



Testing domain general learning in an Australian lizard

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Received: 20 June 2017 / Revised: 8 May 2018 / Accepted: 25 May 2018 / Published online: 2 June 2018
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Abstract

A key question in cognition is whether animals that are proficient in a specific cognitive domain (domain specific hypothesis), such as spatial learning, are also proficient in other domains (domain general hypothesis) or whether there is a trade-off. Studies testing among these hypotheses are biased towards mammals and birds. To understand constraints on the evolution of cognition more generally, we need broader taxonomic and phylogenetic coverage. We used Australian eastern water skinks (*Eulamprus quoyii*) with known spatial learning ability in three additional tasks: an instrumental and two discrimination tasks. Under domain specific learning we predicted that lizards that were good at spatial learning would perform less well in the discrimination tasks. Conversely, we predicted that lizards that did not meet our criterion for spatial learning would likewise perform better in discrimination tasks. Lizards with domain general learning should perform approximately equally well (or poorly) in these tasks. Lizards classified as spatial learners performed no differently to non-spatial learners in both the instrumental and discrimination learning tasks. Nevertheless, lizards were proficient in all tasks. Our results reveal two patterns: domain general learning in spatial learners and domain specific learning in non-spatial learners. We suggest that delineating learning into domain general and domain specific may be overly simplistic and we need to instead focus on individual variation in learning ability, which ultimately, is likely to play a key role in fitness. These results, in combination with previously published work on this species, suggests that this species has behavioral flexibility because they are competent across multiple cognitive domains and are capable of reversal learning.

Keywords Discrimination task · *Eulamprus quoyii* · Instrumental task · Reptile · Spatial learning

Introduction

Cognition is the process whereby animals acquire, process, and store information from the environment and this is thought to have a bearing on fitness (Shettleworth 2010).

There has been some debate about whether animals are good at a multitude of cognitive tasks (domain general learning) or whether they are more commonly good at particular tasks (domain specific learning), perhaps at the expense of others (Macphail and Bolhuis 2001; Galsworthy et al. 2002; Chiappe and MacDonald 2005). The domain general learning hypothesis advocates that the basic processes underlying cognition are associative in nature, therefore, individuals with superior memory and learning ability consistently perform well in all cognitive domains. In contrast, the domain specific hypothesis predicts that learning ability has evolved in concert with recurrent ecological challenges, hence similar cognitive capacities are predicted to evolve in species that experience similar challenges (Macphail and Bolhuis 2001; Galsworthy et al. 2002; Chiappe and MacDonald 2005). Presently, the domain general learning hypothesis has been demonstrated in a range of species including several primates and rodents (Galsworthy et al. 2002; Kolata et al. 2008; Reader et al. 2011). For example, proportional CD-1 mice consistently perform well in spatial, discrimination and

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10071-018-1194-y>) contains supplementary material, which is available to authorized users.

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associative learning (Kolata et al. 2008). Primates are also known to consistently do well across multiple learning tasks (Reader et al. 2011; Herrmann and Call 2012).

Increasing evidence suggests that spatial learning is under varying degrees of selection in diverse taxa (Day et al. 1999; Burns and Rodd 2008; Odling-Smee et al. 2008). For example, habitat stability and predation pressure influences spatial learning and memory in three-spine sticklebacks such that river fish are better at long-term memory than pond fish. Additionally, fish that experienced low predation learnt faster than those under high predation (Burns and Rodd 2008). Because of navigational demands, spatial learning has been regarded as a domain specific adaptation in many birds and mammals. Anatomical evidence comes from the convergent evolution of enlarged hippocampi in food-storing birds and mammals, whose foraging success is largely dependent on spatial learning ability (Sherry et al. 1992; Moser et al. 1995). For example, birds that cache food possess a hippocampus more than twice the size of that of non-food-storing birds (Sherry et al. 1989). Additionally, the hippocampus of homing pigeons is larger than that of non-homing pigeons (Rehkämper et al. 1988). Spatial learning ability is also linked to mating system. For example, in some polygynous species, females have small localized ranges, while males travel more widely in search of multiple mates. Due to intense competition, some males adopt floater tactics, while others defend a territory (Morrison et al. 2002; Keogh et al. 2012; Noble et al. 2013). In these systems, spatial learning is hypothesized to vary with sex and male reproductive tactic due to variation in navigational demands (Carazo et al. 2014; Cummings and Ramsey 2015).

