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Learning outdoors: male lizards show flexible spatial learning under semi-natural conditions

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Spatial cognition is predicted to be a fundamental component of fitness in many lizard species, and yet some studies suggest that it is relatively slow and inflexible. However, such claims are based on work conducted using experimental designs or in artificial contexts that may underestimate their cognitive abilities. We used a biologically realistic experimental procedure (using simulated predatory attacks) to study spatial learning and its flexibility in the lizard *Eulamprus quoyii* in semi-natural outdoor enclosures under similar conditions to those experienced by lizards in the wild. To evaluate the flexibility of spatial learning, we conducted a reversal spatial-learning task in which positive and negative reinforcements of learnt spatial stimuli were switched. Nineteen (32%) male lizards learnt both tasks within 10 days (spatial task mean: 8.16 ± 0.69 (s.e.) and reversal spatial task mean: 10.74 ± 0.98 (s.e.) trials). We demonstrate that *E. quoyii* are capable of flexible spatial learning and suggest that future studies focus on a range of lizard species which differ in phylogeny and/or ecology, using biologically relevant cognitive tasks, in an effort to bridge the cognitive divide between ecto- and endotherms.

Keywords: spatial learning; cognition; reptile; associative learning

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1. INTRODUCTION

The ability to have quick and flexible learning is predicted to arise when animals face complex and variable environmental challenges [1,2]. In consequence, testing animals using biologically relevant cognitive tasks and under conditions where they have access to the full range of stimuli available in their natural environment is particularly important for a realistic understanding of the rate and flexibility of learning [1,2]. Such studies are not easy to implement [1–3] and are therefore relatively uncommon, but they provide valuable insight into learning performance in the environments in which the cognitive traits have evolved. Experimental procedures using cognitive tests that do not adequately consider the animal's biology may thus be misleading. This has often been the case in reptiles, where many cognitive studies have been conducted in the laboratory under conditions that fail to reflect the type of ecological problems faced in the wild, or using experimental paradigms designed for mammals [4]. Not surprisingly, some of these studies have reported comparatively poor learning abilities in some reptile groups, leading to the widespread conclusion that reptile cognition is generally less sophisticated than in other vertebrate groups [4,5].

Particularly striking is the case of spatial cognition in lizards. Lizards are often faced with predatory threats that require them to quickly learn the location of suitable escape routes and refuges within their home range, and flexibly adjust the use of such refuges according to whatever contingencies may arise [6] (e.g. location of predators in their surroundings or obstacles to refuges). Although the available evidence shows that snakes and lizards are capable of learning the spatial location of food items or shelters in the laboratory [4,7–11], some studies seem to suggest that they have limited spatial cognitive abilities and require many training trials to learn simple spatial tasks [4]. Here, we used an ecologically relevant anti-predator context to study whether lizards show evidence of flexible spatial learning using two replicate groups of lizards maintained in large semi-natural outdoor enclosures.

2. MATERIAL AND METHODS

(a) *Study species*

Eastern water skinks (*Eulamprus quoyii*) were collected from five different sites throughout the Sydney region and maintained in a captive colony at Macquarie University. We only used males because they are better spatial learners than females (unpublished data) and occupy larger home ranges, probably experiencing stronger selection/development of spatial cognitive abilities. Sixty adult male lizards were tested in two separate groups (30 males between September 1–10 (10 days) and 30 males between September 12–22 (11 days), 2011).

