines laid out by the Association for the Study of Animal Behavior/Animal Behavior Society for the treatment of animals in behavioral research and Teaching (Association for the Study of Animal Behavior, 2018). Experimental procedures were approved by the Macquarie University Animal Ethics Committee (Animal Research Authority #2013/031). Animal collection from the wild was approved by the New South Wales National Parks and Wildlife Service (Office of Environment and Heritage; License #SL101972).

Results

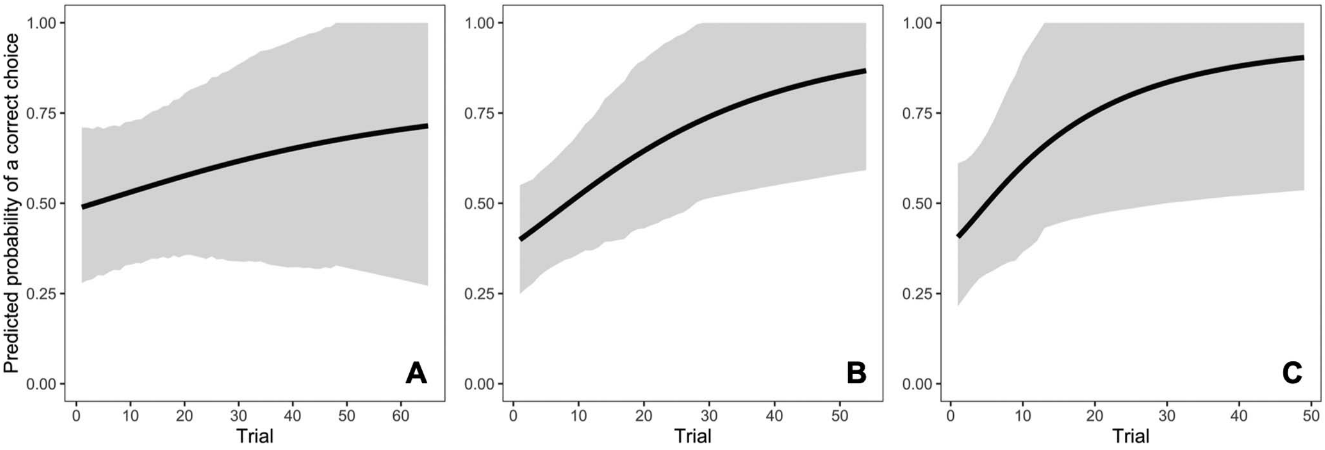
Overall, 12 of 22 lizards (55%) reached the learning criterion during the simple discrimination (SD); eight of 12 (67%) reached criterion during the reversal (SDR), and six (75%) also learnt to discriminate between compound stimuli (CD). However, only one lizard managed to reach the learning criterion during the reversal of the compound discrimination (CDR) and the intradimensional acquisition (ID) when novel colors and shapes were introduced but subsequently failed in the intradimensional reversal (IDR). Lizards that were excluded did make more errors compared with lizards that reached criterion; nonlearners did not show lower food motivation during test trials and neither a side bias or body condition explained learning performance (for details see the online supplemental materials).

In the simple discrimination (SD), the probability of making a correct choice increased from 0.489 in Trial 1 to 0.715 in Trial 65 (Figure 3A). Our lizards improved by 46% across 65 trials, which was not significant (GLMM, $N = 12$, trial $= 0.019$, confidence interval $[\mathrm{CI}]_{\mathrm{low}} = -0.028$, $\mathrm{CI}_{\mathrm{up}} = 0.068$, $p = .362$). During the reversal of the simple discrimination (SDR), in which a change in the stimulus–reward relationship occurred, the probability of lizards making a correct choice increased from 0.399 in Trial 1 to 0.867 in Trial 54 (Figure 3B). Our lizards improved 118% across 54 trials, which was marginally significant (GLMM, $N = 8$, trial $= 0.057$, $\mathrm{CI}_{\mathrm{low}} = -0.008$, $\mathrm{CI}_{\mathrm{up}} = 0.127$, $p = .043$). After the introduction of an irrelevant distractor the probability of lizards choosing correctly increased from 0.406 in Trial 1 to 0.904 in Trial 49 (Figure 3C). Our lizards improved by 123% across 49 trials, which was not significant albeit we had a small sample size at this stage (GLMM, $N = 6$, trial $= 0.098$, $\mathrm{CI}_{\mathrm{low}} = -0.032$, $\mathrm{CI}_{\mathrm{up}} = 0.282$, $p = .083$). Finally, lizards captured at different locations did not differ in their learning performance (GLMM, $p > .05$; Table S2 in the online supplemental materials), and neither did stimulus groups (GLMM, $\mathrm{SG} = 0.237$, $\mathrm{CI}_{\mathrm{low}} = -0.882$, $\mathrm{CI}_{\mathrm{up}} = 1.399$, $p = .674$; $\mathrm{trial}_{\mathrm{SG}} = 0.002$, $\mathrm{CI}_{\mathrm{low}} = -0.063$, $\mathrm{CI}_{\mathrm{up}} = 0.067$, $p = .981$).

