

# Social learning by imitation in a reptile (*Pogona vitticeps*)

Anna Kis · Ludwig Huber · Anna Wilkinson

Received: 26 February 2014 / Revised: 15 August 2014 / Accepted: 20 August 2014  
© Springer-Verlag Berlin Heidelberg 2014

**Abstract** The ability to learn through imitation is thought to be the basis of cultural transmission and was long considered a distinctive characteristic of humans. There is now evidence that both mammals and birds are capable of imitation. However, nothing is known about these abilities in the third amniotic class—reptiles. Here, we use a bidirectional control procedure to show that a reptile species, the bearded dragon (*Pogona vitticeps*), is capable of social learning that cannot be explained by simple mechanisms such as local enhancement or goal emulation. Subjects in the experimental group opened a trap door to the side that had been demonstrated, while subjects in the ghost control group, who observed the door move without the intervention of a conspecific, were unsuccessful. This, together with differences in behaviour between experimental and control groups, provides compelling evidence that reptiles

possess cognitive abilities that are comparable to those observed in mammals and birds and suggests that learning by imitation is likely to be based on ancient mechanisms.

**Keywords** Reptile · Social cognition · Bidirectional control procedure

## Introduction

Learning from the observation of others was long thought to be a distinctive characteristic of humans; it was even suggested that a more appropriate name for the human species would be *Homo imitans*, man who imitates (Meltzoff 1988). Imitation is considered to be the pinnacle of social learning and the basis of cultural transmission (Heyes et al. 2009). Imitation is thought to be cognitively complex because the observer not only has to acquire information, but must also draw inferences about the behaviour observed, the constraints of the situation, and the intentions or goals of the model. There is now evidence that non-human species including apes (Tomasello et al. 1993; Call 2001; Byrne and Tanner 2006), monkeys (Subiaul et al. 2004; Voelkl and Huber 2000, 2007), other mammals (Müller and Cant 2010; Topál et al. 2006; Range et al. 2007; Herman 2002), and birds (Klein and Zentall 2003; Moore 1992; Tchernichovski 2001; Akins and Zentall 1996) are also capable of imitation. However, we know nothing about these abilities of the third amniotic class—reptiles.

Reptiles and mammals evolved from a common amniotic ancestor, and investigation of similarities and differences in their behaviour is essential for understanding the evolution of cognition (Doody et al. 2012, Wilkinson and Huber 2012). Recent advances in the field of reptile

**Electronic supplementary material** The online version of this article (doi:10.1007/s10071-014-0803-7) contains supplementary material, which is available to authorized users.

A. Kis · A. Wilkinson (✉)  
School of Life Sciences, University of Lincoln, Lincoln, UK  
e-mail: AWilkinson@lincoln.ac.uk

A. Kis  
Department of Ethology, Eötvös University, Budapest, Hungary

A. Kis  
Research Centre for Natural Sciences, Hungarian Academy of Sciences, Budapest, Hungary

L. Huber  
Messerli Research Institute, University of Veterinary Medicine, Vienna, Austria

L. Huber  
Department of Cognitive Biology, University of Vienna, Vienna, Austria

cognition have found evidence of sophisticated abilities in this group. The red-footed tortoise (*Chelonoidis*—formerly *Geochelone*—*carbonaria*) is capable of gaze following (Wilkinson et al. 2010a) and can learn to solve an otherwise unsolvable task by observing the actions of a conspecific (Wilkinson et al. 2010b). Furthermore, the Florida redbelly turtle (*Pseudemys nelsoni*) is able to learn to approach a visual object cue by observing conspecifics that had learned the task (Davis and Burghardt 2011). Also, young male skinks (*Eulamprus quoyii*) learn a novel instrumental task (displacing a lid) faster in the presence of a demonstrator than without a demonstrator (Noble et al. 2014). Though these findings provide evidence that reptiles can use social information, the mechanisms that control their behaviour remain unclear.

