

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

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6 **Abstract** The ability to learn through imitation is thought
7 to be the basis of cultural transmission and was long con-
8 sidered a distinctive characteristic of humans. There is now
9 evidence that both mammals and birds are capable of
10 imitation. However, nothing is known about these abilities
11 in the third amniotic class—reptiles. Here, we use a bidi-
12 rectional control procedure to show that a reptile species,
13 the bearded dragon (*Pogona vitticeps*), is capable of social
14 learning that cannot be explained by simple mechanisms
15 such as local enhancement or goal emulation. Subjects in
16 the experimental group opened a trap door to the side that
17 had been demonstrated, while subjects in the ghost control
18 group, who observed the door move without the interven-
19 tion of a conspecific, were unsuccessful. This, together
20 with differences in behaviour between experimental and
21 control groups, provides compelling evidence that reptiles

possess cognitive abilities that are comparable to those 22
observed in mammals and birds and suggests that learning 23
by imitation is likely to be based on ancient mechanisms. 24

Keywords Reptile · Social cognition · Bidirectional 26
control procedure 27

Introduction 28

Learning from the observation of others was long thought 29
to be a distinctive characteristic of humans; it was even 30
suggested that a more appropriate name for the human 31
species would be *Homo imitans*, man who imitates 32
(Meltzoff 1988). Imitation is considered to be the pinnacle 33
of social learning and the basis of cultural transmission 34
(Heyes et al. 2009). Imitation is thought to be cognitively 35
complex because the observer not only has to acquire 36
information, but must also draw inferences about the 37
behaviour observed, the constraints of the situation, and the 38
intentions or goals of the model. There is now evidence 39
that non-human species including apes (Tomasello et al. 40
1993; Call 2001; Byrne and Tanner 2006), monkeys 41
(Subiaul et al. 2004; Voelkl and Huber 2000, 2007), other 42
mammals (Müller and Cant 2010; Topál et al. 2006; Range 43
et al. 2007; Herman 2002), and birds (Klein and Zentall 44
2003; Moore 1992; Tchernichovski 2001; Akins and Zen- 45
tall 1996) are also capable of imitation. However, we know 46
nothing about these abilities of the third amniotic class— 47
reptiles. 48

Reptiles and mammals evolved from a common amni- 49
otic ancestor, and investigation of similarities and differ- 50
ences in their behaviour is essential for understanding the 51
evolution of cognition (Doody et al. 2012, Wilkinson and 52
Huber 2012). Recent advances in the field of reptile 53

