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1 Visual conspecific cues will not help in pygmy bluetongue lizard translocations

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28 **1. Abstract**

29 Where a translocation program is used to reinforce an existing population of an endangered species,  
30 the response of the introduced individuals to cues from conspecific residents will have an important  
31 impact on the success of the translocation. If those cues induce the translocated individuals to stay at  
32 the release site the translocation is more likely to succeed than if the cues cause individuals to move  
33 away. We used conspecific models of the endangered Australian pygmy bluetongue lizard to identify  
34 behavioural parameters relevant to translocation success, that change when the visual conspecific cues  
35 are presented. Pygmy bluetongue lizards typically remain in or at the entrance of their refuge burrows.  
36 In the presence of conspecific models, introduced lizards significantly increased, and nearly doubled,  
37 the number of movements out of their burrows (mean (SE) number of movements with models = 0.44  
38 (0.03); without models = 0.25 (0.03);  $P = 0.012$ ) and more than doubled the number of movements  
39 away from the release area (mean (SE) number of movements with models = 0.28 (0.03); without  
40 models = 0.08 (0.02);  $P = 0.003$ ), suggesting they would be less likely to remain within a resident  
41 population where they were released. We found that, by the end of the first day of experimental trials  
42 11 of 16 lizards in treatments with models present had occupied burrows that did not have a model  
43 nearby, and that number increased to 14 of 16 lizards by the fourth day. The results suggest that cues  
44 from conspecifics will not encourage translocated lizards to stay at a release site.

45 **Key words:** Conspecific models, Behaviour, Lizards, Dispersal

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47 **2. Introduction**

48 A range of behavioural responses to conspecific individuals, particularly responses associated with  
49 agonistic or mating behaviours, are mediated by unique cues, and models that contain features of  
50 those cues can be used to manipulate animal behaviour in practical ways (Craven, 1984), including  
51 their use in conservation related translocations.

52 For many endangered species, one potential management strategy is conservation translocation, the  
53 intentional movement and release of individuals primarily for conservation benefit (IUCN, 2013).

54 Two important problems in any translocation attempt are the initial stress on release, and the tendency

55 to disperse from unfamiliar habitat (Mihoub et al., 2009). Examples of post-release movement in  
56 release habitats include translocated birds (Kemink and Kesler, 2013) and snakes (Reinert and Rupert,  
57 1999). The novel location and resource competition from conspecific residents may increase the stress  
58 level of translocated animals (Letty et al., 2000; Teixeira et al., 2007; Drake et al., 2012), but stress  
59 may be reduced if individuals recognise conspecific cues that allow them to rapidly identify refuge  
60 shelters or feeding locations (Lorenzo and Lazzari, 1996; Göth and Evans, 2004; Gautier et al., 2006;  
61 Kullmann et al., 2008). In those cases the provision of conspecific cues may reduce both stress and  
62 the tendency to disperse. For instance Ahlering et al. (2010) reported that, in 20 of 24 reviewed  
63 studies, songbirds were encouraged to settle in habitat where conspecific songs were played. Alberts  
64 (2007) suggested that captive reared individuals of the endangered Caribbean rock iguana, when  
65 released back into the wild, may be more likely to preferentially settle where there are familiar cues  
66 such as known conspecifics or their odours. On the other hand, in species that are aggressively  
67 territorial, the use of conspecific cues may have the opposite effect, and increase stress. The potential  
68 to use conspecific cues to promote translocation success needs to be examined carefully on a species  
69 by species basis.

70 The endangered pygmy bluetongue lizard (*T. adelaidensis*) is now restricted to a few isolated  
71 fragments of its native grassland habitat in the mid-north region of the state of South Australia,  
72 Australia. Its current distribution is a small part of its previous range, most of which has been taken  
73 over by cereal cropping and grazing farmland. Its endangered status has resulted from the now  
74 restricted geographical range, and from the isolated nature of the few remaining small populations.  
75 Models that explore likely future climate change scenarios within the range of this lizard, show that  
76 reinforcement or reintroduction translocation will be a certain requirement for the future preservation  
77 of this species (Fordham et al., 2012). If we adopt that strategy, we need to know how best to prevent  
78 translocated lizards from dispersing away from release sites. Can we use cues from conspecifics, to  
79 encourage them to preferentially settle close to where they are released?