The present study used a bidirectional control procedure (developed by Dawson and Foss 1965; and later used by many others e.g. Akins and Zentall 1996; Pesendorfer et al. 2009; Wood et al. 2013) to investigate whether bearded dragons (*Pogona vitticeps*) are capable of imitating a conspecific. This task was designed to control for both social influences and emulation/enhancement effects when testing imitation. The paradigm involves comparing the performance of two groups of observers watching demonstrations that differ in their body movements but create identical (or symmetrical) changes in the environment. Imitation occurs when subjects perform the demonstrated action more often than the alternative action, and can be measured either by considering the outcome of the action (Miller et al. 2009) or the details of the specific behaviour performed (e.g. Voelkl and Huber 2007). In the present paper, we define successful imitation as a combination of producing the same outcome as the demonstrator and performing the same behaviour.

## Materials and methods

### Subjects

The bearded dragons either belonged to the Small Animal Unit at the University of Lincoln ( $N = 7$ ) or were privately owned ( $N = 6$ ) but were kept at the university throughout the study. Our subjects were 5 males and 7 females (age range of 1–3 years), and a 3-year-old female was chosen as the demonstrator in order to avoid the possibility of male subjects responding aggressively to the video demonstration. (Females are often housed together and generally show no aggression towards each other.) None of the animals had previously taken part in cognition experiments. All animals were handled by humans on a daily basis. The 12 subjects were divided into three groups ( $N = 4$  individuals each; 2 males and 2 females in each of the two

experimental groups; 1 male and 3 females in the control group).

### Experimental arrangement

Testing was carried out in an experimental arena (100 cm  $\times$  40 cm  $\times$  50 cm) that was divided by the test apparatus into two equal parts: the test area (where the subjects were located) and the demonstration area (where the computer screen was positioned; Fig. 1.). The test apparatus itself was a 40 cm  $\times$  40 cm wooden board with a 12 cm  $\times$  12 cm hole. This was covered by a wire door which could be moved along sliding rails in front of the wooden board in either a leftward or a rightward direction. The door could be moved by using either the head or the foot, making contact at any point and then sliding the door horizontally to either the left or the right side.

### Demonstrator training

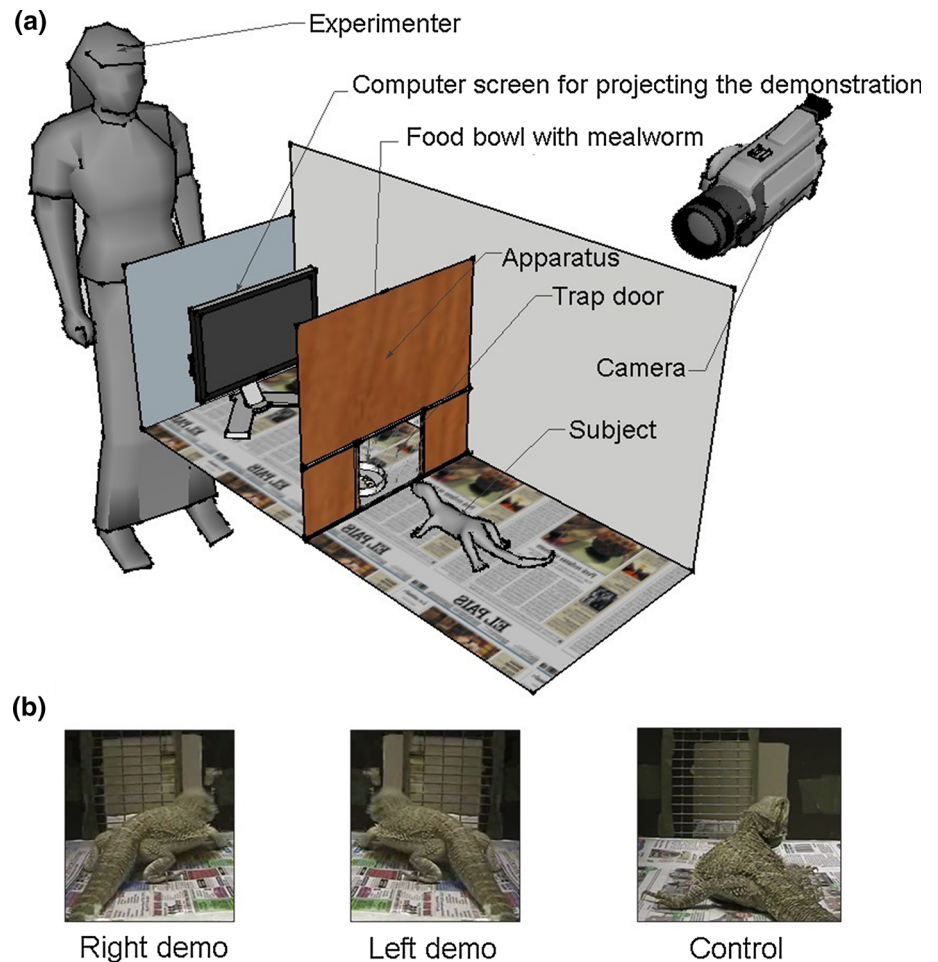
The demonstrator lizard was trained to open the wire door using both shaping and also relying on trial and error learning during a 3-week-long period. After habituation to the experimental arena, meaning when the lizard readily explored and ate mealworms placed in a Petri dish, we introduced the test apparatus. First the lizard had to go through the hole on the wooden board with the wire door completely open in order to get the mealworm placed on the other side, then we gradually closed the door. The lizard had prolonged access (up to 60 min/session) to the apparatus during several days until it could solve each step.