The comparison between the acquisition of the discrimination (SD) to the reversal (SDR) revealed no difference between stages (GLMM, stage $= -0.099$, $\mathrm{CI}_{\mathrm{low}} = -0.387$, $\mathrm{CI}_{\mathrm{up}} = 0.191$, $p = .506$; $\mathrm{trial}_{\mathrm{stage}} = 0.005$, $\mathrm{CI}_{\mathrm{low}} = -0.010$, $\mathrm{CI}_{\mathrm{up}} = 0.020$, $p = .493$). Adding irrelevant features to the cue cards did not affect lizards' performance (GLMM, stage $= -0.078$, $\mathrm{CI}_{\mathrm{low}} = -0.470$, $\mathrm{CI}_{\mathrm{up}} = 0.326$, $p = .696$; $\mathrm{trial}_{\mathrm{stage}} = 0.007$, $\mathrm{CI}_{\mathrm{low}} = -0.012$, $\mathrm{CI}_{\mathrm{up}} = 0.024$, $p = .463$; Fisher's exact test of independence, $p > .05$; Table S3 in the online supplemental materials). Furthermore, improvement when solving similar problems across stages was nonsignificant

Figure 3

Change in the Predicted Probability of Making a Correct Choice From Trial 1 to Trial N *(Last Trial Is Dependent on When Lizards Reach the Learning Criterion) for the First Three Stages*



Note. Panel A: Learning curve of the 12 lizards tested in the simple discrimination (Stage 1—SD). Panel B: Learning curve of the eight lizards tested in the simple discrimination reversal (Stage 2—SDR). Panel C: Learning curve of the six lizards tested in the compound discrimination (Stage 3—CD). Results shown only include lizards that reached the learning criterion, and 95% credible intervals are shown in gray.

(GLMM, $\mathrm{SDR}_{\text{learning rate}} = 0.180$, $\mathrm{CI}_{\text{low}} = -0.276$, $\mathrm{CI}_{\text{up}} = 0.665$, $p = .436$; $\mathrm{CD}_{\text{learning rate}} = 0.296$, $\mathrm{CI}_{\text{low}} = -0.340$, $\mathrm{CI}_{\text{up}} = 0.933$, $p = .341$).

Of the 12 lizards tested in the probe test, only two reached the predetermined learning criterion in Phase 1 within the 30 trials given in this stage. Lizard STOK4 (stimulus group shape) reached the criterion in 10 trials and STOK16 (stimulus group color) in six trials. Within Phase 2, STOK4 chose correctly in 60% (six of 10) of Phase 1 trials and 80% (four of five) of trials in which the novel card was used. STOK16 chose correctly in 40% (four of 10) of Phase 1 trials and 80% (four of five) in those trials in which the novel card was used.

Discussion

Gidgee skinks showed evidence of behavioral flexibility by completing a minimum of one reversal and learnt a discrimination using compound stimuli. However, only one lizard learnt a second reversal and an intradimensional acquisition, although it failed at the third (intradimensional) reversal. Because gidgee skinks live in family groups that are genetically distinct from other groups (Gardner et al., 2001), we also hypothesized that groups might differ in cognitive performance. Capture location did, however, not predict differences in performance, at least not in this task.