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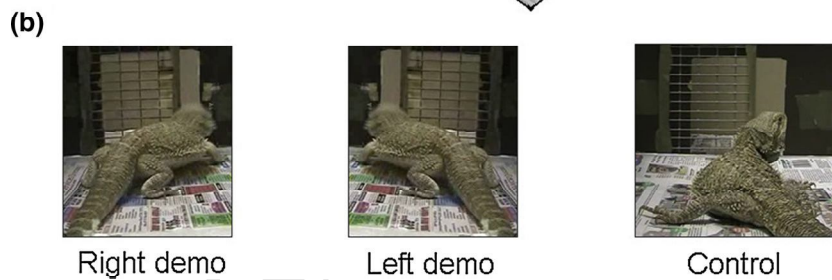
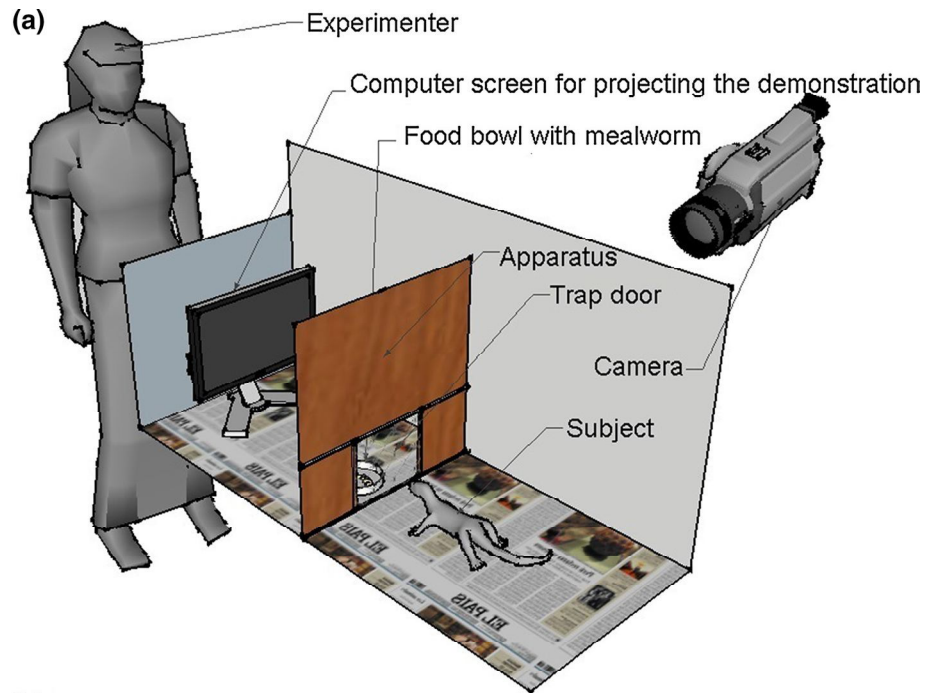
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54	cognition have found evidence of sophisticated abilities in	experimental groups; 1 male and 3 females in the control	103
55	this group. The red-footed tortoise (<i>Chelonoidis</i> —formerly	group).	104
56	<i>Geochelone</i> — <i>carbonaria</i>) is capable of gaze following		
57	(Wilkinson et al. 2010a) and can learn to solve an other-	Experimental arrangement	105
58	wise unsolvable task by observing the actions of a con-		
59	specific (Wilkinson et al. 2010b). Furthermore, the Florida	Testing was carried out in an experimental arena	106
60	redbelly turtle (<i>Pseudemys nelsoni</i>) is able to learn to	(100 cm × 40 cm × 50 cm) that was divided by the test	107
61	approach a visual object cue by observing conspecifics that	apparatus into two equal parts: the test area (where the	108
62	had learned the task (Davis and Burghardt 2011). Also,	subjects were located) and the demonstration area (where	109
63	young male skinks (<i>Eulamprus quoyii</i>) learn a novel	the computer screen was positioned; Fig. 1.). The test	110
64	instrumental task (displacing a lid) faster in the presence of	apparatus itself was a 40 cm × 40 cm wooden board with	111
65	a demonstrator than without a demonstrator (Noble et al.	a 12 cm × 12 cm hole. This was covered by a wire door	112
66	2014). Though these findings provide evidence that reptiles	which could be moved along sliding rails in front of the	113
67	can use social information, the mechanisms that control	wooden board in either a leftward or a rightward direction.	114
68	their behaviour remain unclear.	The door could be moved by using either the head or the	115
69	The present study used a bidirectional control procedure	foot, making contact at any point and then sliding the door	116
70	(developed by Dawson and Foss 1965; and later used by	horizontally to either the left or the right side.	117
71	many others e.g. Akins and Zentall 1996; Pesendorfer et al.		
72	2009; Wood et al. 2013) to investigate whether bearded	Demonstrator training	118
73	dragons (<i>Pogona vitticeps</i>) are capable of imitating a		
74	conspecific. This task was designed to control for both	The demonstrator lizard was trained to open the wire door	119
75	social influences and emulation/enhancement effects when	using both shaping and also relying on trial and error	120
76	testing imitation. The paradigm involves comparing the	learning during a 3-week-long period. After habituation to	121
77	performance of two groups of observers watching demon-	the experimental arena, meaning when the lizard readily	122
78	strations that differ in their body movements but create	explored and ate mealworms placed in a Petri dish, we	123
79	identical (or symmetrical) changes in the environment.	introduced the test apparatus. First the lizard had to go	124
80	Imitation occurs when subjects perform the demonstrated	through the hole on the wooden board with the wire door	125
81	action more often than the alternative action, and can be	completely open in order to get the mealworm placed on	126
82	measured either by considering the outcome of the action	the other side, then we gradually closed the door. The	127
83	(Miller et al. 2009) or the details of the specific behaviour	lizard had prolonged access (up to 60 min/session) to the	128
84	performed (e.g. Voelkl and Huber 2007). In the present	apparatus during several days until it could solve each step.	129
85	paper, we define successful imitation as a combination of		
86	producing the same outcome as the demonstrator and	Procedure	130
87	performing the same behaviour.		
88	Materials and methods		
89	Subjects		
90	The bearded dragons either belonged to the Small Animal	All subjects were habituated to the experimental arena	131
91	Unit at the University of Lincoln ($N = 7$) or were privately	before the onset of the experiment. They were considered	132
92	owned ($N = 6$) but were kept at the university throughout	habituated when they readily explored and ate mealworms	133
93	the study. Our subjects were 5 males and 7 females (age	placed in a Petri dish (used later as a reward in the test	134
94	range of 1–3 years), and a 3-year-old female was chosen as	trials) in the experimental arena. During this time, they	135
95	the demonstrator in order to avoid the possibility of male	were not exposed to the apparatus used in the test as	136
96	subjects responding aggressively to the video demonstra-	habituation was carried out in the empty arena (without the	137
97	tion. (Females are often housed together and generally	wooden wall) with a Petri dish placed at varying locations.	138
98	show no aggression towards each other.) None of the ani-	The subjects received two trials a day separated by a	139
99	mals had previously taken part in cognition experiments.	break. Testing took place on five consecutive days resulting	140
100	All animals were handled by humans on a daily basis. The	in ten experimental trials for each animal. Each trial started	141
101	12 subjects were divided into three groups ($N = 4$ indi-	with a short (30 s) habituation phase when the experi-	142
102	viduals each; 2 males and 2 females in each of the two	menter placed the subjects in the experimental arena and	143
		they were allowed to explore freely. This was followed by	144
		the demonstration phase, when an 11-s video was presented	145
		via a computer monitor (please see supplementary videos	146
		S1-3). In the two experimental groups, the demonstration	147
		showed a conspecific approaching the test apparatus,	148
		opening the door rightwards (or leftwards) with a sliding	149