In contrast to mammals and birds, studies of reptile spatial learning are limited (see reviews in Wilkinson and Huber 2012; Matsubara et al. 2017) and most studies are conducted using lizards (e.g., Carazo et al. 2014; LaDage et al. 2012; Noble et al. 2012, 2014). In an important early study, Day et al. (1999) demonstrated that an active foraging lizard, *Acanthodactylus boskianus*, was superior at spatial learning compared to a congeneric sit-and-wait forager, *A. scutellatus*. Noble et al. (2012) demonstrated flexible spatial learning in the lizard *Eulamprus quoyii* under semi-natural conditions and a related study showed male *E. quoyii* performed better than females in a spatial learning task (Carazo et al. 2014). Finally, spatial memory was demonstrated in the side-blotched lizard (*Uta stansburiana*) (LaDage et al. 2012), a lizard in which spatial demands correlate with reproductive tactics and dorsal cortical volumes (LaDage et al. 2009). Furthermore, neurogenesis in the medial and dorsal cortex (reptile hippocampus homologue) is dependent on spatial requirements, with territorial males in larger enclosures experiencing higher rates of neurogenesis than their siblings in smaller enclosures (LaDage et al. 2013). It is clear from these and other studies that many lizard species

experience selection on spatial learning ability. What is less clear, is whether lizards that are proficient at spatial learning also perform well at other learning tasks (domain general learning) or whether there is a trade-off in which they perform less proficiently in other cognitive domains (domain specific learning).

To answer this question, we used male eastern water skinks (*E. quoyii*) of known spatial learning ability. This species is a good model system for cognition studies because they are capable of flexible spatial learning, they can manipulate objects (removal of a lid), their spatial ability is variable, and they also show age-dependent social learning in which juveniles but not adults use social information (Carazo et al. 2014; Noble et al. 2012, 2014). Furthermore, males adopt alternate reproductive tactics in which males vary in their movement and activity, potentially affecting demands on spatial learning (Noble et al. 2013). This species has a widespread distribution along the east coast of Australia (Cogger 2014) and is common in urban environments near streams. We had one group of lizards ($n = 7$) that attained our spatial learning criterion and a second group ($n = 8$) that did not (Carazo et al. 2014). Here, we tested whether spatial learners and non-learners could learn to extract a food reward in an instrumental task and their ability to learn to discriminate colors in an association task. If spatial learning is domain specific, we predicted that lizards proficient in spatial learning would perform less well in the instrumental and discrimination tasks. Likewise, we predicted that lizards that did not meet our criterion for spatial learning ('social non-learners') would perform better in these tasks. Conversely, if spatial learning is domain general, we predicted that spatial learners would perform better than spatial non-learners across different tasks. We also examined whether spatial learners use similar cues to solve a task, regardless of context. If the spatial learners use spatial cues in the discrimination learning task, we predicted that spatial learners would make more incorrect choices compared to spatial non-learners when spatial cues are removed.

Materials and methods

Spatial learning

We used a subset (15/32) of adult, sexually mature male lizards from a previous study of spatial learning and personality by Carazo et al. (2014) in which lizards were classified as spatial learners or non-learners. In this study, lizards were given the choice between a designated safe and unsafe refuge and were chased until they took refuge (aversive learning). Full details of methods are in that paper and are summarized in the online supplementary material (OSM). Lizards were considered spatial learners if they met a learning criterion

in which the ratio of correct/incorrect choices followed a binomial distribution (5/5, 7/8, etc.) and this distribution remained significant until a trial was complete. For example, a lizard could score 7/8, but end up with a tally of 10/14 and be categorized as a non-learner. The number of trials to learn in spatial learners was 10.57 ± 1.46 ($n = 7$), while spatial non-learners ($n = 8$) did not reach acquisition in 20 trials. We had seven spatial learners and eight spatial non-learners of the lizards we had available from Carazo et al. (2014).