(b) *Learning tasks*

Each lizard was housed individually in a large outdoor tub measuring 3.2 m in diameter and 0.5 m high (approx. 8 m^2). Each tub contained mulch substrate and two water bowls (15 × 9.5 × 7 cm) with three separate stacks of two terra-cotta roofing tiles, which were used as refuges by the lizards (see the electronic supplementary material, figure S1). Refuges were separated by approximately 1 m and were spread out along the edges of the arena. Each lizard was subjected to two consecutive learning tasks. In task 1 (spatial learning), lizards were trained to learn the location of a randomly chosen 'safe' refuge over four consecutive days (3 trials per day). In task 2 (reversal spatial-learning), we conducted a choice reversal by randomly choosing a new 'safe' refuge and repeating the protocol for up to six more consecutive days (3 trials per day). A reversal-learning task is one in which positive and negative contingencies are switched (but still present) with respect to a previous learning task so that individuals have to reverse previously created associations. Conducting a reversal allowed us to ask whether spatial cognitive ability under semi-natural conditions is flexible. We simulated predatory attacks by entering tubs and approaching and chasing lizards around their enclosure and/or by lifting incorrect refuges until lizards entered the 'safe' refuge (refuges were immediately replaced in their original position). Although it was not possible to scare lizards following a blind protocol, we made every attempt to reduce observer bias. First, the approach direction and order that each unsafe refuge was lifted were both randomized and different for each trial to prevent biases in flight direction. Second, each lizard was scared following a standardized protocol. Lizards were always scared from behind and gently tapped on the pelvic girdle. We followed each lizard closely from behind (within an arms length) and allowed lizards to choose their flight direction to

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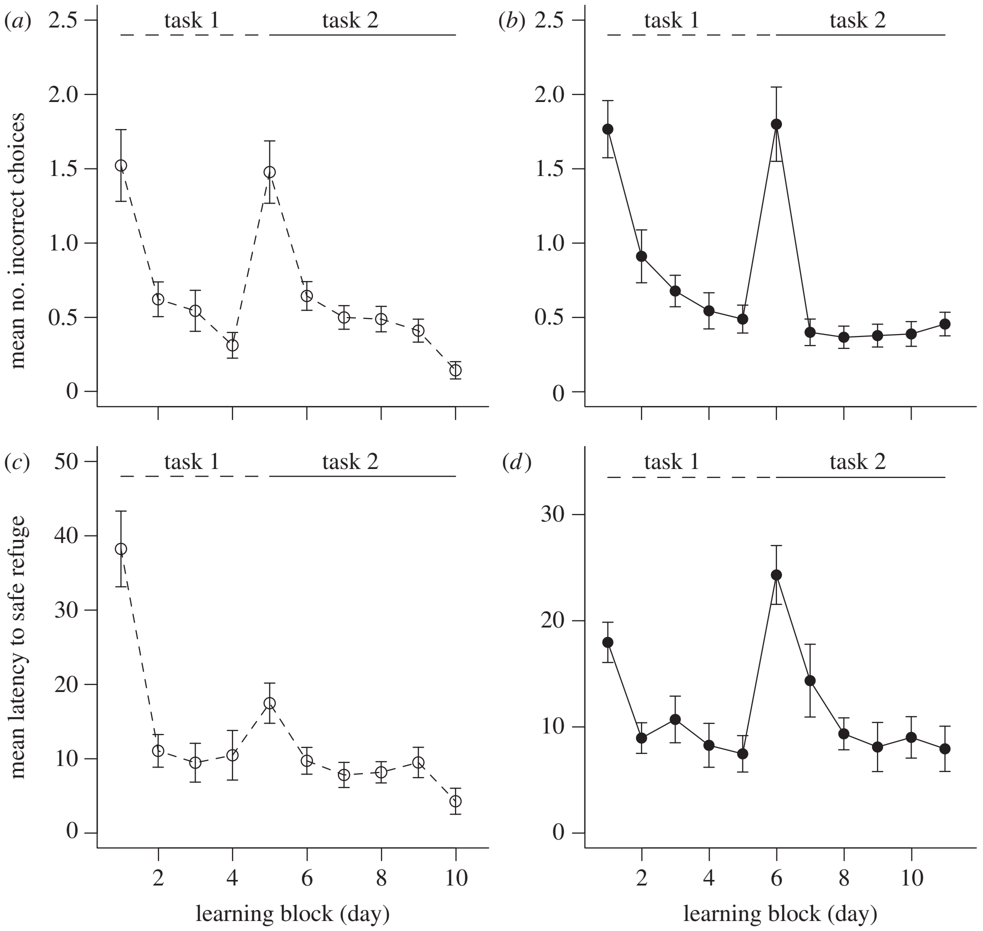