### Procedure

All subjects were habituated to the experimental arena before the onset of the experiment. They were considered habituated when they readily explored and ate mealworms placed in a Petri dish (used later as a reward in the test trials) in the experimental arena. During this time, they were not exposed to the apparatus used in the test as habituation was carried out in the empty arena (without the wooden wall) with a Petri dish placed at varying locations.

The subjects received two trials a day separated by a break. Testing took place on five consecutive days resulting in ten experimental trials for each animal. Each trial started with a short (30 s) habituation phase when the experimenter placed the subjects in the experimental arena and they were allowed to explore freely. This was followed by the demonstration phase, when an 11-s video was presented via a computer monitor (please see supplementary videos S1–3). In the two experimental groups, the demonstration showed a conspecific approaching the test apparatus, opening the door rightwards (or leftwards) with a sliding

**Fig. 1** Test set-up. **a** The experimental arena was divided into two parts by the apparatus. The subject was located in the test arena where it had access to the wire door, through which it could see the mealworm. The demonstration arena contained the computer screen used for projecting the video demonstration and a Petri dish with the mealworm. **b** Frame-grabs from the demonstration videos showing a conspecific opening the wire door to the *right* or the *left* or a passive conspecific while the door opened by itself



head movement (see later for definition) and going through it. To ensure that the lizards learned about the behaviour of the conspecific and not a simple rule of moving the door towards (or away from) a salient part of the apparatus, the demonstrator was trained to open the door in one direction (right) and the stimulus video was flipped and appeared as a mirror image for presentation of the leftward opening (using the “flip horizontally” filter in the VirtualDub program). In the control group, the demonstration showed a conspecific standing in front of the apparatus and the door opening by itself to the right side. None of the videos showed the demonstrator being rewarded.

Following the demonstration, the subject was moved to the test area part of the experimental arena and a white plastic board was placed in front of the lizard while the test apparatus was placed in the arena (this took approximately 5 s). Afterwards, the subjects were allowed free access to the test apparatus, and their behaviour was recorded for 5 min. During this time, the monitor used for demonstration remained in the same place, but showed only a blank screen. The trials were terminated and the subjects were returned to their home enclosures if they successfully

opened the sliding door to any side and went through it or if the 5 min were over. If subjects were not able to get to the mealworm (by opening the sliding door to any side and going through it), they were not rewarded, even if they opened the sliding door.

#### Behavioural coding and analysis

##### Success

In all trials, we coded the side to which subjects opened the door with: +1 for left, −1 for right and 0 for no opening. In those rare cases (6 out of 120 trials) when a subject opened the door to both sides in the same trial, it received both scores +1 and −1 (=0). Opening was defined as a visible gap at either side of the door. Behavioural coding was blind to experimental condition and the inter-observer reliability (based on double coding of 20 % of the test trials—2 trials/subject) was high ( $\kappa = 0.92$ ). The side of opening on the first successful trial (when the first opening occurred) was compared to 50 % chance level using a Binomial test (for this analysis, the opening score was converted to 0/1 so that