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



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

162 Following the demonstration, the subject was moved to
 163 the test area part of the experimental arena and a white
 164 plastic board was placed in front of the lizard while the test
 165 apparatus was placed in the arena (this took approximately
 166 5 s). Afterwards, the subjects were allowed free access to
 167 the test apparatus, and their behaviour was recorded for
 168 5 min. During this time, the monitor used for demonstra-
 169 tion remained in the same place, but showed only a blank
 170 screen. The trials were terminated and the subjects were
 171 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

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191 subjects received a score of 1 for opening to the demon-
 192 strated side and a score of 0 for opening to the non-demon-
 193 strated side; data of the two experimental groups were
 194 pooled together). Opening score (reflecting the sum of all
 195 ten trials) was compared to the chance level of 0 using a
 196 Wilcoxon Test (for this analysis, the opening score was
 197 converted to 0/1 and subjects received a score of 1 for
 198 opening to the demonstrated side and a score of 0 for
 199 opening to the non-demonstrated side or not opening; data
 200 of the two experimental groups were pooled together). The
 201 three groups were compared by Kruskal–Wallis test (fol-
 202 lowed by pair wise Mann–Whitney post hoc tests) using
 203 the sum of the $-1, 0, +1$ opening scores. The correlation
 204 between the number of successful experimental subjects in
 205 a given trial and the number of previous trials administered
 206 was assessed in order to check for the effect of repeated
 207 exposure to the task (Kendall's tau). To investigate the
 208 impact of learning within a day, the number of successful
 209 experimental subjects was compared within a daily session
 210 between the first (trials 1, 3, 5, 7, 9) and second (trials 2, 4,
 211 6, 8, 10) trials administered on that day (Wilcoxon test).