Figure 1. (*a*,*b*) Mean (±s.e.) number of incorrect choices and (*c*,*d*) the mean (±s.e.) latency until entering the safe refuge across trials for group 1 (*a*,*c*; open circle and dashed line) and group 2 (*b*,*d*) filled circle and solid line) for learners and non-learners combined. Refer to the GLMM results for statistical significance.

the safe refuge. In many cases, lizards ran past the unsafe refuge in the direction of the safe refuge. Since trials were conducted under semi-natural conditions, we could not completely control for chemical cues. We implemented a control prior to the reversal task for group 2, which strongly suggests that lizards were using spatial cues to locate the 'safe' refuge. In addition, lizards did not tongue flick during scares, and flight responses were too quick to suggest the use of chemical tropotaxis (see the electronic supplementary material). Trials were conducted during the active period of the day (11.00–17.00 h) with at least 1 h between trials. During each trial, we recorded: (i) whether the lizard was in the safe refuge; (ii) the first refuge chosen by the lizard; (iii) the number of incorrect choices; and (iv) the latency to enter the safe refuge. For each lizard, we designated its learning trial as the last in a run of five successive correct trials in a row. Only lizards that were successful at both the spatial learning and choice reversal tasks were included in the learner group.

Our learning criteria and curves considered lizards found within the 'safe' refuge at the start of the trial as having made a correct choice (see electronic supplementary material, for details). We believe that this is a biologically sensible interpretation because learners are predicted to take refuge in the 'safe' refuge. However, we acknowledge that this scoring method might inflate apparent learning (see electronic supplementary material). To ensure that this was not the case, we replicated our original statistical analysis of learning curves, but considering lizards already found within the safe refuge to have made 'no choice'. Results of this analysis are similar (see electronic supplementary material) and did not affect our final conclusion. Lizards already in the safe refuge were considered to have zero latency to enter the safe refuge and these values were subsequently removed prior to analysis.

(c) *Data analysis*

We used generalized linear mixed models (GLMM) to test for significant decreases in mean number of incorrect choices (ICC) and mean latency to enter the safe refuge (LSR) across learning blocks (see electronic supplementary material, for details).

3. RESULTS

Body size and mass did not differ significantly between the groups (Wilcoxon test; SVL: $W = 144$, $p = 0.52$ and mass: $W = 143.5$, $p = 0.59$). Lizards in group 1 exhibited a significant decrease in both ICC and LSR from day 1 to day 2 in task 1 (ICC: $\beta = -0.98 \pm 0.42$, $p = 0.02$ and LSR: $\beta = -1.36 \pm 0.45$, $p = 0.002$; figure 1*a*,*c*); however, in task 2 (choice reversal) a significant decrease in ICC was observed by day 3 ($\beta = -1.03 \pm 0.43$, $p = 0.017$; figure 1*a*) whereas LSR did not decrease significantly until day 10 ($\beta = -1.66 \pm 0.51$, $p = 0.001$; figure 1*c*). In group 2, ICC and LSR decreased significantly by day 2 in task 1 (ICC: $\beta = -0.78 \pm 0.33$, $p = 0.02$ and LSR: $\beta = -0.76 \pm 0.32$, $p = 0.02$; figure 1*b*,*d*) and in task 2 (ICC: $\beta = -1.52 \pm 0.36$, $p < 0.001$ and LSR: $\beta = -1.13 \pm 0.34$, $p = 0.001$; figure 1*b*,*d*). The proportion of lizards outside the unsafe refuges in tasks 1 and 2 for both groups decreased across trials (figure 2*a*,*b*).