subjects received a score of 1 for opening to the demonstrated side and a score of 0 for opening to the non-demonstrated side; data of the two experimental groups were pooled together). Opening score (reflecting the sum of all ten trials) was compared to the chance level of 0 using a Wilcoxon Test (for this analysis, the opening score was converted to 0/1 and subjects received a score of 1 for opening to the demonstrated side and a score of 0 for opening to the non-demonstrated side or not opening; data of the two experimental groups were pooled together). The three groups were compared by Kruskal–Wallis test (followed by pair wise Mann–Whitney post hoc tests) using the sum of the  $-1$ ,  $0$ ,  $+1$  opening scores. The correlation between the number of successful experimental subjects in a given trial and the number of previous trials administered was assessed in order to check for the effect of repeated exposure to the task (Kendall's tau). To investigate the impact of learning within a day, the number of successful experimental subjects was compared within a daily session between the first (trials 1, 3, 5, 7, 9) and second (trials 2, 4, 6, 8, 10) trials administered on that day (Wilcoxon test).

### Behaviour analysis

The subjects' behaviour was coded during the test phase.

**Contact behaviour** The number of times a subject made contact with the wire door in each trial was compared across the three groups (ANOVA). The position of the subjects when making contact with the wire door, that is, the side of the wire door the subjects touched, was also recorded, and we compared the proportion of contacts made to the left or right side across the three groups (ANOVA). For the experimental subjects, we also compared the number of contacts with the wire door for the successful and unsuccessful trials using a paired samples  $t$  test. This was only done in the case of the trials when the subjects made contact with the wire door and thus had a chance to open it.

**Opening behaviour** The occurrence of a specific sliding head movement behaviour which the demonstrator used to open the wire door (a fast ( $<1$  s), horizontal head movement of at least 1 cm) was recorded for all three groups. For the experimental subjects, we compared the number of sliding head movements in the successful and unsuccessful trials using a paired samples  $t$  test. Behavioural coding was blind to experimental condition, and the inter-observer reliability (based on double coding of 20 % of the test trials—2 trials/subject) was high for all variables (contact with the wire door:  $\kappa = 0.83$ ; contact at left/right side of the wire door:  $\kappa = 1.00$ ; sliding head movement:

$\kappa = 0.91$ ); in case of disagreement, the assessment of the first coder (AK) was used.

Please see supplementary videos 4 (S4 experimental group—right) and 5 (S5 control group) as examples of the responses to the different conditions.

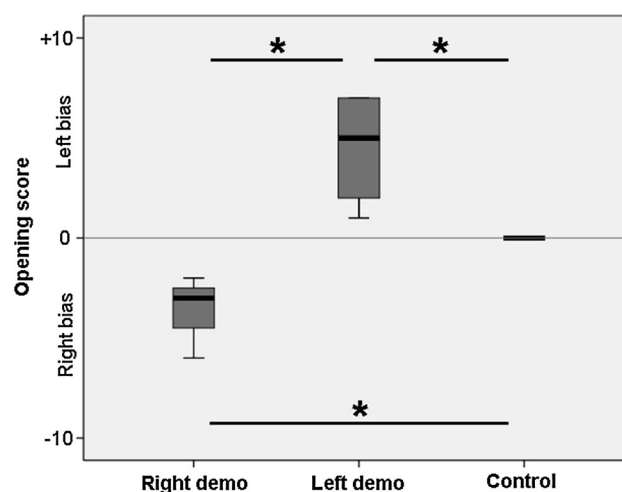
## Results

### Success

All experimental subjects successfully opened the sliding door, whereas none of the control subjects did. Furthermore, on their first successful trial, all 8 experimental subjects opened the door to the side that they had observed the demonstrator opening (Binomial test,  $P = 0.008$ ). This side preference was consistent across the entire experiment (67–100 %) with a significant bias towards the demonstrated side (Wilcoxon Test,  $T+ = 37$ ,  $P = 0.007$ ). The three groups also differed from each other in the side of opening (Kruskal–Wallis Test,  $\chi^2 = 10.277$ ,  $P = 0.006$ ; Fig. 2).

However, considerable individual variation was observed (Table 1.). Of the eight experimental animals, the number of successful openings varied from 2/10 to 10/10, and the first successful opening varied from trial 1 to trial 5.