80 The pygmy bluetongue lizard is normally solitary and lizards spend most of their time associated with  
81 single entrance burrows constructed by lycosid and mygalomorph spiders (Hutchinson et al., 1994;

82 Fenner and Bull, 2011b). Individuals usually occupy a single burrow for extended periods of time and  
83 most suitable burrows are taken by lizards (Hutchinson et al., 1994; Milne et al., 2003; Souter et al.,  
84 2004; Fellows et al., 2009). This suggests there is competition between lizards for limited high quality  
85 burrows, and although occupied burrows can be as close as 1 m apart (Fenner and Bull, 2009) lizards  
86 actively defend a very small area with a radius of less than 15 cm around their burrow entrance from  
87 approaching conspecifics (and from conspecific models) (Fenner and Bull, 2011a). This would  
88 suggest that conspecific cues might increase stress in newly introduced lizards. On the other hand,  
89 when in a novel environment, lizards recognise conspecific olfactory signals and prefer to choose  
90 unoccupied burrows that have previously held a conspecific (Fenner and Bull, 2011b); that is they  
91 select refuges where other lizards have been. In that case, conspecific cues that are not directly  
92 challenging might help lizards adjust to a novel environment. In the current study we asked whether  
93 the provision of conspecific models near some, but not all burrows in a novel habitat, might reduce or  
94 increase movements and dispersal among newly introduced pygmy bluetongue lizards.

### 95 **3. Methods**

#### 96 *3.1 Experimental trials*

97 We used eight male (average snout-to-vent length (SVL)  $85.1 \pm 0.2$  mm) and eight female (average  
98 SVL  $89.2 \pm 0.2$  mm) pygmy bluetongue lizards that had been captured from two natural populations  
99 near Burra, South Australia ( $33^{\circ}42'S$ ;  $138^{\circ}56'E$ ). These lizards had been used in several other short  
100 behavioural experiments during the austral spring and summer of 2009/10 and 2010/11 (Ebrahimi and  
101 Bull, 2012; 2013a; b; c), and so had briefly experienced the experimental habitat of the current  
102 experiment (total of 60 days in the cages over a two year period). Before the current experiment the  
103 lizards were held in individual cages (52.5 x 38 x 31cm) in ambient conditions and fed every day with  
104 crickets and mealworms.

105 The experimental cages have been described previously (Ebrahimi and Bull, 2013b) as four, 15 m  
106 diameter cages at Monarto Zoo, 70 km SE of Adelaide, South Australia ( $35^{\circ}06'S$ ;  $139^{\circ}09'E$ ). Each  
107 cage had a 1 m high galvanized wall and a bird-proof wire roof. Each cage was divided into three  
108 areas; a 2 m radius central area where lizards were released, which was lightly vegetated with annual

109 grass cut to ground level before the experiment started, and where burrows were provided, a 5 m wide  
110 ring of marginal habitat, similarly vegetated but with no burrows, and a 0.5 m wide perimeter area  
111 around the inside cage wall, again similarly vegetated but with burrows. We considered the no-burrow  
112 habitat marginal because we assumed that lizards would perceive they were exposed and at risk where  
113 there were no burrows. We placed 41 artificial burrows into the central area, one in the centre and 40  
114 in three concentric rings, so that burrows were 65-75 cm apart. We also spaced 30 burrows evenly  
115 around the inside cage perimeter (Fig 1). Burrows were made from 30 cm lengths of 3 cm diameter  
116 wooden dowling with the central 2 cm diameter drilled out. These were hammered into 30 cm deep, 3  
117 cm diameter holes drilled into the soil surface. The burrows in the perimeter area allowed us to detect  
118 lizards that had dispersed from the central area.

119 We made 40 polyurethane models from a previously produced mould of a male pygmy bluetongue  
120 lizard. To produce a model colour that resembled that of the lizards, we added 1 mg of oxide brown  
121 colour (Diggers oxide colouring, Recochem, Australia) to 500 mL polyurethane (Easy Flo 60 Casting  
122 Polyur-ethane, Polytek Development Corp., Solid Solutions, Australia). Fenner and Bull (2011a) have  
123 previously reported that pygmy bluetongue lizards attacked these models if they were placed 5 cm  
124 from their burrow entrances, and that they differentiated between these models (that they attack), and  
125 models of a similar sized sympatric skink species, or a similar sized inanimate stick (that they do not  
126 attack).

127 Two replicate trials were conducted to test whether the behaviours of lizards differed in the presence  
128 or absence of the model lizards. At the start of each trial we placed 20 models in the central area of  
129 each of two cages. Models were located 5 cm from the entrance of alternate burrows. We considered  
130 the models were located at a position relative to the burrow entrance that a basking lizard might adopt.  
131 There were four models spaced around the inner concentric ring of eight burrows, and eight models  
132 spaced around the two outer rings, each of 16 burrows (Fig 1). The other two cages were left with no  
133 models. In the first trial, we released four lizards (two males and two females) into the central region  
134 of each cage at 07:00 h on 17 January 2011 and confined them for 24 h in the release area with a  
135 temporary, 20 cm high, black plastic wall. This allowed the lizards to become familiar with the release

136 environment (Ebrahimi and Bull, 2013b) and the models. Then we removed the wall and recorded  
137 lizard behaviour for the next 4 days. Thus day 1 of the trial was the day after the wall had been  
138 removed. Because filming was continuous while lizards were active we could follow the behaviours  
139 of each individual lizard over the four days of each trial. At the completion of the first trial, on the  
140 evening of 21 January 2011, we removed lizards from their burrows and kept them individually in  
141 their holding cages, with ambient temperature and light, and fed them for 3 days. Then, for the second  
142 replicate trial, we randomly chose new combinations of two male and two female lizards, and released  
143 them into the same four cages (two with and two without models).