Nineteen lizards (32%) were categorized as learners (group 1, $n = 11$; group 2, $n = 8$; see table S1 in electronic supplementary material). In task 1, lizards learnt the position of the safe refuge within 5–14 trials (mean = 8.16 ± 0.69; $n = 19$). In task 2, lizards learned the position of the new safe refuge after 6–17 trials (mean = 10.74 ± 0.98; $n = 19$). The difference in median learning trial between tasks was marginally non-significant ($V = 30$, $p = 0.052$).

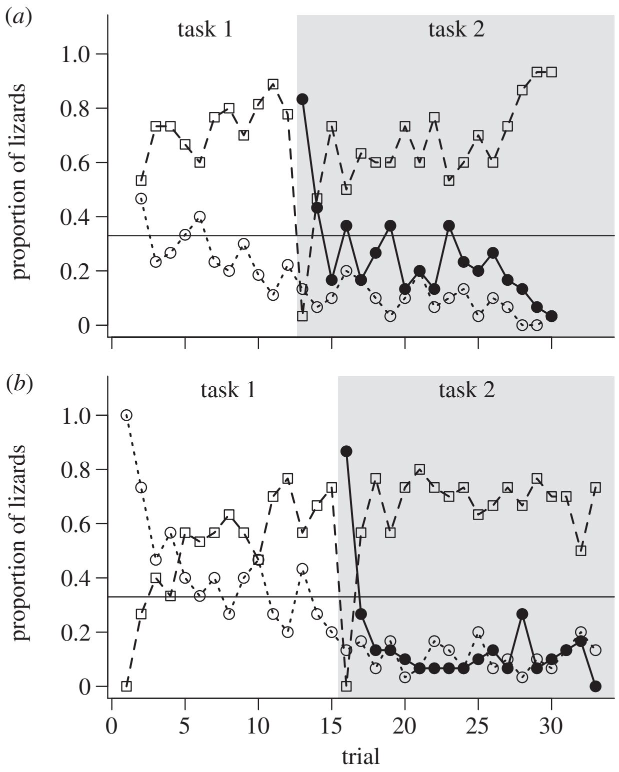

Figure 2. (*a*) Group 1; (*b*) group 2. Proportion of lizards in the correct safe refuge (open square and dashed line), in the incorrect refuge (open circle and dotted line) and in the former safe refuge (filled circle and solid line) in successive trials for learners and non-learners combined. In task 2, the sum of the lizards near the former safe refuge and lizards near the incorrect refuge equals the lizards near the incorrect refuge in task 1. Each refuge is predicted to be chosen by chance 33% of the time and this is represented by the horizontal solid line.

4. DISCUSSION

The long-standing idea that squamates (lizards and snakes) have poor cognitive abilities has been spurred in part by the use of inadequate or ecologically irrelevant cognitive tasks [4,5], and is being challenged by recent studies [11–14]. Here, we provide evidence of flexible spatial learning in lizards tested under a biologically meaningful anti-predatory context in semi-natural conditions. In both tasks, lizards were performing above chance in the span of only 3–4 days (3 trials per day), and at least 19 out of 60 lizards learned to avoid unsafe refuges in both the spatial and the reversal task. It is important to note that our data do not provide insight into the mechanism(s) that may be responsible for spatial learning. Nonetheless, our findings contrast with previously available studies reporting that lizards require dozens of trials before learning a relatively simple spatial task if they learn at all [4,8]. This may be due to the larger spatial scale of our experiment, or to the fact that lizards had access to the whole range of spatial cues that they would have access to in their natural habitat (e.g. landmarks, distal cues, geometric cues), whereas laboratory experiments usually focus on a restricted range of cues.

Our data fit well with theoretical expectations given that, in the wild, most lizards need to process complex spatial information that is crucial to fitness [11]. For example, some lizard species exhibit wide-ranging mate searching while others defend territories, both of which require knowledge of the spatial location of mates and resources. Comparative cognition studies of lizards from a range of clades and with diverse mating systems and ecology will enable us to test the generality of these findings and allow us to better understand how lizard spatial cognition stacks up with the traditional bird and mammal model systems.

All research was carried out under the approval of the AEC committee of Macquarie University (2011–018).