The number of successful experimental subjects in a given trial was not related to the number of previous trials administered ( $r = -0.025$ ,  $P = 0.926$ ). There was no difference in the number of successful experimental

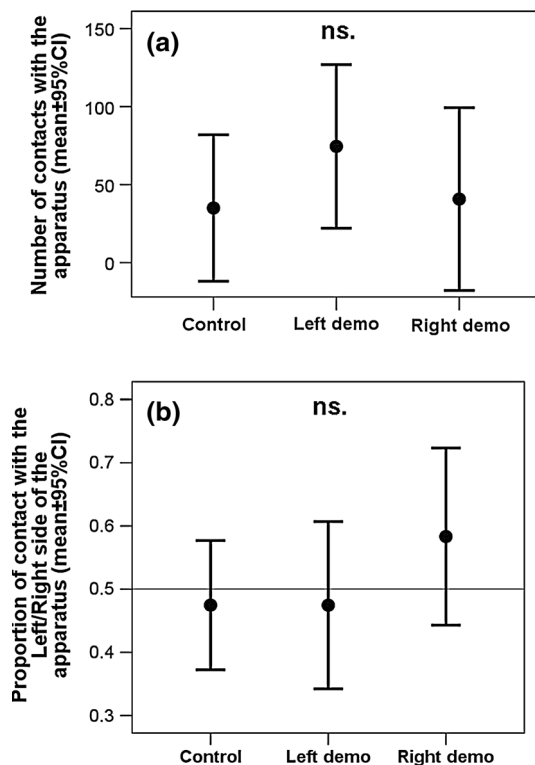


**Fig. 2** Side preferences for the three groups calculated from the 10 trials. The right demo group saw the demonstrator opening the door to the *right side*, the left demo group saw the demonstrator opening the door to the *left side*, while the control group saw a passive demonstrator while the door opened by itself to the right side. \* $P = 0.029$

**Table 1** Individual data on subjects' performance in the two experimental groups

ID	Gender	Housing	Group	Trial1	Trial2	Trial3	Trial4	Trial5	Trial6	Trial7	Trial8	Trial9	Trial10
1	f	U	R	<b>R</b>	L R	<b>R</b>	<b>R</b>	L R	0	R	0	R	R
2	m	U	L	0	0	<b>L</b>	L	L	<b>L</b>	<b>L</b>	<b>L</b>	L	0
3	f	U	L	0	<b>L</b> R	0	0	0	0	0	0	L	0
4	m	U	L	0	0	0	<b>L</b>	L	0	0	L	0	0
5	f	U	R	0	<b>R</b>	0	R	0	0	0	0	0	0
6	m	U	R	0	0	0	0	<b>R</b>	R	0	R	0	0
7	m	P	R	0	<b>R</b>	R	<b>R</b>	0	0	0	R	0	0
8	f	P	L	<b>L</b>	L	L	L	<b>L</b>	L	L	L R	<b>L</b>	L R

Control subjects performed no door openings in any of the ten trials and are thus not included in the table. Gender of the subjects: f—female, m—male; Housing: U—university owned, P—privately owned; Group: R—right demonstration, L—left demonstration. The side of opening during the ten trials is indicated with R/L for right/left. In case of the trials when subjects opened the wire door to both sides, the two openings are presented in the order in which they occurred. The first successful opening is marked with bold. Bolditalic indicates that the subject in the given trial not only opened the door, but also went through it



**Fig. 3** Contact behaviour. **a** The number of contacts subjects made with the apparatus during the ten trials in the control, left demo and right demo groups. ns.:  $P = 0.245$ . **b** The proportion of making contact with the *left/right side* of the apparatus during the ten trials in the control, left demo and right demo groups. ns.:  $P = 0.136$

subjects in the first and second trial of a daily session ( $Z = 0.141$ ,  $P = 0.888$ ).

