

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

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10 **The ability to learn through imitation is thought to be the basis of cultural transmission**
11 **and was long considered a distinctive characteristic of humans. There is now evidence**
12 **that both mammals and birds are capable of imitation. However nothing is known about**
13 **these abilities in the third amniotic class – reptiles. Here we use a bidirectional control**
14 **procedure to show that a reptile species, the bearded dragon (*Pogona vitticeps*), is**
15 **capable of social learning that cannot be explained by simple mechanisms such as local**
16 **enhancement or goal emulation. Subjects in the experimental group opened a trap door**
17 **to the side that had been demonstrated, while subjects in the ghost control group were**
18 **unsuccessful. This, together with differences in behaviour between experimental and**
19 **control groups, provides compelling evidence that reptiles possess cognitive abilities that**
20 **are comparable to those observed in mammals and birds and suggests that learning by**
21 **imitation is likely to be based on ancient mechanisms.**

22

23 **Key words:** reptile, social cognition, bidirectional control procedure

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25

26 **Introduction**

27 Learning from the observation of others was long thought to be a distinctive characteristic
28 of humans; it was even suggested that a more appropriate name for the human species would
29 be *Homo imitans*, man who imitates (Meltzoff 1988). Imitation is considered to be the
30 pinnacle of social learning and the basis of cultural transmission (Heyes et al. 2009). Imitation
31 is thought to be cognitively complex because the observer not only has to acquire
32 information, but must also draw inferences about the behaviour observed, the constraints of
33 the situation, and the intentions or goals of the model. There is now evidence that non-human
34 species including apes (Tomasello et al. 1993; Call 2001; Byrne and Tanner 2006), monkeys
35 (Subiaul et al. 2004; Voelkl and Huber 2000; 2007), other mammals (Müller & Cant 2010;
36 Topál et al. 2006; Range et al. 2007; Herman 2002) and birds (Klein & Zentall 2003; Moore
37 1992; Tchernichovski 2001; Akins & Zentall 1998) are also capable of imitation. However,
38 we know nothing about these abilities of the third amniotic class – reptiles.

39 Reptiles and mammals evolved from a common amniotic ancestor and investigation of
40 similarities and differences in their behaviour is essential for understanding the evolution of
41 cognition (Doody et al. 2012, Wilkinson and Huber 2012). Recent advances in the field of
42 reptile cognition have found evidence of sophisticated abilities in this group. The red-footed
43 tortoise (*Chelonoidis* – formerly *Geochelone* – *carbonaria*) is capable of gaze following
44 (Wilkinson et al. 2010a) and can learn to solve an otherwise unsolvable task by observing the
45 actions of a conspecific (Wilkinson et al. 2010b). Furthermore, the Florida redbelly turtle
46 (*Pseudemys nelsoni*) is able to learn to approach a visual object cue by observing conspecifics
47 that had learned the task (Davis et al. 2011). Also, young male skinks (*Eulamprus quoyii*)
48 learn a novel instrumental task (displacing a lid) faster in the presence of a demonstrator than
49 without a demonstrator (Noble et al. 2014). Though these findings provide evidence that

50 reptiles can use social information, the mechanisms that control their behaviour remain
51 unclear.

52 The present study used a bidirectional control procedure (developed by Dawson and Foss
53 1965; and later used by many others e.g. Akins & Zentall 1996, Pesendorfer et al. 2009,
54 Wood et al. 2013) to investigate whether bearded dragons (*Pogona vitticeps*) are capable of
55 imitating a conspecific. This task was designed to control for both social influences and
56 emulation/enhancement effects when testing imitation. The paradigm involves comparing the
57 performance of two groups of observers watching demonstrations that differ in their body
58 movements but create identical (or symmetrical) changes in the environment. Imitation occurs
59 when subjects perform the demonstrated action more often than the alternative action, and can
60 be measured either by considering the outcome of the action (Miller et al. 2009) or the details
61 of the specific behaviour performed (e.g. Voelkl and Huber 2007). In the present paper we
62 define successful imitation as a combination of producing the same outcome as the
63 demonstrator and performing the same behaviour.