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SUPPLEMENTARY MATERIAL

Learning criteria

Within each learning task (i.e. spatial learning and choice reversal learning), we considered the lizard to have learnt the position of the safe refuge when he chose the correct refuge five times in a row. For the purpose of categorizing learners, we considered a lizard to have chosen the correct refuge if a) it was found already inside the 'safe' refuge or b) it was found outside the 'safe' refuge but ran directly inside it when scared (but see "*Data analysis*" section below). We considered the last trial in this run as the 'learning trial' for each lizard. As an additional precaution, and starting from this 'learning trial', we kept a correct/incorrect tally until the end of the task and only lizards that ended with a significant tally were scored as learners. In order to be conservative, and despite the fact that lizards faced a three-refuge choice (i.e. 0.33 chance of choosing the correct refuge), we used the binomial distribution for significance testing. Because some lizards learnt towards the end of each learning period, they ended up with a running tally that included less than 10 trials. For these individuals, we conservatively included as many of the trials immediately preceding their 'learning trial' as was necessary to end up with an overall correct/incorrect choice tally of at least 10 trials (see table S1 below).

We considered a lizard already in safe refuge to have made a correct choice because it makes biological sense to consider lizards in the safe refuge as having chosen correctly even though they were not observed entering the safe refuge. Also, because the outdoor enclosures were close to each other it is likely that many lizards were outside but ran into the safe refuge as they heard or possibly saw us scaring lizards in nearby enclosures. Although we attempted to avoid this during the scaring of surrounding lizards, it was difficult to control because the sides of each tub were not very high (~ 50 cm) and each tub was close together (~1 m apart). This being so, not considering a lizard found in the safe refuge as having made a correct choice could seriously underestimate learning. Conversely, considering a lizard found in the safe refuge as having made a correct choice could be a problem if lizards were not moving around between trials or if, when not scared, lizards were using chemical cues to go back to the most heavily scented refuge (see below), in which case we would be overestimating learning. We believe the former is unlikely because we only scared lizards three times per day and trials were conducted in good weather conditions and at a time in the year when lizards are active. In addition, all the enclosures in the outdoor experimental area were in a single area enclosed in mesh (figure S1) and accessible through a locked gate, thereby preventing access by people or predators. Given these factors, it seems unlikely that lizards were not coming out to bask and forage between trials.

Nonetheless, we decided to err on the side of caution and implemented a series of double-checks to ensure we were picking up learning, and not a spurious result. First, we only counted learners as those lizards that, during the first two trials of the reversal phase (i.e. first reversal day), repeatedly went back into the former ‘safe’ refuge (see table S1 below), which was the case in most lizards. We would predict lizards to exhibit this choice if they learned to associate the previous refuge as being safe, and they used spatial cues to locate it (see below). Second, to test whether lizards were moving around between trials we randomly selected 15 lizards in group 2 and placed mealworms in deep petri-dishes at the centre of their enclosure (i.e. equidistant from all of the refuges) over a 7-day period. We checked and replaced mealworms on a daily basis and found that 73% of the lizards ate mealworms on at least 3-5 of the 7 days, suggesting that lizards were moving through their enclosure and were not just staying within their refuge (Note that birds were excluded by netting and only lizards had access to mealworms). Finally, and most importantly, we re-analysed our data for our learning curves scoring lizards already found within the safe refuge as having made “no-choice”; thus ensuring that these values were not contributing to the population-level mean (see “*Data analysis*” section below). We did not find any major difference between our two learning curve analyses, which shows our initial learning criterion was adequate.

