

## On the flexibility of lizards' cognition: a response to Vasconcelos *et al.*

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*Invited reply***On the flexibility of lizards' cognition: a response to Vasconcelos *et al.***

In their commentary, Vasconcelos *et al.* [1] questioned the validity of our interpretation that *Anolis evermanni* exhibits problem-solving across multiple tasks, rapid associative learning and behavioural flexibility [2]. We will address each of these points in turn.

In our paper, we presented two pieces of evidence to support problem-solving across multiple tasks. First, individuals of *A. evermanni* were capable of solving a motor task in which they were challenged with the novel problem of dislodging a tightly fitted disc to gain access to a food reward. Individuals who successfully completed this task did so by modifying what previously was characterized as a highly stereotyped prey-striking behaviour (see movies in Leal & Powell [2]). This is indicative of behavioural flexibility, the ability of an individual to modify a behaviour in response to novel conditions.

Second, lizards were capable of completing a choice reversal task. Vasconcelos *et al.* contend that the behavioural paradigm we used to document choice reversal only demonstrates associative learning and not behavioural flexibility. At the centre of their critique is the implementation of our methodology, which differs from the one typically used in studies of reversal learning. In our methodology, previous contingencies (i.e. positive or negative associations) were not formed for both stimuli during the habituation trials. Instead, as a result of the discrimination trials, in our experimental design there was a positive contingency for one stimulus (i.e. previously rewarded disc) and a lack of contingency for the previously unrewarded disc [2]. To successfully complete the choice reversal task, individuals needed to develop a new association with the previously unrewarded disc, which required extinguishing the previously formed association with the rewarded disc; this took place while both stimuli were present. Under this condition, individuals are exposed to a negative transfer effect, in which the previous association interferes with the formation of the new association, as is the case during typical reversal learning. Thus, we disagree with the conclusion made by Vasconcelos *et al.* that this experiment only demonstrates associative learning and provides no evidence for behavioural flexibility. However, although behavioural flexibility is required to successfully complete both paradigms, it is conceivable that the degree of difficulty of our behavioural paradigm is different from a typical reversal paradigm. We are unaware of a study,

particularly in reptiles, that has evaluated if methodological differences of this sort affect the ability of individuals to complete the task and/or indicate differences in the degree of behavioural flexibility.

In any case, we are currently in the midst of a study that is functionally equivalent to the experimental protocol that Vasconcelos *et al.* endorse (see current results in table 1, *A. evermanni* males A–E). In this study, the experimental methodology and sequence of experiments up to and including the first discrimination task is identical to the one presented in Leal & Powell [2]. At the conclusion of the first discrimination, the lizards were presented with a choice reversal task, in which blue became the unrewarded disc and yellow became the rewarded disc (i.e. first choice reversal task). We then conducted a second choice reversal task; at this point, the lizards had formed contingencies to both stimuli (i.e. blue and yellow discs). At the present, four lizards have performed the first choice reversal and three of those have performed the second choice reversal. These three lizards performed both the first and second choice reversals in a similar number of trials (table 1), suggesting that both trials are functionally comparable. More generally, both studies provide evidence for the ability of individuals to reverse a pre-existing association and to do so under conditions in which the previous association interferes with the formation of the new association. We interpret these results as providing further evidence for behavioural flexibility.

With regard to rapid associative learning, Vasconcelos *et al.* pointed out that a reader could not know the exact number of trials that each lizard performed during the habituation phase of the experiment. The omission of information on the number of trials was an oversight which is now presented in table 1.

In summary, Vasconcelos *et al.* argued that the results of our experiments do not provide evidence for problem-solving across multiple tasks, rapid associative learning and more generally behavioural flexibility. We respectfully disagree with their interpretation; however, we welcome their criticism as it may refine our future work in this area. Moreover, our study is not the first addressing cognitive abilities of lizards, or reptiles in general (see references in Leal & Powell [2] and Vasconcelos *et al.* [1]). The novelty of our study lies in testing behavioural flexibility by evaluating the ability of individuals to solve multiple cognitive tasks, an active area of study in birds and mammals but overlooked in this clade. We hope that this discussion will serve to spark further studies on cognitive abilities across a diversity of taxa, including a reconsideration of possible factors favouring the evolution of behavioural flexibility.

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- 1 Vasconcelos, M., Monteiro, T. & Kacelnik, A. 2012 On the flexibility of lizards' cognition: a comment on Leal & Powell (2011). *Biol. Lett.* 8, 42–43. (doi:10.1098/rsbl.2011.0848)
- 2 Leal, M. & Powell, B. J. 2012 Behavioural flexibility and problem-solving in a tropical lizard. *Biol. Lett.* 8, 28–30. (doi:10.1098/rsbl.2011.0480)

The accompanying comment can be viewed at <http://dx.doi.org/10.1098/rsbl.2011.0848>.

Table 1. Number of trials performed by individuals of *Anolis evermanni* to complete each task (n.a., individual stopped performing the experiment; parentheses indicate the number of trials performed before extinction; italics indicate the number of trials an individual has performed at present without completing the task; asterisk indicates that the individual was not presented with that task).

lizard	near cover	partial cover	motor task	discrimination		choice reversal	
				first experiment	second experiment	first experiment	second experiment
male 3	6	6	19	6	6	64	*
male 5	6	6	36	7	6	65	*
female 8	6	6	39	6	6	n.a.(38)	*
female 10	7	6	19	6	6	n.a.(60)	*
male A	6	6	7	6	*	16	32
male B	36	6	19	12	*	105	*
male C	6	6	6	6	*	11	18
male D	6	6	33	7	*	38	32
male E	11	10	17	19	*	30	90