64

65 **Material and Methods**

66 *Subjects*

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

74 were divided into three groups (N=4 individuals each; 2 males and 2 females in each of the
75 two experimental groups, 1 male and 3 females in the control group).

76 *Experimental arrangement*

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

85 *Demonstrator training*

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

93 *Procedure*

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

99 The subjects received two trials a day separated by a break. Testing took place on five
100 consecutive days resulting in ten experimental trials for each animal. Each trial started with a
101 short (30 sec) habituation phase when the experimenter placed the subjects in the
102 experimental arena and they were allowed to explore freely. This was followed by the
103 demonstration phase, when an 11 second video was presented via a computer monitor (please
104 see supplementary videos S1-3). In the two experimental groups the demonstration showed a
105 conspecific approaching the test apparatus, opening the door rightwards (or leftwards) with a
106 sliding head movement (see later for definition) and going through it. To ensure that the
107 lizards learned about the behaviour of the conspecific and not a simple rule of moving the
108 door towards (or away from) a salient part of the apparatus, the demonstrator was trained to
109 open the door in one direction (right) and the stimulus video was flipped and appeared as a
110 mirror image for presentation of the leftward opening (using the “flip horizontally” filter in
111 the VirtualDub program). In the control group the demonstration showed a conspecific
112 standing in front of the apparatus and the door opening by itself to the right side. None of the
113 videos showed the demonstrator being rewarded.

114 Following the demonstration, the subject was moved to the test area part of the experimental
115 arena and a white plastic board was placed in front of the lizard whilst the test apparatus was
116 placed in the arena (this took approximately 5 seconds). Afterwards the subjects were allowed
117 free access to the test apparatus and their behaviour was recorded for 5 minutes. During this
118 time the monitor used for demonstration remained in the same place, but showed only a blank
119 screen. The trials were terminated and the subjects were returned to their home enclosures if
120 they successfully opened the sliding door to any side and went through it or if the 5 minutes
121 were over. If subjects were not able to get to the mealworm (by opening the sliding door to
122 any side and going through it), they were not rewarded, even if they opened the sliding door.

123 *Behavioural coding and analysis*

124 *Success.* In all trials we coded the side to which subjects opened the door with: +1 for left, -1
125 for right and 0 for no opening. In those rare cases (6 out of 120 trials) when a subject opened
126 the door to both sides in the same trial it received both scores +1 and -1 (=0). Opening was
127 defined as a visible gap at either side of the door. Behavioural coding was blind to
128 experimental condition and the inter-observer reliability (based on double coding of 20 % of
129 the test trials – 2 trials / subject) was high ($\kappa=0.92$). The side of opening on the first successful
130 trial (when the first opening occurred) was compared to 50% chance level using a Binomial
131 test (for this analysis the opening score was converted to 0/1 so that subjects received a score
132 of 1 for opening to the demonstrated side and a score of 0 for opening to the non-
133 demonstrated side; data of the two experimental groups were pooled together). Opening score
134 (reflecting the sum of all ten trials) was compared to the chance level of 0 using a Wilcoxon
135 Test (for this analysis the opening score was converted to 0/1 and subjects received a score of
136 1 for opening to the demonstrated side and a score of 0 for opening to the non-demonstrated
137 side or not opening; data of the two experimental groups were pooled together). The three
138 groups were compared by Kruskal-Wallis test (followed by pair wise Mann-Whitney post-
139 hoc tests) using the sum of the -1, 0, +1 opening scores. The correlation between the number
140 of successful experimental subjects in a given trial and the number of previous trials
141 administered was assessed in order to check for the effect of repeated exposure to the task
142 (Kendall's tau). To investigate the impact of learning within a day, the number of successful
143 experimental subjects was compared within a daily session between the first (trials 1, 3, 5, 7,
144 9) and second (trials 2, 4, 6, 8, 10) trials administered on that day (Wilcoxon test).