#### Behaviour analysis; contact behaviour

All subjects in the control group and all but one subject in the experimental groups had trials when they did and did not make

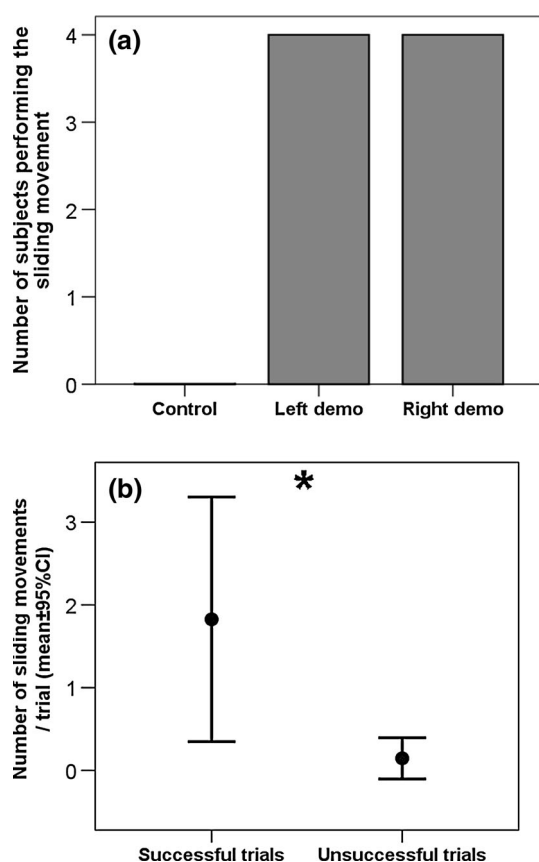
contact with the wire door (the one subject that opened the sliding door in all ten trials naturally touched the wire door in all of these trials). The three groups did not differ in the average number of contacts with the apparatus ( $F_{(2,9)} = 1.651$ ,  $P = 0.245$ ; Fig. 3a). However, in the trials when they did touch the wire door, the experimental subjects tended to make more contact with the wire door in their successful compared to their unsuccessful trials ( $t_{(5)} = 2.119$ ,  $P = 0.088$ ), though this difference was not significant.

The three groups did not differ in how often they made contact with the left/right side of the apparatus ( $F_{(2,9)} = 2.509$ ,  $P = 0.136$ ; Fig. 3b); no systematic side bias was observed in any of the groups (control group:  $0.47 \pm 0.03$ , left demo group:  $0.47 \pm 0.04$ , right demo group:  $0.58 \pm 0.04$ ). This suggests that the bias of experimental subjects to open to the left/right side was not due to a local preference or enhancement effect towards a specific side of the apparatus. Also subjects in the two experimental groups showed no individual difference in side bias between successful and unsuccessful trials (paired samples t-test,  $t_{(5)} = 1.398$ ,  $P = 0.221$ ).

#### Opening behaviour

A key difference between the control and the experimental groups was that, while sliding head movement occurred in the case of all experimental subjects, it was never observed in the control subjects (Fisher exact test,  $P = 0.002$ ; Fig. 4a). As this was the movement that the demonstrator performed in order to open the sliding door, this suggests that experimental subjects copied an action that was not part of their spontaneous behavioural repertoire. Further, more sliding behaviour was observed in the successful compared to the unsuccessful trials of the experimental subjects ( $t_{(6)} = 3.034$ ,  $P = 0.023$ ; Fig. 4b).





**Fig. 4** Door opening behaviour. **a** The number of subjects in the three groups that performed the sliding head movement presented by the demonstrator in the left and right demo groups.  $**P = 0.002$ . **b** The number of sliding head movements in the successful and unsuccessful trials of the experimental subjects in the left and right demo groups pooled together.  $*P = 0.023$

## Discussion

These results reveal the first evidence of imitation in a reptile species and suggest that reptiles can use social information to learn through imitation. This is evidenced by (1) the specific direction in which the bearded dragons opened the wire door (2) the success of the experimental group in comparison with poor performance of the control group and (3) the observation of a novel opening behaviour in the experimental group which was not present in the control group. This finding is not compatible with the frequently repeated claim that only humans, and to some lesser extent great apes, are able to imitate (Byrne 2003). Rather, they indicate the adaptive nature of socially aided learning, which provides a shortcut to finding a solution and avoids the costly process of trial and error learning (Boyd and Richerson 1988). Previous studies have already revealed evidence of social learning in chelonian (Wilkinson et al. 2010b; Davis and Burghardt 2011). However, the present study is the first to investigate the role that imitation may play in social learning in reptiles.