#### 144 *4.2 Behavioural parameters*

145 In each trial, we observed lizard behaviour using four surveillance cameras suspended above each  
146 cage (CCD video camera, LICS23HF and lens 3.6 mm, Normal recording mode (continues), 30 fps,  
147 Longse, China). The cameras had a combined field of view covering the complete central area, and  
148 we used them to record continuously lizard behaviour from 07:00h to 17:00h during each day of each  
149 trial. We also confirmed the location of each lizard every day in the early morning and late afternoon  
150 by inspecting each burrow with a small torch. In the cages with models, we recorded, at the end of  
151 each day, how many lizards were in the 20 burrows with adjacent models, and how many were in the  
152 21 burrows without models. We did not add supplementary food during the experiment, but lizards  
153 could prey on naturally occurring invertebrates.

154 We derived six behavioural parameters from the video recordings in each cage during each replicate  
155 trial; 1) Total activity time ( $\text{h d}^{-1}$ ) which was defined as the period from the first time the head of a  
156 lizard emerged from its burrow to the last time that lizard retreated completely into its burrow on that  
157 day; 2) Basking time ( $\text{min h}^{-1}$ ) which was defined as the period of time when the lizard was at least  
158 partially emerged (5 -98% of body outside of the burrow) and was located at the entrance of its  
159 burrow. We divided the total min spent basking each day by 11 (the total h of filming in a day) to  
160 calculate the basking time as  $\text{min h}^{-1}$ ; 3) Number of movements around burrow. In some cases lizards  
161 fully emerged from their burrow, moved about, usually for a very short distance, no more than 10 cm  
162 from the burrow entrance, and then returned to the same burrow. These movements included lizards

163 that just walked around the burrow entrance no more than 5 cm from it, lizards that basked while fully  
164 emerged, and lizards that moved 10 cm away from the burrow entrance for defecation or darted out to  
165 catch prey within 10 cm of the burrow entrance. We recorded the number of movements by each  
166 lizard on each day; 4) Number of burrow changes. In some cases, lizards fully emerged from their  
167 burrow, moved more than 10 cm from that burrow (distance of actual moves are given in the results),  
168 and entered another burrow in the central area. We recorded the number of burrow changes for each  
169 lizard on each day; 5) Distance moved. If a lizard had moved to one or more different burrows within  
170 the central area during a day we measured the distance moved as the direct line distance between the  
171 burrow the lizard was in at the start of the day to the burrow it was in at the end of the day; 6) Number  
172 of movements to the perimeter area, which was defined as the number of times a lizard left the central  
173 area, moved across the habitat matrix, and was subsequently discovered occupying a burrow in the  
174 perimeter region. In terms of the translocation simulation, we considered that these represented  
175 dispersal events away from the release site, because lizards normally move less than 1 m from their  
176 occupied burrows (Milne et al., 2003; Fenner and Bull, 2011a) and because lizards that ended in  
177 perimeter burrows had to leave the central area where burrow refuges were available and cross the  
178 burrow-less matrix.

179 For each cage, on each day, we calculated a mean value per lizard of each parameter, and used that  
180 mean value for the cage in subsequent analyses. Normally this was a mean from four lizards, although  
181 in some cases, when a lizard had moved to the perimeter ring, and out of the field of view of the  
182 cameras, the mean for that day was derived from three or fewer lizards. On the first, second and fourth  
183 day, data from one cage had to be calculated from just three lizards and on the second and fourth day  
184 from one other cage data had to be calculated from just two lizards. We observed no agonistic  
185 interactions among live lizards in any cages, but recorded the number of attacks that lizards made on  
186 the model lizards.

187 We also recorded the overall number of behavioural activities by the lizards, including emerging to  
188 bask, movement around the burrow, burrow changes, movements to the perimeter area, and attacks on  
189 models. Although we used the same lizards, they were in different combinations in the second trial



190 and we considered that we had four independent replicates, two from each trial, of each treatment  
191 (with or without models). Thus data from the two sets of replicate trials were combined in the  
192 analyses to ask two questions. We first asked whether lizards in cages with models (four cages total;  
193 two cages in each of the two trials) showed any specific responses to those models, and if this  
194 response changed with experience over the 4-day trials. We then asked if lizards differed in their  
195 behaviours if they were in cages with (four cages) or without (four cages) conspecific models.

