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

24

25

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 & Cant 2010; Topál et al. 2006; Range et al. 2007; Herman 2002) and birds (Klein & Zentall 2003; Moore 1992; Tchernichovski 2001; Akins & Zentall 1998) 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 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 et al. 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

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).

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.

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.

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.

4

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 (κ=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 Kruskall-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

6

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: κ=0.83; contact at left/right side of the

161 wire door: κ=1.00; sliding head movement: κ=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, χ^2=10.277,

173 *P*=0.006; Figure 2).

However, considerable individual variation was observed (Table 1.). Of the 8 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 subject 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; Figure 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; Figure 3b); no systematic side bias was observed in any of the groups (control group: 0.47±0.03, left demo group: 0.47±0.04, right demo group: 0.58±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. However, if we repeat this comparison using successful trials only in case of the experimental group than we do find an effect ($F_{(2,9)}$=7.453, P=0.012), with the right demo group showing a stronger preference to the left side compared to the left demo group (Tukey post hoc test P=0.012), but neither of the experimental groups showing a significantly 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.

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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.

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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