Husbandry and general methods

Instrumental and discrimination tasks were designed to test the learning ability of spatial learners and spatial non-learners in other learning domains. We carried out all trials in each lizard’s home enclosure which consisted of a plastic tub [683 (L) × 483 (W) × 385 (H) mm] with bark chips as a substrate and a hide box where they could take refuge. Each lizard tub was positioned in the same position and orientation within the room to control the effects of other spatial factors. Lizards always had access to a bowl of water and obtained all their food (mealworms) from the trials, which we conducted twice daily (for all tasks; appetitive learning). The first trial began at 10:30 h, and the second trial at 13:30 h. Lizards were given an hour to complete the task and a 2-h break before the second trial. Immediately before each trial, we shuffled the mulch around to spread around any chemical cues. We also provided lizards with a

thermal gradient using heat wire under their tub. All trials were video recorded using CCTV cameras linked to a digital video recorder (DVR).

Instrumental and discrimination tasks

Our instrumental tasks were similar in design to Leal and Powell (2012) and Clark et al. (2014; Fig. 1) in which lizards had to access a food reward from an opaque dish which was covered by a colored lid. During each trial, we recorded: (1) whether the lizard removed the lid on the reward dish (0: did not remove; 1: remove); and (2) the latency (s) to remove the lid from the reward dish. Only lizards that successfully performed at least five out of the previous six trials were considered to have learnt the task and advanced to the next task. We gave lizards a maximum of 50 trials to complete a task and lizards that did not learn within this period were removed from the experiment ($n = 2$). We first trained lizards to the reward dish prior to beginning the instrumental task. During training phase 1, we first ushered the lizards into their refuge and placed a single dish (spray painted black around the sides to remove visual cues) in the enclosure with a single mealworm inside (Fig. 1). Lizards had to eat mealworms from this dish at least 5/6 times before moving onto training phase 2. Training phase 2 was identical to training phase 1 except that a yellow lid covered 75% of the dish (Fig. 1). Lizards again had to successfully eat mealworms 5/6 times to move to task 1. Our previous work has shown

Fig. 1 Schematic of learning tasks including training phase 1 and 2, with a brief description for each. The reward is a mealworm placed into the dish. The covers corresponding to the reward were yellow (training phase 1 and 2, task 1) and blue (tasks 2 and 3)

Training phase 1		Successful completion: eating a mealworm from the well.
Training phase 2		Successful completion: eating a mealworm from the well.
Task 1		Successful completion: removal of the cover and eating a mealworm from the well.
Task 2		Successful completion: mealworm was always under the blue cover whose position remained the same each trial, lizard had to remove the cover and eat a mealworm.
Task 3		Successful completion: mealworm was always under the blue cover whose position was randomized each trial, lizard had to remove the cover and eat a mealworm.

that animals would consistently flip the lids on the rewarded dish so long as they experienced two-stage training (Noble et al. 2014). In task 1 (instrumental task), the yellow lid completely covered the dish, preventing lizards from using visual cues from the mealworms (Fig. 1). Lizards had to successfully learn how to displace the yellow lid of the reward dish to access the food item.

The discrimination task followed a similar paradigm to the instrumental task (Fig. 1). To understand whether spatial learners learn a different task using spatial cues, we used two different tasks to answer this question. The first part of the discrimination task, task 2, involved the use of three separate dishes placed beside each other. All three dishes were spray painted black, similar to task 3, however, each dish had a different colored lid (blue, white or gold) and only the blue lid contained the food reward. We used neutral colors to avoid sensory bias towards ‘attractive’ colors (e.g., yellow, red). We initiated trials by ushering lizards into their refuge. After that, we put one mealworm into the dish with the blue lid, while also adding mealworm-scented bran into the other two dishes to control the effect of odor. Only lizards that opened the reward dish first were considered to have chosen correctly. We recorded: (1) whether the lizard made the correct choice and removed the lid on the reward dish (0: incorrect choice; 1: correct choice); and (2) the latency to remove the lid covering the reward dish. Only lizards that correctly performed at least five out of the previous six trials were considered to have learnt the task and advanced to the next task.

In task 2, the position of each of the colored dishes were randomly determined and remained the same across trials for each lizard. This confounded location and the color of the reward dish. In task 3, we disambiguated location and color by keeping the same reward color in each trial but randomizing spatial position with the proviso that the reward lid was not in the same position two times in a row. If spatial learners use a similar cognitive mechanism to learn different tasks, we predicted that spatial learners would cue on the spatial position of the reward dish in task 2 and would do less well in task 3. More specifically, we predicted that, on average, spatial learners would make more incorrect choices to successfully learn task 3 compared with spatial non-learners, and similarly, spatial learners would need more time to make the correct choice in task 3 compared with spatial non-learners.