### 196 *4.3 Statistical analyses*

197 In the cages with models we used contingency chi-squared analysis to determine if burrow choice was  
198 random or was influenced by the presence of the models. Then, after the first day of each trial, we  
199 compared by t-test the behavioural parameters of those lizards that were in burrows with models and  
200 those in burrows without models. We did not repeat these analyses for days 2 to 4 because of the low  
201 numbers of lizard that remained in burrows with models on those days. In the cages with models, we  
202 used repeated measures ANOVA (Hand and Taylor, 1987) to determine whether attack rate on models  
203 changed with day of the trial. To compare other behavioural parameters between those lizards that did  
204 or did not attack models at least once, we used a repeated measures ANOVA for each of the six  
205 behavioural parameters, with day of trial as a within subjects factor and lizard response to the model  
206 (attacked model/did not attack model) as a between subjects factor.

207 We again used repeated measure ANOVA to examine whether the treatment of adding conspecific  
208 models to cages altered lizard behaviour, for each of the six behavioural parameters. We used the  
209 average behavioural parameter value per cage (eight cages in total, four cages in each of the two  
210 trials) per day as the dependent variable, day (1-4) as a within subjects factor and cage treatment  
211 (model/no model) as the between subjects factor. For all repeated measures ANOVA's we applied the  
212 Greenhouse-Geisser correction when data were non- spherical.

## 213 **4. Results**

### 214 *4.1. Do lizards respond to the models?*

215 From 16 lizards (in four replicate cages with models present), five occupied burrows with models 5  
216 cm from the burrow entrance at the end of the first day (two in the first and three in the second trial).

217 This was reduced to three lizards on the second day, and to two lizards on the third and fourth days  
218 (one in each trial) of the experiment. While chi squared tests showed no significant deviation from  
219 random choice on the first day ( $X^2 = 2.25$ , d.f. = 1,  $P = 0.13$ ) lizards had a significant preference for  
220 burrows without models by the second day ( $X^2 = 6.25$ , d.f. = 1,  $P = 0.012$ ), and the third and fourth  
221 days ( $X^2 = 9.0$ , d.f. = 1,  $P = 0.002$ ). In the cages with models, the mean number of lizards that stayed in  
222 burrows near models significantly reduced from the first to the fourth day of the trials ( $F_{3,9} = 9.00$ ,  
223  $P < 0.005$ ; Fig. 2a).

224 On the first day of each trial, in cages with conspecific models, lizards that had chosen burrows with  
225 models had significantly shorter overall activity time and spent significantly less time basking than  
226 lizards that had chosen burrows without models (Table 1). Additionally those lizards that ended the  
227 day in burrows with models had changed burrows significantly more often on that day, than lizards  
228 that ended the day in burrows without models (Table 1). Two different lizards (two females) that  
229 occupied burrows with a conspecific model 5cm from the burrow entrance, attacked the models  
230 during days 1, 2 and 4 (a total of five times for both females and all days) and appeared to be trying to  
231 push the models further away. There was no significant effect of day on the mean number of attacks  
232 on models ( $F_{3,9} = 0.60$ ,  $P = 0.63$ ).

233 Repeated measure analyses showed significant effects of the response of lizards to models (whether  
234 they did or did not attack the models) on three behavioural parameters (Table 2). The lizards that  
235 attacked the models stayed active for longer (mean  $3.71 \pm \text{SE } 0.03 \text{ h d}^{-1}$ ) than those that did not ( $2.98$   
236  $\pm 0.11 \text{ h d}^{-1}$ ), and changed burrows more often (Fig. 2b; Table 2). The lizards that attacked the models  
237 were also significantly more likely to stay in the central release area (0.0 movements to the perimeter  
238 area per day) than those that did not ( $0.56 \pm 0.11$  movements to the perimeter area lizard $^{-1}$  day $^{-1}$ )  
239 (Table 2). There was also a significant effect of day on total activity time, and a significant interaction  
240 effect between day and response to models, for the number of burrow changes (Table 2).

241 Note that these results are derived from a small sample size (only two lizards attacked models), and an  
242 uneven distribution of lizards between the two categories attacked model (two lizards) or did not  
243 attack model (14 lizards).

244 4.2. *Do lizards behave differently with and without models present?*

245 We recorded 429 separate behavioural activities from 1280 hours of recordings. Emerging to bask  
246 was the most common lizard activity (234 basking events) followed by movement around the burrow  
247 (135 movement events). The experimental treatment (with or without models) did not affect total  
248 activity time, basking time, or distance moved when changing burrows (Table 3). There was a  
249 significant interaction of treatment x day for the number of lizard movements around the burrow  
250 (Table 3); lizards consistently made more movements around the burrow in the cages with models,  
251 although the difference between treatments was much smaller on the first day of the trials (Fig. 3).  
252 Also lizards changed burrows significantly more (Fig. 4a), and made significantly more movements to  
253 the perimeter area (Fig. 4b) in cages with models than in cages with no models (Table 3).