A potential confound could be that lizards used chemical cues to locate the ‘safe’ refuge each time they were scared. This is very unlikely because, as expected, fleeing times were simply too quick for lizards to use tropotaxis to navigate their way into the ‘safe’ refuges. Also, *E. quoyii* very rarely tongue-flicked immediately before or during scares. Chemical cues would be expected to play a role prior to the start of each lizard’s trial, where lizards were able to explore the enclosure and choose a refuge. This may also explain the occurrence of lizards already in the safe refuge at the start of their trial. However, our re-analysis (see “*Data analysis*” section below) still shows declines in the mean number of incorrect choices and latency to enter the safe refuge suggesting that chemical cues cannot explain these data. In addition, for the lizards in the second group we reshuffled the tiles and substrate of the three refuges to scatter available scent marks before beginning the second learning task (i.e. where we changed the location of the safe refuge). Dispersing chemical cues did not change the outcome of the results for lizards in the second group. Most of the lizards (all of those considered as learners) repeatedly went back into their ‘former safe’ refuge when scared during the first trials of the first reversal day, which can only be explained if lizards had learnt the spatial location of the safe refuge (now former safe) during the first task (see table S1).

Data analysis

We tested whether the mean number of incorrect choices (ICC) and the mean latency to enter the safe refuge (LSR) significantly decreased through time, as predicted if the lizards were learning the tasks. We rounded latency to the nearest whole number so that it could be more easily modeled and removed lizards that were already found within the safe refuge from the latency analyses (i.e. that had a latency to correct refuge as zero). We used generalized linear mixed models (GLMM) with the number of incorrect choices and latency to safe refuge as dependent variables and the learning block 'Day' as a fixed predictor variable. We choose to analyse the lizard groups separately because: 1) we were interested in whether patterns were repeatable between groups; and 2) pooling groups would make our models unnecessarily complex since we treated day as a categorical predictor variable and interactions between group and day would over-parameterise models. Individual identity, identity nested within day, and trial nested within day, were included as random effects to account for the non-independence in the data. We fitted models using a Poisson error distribution ('log' link) and estimated model coefficients using restricted maximum likelihood (REML). All analyses were carried out using the 'lme4' package in R [1, 2]. Data for these analyses are deposited in Dryad (DOI: doi:10.5061/dryad.n5b32)

Importantly, we were interested in testing whether lizards could learn our spatial tasks and whether this learning was flexible under semi-natural conditions and our question was not directed at understanding the mechanisms responsible for learning, as this would require greater control of confounding variables. As stated above, we explored the possibility that we may have inflated the apparent rate of learning in our original analysis if lizards remained in the safe refuge as a response to predation. In addition to the GLMM analysis with our initial learning scoring (i.e. correct choice if lizards were already in the safe refuge), we also conducted a much more conservative analysis to control for this confound. In this analysis each occurrence of a lizard being found in the 'safe' refuge at the beginning of the trial was categorized as that lizard having made 'no choice' and these values did not contribute to the average score of the mean incorrect number of choices. In group 1 lizards, there was a significant decrease in the number of incorrect choices by day 2 ($\beta = -0.76 \pm 0.30$, $p = 0.01$; figure S2 a) while in group 2 lizards a significant decrease in the number of incorrect choices was not observed until day 3 ($\beta = -0.38 \pm 0.18$, $p = 0.03$; figure S2 b) for task 1. Group 1 lizards in task 2 showed a marginally significant decrease in the number of incorrect choices by day 2 ($\beta = -0.59 \pm 0.31$, $p = 0.056$; Fig. 2A), however a significant drop was not observed until day 9 ($\beta = -0.65 \pm 0.33$, $p = 0.048$; figure S2 a). In contrast, group 2 lizards showed a significant drop in the number of incorrect choices by day 2 ($\beta = -0.98 \pm 0.21$, $p < 0.001$) for task 2 (figure S2 b). Importantly, these results are qualitatively congruent with our original analysis of learning curves where lizards found in the 'safe' refuge at the beginning of the trial were considered to have made a correct choice, supporting our use of categorizing trials where lizards were already in the safe refuge as correct choices as well as our final conclusions.

We compared the average learning trial between task 1 and task 2 using a Wilcoxon sign rank test. Only the 19 lizards that learned both task 1 and 2 were used for this analysis and therefore it was a paired test. Snout-vent length (SVL) and body mass between our two groups of lizards were compared using a Wilcoxon rank sum test because groups did not have equal variances and were not normally distributed.