Data analysis

All data analysis was carried out in R version 2.14 (R Development Core Team 2011). Means (\pm 1SE) are reported throughout. For the instrumental task (task 1) and discrimination tasks (tasks 2 and 3), we compared the mean number of incorrect choices to criterion between spatial learners

and spatial non-learners using a Wilcoxon rank sum test. We also used Wilcoxon rank sum tests to compare (a) the mean latency to remove the lid from the reward dish between spatial learners and spatial non-learners; (b) the mean number of incorrect choices to reach criterion; and (c) the mean latency to remove the lid from the reward dish between task 2 and 3 for spatial learners and spatial non-learners. It is common to use these two measures because both come with predictions associated with learning (Carazo et al. 2014; LaDage et al. 2012; Noble et al. 2012, 2014). The number of errors is the most important metric for learning, and we predicted fewer errors with time, as lizards learn. Likewise, we also predicted that latency to acquisition also reduces with time, as lizards learn, although it may also be indicative of motivation. We tested the number of incorrect choices and the mean latency to acquisition in spatial learners and spatial non-learners using Spearman rank correlation tests. To establish any association between spatial learning ability and learning probability in tasks 2 and 3, we compared the frequency of spatial learners and spatial non-learners in relation to whether they learnt task 2 and 3 using a Fisher’s exact test. In task 2, we blocked every 6 trials and plotted learning curves across learning blocks for each individual using the number of incorrect choices and the mean latency to correct choice. We also examined the choices lizards made in task 2, where they were first exposed to the blue reward lid, to determine if they had a preference for blue. Given that lizards had a choice of three dishes, we would expect a probability of 0.3 (33%) that a lizard would select the blue lid by chance, but because of small sample sizes, this number can easily deviate from this expectation. In the case of the very first trial in task 2, 47% (7/15) of lizards chose the blue lid, which was not significantly different from the white or gold well covers ($\chi^2 = 1.6$, $df = 2$, $p = 0.449$). After 3 days (6 trials), 53% (8/15) of lizards had chosen the blue dish in less than 33% of trials and this was not significantly different among treatments ($\chi^2 = 4.467$, $df = 2$, $p = 0.107$). After 5 days (10 trials), 46% (6/13) of lizards had chosen the blue dish in less than 33% of trials and this was significantly different among treatments, but in favor of white ($\chi^2 = 6.2$, $df = 2$, $p = 0.045$). Importantly, we did not find any significant evidence of a bias for the blue (reward) lid (also see results). We also present the number of incorrect choices for each individual lizard for both spatial learners and spatial non-learners by learning block (Fig. S1), which shows higher error rates at the start of trials, prior to learning.

Spatial non-learner 207 was removed after task 2, because it took 49 trials to successfully learn task 2 and seemed fatigued and disengaged with the experiment. Spatial learner 168 and spatial non-learner 55 completed task 2, but not task 3 and were, therefore, excluded from the analysis comparing performance in task 2 and 3.

Results

All spatial learners and spatial non-learners successfully completed both the instrumental task (task 1) and task 2 (discrimination task 1). Six (86%) spatial learners and six (75%) spatial non-learners successfully completed task 3 (discrimination task 2) (Table 1).

Table 1 Number of trials performed by male *Eulamprus quoyii* to reach criterion in each task

ID	Spatial learner	Task 1	Task 2	Task 3
16	N	6 (1)	42 (23)	6 (1)
36	N	6 (0)	6 (1)	29 (15)
37	N	6 (0)	19 (9)	26 (14)
55	N	6 (1)	9 (4)	50 (37)
66	N	6 (0)	6 (1)	6 (1)
155	N	6 (0)	30 (17)	24 (14)
179	N	6 (0)	27 (15)	12 (3)
207	N	6 (0)	49 (35)	–
46	Y	6 (0)	30 (11)	48 (28)
65	Y	7 (2)	37 (20)	14 (5)
72	Y	6 (1)	38 (25)	6 (1)
76	Y	9 (4)	10 (4)	11 (6)
168	Y	6 (0)	15 (9)	50 (31)
182	Y	6 (0)	30 (20)	34 (17)
230	Y	6 (1)	7 (2)	33 (17)

Numbers within parentheses are the number of incorrect choices made during the task. Trials where a lizard did not attempt the task are not included in these tallies

Y spatial learner, N spatial non-learner

Is spatial learning domain specific or general?