254 **5. Discussion**

255 First considering the lizards in the cages with models present, our results showed that lizards  
256 responded to the conspecific models. They tended to avoid burrows that were close to the models,  
257 and, rarely, they attacked the models. This is consistent with the report of Fenner and Bull (2011a)  
258 who suggested that pygmy bluetongue lizards defend a small area immediately around their burrow  
259 entrance (radius less than 15 cm) and that they aggressively attacked conspecific models placed 5 cm  
260 from their burrows. We deduced from the current study, that lizards in a new habitat will reduce  
261 agonistic interactions with conspecifics by avoiding burrows they perceive to be occupied. Those  
262 lizards that occupied burrows close to models at the end of the first day, showed behaviours consistent  
263 with being negatively affected by the presence of a conspecific; they were active over a shorter time,  
264 and basked for shorter periods than lizards in the same cages but in burrows without models close by.  
265 Comparing lizards in cages with models and in cages without models, we found that the presence of  
266 models did not affect total time active or basking time. Perhaps this was because, after the first day,  
267 most of the lizards in cages with models had selected burrows that did not have a model 5 cm from  
268 the burrow entrance, and there was no immediate perceived threat from closely adjacent conspecifics.  
269 However the presence of models significantly altered movement behaviours. Lizards in cages with  
270 models moved around the burrow more, changed burrows more, and moved to the perimeter area

271 more. Thus, even with apparently unoccupied burrows available, the presence of an apparent  
272 conspecific in another burrow within 65 – 75 cm induced this extra activity. We have previously  
273 shown a similar result (Ebrahimi and Bull, 2013c), that lizards changed burrows more, and made  
274 more moves to the perimeter area if they released into burrows that were close together than if they  
275 were released into burrows that were further apart.

276 We can draw three broad conclusions from our results about the use of conspecific models for the  
277 translocation of pygmy bluetongues, and the translocation of other species that have a similar solitary  
278 social organisation, and with defence of a central refuge. First, the lizards responded to visual cues  
279 from models as if they were real conspecifics. This confirms our earlier studies on this species  
280 (Fenner and Bull, 2011a), and the reports of many other behavioural ecologists since Tinbergen  
281 (1948). In any conservation program where increased conspecific presence is a management option to  
282 enhance retention of translocated individuals at the release site, models are adequate substitutes even  
283 if they contain less than the complete sensory signal range of real conspecifics.

284 Second, in the case of pygmy bluetongue lizards, models induced more movements among lizards that  
285 had been introduced to a release site. There were more movements away from the burrow entrances  
286 when models were present than when models were absent, both for lizards that returned to the same  
287 burrow (movements around the burrow) and for lizards that changed burrows. And there were more  
288 movements to the perimeter area when models were present than when models were absent, out of the  
289 central release area and across a burrow free area. In terms of translocations, these movements would  
290 increase the exposure of the lizards to visual predators such as birds (Fenner et al., 2008), and increase  
291 their probability of leaving the release site. Although our experiments were conducted over a  
292 relatively brief period, we suggest that behaviours immediately after release are likely to be most  
293 significant in determining the success of a translocation. The likely drivers of this behavioural change  
294 (increased movement by lizards when models are present than when models are absent) are either a  
295 perceived increase in the threat to burrow security, a perceived increase in the likelihood of aggressive  
296 encounters, or a perceived increase in competition for invertebrate prey. Whatever the mechanism, the  
297 message for conservation management is that, for this species, a high density, or a perceived high

298 density at the release site is likely to lead to behaviours that will reduce the chance of a translocated  
299 individual staying and surviving. The broader implication for any translocation program is that it will  
300 be important to understand the local density that can be tolerated by a target species, and whether  
301 conspecific cues will negatively impact translocation success at those densities. This might be  
302 particularly important in reinforcement translocation programs designed to augment existing  
303 populations, where resident individuals may inhibit the settlement of introduced individuals. A novel,  
304 but as yet unexplored suggestion from the current study, is that the placement of conspecific models  
305 in locations surrounding a release site might inhibit dispersal away from that site if an initial aim is to  
306 retain released animals near to the release site.

307 A third conclusion is that the presence of conspecific cues at the release site would be detrimental to  
308 any translocation program for pygmy bluetongue lizards. This contrasts with studies of other species  
309 such as Caribbean rock iguanas (Alberts, 2007; Ahlering et al., 2010) where conspecific cues have  
310 reduced the stress levels and allowed translocated animals to adjust more rapidly to their new habitat  
311 at the translocation site. Our third conclusion emphasises the need for detailed understanding of the  
312 social structure of the species before embarking on any translocation attempt.