Table S1- Results for all lizards tested in both groups (n = 60). Tallies are only shown for lizards that learnt both tasks, or that achieved significant tallies in one or both tasks but were not counted as learners because they did not fully comply with the learning criterion (see text above). PFS- Proportion of times that a lizard chose the ‘former safe’ refuge during the two first trials of the reversal. It is important to note that chemical cues were not available during the first two trials, in which lizards were scared into a new ‘safe refuge’. Lizards could make multiple incorrect choices while being scared because they could return to the former safe refuge. Hence, the fact that lizards go back into the ‘former safe’ can only be explained if they had learnt the spatial location of the ‘safe refuge’ in task one (i.e. now the ‘former safe’). Under the learner column: Y = classified as learner; N = classified as non-learner.

Lizard	**Group**	**Task 1**			**PFS**	**Task 2**			**Learner**
		Learning trial (LT)	**Tally since LT**	**Last 10**		**Learning trial (LT)**	**Tally since LT**	**Last 10**	
1	1	11	6/6	8/10	0.75	13	9/10	9/10	Y
2	1	6	11/11	10/10					N
3	1	10	7/7	9/10	1.00	8	14/15	9/10	Y
4	1	5	12/12	10/10	1.00	10	12/13	9/10	Y
5	1	5	12/12	10/10	0.70	11	10/12	8/10	Y
6	1								N
7	1	5	12/12	10/10	0.67				N
8	1								N
9	1								N
10	1	6	10/10	10/10	1.00	6	16/17	9/10	Y
11	1								N
12	1		4/4	7/10	1.00	6	11/17	5/5	N
13	1	7	10/10	10/10	0.87				N
14	1	9	8/8	8/10	0.88				N
15	1	11	6/6	8/10	1.00	6	17/17	10/10	Y
16	1								N
17	1	6	11/11	10/10	1.00	16	7/7	9/10	Y
18	1								N
19	1	6	11/11	10/10	0.80				N
20	1	5	12/12	10/10	0.67	6	16/17	9/10	Y
21	1	6	11/11	10/10		6	17/17	10/10	Y
22	1	5	12/12	10/10		16	7/7	8/10	Y
23	1	7	10/10	10/10	0.60		4/4	5/5	N
24	1	9	8/8	8/10	0.80	17	6/6	8/10	Y

25	1	6	11/11	10/10		13	10/10	10/10	N
26	1								N
27	1								N
28	1	6	8/8	8/10	0.67			7/10	N
29	1								N
30	1								N
31	2	12	8/8	8/10	1.00	9	10/14	6/10	Y
32	2	7	10/13	7/10					N
33	2								N
34	2								N
35	2	12	8/8	9/10	0.67	16	6/7	8/10	Y
36	2								N
37	2	9	10/11	9/10					N
38	2	6	12/14	8/10	0.67	7	16/16	10/10	Y
39	2	11	9/9	9/10	0.55	13	8/10	8/10	Y
40	2	6	13/14	9/10	0.75	15	7/8	8/10	Y
41	2								N
42	2								N
43	2								N
44	2								N
45	2								N
46	2								N
47	2	9	9/11	8/10	0.50	16	7/7	8/10	Y
48	2	14	6/6	9/10	0.67	7	16/16	10/10	Y
49	2								N
50	2	7	12/13	9/10		9	14/14	10/10	N
51	2								N
52	2								N
53	2								N
54	2								N
55	2								N
56	2	10	9/10	9/10					N
57	2								N
58	2	6	13/14	9/10	0.63	6	17/17	10/10	Y
59	2								N
60	2								N