212 Behaviour analysis

213 The subjects' behaviour was coded during the test phase

214 Contact behaviour

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

227 Opening behaviour

228 The occurrence of a specific sliding head movement
 229 behaviour which the demonstrator used to open the wire
 230 door (a fast (<1 s), horizontal head movement of at least
 231 1 cm) was recorded for all three groups. For the experi-
 232 mental subjects, we compared the number of sliding head
 233 movements in the successful and unsuccessful trials using a
 234 paired samples *t* test. Behavioural coding was blind to
 235 experimental condition, and the inter-observer reliability
 236 (based on double coding of 20 % of the test trials—2 trials/
 237 subject) was high for all variables (contact with the wire

238 door: $\kappa = 0.83$; contact at left/right side of the wire door: 238
 239 $\kappa = 1.00$; sliding head movement: $\kappa = 0.91$); in case of 239
 240 disagreement, the assessment of the first coder (AK) was 240
 241 used. 241

242 Please see supplementary videos 4 (S4 experimental 242
 243 group—right) and 5 (S5 control group) as examples of the 243
 244 responses to the different conditions. 244

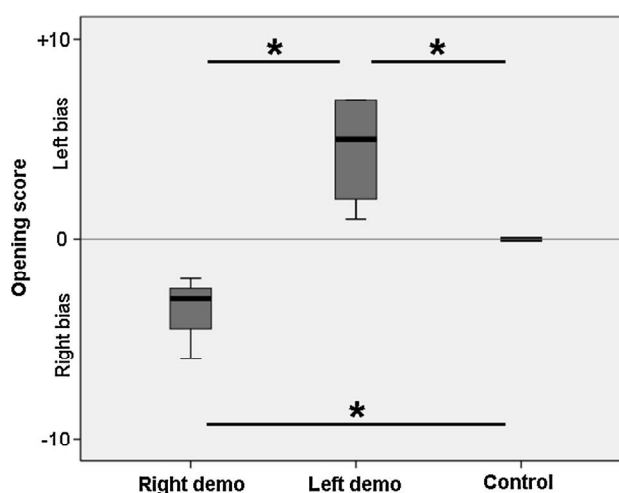
245 Results

246 Success

247 All experimental subjects successfully opened the sliding 247
 248 door, whereas none of the control subjects did. Furthermore, 248
 249 on their first successful trial, all 8 experimental subjects 249
 250 opened the door to the side that they had observed the 250
 251 demonstrator opening (Binomial test, $P = 0.008$). This side 251
 252 preference was consistent across the entire experiment 252
 253 (67–100 %) with a significant bias towards the demonstrated 253
 254 side (Wilcoxon Test, $T+ = 37$, $P = 0.007$). The three 254
 255 groups also differed from each other in the side of opening 255
 256 (Kruskal–Wallis Test, $\chi^2 = 10.277$, $P = 0.006$; Fig. 2). 256

257 However, considerable individual variation was 257
 258 observed (Table 1.). Of the eight experimental animals, the 258
 259 number of successful openings varied from 2/10 to 10/10, 259
 260 and the first successful opening varied from trial 1 to trial 260
 261 5. 261

262 The number of successful experimental subjects in a 262
 263 given trial was not related to the number of previous trials 263
 264 administered ($r = -0.025$, $P = 0.926$). There was no 264
 265 difference in the number of successful experimental 265



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

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	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	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	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

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. Italic indicates that the subject in the given trial not only opened the door, but also went through it