## 313 **6. Conclusion**

314 In cages with conspecific models we found lizards responded to the models by avoiding occupancy of  
315 burrows with a model near the entrance. The visual cue from the model appeared to induce  
316 behavioural avoidance. In the presence of conspecific models, compared to the absence of models,  
317 introduced lizards significantly increased the number of movements around burrows, the number of  
318 burrow changes and the number of movements to the perimeter area of the experimental cages. These  
319 behavioural changes could decrease the success of a translocation by increasing exposure to predation  
320 and dispersal from the release site. The results suggest that cues from conspecifics will not encourage  
321 translocated lizards to stay at a release site. This contrasts with other studies where conspecific cues  
322 have increased translocation success, and our results suggest that a careful assessment of reactions to  
323 conspecific cues will be required before they are considered in any translocation program.

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406 Table 1. Two sample t-tests, for lizards in cages with models, comparing, for each of six  
 407 behavioural parameters, the five lizards, that , by the end of the first day of the trials,  
 408 occupied burrows with models located 5 cm from the burrow entrance, with the 11 lizards  
 409 that occupied burrows without adjacent models. Values in bold indicate significant effects ( $P$   
 410  $< 0.05$ ).

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Behavioural parameter	Burrow occupied	Mean	SE	df	t	P
Total activity time (h d <sup>-1</sup> )	No Model	4.19	0.16	14	2.402	<b>0.031</b>
	Model	0.76	0.20			
Basking time (min h <sup>-1</sup> )	No Model	18.13	0.27	14	2.628	<b>0.020</b>
	Model	7.63	0.18			
No. movements around burrow	No Model	1.82	0.15	14	0.745	0.469
	Model	0.88	0.19			
No. burrow changes	No Model	0.75	0.09	14	-2.650	<b>0.019</b>
	Model	2.00	0.01			
Distance moved (cm)	No Model	12.46	0.47	14	0.173	0.865
	Model	10.00	0.94			
No. movements to perimeter area	No Model	0.28	0.05	14	-0.959	0.354
	Model	0.48	0.13			

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424 Table 2. Repeated-measure analyses of variance for behavioural parameters comparing the two lizards  
 425 that attacked models and the 14 lizards that did not attack models, in the cages with model lizards. Day  
 426 (1-4) was the repeated measure, and response to model (did or did not attack) was the between  
 427 subjects factor. Values of P in bold indicate significant effects ( $P < 0.05$ ).

