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Behavioural flexibility and problem-solving in a tropical lizard

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The role of behavioural flexibility in responding to new or changing environmental challenges is a central theme in cognitive ecology. Studies of behavioural flexibility have focused mostly on mammals and birds because theory predicts that behavioural flexibility is favoured in species or clades that exploit a diversity of habitats or food sources and/or have complex social structure, attributes not associated with ectothermic vertebrates. Here, we present the results of a series of experiments designed to test cognitive abilities across multiple cognitive modules in a tropical arboreal lizard: *Anolis evermanni*. This lizard shows behavioural flexibility across multiple cognitive tasks, including solving a novel motor task using multiple strategies and reversal learning, as well as rapid associative learning. This flexibility was unexpected because lizards are commonly believed to have limited cognitive abilities and highly stereotyped behaviour. Our findings indicate that the cognitive abilities of *A. evermanni* are comparable with those of some endothermic species that are recognized to be highly flexible, and strongly suggest a re-thinking of our understanding of the cognitive abilities of ectothermic tetrapods and of the factors favouring the evolution of behavioural flexibility.

Keywords: behavioural flexibility; cognition; evolution; reptile; radiation; *Anolis*

1. INTRODUCTION

Behavioural flexibility—i.e. the ability of an individual to change its behaviour by developing new responses to novel stimuli or altering existing responses to familiar stimuli—has become a central focus in cognitive ecology, and it is commonly associated with advanced cognition [1,2], including problem-solving. In vertebrates, studies of behavioural flexibility have mostly focused on mammals and birds (e.g. [3–6]), because theory predicts that behavioural flexibility is favoured in species or clades that exploit diverse food sources, have complex social structure, or inhabit environments with highly unpredictable resources [7], attributes not associated with ectothermic vertebrates.

Two types of evidence have been used to document behavioural flexibility. First, studies have examined anecdotal evidence of behavioural plasticity (i.e. behavioural innovations, *sensu* Lefebvre *et al.* [8]), particularly in feeding behaviour within a given clade [4].

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Second, experimental data, usually under laboratory conditions, have been collected to evaluate behavioural flexibility [1]. In this case, studies have addressed a variety of cognitive modules, such as flexibility of motor skills, spatial learning, associative learning and reversal learning (see [1,7] and references therein). In studies in which multiple cognitive tasks have been used, results indicate that the ability of an individual to solve one cognitive task is not a predictor of success across multiple cognitive tasks [9,10]. Thus, a robust demonstration of behavioural flexibility should show that individuals are capable of solving multiple cognitive tasks, an approach that is not commonly used, especially in ectothermic vertebrates (see [11,12] and references therein).

Here, we present the results of a series of experiments, designed to test behavioural flexibility by evaluating cognitive abilities on multiple cognitive tasks in the arboreal lizard *Anolis evermanni*. The results not only demonstrate problem-solving and behavioural flexibility across multiple tasks, but also indicate that the cognitive abilities of this lizard are comparable with those of some endothermic species, including species recognized as having highly flexible behaviours.

2. MATERIAL AND METHODS

Anolis evermanni, three males and three females, were collected in Puerto Rico and transported to our laboratory. Lizards were housed independently in cages (29 L, 21 W and 21 H cm), and kept under 12 L:12 D photoperiod cycle, at 28°C and 60 per cent relative humidity, watered daily and fed crickets on a regular schedule throughout the experimental period.

Behavioural experiments were conducted in the cage where the lizards were housed. The behavioural testing apparatus was placed inside the cage, and lizards had 15 min to perform the task. The apparatus was an opaque grey platform (12 L, 5.5 W cm) containing two wells, each 1.6 cm in diameter and 1 cm deep. The wells were covered by a tight-fitting 2.5 cm diameter opaque-coloured circular disc, concealing their contents (figure 1). A reward (freshly killed, intact larva of *Hermetia illucens*) was placed inside a well, and the lizard had to remove the disc to reach the larva.

Individuals were habituated to the testing apparatus before conducting the experiments. Habituation was performed in three sequential steps: (i) the apparatus was placed inside the cage with a reward inside one well; (ii) the blue disc was positioned next to the well containing the reward; (iii) the blue disc was positioned covering half of the well containing the reward. During the habituation period, individuals did not need to manipulate the disc to access the worm. Individuals advanced stages or completed an experiment when they correctly performed the task six consecutive times. Trials were video-recorded.

Once the habituation period was completed, a uniform-coloured blue disc was tightly fitted to one of the wells and the lizards were presented with the novel problem of dislodging the target to access the larva. Only one disc was used and its position was randomly determined before each trial. Individuals conducted one trial per day.

Lizards that learned to dislodge the disc performed two discrimination experiments in which a target (i.e. stimulus used for the motor task) and a distracter (i.e. a solid-coloured yellow disc for experiment 1 and a disc formed by yellow and blue concentric rings for experiment 2) were presented simultaneously. Position of the stimuli was randomly determined before each trial. The reward was placed under the target, and larva odour was placed inside both wells. Choice was scored as the first stimulus dislodged by the lizard. To further control for smell, in 25 of the trials a larva was placed under both stimuli; each lizard performed a minimum of five trials under this condition. In 23 out of the 25 trials ($p < 0.001$, binary choice test), the lizards chose the target.

The same paradigm was used to test reversal learning. However, in these experiments, the reward was placed under the disc formed by yellow and blue concentric rings rather than the uniform-coloured blue disc, reversing the conditions previously presented to the lizards. A lizard was removed from the experiment when it did not attempt to perform the task in six consecutive presentations.