In task 1, the number of incorrect choices prior to reaching acquisition between spatial learners (mean = 1.14 ± 0.55 , $n = 7$) and spatial non-learners (mean = 0.25 ± 0.16 , $n = 8$) was not significantly different ($W = 39$, $p = 0.15$; Fig. 2a). While spatial learners took longer to do the task (mean = 12.63 ± 7.18 , $n = 7$), the mean latency to remove the lid on the reward was not significantly ($W = 29$, $p = 0.91$; Fig. 2b) different from spatial non-learners (mean = 5.73 ± 1.12 , $n = 8$).

In task 2, we did not find significant ($W = 31$, $p = 0.73$; Fig. 2a) differences in the number of incorrect choices prior to reaching acquisition between spatial learners (mean = 13.00 ± 3.32 , $n = 7$) and spatial non-learners (mean = 13.13 ± 4.20 , $n = 8$). We also did not find significant ($W = 19$, $p = 0.30$; Fig. 2b) differences in the mean latency to remove the lid from the reward dish between spatial learners (mean = 10.03 ± 2.38 , $n = 7$) and spatial non-learners in task 2 (mean = 14.07 ± 3.10 , $n = 8$). This lack of a difference is also evidence against any difference in a blue color preference between the two treatment groups (also see Fig. S1).

In task 3, both the number of incorrect choices prior to acquisition and mean latency to remove the lid on the reward dish were not significantly different between spatial learners and spatial non-learners (number of incorrect choices prior to acquisition: spatial learner: mean = 15.00 ± 4.39 , $n = 7$; spatial non-learner: mean = 12.14 ± 4.79 , $n = 7$; $W = 31$, $p = 0.40$; mean latency: spatial learner: mean = 6.67 ± 1.77 , $n = 7$; spatial non-learner: mean = 8.02 ± 2.13 , $n = 7$; $W = 20$, $p = 0.57$; Fig. 2a, b).

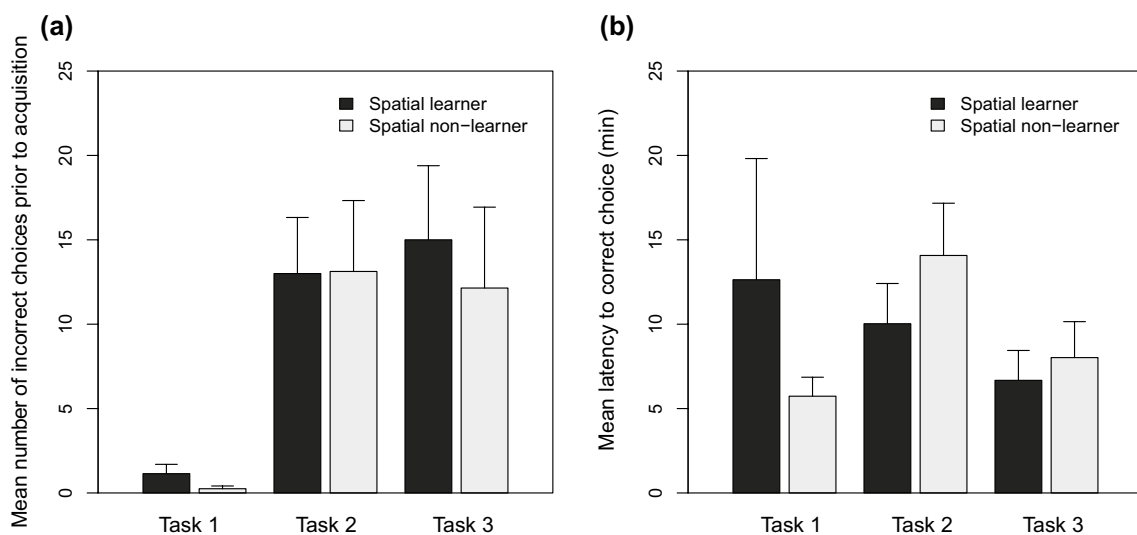


Fig. 2 Comparison of cognitive performance between spatial learners and spatial non-learners. **a** Mean (\pm ISE) number of incorrect choices to acquisition; **b** mean (\pm ISE) latency to correct choice

The number of incorrect choices prior to acquisition was not associated with the mean latency to remove the lid on the reward in spatial learners ($S=115.19$, $p=0.37$) and spatial non-learners ($S=41.41$, $p=0.20$). The probability of learning in task 2 and 3 was not associated with spatial learning ability (Fisher exact test, $p=0.72$).