We were also interested in what stimuli lizards relied upon while learning to discriminate compound cues, a factor largely ignored in lizard learning studies. Lizards selected the card showing the novel pairing between the relevant and irrelevant feature in four out of five trials. Some studies have implemented probe tests similar to what we have tested here, to evaluate what stimuli animals attend to during ID/ED attentional set-shifting tasks (Dias et al., 1996, 1997; Roberts et al., 1988). In these studies, animals were probe tested after they had finished their first intradimensional acquisition. During the probe test, the relevant (reinforced) features were kept the same as in the previous stage, but the irrelevant features were replaced with novel exemplars. Common marmosets (*Cullithrix jucchus*) do not change performance compared with the preceding ID stage, showing that they were unaffected by the change in the irrelevant features (Dias et al., 1996, 1997; Roberts et al., 1988). The two lizards that were tested on Phase 2 probe trials both showed greater accuracy (higher proportion of correct choices) in probe trials as compared with trials in which Phase 1 cards were presented, which suggests that they might have learnt to ignore irrelevant information (learnt irrelevance), as did marmosets. The added irrelevant information had previously been associated with the incorrect stimulus. Had lizards attended to the irrelevant features they might have mistakenly valued it as incorrect based on previous experience. One alternative explanation for our lizards' good performance during the five probe trials could be that they were attracted to the novel stimulus combination. However, trials were 1.5 hr long increasing the likelihood that lizards had habituated to the sight of, or familiarized themselves with, the novel feature combination after experience in the first trial. Nonetheless, novelty of the stimulus combination could have caused our result. Testing lizards using a similar approach such as the one used in common marmosets (Dias et al., 1996, 1997; Roberts et al., 1988) would give further insights into whether novelty affected our lizards' performance in probe trials. Another alternative explanation for our result could be that lizards had learnt which stimuli were incorrect based on their experience in test stages and Phase 1 of the probe test. Studies using a midsession reversal approach, in which the reversal of a simultaneous two-choice discrimination takes place in the middle of each session, have shown that rats develop a win-stay/loose-shift strategy to reverse effectively in each session and pigeons use timing instead of the result of their choice (McMillan & Roberts, 2012; Rayburn-Reeves et al., 2013). Consequently, rats eventually only make one mistake per session (first reversal trial) and pigeons make a number of anticipatory errors (before the reversal occurs) as well as perseverative errors (after the reversal occurs; McMillan & Roberts, 2012; Rayburn-Reeves et al., 2013). Other studies suggest that the errors made by pigeons are caused by problems learning to inhibit responding. Pigeons learn which stimuli to reject instead of which stimuli to choose (McMillan et al., 2015; Zentall et al., 2020). Because lizards are more closely related to birds than mammals (Alföldi et al., 2011), it would, therefore, not be surprising to find that lizards also rely more on information about which stimuli to reject rather than which stimuli to choose. If this is the case, then it is not surprising that lizards had no problem choosing the novel, correct stimulus combination, because the information needed for lizards to make the appropriate response (which stimuli to reject) in probe trials had not changed. Importantly, only one of the two successful individuals had previous experience with compound cues, the other lizard had only been tested with single feature cards. Furthermore, one lizard was tested with color as the relevant feature and the second with shape indicating that both colors and shapes were of similar discriminability to lizards. This is also confirmed by our analysis showing no difference in performance between stimulus groups. With data on only two lizards, however, we are unable to determine exactly how lizards learn compound cues. Furthermore, their low accuracy in trials with Phase 1 stimuli indicates that these two lizards had not fully learnt the compound discrimination which might be connected with our learning criterion (discussed below). More tests are certainly needed to better understand the processes involved when lizards learn compound stimuli and this is likely to be a highly rewarding line of study in the future.

Our results show that gidgee skinks are able to learn discriminations based on visual cues and that they possess some reversal learning ability. However, our results also highlight some potential issues with applying our learning criterion. Lizards' performance had not plateaued at the point when they were considered to have learnt the discrimination, especially given the very slow increase in the probability of making a correct choice that we observed (see Figure 3). Consequently, they may have been moved to the next stage too early. Using a set learning criterion (fixed number of correct trials) might only be sufficient after running pilots to determine its appropriateness for a given species. Our methods can, however, be improved by giving animals more than two to three trials a day and testing until a certain performance threshold is reached across multiple testing days (e.g., 80–90% correct across 2–3 days; Reiner & Powers, 1978; Roberts et al., 1988). If only a limited number of trials can be given within a day, we suggest giving animals multiple post criterion trials to evaluate the stability of performance after the criterion is reached (Szabo, Noble, & Whiting, 2019). Applying set learning criteria to decide on when to advance animals to more advanced tasks is common in studies across vertebrates (Ashton et al., 2018; Batabyal & Thaker, 2019; Day et al., 1999; Logan, 2016; Roberts et al., 1988; Tebbich et al., 2010), but further study is needed to determine the effectiveness of these procedures in lizards.

Previously, we used the same methodology to test set shifting in two other, relatively closely related lizard species, the tree skink (*Egernia striolata*; Szabo et al., 2018) and the eastern blue-tongue lizard (*Tiliqua s. scincoides*; Szabo, Noble, Byrne, et al., 2019). Both tree skinks and blue-tongue lizards were able to learn multiple acquisition and reversal stages including an intra- and extradimensional shift. Lizards started each stage choosing correctly at or below chance and gradually improved until reaching the learning criterion. Tree skinks and blue-tongue lizards showed significant evidence of learning at least in the early stages. Similar to the current study, however, sample sizes decreased across stages and so did the power to detect learning. Furthermore, in tree skinks, blue-tongue lizards and gidgee skinks, we did not find differences in stage comparisons or training effects across stages using the same exemplars of relevant stimulus features (e.g., X and triangle across the first four stages; Figure 2). It is possible that our methodology is not well suited to test reversal learning, habit formation (training effect), and behavioral flexibility (reversal learning and set shifting) in lizards and is, therefore, not sensitive enough to detect changes in learning rate. Simply increasing statistical power by testing higher numbers of individuals, however, might lead to statistical results showing the expected differences between test stages.