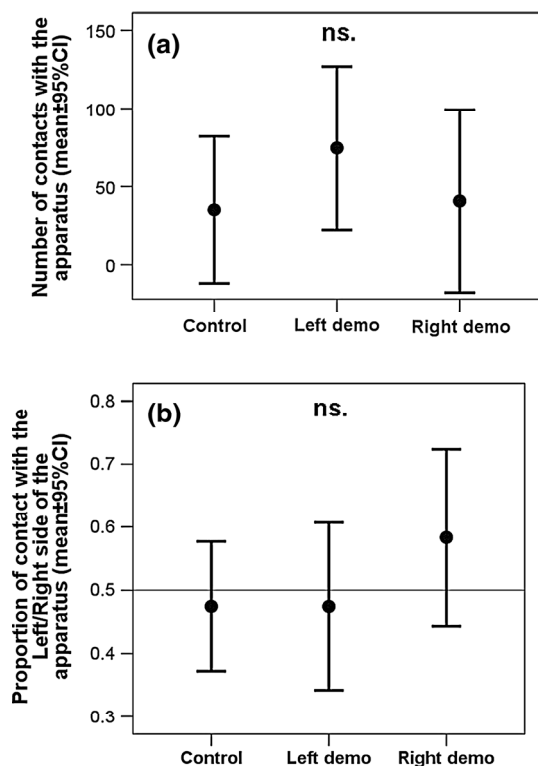


Fig. 3 Contact behaviour. **a** The number of contacts subjects made with the apparatus during the ten trials in the control, left demo and right demo groups. ns.: $P = 0.245$. **b** The proportion of making contact with the left/right side of the apparatus during the ten trials in the control, left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

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

268 Behaviour analysis; contact behaviour

269 All subjects in the control group and all but one subject in
270 the experimental groups had trials when they did and did

not make contact with the wire door (the one subject that 271
opened the sliding door in all ten trials naturally touched 272
the wire door in all of these trials). The three groups did not 273
differ in the average number of contacts with the apparatus 274
($F_{(2,9)} = 1.651$, $P = 0.245$; Fig. 3a). However, in the trials 275
when they did touch the wire door, the experimental sub- 276
jects tended to make more contact with the wire door in 277
their successful compared to their unsuccessful trials 278
($t_{(5)} = 2.119$, $P = 0.088$), though this difference was not 279
significant. 280

The three groups did not differ in how often they made 281
contact with the left/right side of the apparatus 282
($F_{(2,9)} = 2.509$, $P = 0.136$; Fig. 3b); no systematic side 283
bias was observed in any of the groups (control group: 284
 0.47 ± 0.03 , left demo group: 0.47 ± 0.04 , right demo 285
group: 0.58 ± 0.04). This suggests that the bias of exper- 286
imental subjects to open to the left/right side was not due to 287
a local preference or enhancement effect towards a specific 288
side of the apparatus. Also subjects in the two experimental 289
groups showed no individual difference in side bias 290
between successful and unsuccessful trials (paired samples 291
t-test, $t_{(5)} = 1.398$, $P = 0.221$). 292

Opening behaviour 293

A key difference between the control and the experimental 294
groups was that, while sliding head movement occurred in 295
the case of all experimental subjects, it was never observed 296
in the control subjects (Fisher exact test, $P = 0.002$; 297
Fig. 4a). As this was the movement that the demonstrator 298
performed in order to open the sliding door, this suggests 299
that experimental subjects copied an action that was not 300
part of their spontaneous behavioural repertoire. Further, 301
more sliding behaviour was observed in the successful 302
compared to the unsuccessful trials of the experimental 303
subjects ($t_{(6)} = 3.034$, $P = 0.023$; Fig. 4b). 304

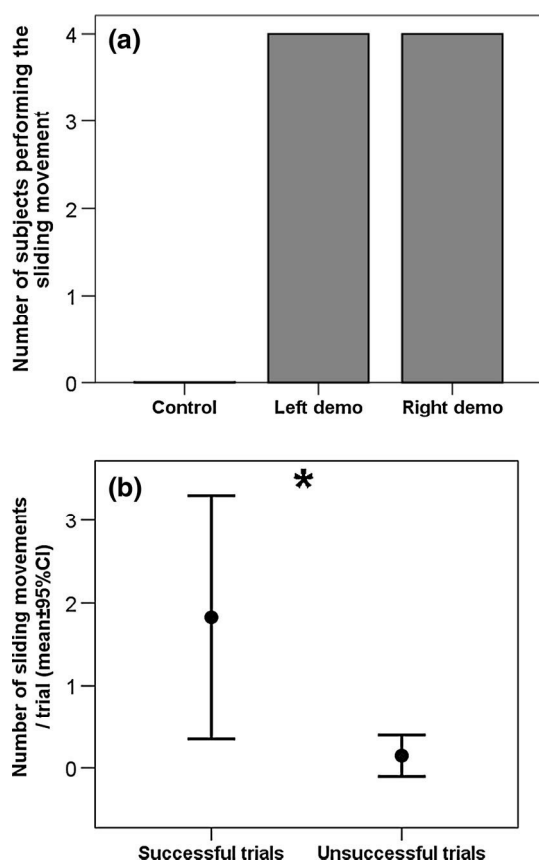


Fig. 4 Door opening behaviour. **a** The number of subjects in the three groups that performed the sliding head movement presented by the demonstrator in the left and right demo groups. $**P = 0.002$. **b** The number of sliding head movements in the successful and unsuccessful trials of the experimental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