Figure S1**-** Setup of outdoor experimental enclosures used in learning trials

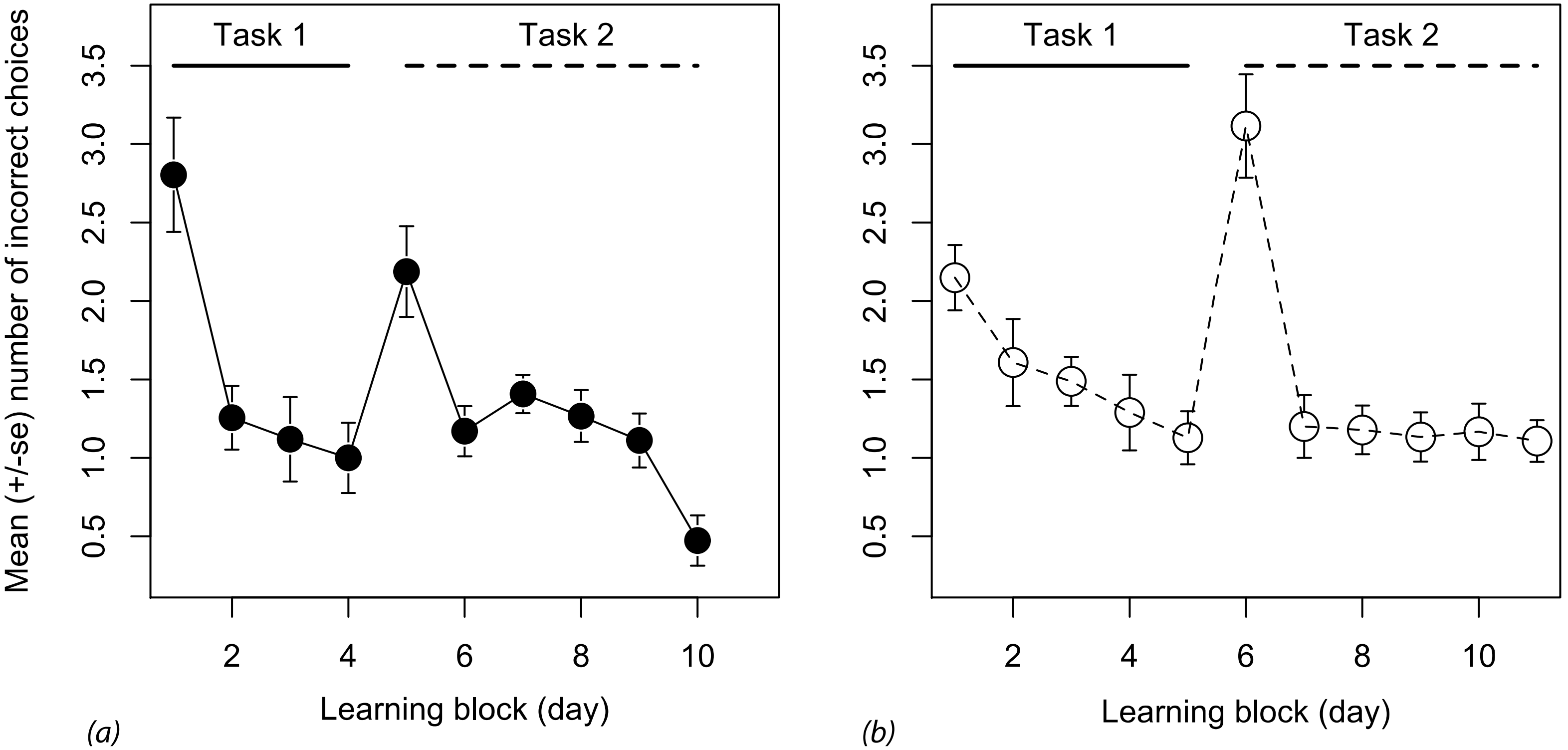

Figure S2- *(a)* group 1 lizards; *(b)* group 2 lizards. Mean (± standard error [se]) number of incorrect choices after categorizing lizards already found within the 'safe' refuge as having made "no choice". This test is meant to be conservative because zero scores do not contribute to the mean value in each learning block. It is important to note that standard errors are small because this is simply a plot of means and standard errors and does not control for non-independence in the data. Refer to the GLMM analysis for statistical significance.

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