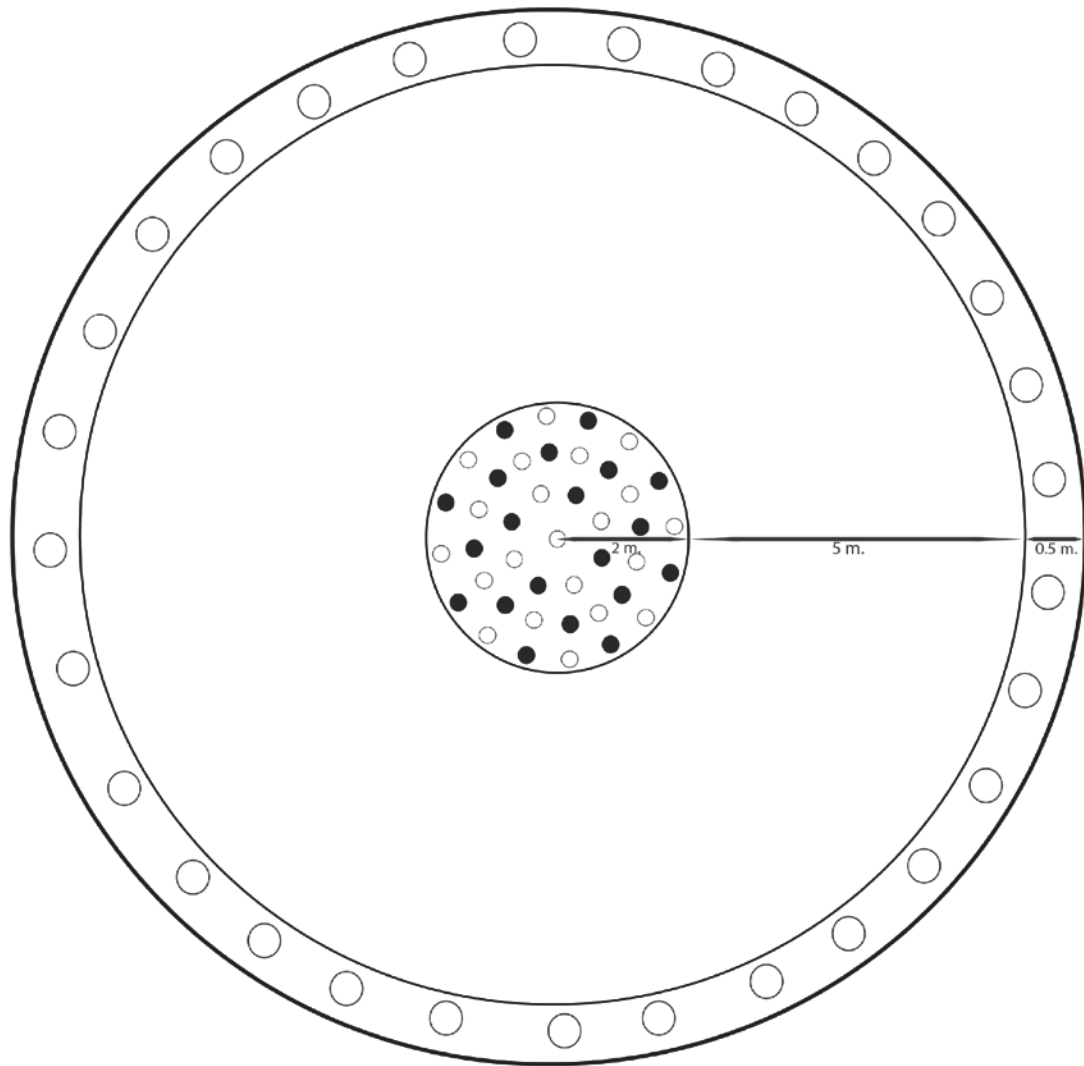
	df	Total activity time (h d <sup>-1</sup> )		Basking time (min h <sup>-1</sup> )		No. movements around burrow		No. burrow changes		Distance moved (cm)		No. movements to perimeter area	
		<i>F</i>	<b>P</b>	<i>F</i>	<b>P</b>	<i>F</i>	<b>P</b>	<i>F</i>	<b>P</b>	<i>F</i>	<b>P</b>	<i>F</i>	<b>P</b>
Response to model	1, 14	6.57	<b>0.022</b>	0.05	0.824	1.30	0.272	21.06	<b>0.001</b>	0.06	0.809	6.95	<b>0.020</b>
Day	3, 42	5.20	<b>0.004</b>	1.19	0.324	1.23	0.311	3.66	<b>0.020</b>	0.05	0.904	0.13	0.938
Response to model x Day	3, 42	1.85	0.153	1.34	0.272	0.29	0.827	4.17	<b>0.006</b>	1.29	0.287	0.29	0.826

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443 Table 3. Repeated-measure analyses of variance for behavioural parameters comparing mean daily  
 444 values for lizards in four cages with models and four cages without models. Day (1-4) was the  
 445 repeated measure, and treatment (models present or models absent) was the between subjects factor.  
 446 Values in bold indicate significant effects ( $P < 0.05$ ).

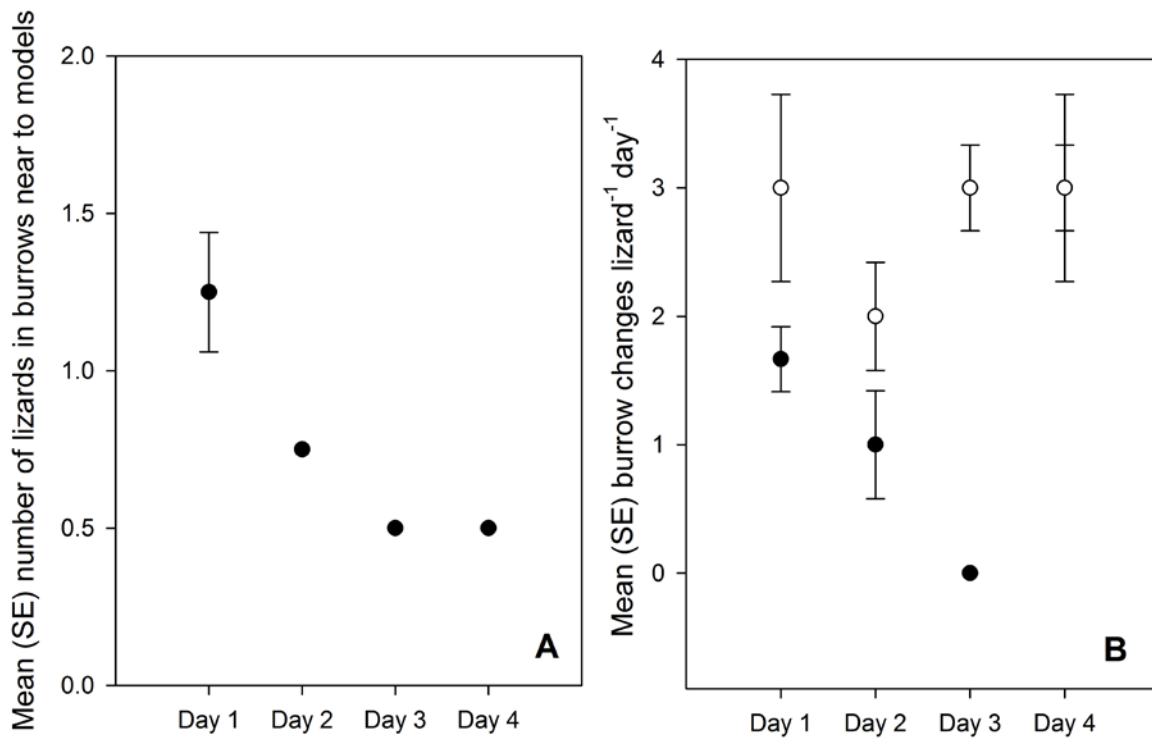
	df	Total activity time (h d <sup>-1</sup> )		Basking time (min h <sup>-1</sup> )		No. movements around burrow		No. burrow changes		Distance moved (cm)		No. movements to perimeter area	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment	1, 6	2.103	0.197	0.001	0.988	7.199	<b>0.036</b>	51.76	<b>0.012</b>	0.150	0.710	22.04	<b>0.003</b>
Day	3, 18	0.788	0.516	0.893	0.464	1.881	0.169	3.120	0.052	0.147	0.930	1.387	0.279
Treatment x Day	3, 18	1.126	0.365	0.269	0.847	27.18	<b>0.005</b>	0.724	0.529	1.826	0.179	2.677	0.078