Do spatial learners rely on spatial cues during discrimination learning?

We found that spatial learners and spatial non-learners made a similar number of incorrect choices prior to acquisition in task 2 and task 3 (spatial learners: task 2: mean = 13.66 ± 3.85 , $n=6$; task 3: mean = 12.33 ± 4.12 , $n=6$; $V=11.5$, $p=0.92$; spatial non-learners: task 2: mean = 11.00 ± 3.65 , $n=6$; task 3: mean = 8.00 ± 2.85 , $n=6$; $V=9$, $p=0.79$, Fig. 3a). Similarly, no significant difference was found in the mean latency to remove the lid on the reward between task 2 and task 3 for spatial learners (task 2: mean = 10.17 ± 2.81 , $n=6$; task 3: mean = 6.87 ± 2.08 , $n=6$; $V=16$, $p=0.29$) and spatial non-learners (task 2: mean = 13.41 ± 2.89 , $n=6$; task 3: mean = 8.27 ± 2.50 , $n=6$; $V=18$, $p=0.14$, Fig. 3b).

Discussion

We tested whether learning in one task was predictive of a lizard's ability to learn across different cognitive tasks (domain general learning). The results were mixed. First, if we compare within treatment groups, all spatial learners, bar one, reached criterion in all tasks. This result supports the domain general hypothesis for spatial learners.

Likewise, in the case of spatial non-learners, all but two individuals reached criterion in the three tasks in this study. However, their classification as spatial non-learners from previous work (Carazo et al. 2014) suggests domain specific learning whereby they did better at instrumental and discrimination tasks, but poorly in a spatial learning task. When we compare between treatments, performance in the instrumental and discrimination learning tasks were similar for spatial learners and non-spatial learners. This is contrary to the domain general hypothesis which predicts that spatial learners would perform better than non-spatial learners at the instrumental and discrimination tasks. In addition, we also found that spatial learners did not preferentially rely on spatial cues during discrimination learning. When space and color cues were disassociated (task 2 compared to task 3), any increase in the number of mistakes or the time taken to make the correct choice for spatial learners was not significantly different.

Spatial learning ability in male *E. quoyii* is not a clear predictor of an individual's learning ability in other cognitive domains. Proficiency in a single domain is not always predictive of ability in other domains (Boogert et al. 2010, 2011), despite some evidence that it can be (Kolata et al. 2008; Reader et al. 2011; Leal and Powell 2012). At the individual level, our results provide support for multiple hypotheses (e.g., domain general learning in spatial learners and domain specific learning in non-spatial learners) and we suggest that delineating learning into domain general and domain specific may be overly simplistic. We suggest focusing instead on individual variation in learning ability, which ultimately, is likely to play a key role in fitness. *E. quoyii* has a relatively high level of variance in cognitive ability not only between the sexes (Carazo et al. 2014), but