145 *Behaviour Analysis.* The subjects' behaviour was coded during the test phase.

146 *Contact Behaviour.* The number of times a subject made contact with the wire door in
147 each trial was compared across the three groups (ANOVA). The position of the subjects when
148 making contact with the wire door, that is, the side of the wire door the subjects touched, was

149 also recorded, and we compared the proportion of contacts made to the left or right side
150 across the three groups (ANOVA). For the experimental subjects, we also compared the
151 number of contacts with the wire door for the successful and unsuccessful trials using a paired
152 samples t-test. This was only done in the case of the trials when the subjects made contact
153 with the wire door and thus had a chance to open it.

154 *Opening Behaviour.* The occurrence of a specific sliding head movement behaviour
155 which the demonstrator used to open the wire door (a fast (< 1 sec), horizontal head
156 movement of at least 1 cm) – was recorded for all three groups. For the experimental subjects
157 we compared the number of sliding head movements in the successful and unsuccessful trials
158 using a paired samples t-test. Behavioural coding was blind to experimental condition and the
159 inter-observer reliability (based on double coding of 20 % of the test trials – 2 trials / subject)
160 was high for all variables (contact with the wire door: $\kappa=0.83$; contact at left/right side of the
161 wire door: $\kappa=1.00$; sliding head movement: $\kappa=0.91$); in case of disagreement the assessment
162 of the first coder (AK) was used.

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

165

166 **Results**

167 *Success.* All experimental subjects successfully opened the sliding door whereas none of the
168 control subjects did. Furthermore, on their first successful trial all 8 experimental subjects
169 opened the door to the side that they had observed the demonstrator opening (Binomial test,
170 $P=0.008$). This side preference was consistent across the entire experiment (67-100%) with a
171 significant bias towards the demonstrated side (Wilcoxon Test, $T+=37$, $P=0.007$). The three
172 groups also differed from each other in the side of opening (Kruskall-Wallis Test, $\chi^2=10.277$,
173 $P=0.006$; Figure 2).

174 However, considerable individual variation was observed (Table 1.). Of the 8 experimental
175 animals the number of successful openings varied from 2/10 to 10/10 and the first successful
176 opening varied from trial 1 to trial 5.

177 The number of successful experimental subjects in a given trial was not related to the
178 number of previous trials administered ($r=-0.025$, $P=0.926$). There was no difference in the
179 number of successful experimental subject in the first and second trial of a daily session
180 ($Z=0.141$, $P=0.888$).

181 *Behaviour Analysis; Contact Behaviour.* All subjects in the control group and all but one
182 subject in the experimental groups had trials when they did and did not make contact with the
183 wire door (the one subject that opened the sliding door in all ten trials, naturally touched the
184 wire door in all of these trials). The three groups did not differ in the average number of
185 contacts with the apparatus ($F_{(2,9)}=1.651$, $P=0.245$; Figure 3a). However, in the trials when
186 they did touch the wire door, the experimental subjects tended to make more contact with the
187 wire door in their successful compared to their unsuccessful trials ($t_{(5)}=2.119$, $P=0.088$),
188 though this difference was not significant.

189 The three groups did not differ in how often they made contact with the left/right side of the
190 apparatus ($F_{(2,9)}=2.509$, $P=0.136$; Figure 3b); no systematic side bias was observed in any of
191 the groups (control group: 0.47 ± 0.03 , left demo group: 0.47 ± 0.04 , right demo group:
192 0.58 ± 0.04). This suggests that the bias of experimental subjects to open to the left/right side
193 was not due to a local preference or enhancement effect towards a specific side of the
194 apparatus. However, if we repeat this comparison using successful trials only in case of the
195 experimental group than we do find an effect ($F_{(2,9)}=7.453$, $P=0.012$), with the right demo
196 group showing a stronger preference to the left side compared to the left demo group (Tukey
197 post hoc test $P=0.012$), but neither of the experimental groups showing a significantly
198 different side bias compared to the unsuccessful control group (left demo: $P=0.615$, right

199 demo: $P=0.053$). Also subjects in the two experimental groups showed no individual
200 difference in side bias between successful and unsuccessful trials (paired samples t-test,
201 $t_{(5)}=1.398$, $P=0.221$).