Large individual differences in performance might have factored into our inability to detect differences between stages. Unfortunately, our study precluded investigating among-individual differences in learning in detail given our sample size (van de Pol, 2012). Individual variation might, however, be caused by cognitive as well as noncognitive factors such as food motivation, neophobia, or behavioral type (Boogert et al., 2018; Dougherty & Guillette, 2018). Larger samples of independent animals will be necessary to statistically explore among-individual differences, and how cognitive and noncognitive factors impact learning (van de Pol, 2012). Looking at individual differences in learning is beginning to receive greater attention across taxa, but less so in reptiles. Nonetheless, recent research is starting to close this gap (Carazo et al., 2014; Chung et al., 2017; Goulet et al., 2018; Munch et al., 2018; Noble et al., 2014).

One striking difference with our two previous studies is the high dropout rate of gidgee skinks from the beginning of the first stage. We investigated possible causes analyzing error rates, motivation (eating the reward), body condition, and the influence of a side bias. We found that animals removed as nonlearners made more errors but did not differ from learners in motivation, side bias or body condition (see online supplemental materials). One factor causing lowered motivation to participate might have been the chosen reward (baby food), where a different reward might have been more suitable. We did not test food preference a priori in these lizards because we did not expect baby food to be less desirable than other foods. Nonetheless, it could have factored into the high dropout rate. Moreover, although we found similar patterns of performance as in previous studies (Szabo et al., 2018, Szabo, Noble, Byrne, et al., 2019), our methodology might have been less well-suited to test gidgee skinks compared with tree skinks and blue-tongue lizards. We previously found similarly high dropout rates in sleepy lizards (*Tiliqua r. asper*), also a member of the Egernia group, learning to discriminate simpler stimuli (Szabo & Whiting, 2020) although many of these were captive-bred individuals which may have contributed to their high dropout. With data on only four species we are unable to make distinct conclusions on the underlying cause of the differences between species. Using a different methodology to test visual discrimination learning in these species could help establish whether gidgee skinks and sleepy lizards are poor at visual discrimination learning compared with other relatively closely related lizard species. Additionally, the different species tested might simply differ in, for example, how long they need to be habituated to captivity and testing procedures. Furthermore, they might differ in food motivation or neophobia and might even have different preferences for visual stimuli, all of which might have attributed to the species differences.

One goal of testing gidgee skinks to discriminate simple and compound stimuli was to compare their performance to that of tree skinks and the eastern blue-tongue lizards, all of which differ in sociality. Tree skinks live in small groups (Chapple, 2003) whereas blue-tongue lizards are solitary (Koenig et al., 2001). Set-shifting tasks test for flexibility in behavior and attention, and we hypothesized that such cognitive skills might be enhanced in social species because of their need to identify, track, and remember individuals and their relationships within their social group ("Social Intelligence Hypothesis"; Byrne & Whiten, 1988; Humphrey, 1976). In other vertebrates, group size has been linked to increased cognitive ability including associative and reversal learning (Ashton et al., 2018). Evidence shows that gidgee skinks can discriminate between group and nongroup members (Bull et al., 2000) and that mothers recognize their offspring (Main & Bull, 1996) based on chemical cues. Whether visual cues are involved in individual recognition is unknown. We can therefore not exclude the possibility that flexible use of visual information is important for group cohesion. Although we did not compare learning performance directly across species, behavioral flexibility and learning does not seem to be enhanced in group-living lizards (i.e., gidgee skinks). In the future, testing social–cognitive abilities (e.g., social learning), which are more closely linked to sociality, will help us understand how cognition might relate to group size in lizards. However, the social life of lizards might not pose the same selective pressures to enhance cognition such as in other vertebrates (Byrne & Whiten, 1988; Humphrey, 1976; Jolly, 1966). Furthermore, testing a broader range of lizard species could prove informative with respect to alternative hypotheses such as the "Ecological Intelligence Hypothesis," which links enhanced cognition to a species' ecology (Byrne, 1997; Gibson, 1986; Rosati, 2017).

Taken together, this is the third study looking at discrimination learning of multifeatured cues in lizards. We show that some gidgee skinks might be able to differentiate feature sets when tested with compound stimuli without needing extensive preexperience with such cues, but further testing is needed to confirm our hypothesis. Such investigations are important for evaluating how animals learn and what cognitive processes they use to solve complex tasks. Understanding reptile cognition more broadly will help us better understand the evolution of cognition in vertebrates and whether animals with different evolutionary history have evolved learning processes convergently.

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