The fact that our subjects were exposed to multiple trials during the experiment does raise the possibility that individual learning may contribute to the performance of the bearded dragons; however, we could not find any association between the performance of subjects and the number of previously administered trials, suggesting that this is unlikely to account for our findings. Further, our results show that the first successful opening occurred to the demonstrated side; this, in combination with presence of the sliding head movement in the experimental but not control subjects, indicates that the mechanism underlying the behaviour of the bearded dragons was imitation. This, of course, does not rule out the possibility that bearded dragons are able to learn by individual learning (and in fact our results indicate a tendency that trial and error learning might also play a role in their performance), but suggests that, in the current setup, the task was learned through observation. A further interesting condition would be to observe animals solve the task without a social demonstration (e.g. by allowing them more time than what our subjects had), and see whether the wire door can be opened by alternative actions, not the sliding head movement that the demonstrator used in the present study. We should also note that control subjects did not see the demonstrator going through the door, while experimental subjects did. It is thus possible that the demonstrator going through the door might have increased the salience of the directional information (door opening) in the experimental groups, although this alone would not explain the copying of the sliding head movement.

In the classic literature, imitation has been defined as the learning of an act by seeing it performed (Thorndike 1898) or, more specifically, as the copying of a novel or otherwise improbable act (Thorpe 1956). In contrast to the simplicity of these definitions, producing experimental evidence to support these ideas has been difficult. Only a few studies have shown that the observer has learned about the response topography, i.e. the specific action by which the response is made (e.g. Custance et al. 1995; Moore 1992; Myowa-Yamakoshi and Matsuzawa 2000). Imitative performance can vary greatly according to the copying fidelity—the degree of matching between the topographies of the demonstrated action and the observer's copy (Huber et al. 2009). Animals have been found to either reproduce the result or effect of a demonstration or by copying the demonstrated actions roughly (e.g. using the same body part) or as copying the action very precisely, matching the movement trajectory. For instance, Voelkl and Huber (2000) showed that marmosets are capable of imitating the overall feature of the opening action, that is, of using the same body part as the model to open a food container. Later they quantitatively assessed the degree of matching between the actions of the model and the observers. Employing detailed motion analyses, they showed that the observers precisely copied the

movement patterns of the novel action demonstrated by the model (Voelkl and Huber 2007). Behavioural analysis of the bearded dragons in this study revealed that the experimental group copied a specific movement pattern of the demonstrator; this was not observed in any control animal. Thus, our findings suggest that the social learning shown by this species is not goal emulation but fulfils the criteria of imitation (Zentall 2006). In summary, the present findings suggest that reptiles exhibit complex cognitive behaviour equivalent to that observed in mammals and birds and suggests that learning by imitation is based on ancient mechanisms.

**Acknowledgments** We thank L. Stepniewska, V. Clarke, J. Murray, M. Gácsi for assistance and Boróka Bereczky for reliability coding. Supported by ESF Programme “The Evolution of Social Cognition”.

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics standard** The experiment reported in this paper complies with the laws of the country in which it was performed (UK).