Figure 1. *Anolis evermanni* performing a discrimination trial.

3. RESULTS

Four lizards were able to solve the novel problem of removing the disc to access the reward (table 1). Two distinct strategies were used to dislodge the disc: individuals learned to bite the edge of the disc to dislodge it or to use their snout as a lever (see electronic supplementary material, movies S1 and S2). The two lizards that could not solve the motor task failed to do so because they continually struck at the target from above, a behaviour that was ineffective at dislodging the disc.

All lizards that completed the motor tasks were able to discriminate between the target and a distracter (figure 1). Three out of four individuals were able to do so without making any mistakes, and the other individual only made one mistake (table 1, first experiment). Discrimination was further evaluated by testing a second distracter: a disc formed by two concentric rings. The centre of the new distracter was of the same colour and shape as the target, increasing the similarity between the two stimuli. Again, lizards were able to correctly choose the target without making any mistakes (table 1, second experiment).

Two out of four lizards exhibited reversal learning (table 1). Lizards that did not reverse their association never tried to dislodge the concentric rings; instead, they consistently removed the uniform disc (i.e. previous target) until they stopped responding owing to lack of reinforcement.

4. DISCUSSION

Our results show that *A. evermanni* exhibits behavioural flexibility across multiple cognitive tasks, including solving a novel motor task using multiple strategies and reversal learning, plus rapid associative learning. This degree of flexibility is commonly associated with bird or mammal species considered highly flexible [1,7,8], but is not predicted to be exhibited by a species that lacks complex social structure and has a relatively simple foraging strategy (i.e. sit-and-wait), suggesting that behavioural flexibility might be favoured by a wider set of life-history traits than previously proposed.

The ability of *A. evermanni* to solve the novel motor problem presented here was completely unexpected. The correct response required major changes to what

Table 1. Number of trials performed by individuals of *Anolis evermanni* to complete each experiment. (n.a., individual stopped performing the experiment; parentheses indicate the number of trials performed).

lizard	motor task	discrimination		
		first experiment	second experiment	choice reversal
male 3	19	6	6	64
male 5	36	7	6	65
female 8	39	6	6	n.a.(38)
female 10	19	6	6	n.a.(60)

has previously been considered highly stereotyped foraging behaviour [13], which consists of scanning the environment for moving prey items and striking them from above. In our experiment, motion cues were absent and striking from above was ineffective at dislodging the disc. Lizards used multiple strategies to remove the disc. The first was a modified strike, laterally biting the disc and lifting it away from the reward. The second strategy required the lizard to advance on the disc with its head held against the substrate, using its snout as a lever to push the disc out of the way (see electronic supplementary material, movie S1). This strategy is not a natural foraging behaviour that has at least been witnessed, and may demonstrate an entirely novel solution, which is one of the main criteria used to recognize behavioural flexibility [4].

The four lizards that successfully completed the motor task were all immediately able to discriminate the rewarded disc from the novel, unrewarded disc (table 1). The fact that individuals of *A. evermanni* rarely made mistakes during the discrimination tasks shows that individuals were able to quickly form a strong association between a non-ecologically relevant stimulus (i.e. a non-moving coloured circle) and a food reward, and demonstrates rapid acquisition of non-spatial memory. The behavioural paradigm used in our experiment is similar to that used in studies evaluating cognitive abilities of birds (e.g. [10,14]), which provides an opportunity to evaluate similarities and/or differences in cognitive performance across the two groups [4]. However, because distinct taxa might perceive the same cognitive task differently, we only explore the most basic aspect of the task: number of presentations. Although individuals of *A. evermanni* only performed one task per day (i.e. a single presentation), they needed at least three times fewer presentations to successfully complete the associative learning tasks than what is commonly used in studies testing similar abilities in bird species (e.g. [9,10,14,15] and references therein). This result was unexpected and suggests a possible difference in the tempo at which associations are formed between these groups; further studies are needed to explore the generality of these results.

The final experiment demonstrated that individuals of *A. evermanni* were capable of reversing their previously learned colour associations. Two individuals were able to reverse their association, while two individuals

continued to remove the previously rewarded stimulus and never manipulated the new target (table 1). Studies of reptilian cognition are extremely limited; however, evidence suggests that spatial reversal is an easier cognitive task than reversal based on visual feature cues (reviewed in Day *et al.* [12]). In our reversal task, the degree of similarity between the cues was higher than that previously used in reptiles (reviewed in Day *et al.* [12]), suggesting that reptiles might be more efficient than previously reported at discriminating the features of visual stimuli (i.e. colour and pattern). Also, our results demonstrate that performance of a given cognitive task (i.e. motor task and associative learning) was not a predictor of the ability to solve the reversal learning experiment, illustrating the need to measure individuals' cognitive abilities across multiple tasks.

In summary, our results provide evidence that cognitive abilities of *A. evermanni* are comparable with those of some endothermic species known for their behavioural flexibility. As a group, *Anolis* is known for exploiting a diversity of ecological niches and exhibiting complex behavioural repertoires [13], attributes that can favour the evolution of behavioural flexibility [7,16]. Alternatively, behavioural flexibility might have contributed to the radiation of this clade by facilitating the exploration of novel environments and promoting diversification of habitat use [17]. Finally, our findings and those of Wilkinson *et al.* [18] force a re-thinking of our understanding of the cognitive abilities of ectothermic tetrapods.

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