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

209

210 **Discussion**

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

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

242 In the classic literature, imitation has been defined as the learning of an act by seeing it
243 performed (Thorndike 1898) or, more specifically, as the copying of a novel or otherwise
244 improbable act (Thorpe 1956). In contrast to the simplicity of these definitions, producing
245 experimental evidence to support these ideas has been difficult. Only a few studies have
246 shown that the observer has learned about the response topography, i.e., the specific action by
247 which the response is made (e.g. Custance et al. 1995; Moore 1992; Myowa-Yamakoshi &

248 Matsuzawa 2000). Imitative performance can vary greatly according to the copying fidelity—
249 the degree of matching between the topographies of the demonstrated action and the
250 observer’s copy (Huber et al. 2009). Animals have been found to either reproduce the result
251 or effect of a demonstration or by copying the demonstrated actions roughly (e.g. using the
252 same body part) or as copying the action very precisely, matching the movement trajectory.
253 For instance, Voelkl and Huber (2000) showed that marmosets are capable of imitating the
254 overall feature of the opening action, that is, of using the same body part as the model to open
255 a food container. Later they quantitatively assessed the degree of matching between the
256 actions of the model and the observers. Employing detailed motion analyses they showed that
257 the observers precisely copied the movement patterns of the novel action demonstrated by the
258 model (Voelkl & Huber 2007). Behavioural analysis of the bearded dragons in this study
259 revealed that the experimental group copied a specific movement pattern of the demonstrator;
260 this was not observed in any control animal. Thus, our findings suggest that the social
261 learning shown by this species is not goal emulation but fulfils the criteria of imitation
262 (Zentall 2006). In summary, the present findings suggest that reptiles exhibit complex
263 cognitive behaviour equivalent to that observed in mammals and birds and suggests that
264 learning by imitation is based on ancient mechanisms.

265

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270

271 **Ethics statement**

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

274 **Conflict of interest**

275 The authors declare that they have no conflict of interest.

276

277

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353

354 **Figure legend**

355 *Figure 1.* Test setup.

356 a) The experimental arena was divided into two parts by the apparatus. The subject was
357 located in the test arena where it had access to the wire door, through which it could see the
358 mealworm. The demonstration arena contained the computer screen used for projecting the
359 video demonstration and a Petri dish with the mealworm.

360 b) Frame-grabs from the demonstration videos showing a conspecific opening the wire door
361 to the right or the left or a passive conspecific while the door opened by itself

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

366 *Figure 3.* Contact behaviour

367 a) The number of contacts subjects made with the apparatus during the ten trials in the
368 control, left demo and right demo groups. ns.: $P=0.245$

369 b) The proportion of making contact with the left/right side of the apparatus during the ten
 370 trials in the control, left demo and right demo groups. ns.: $P=0.136$

371 *Figure 4. Door opening behaviour*

372 a) The number of subjects in the three groups that performed the sliding head movement
 373 presented by the demonstrator in the left and right demo groups. **: $P=0.002$

374 b) The number of sliding head movements in the successful and unsuccessful trials of the
 375 experimental subjects in the left and right demo groups pooled together. *: $P=0.023$

376

377 *Table 1. Individual data on subjects' performance in the two experimental groups. Control*
 378 *subjects performed no door openings in any of the ten trials and are thus not included in the*
 379 *table.*

380 Gender of the subjects: f – female, m – male; Housing: U – university-, P – privately-owned;
 381 Group: R – right demonstration, L – left demonstration. The side of opening during the ten
 382 trials is indicated with R/L for right/left. In case of the trials when subjects opened the wire
 383 door to both sides, the two openings are presented in the order in which they occurred. The
 384 first successful opening is marked with bold. Gray background indicates that the subject in the
 385 given trial not only opened the door, but also went through it.

386 **Table 1.**

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

387