## References

- Akins CK, Zentall TR (1996) Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *J Comp Psychol* 110:316–320
- Boyd R, Richerson PJ (1988) An evolutionary model of social learning: the effects of spatial and temporal variation. In: Zentall TR, Galef BG Jr (eds) *Social learning: psychological and biological perspectives*, pp 29–48
- Byrne RW (2003) Imitation as behaviour parsing. *Philos Trans R Soc Lond B Biol Sci* 358:529–536
- Byrne RW, Tanner JE (2006) Gestural imitation by a gorilla: evidence and nature of the capacity. *Int J Psychol Psychol Ther* 6:215–231
- Call J (2001) Body imitation in an enculturated orangutan (*Pongo pygmaeus*). *Cybernet Syst* 32:97–119
- Custance D-M, Whiten A, Bard KA (1995) Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes and Hayes (1952) revisited. *Behaviour* 132:837–859
- Davis KM, Burghardt GM (2011) Turtles (*Pseudemys nelsoni*) learn about visual cues indicating food from experienced turtles. *J Comp Psychol* 125:404–410
- Dawson BV, Foss BM (1965) Observational learning in Budgerigars. *Anim Behav* 13:470–474
- Doody JS, Burghardt GM, Dinets V (2012) Breaking the social-non-social dichotomy: a role for reptiles in vertebrate social behavior research? *Ethology* 119:95–103
- Herman LM (2002) Vocal, social, self-imitation by bottle-nosed dolphins. In: Dautenhahn K, Nehaniv CL (eds) *Imitation in animals and artifacts*. MIT Press, Cambridge
- Heyes C, Huber L, Gergely G, Brass M (2009) Evolution, development and intentional control of imitation (special issue). *Philos Trans R Soc Lond B Biol Sci* 364:2291–2443
- Huber L, Range F, Voelkl B, Szucsich A, Viranyi Z, Miklósi A (2009) The evolution of imitation: what do the capacities of nonhuman animals tell us about the mechanisms of imitation? *Philos Trans R Soc Lond B Biol Sci* 364:2299–2309
- Klein ED, Zentall TR (2003) Imitation and affordance learning by pigeons (*Columba livia*). *J Comp Psychol* 117:414–419
- Meltzoff AN (1988) The human infant as homo imitans. In: Zentall TR, Galef BG Jr (eds) *Social learning: psychological and biological perspectives*, pp 319–341
- Miller HC, Rayburn-Reeves R, Zentall TR (2009) Imitation and emulation by dogs using a bidirectional control procedure. *Behav Proc* 80:109–114
- Moore BR (1992) Avian movement imitation and a new form of mimicry: tracing the evolution of a complex form of learning. *Behaviour* 122:231–263
- Müller C, Cant M (2010) Imitation and traditions in wild banded mongooses. *Curr Biol* 20:1171–1175
- Myowa-Yamakoshi M, Matsuzawa T (2000) Imitation of intentional manipulatory actions in chimpanzees (*Pan troglodytes*). *J Comp Psychol* 114:381–391
- Noble DWA, Byrne RW, Whiting MJ (2014) Age-dependent social learning in a lizard. *Biol Lett* 10:20140430
- Pesendorfer MB, Gunhold T, Schiel N, Souto A, Huber L, Range F (2009) The maintenance of traditions in marmosets: individual habit, not social conformity? A field experiment. *PLoS ONE* 4:e4472
- Range F, Viranyi Z, Huber L (2007) Selective imitation in domestic dogs. *Curr Biol* 17:1–5
- Subiaul F, Cantlon JF, Holloway RL, Terrace HS (2004) Cognitive imitation in rhesus macaques. *Science* 305:407–410
- Tchernichovski O (2001) Dynamics of the vocal imitation process: how a zebra finch learns its song. *Science* 291:2564–2569
- Thorndike EL (1898) Animal intelligence: an experimental study of the associative processes in animals. *Psychol Rev Monogr Suppl* 2:79
- Thorpe WH (1956) *Learning and instinct in animals*. Methuen, London
- Tomasello M, Savage-Rumbaugh ES, Kruger AC (1993) Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Dev* 64:1688–1705
- Topál J, Byrne RW, Miklósi Á, Csányi V (2006) Reproducing human actions and action sequences: “Do as I Do!” in a dog. *Anim Cogn* 9:355–367
- Voelkl B, Huber L (2000) True imitation in marmosets. *Anim Behav* 60:195–202
- Voelkl B, Huber L (2007) Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE* 2:e611
- Wilkinson A, Huber L (2012) Cold-blooded cognition: Reptilian cognitive abilities. In: Vonk J, Shackelford TK (eds) *The Oxford Handbook of Comparative Evolutionary Psychology*. Oxford University Press, New Jersey, pp 129–143
- Wilkinson A, Mandl I, Bugnyar T, Huber L (2010a) Gaze following in the red-footed tortoise (*Geochelone carbonaria*). *Anim Cogn* 13:765–769
- Wilkinson A, Kuenstner K, Mueller J, Huber L (2010b) Social learning in a non-social reptile (*Geochelone carbonaria*). *Biol Lett* 6:614–616
- Wood LA, Kendal RL, Flynn EG (2013) Copy me or copy you? The effect of prior experience on social learning. *Cognition* 127:203–213
- Zentall TR (2006) Imitation: definitions, evidence, and mechanisms. *Anim Cogn* 9:335–353