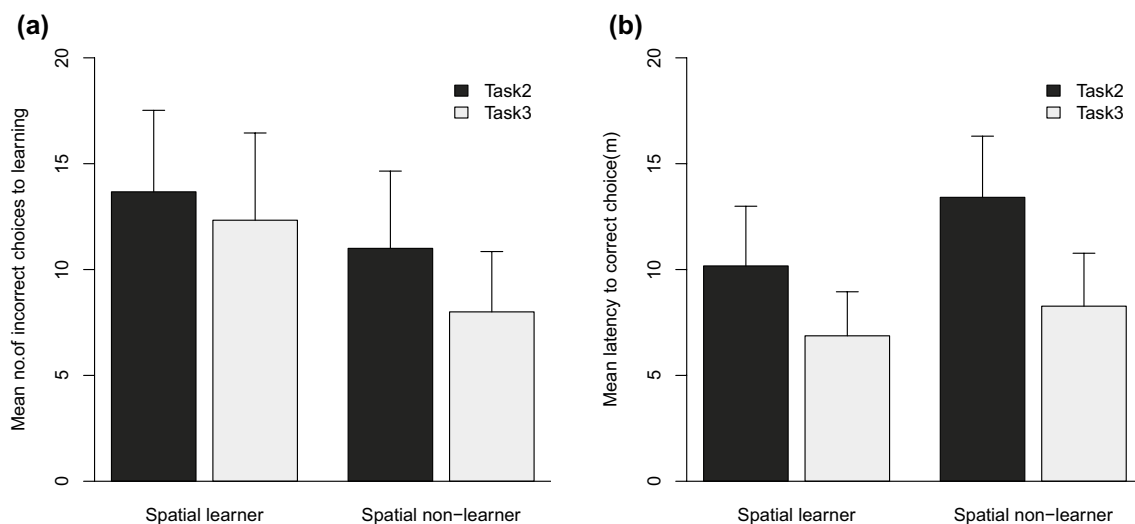


Fig. 3 Comparison of cognitive performance between task 2 and task 3 for spatial learners and spatial non-learners. **a** Mean (\pm 1SE) number of incorrect choices to acquisition; **b** mean (\pm 1SE) latency to correct choice

also within a sex. In the case of males, this variance may be related to alternate reproductive tactics because territorial males actively defend space from other males while floater males are more active and cover more ground (Noble et al. 2013), potentially setting the stage for different developmental or selective pressures on cognition. Although we do not have data on the relationship between spatial learning and male alternative reproductive tactics, we expect that floater males may be more accomplished spatial learners because of their higher activity levels and consequently, greater navigational demands (Sherry et al. 1992; Day et al. 1999). The lack of difference in discrimination learning and their ability to solve an instrumental task likely reflects their similarity in foraging behavior (this species is an ambush forager) and general habitat use.

Eulamprus quoyii that were spatial learners did not use spatial cues in different contexts to solve novel tasks. Spatial learning largely depends on spatial cues (e.g., moon, sun, visual landmarks) (Keeton 1971; Collett et al. 1986; Dyer and Dickinson 1994; Collett 2002), while visual cues are also required for associative learning (e.g., color, shape, spatial setting; Day et al. 1999; Leal and Powell 2012; Clark et al. 2014). For example, color is used in associative and reversal learning in the lizard *Bassiana duperreyi* (Clark et al. 2014). In our experiment, both spatial learners and spatial non-learners did not differ in their performance in the discrimination tasks when color and spatial cues were disambiguated. This suggests that both groups are equally adept at switching to other cues when spatial cues are no longer reliable, as was the case in task 3 when the blue dish was the reward and was spatially randomized during each trial. There is a possibility that using an aversive learning task in the spatial learning experiment (Carazo et al. 2014) could confound our results from the experiments conducted using appetitive tasks. We doubt this is the case because lizards were motivated to engage with all tasks. We are also unaware of any evidence suggesting that lizards that perform well in an aversive task do not also perform well in an appetitive task.

While we did not detect differences in learning ability among spatial and non-spatial learners in either the instrumental or discrimination task, both groups reached criterion. Although the spatial non-learner group did not reach criterion in the previous spatial task (Carazo et al. 2014), in an earlier study this species demonstrated flexibility in spatial learning (Noble et al. 2012), and young males solved a foraging task more quickly using social information (Noble et al. 2014). These previous findings, together with their ability to solve both the instrumental and discrimination task in this study, support the notion that *E. quoyii* has behavioral flexibility. Behavioral flexibility is defined as the ability to solve novel tasks or existing problems using novel means (Reader and Laland 2002; Shettleworth 1998a). However,

there are several metrics for behavioral flexibility that typically include the ability to solve novel tasks across multiple cognitive domains, including reversals, and/or the use of multiple strategies to solve a task (Leal and Powell 2012). By solving tasks across multiple cognitive domains, including reversal learning, *E. quoyii* meets this criterion, which was first demonstrated for lizards in *Anolis evermanni* (Leal and Powell 2012). We need more tests of behavioral flexibility incorporating multiple cognitive domains in a greater range of species with differing ecological constraints and social organization to better understand the generality of our findings.

Acknowledgements This study was funded by the National Natural Science Foundation of China (31572273) to YQ, a Talent Reward Grant from the Sichuan provincial government (Y1D3011) to JF, and funding from Macquarie University to MJW.

Data availability The datasets generated during and/or analyzed during the current study are available in Table 1 and on Figshare: <https://doi.org/10.6084/m9.figshare.6394892>.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest regarding this study.

Ethical approval This work was approved by the Animal Ethics Committee at Macquarie University (ARA2011/018) and lizards were collected under a permit from the Wildlife Licensing and Management Unit, Office of Environment and Heritage of New South Wales (scientific collection permit S13150).

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