305 Discussion

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

The fact that our subjects were exposed to multiple trials 324
 during the experiment does raise the possibility that indi- 325
 vidual learning may contribute to the performance of the 326
 bearded dragons; however, we could not find any association 327
 between the performance of subjects and the number of 328
 previously administered trials, suggesting that this is unli- 329
 kely to account for our findings. Further, our results show 330
 that the first successful opening occurred to the demonstrator 331
 side; this, in combination with presence of the sliding head 332
 movement in the experimental but not control subjects, 333
 indicates that the mechanism underlying the behaviour of 334
 the bearded dragons was imitation. This, of course, does not 335
 rule out the possibility that bearded dragons are able to learn 336
 by individual learning (and in fact our results indicate a 337
 tendency that trial and error learning might also play a role 338
 in their performance), but suggests that, in the current setup, 339
 the task was learned through observation. A further inter- 340
 esting condition would be to observe animals solve the task 341
 without a social demonstration (e.g. by allowing them more 342
 time than what our subjects had), and see whether the wire 343
 door can be opened by alternative actions, not the sliding 344
 head movement that the demonstrator used in the present 345
 study. We should also note that control subjects did not see 346
 the demonstrator going through the door, while experi- 347
 mental subjects did. It is thus possible that the demonstrator 348
 going through the door might have increased the salience of 349
 the directional information (door opening) in the experi- 350
 mental groups, although this alone would not explain the 351
 copying of the sliding head movement. 352

In the classic literature, imitation has been defined as the 353
 learning of an act by seeing it performed (Thorndike 1898) 354
 or, more specifically, as the copying of a novel or otherwise 355
 improbable act (Thorpe 1956). In contrast to the simplicity of 356
 these definitions, producing experimental evidence to sup- 357
 port these ideas has been difficult. Only a few studies have 358
 shown that the observer has learned about the response 359
 topography, i.e. the specific action by which the response 360
 is made (e.g. Custance et al. 1995; Moore 1992; Myowa- 361
 Yamakoshi and Matsuzawa 2000). Imitative performance 362
 can vary greatly according to the copying fidelity—the 363
 degree of matching between the topographies of the dem- 364
 onstrated action and the observer's copy (Huber et al. 2009). 365
 Animals have been found to either reproduce the result or 366
 effect of a demonstration or by copying the demonstrated 367
 actions roughly (e.g. using the same body part) or as copying 368
 the action very precisely, matching the movement trajectory. 369
 For instance, Voelkl and Huber (2000) showed that mar- 370
 mosets are capable of imitating the overall feature of the 371
 opening action, that is, of using the same body part as the 372
 model to open a food container. Later they quantitatively 373
 assessed the degree of matching between the actions of the 374
 model and the observers. Employing detailed motion anal- 375
 yses, they showed that the observers precisely copied the 376

377 movement patterns of the novel action demonstrated by the
378 model (Voelkl and Huber 2007). Behavioural analysis of the
379 bearded dragons in this study revealed that the experimental
380 group copied a specific movement pattern of the demon-
381 strator; this was not observed in any control animal. Thus,
382 our findings suggest that the social learning shown by this
383 species is not goal emulation but fulfils the criteria of imi-
384 tation (Zentall 2006). In summary, the present findings
385 suggest that reptiles exhibit complex cognitive behaviour
386 equivalent to that observed in mammals and birds and sug-
387 gests that learning by imitation is based on ancient
388 mechanisms.

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

394 **Ethics standard** The experiment reported in this paper complies
395 with the laws of the country in which it was performed (UK).
396

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