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Fig. 1. The layout of each cage used in the experimental trials, showing burrows with models placed 5 cm from the burrow entrance (in the model addition treatment; filled circles) and the burrows with no models (open circles)



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474 Fig. 2. For cages with models: A) Mean number of lizards in burrows near to models on each day. B)

475 Mean number of burrow changes of two lizards that attacked the model (open circles) and 14 lizards

476 that did not attack the model (closed circles).

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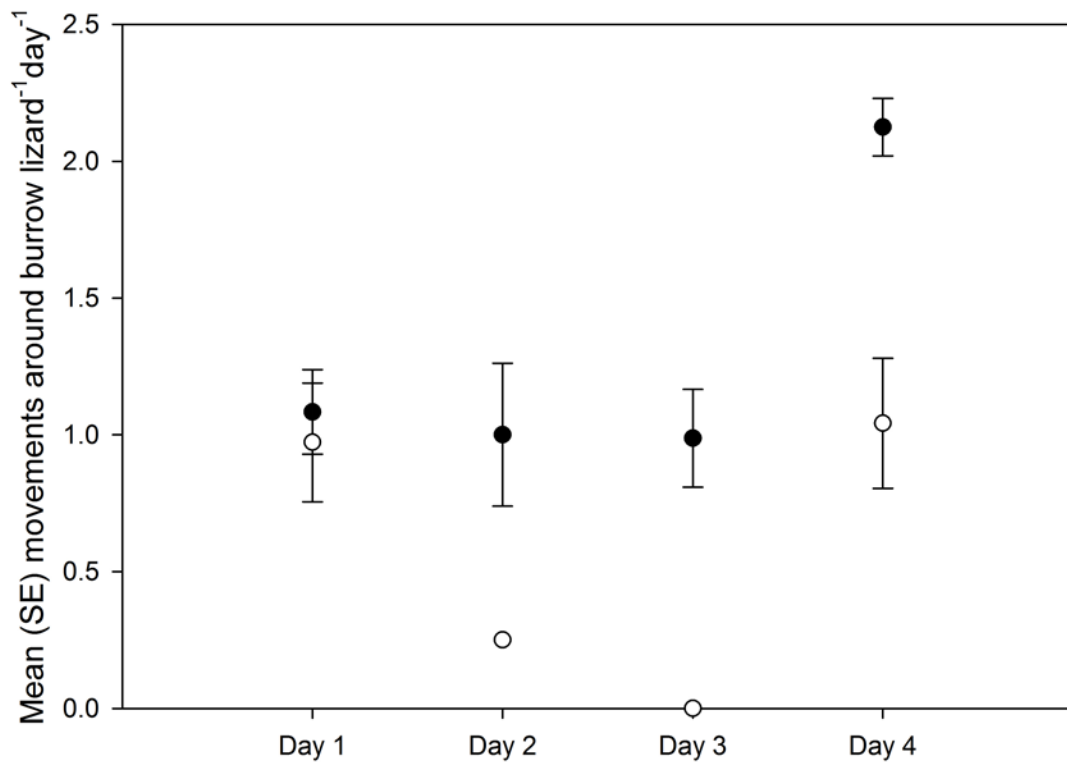
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490 Fig. 3. Mean number of movements around burrows per lizard on each trial day in cages with models  
491 (filled circles) and without models (open circles).

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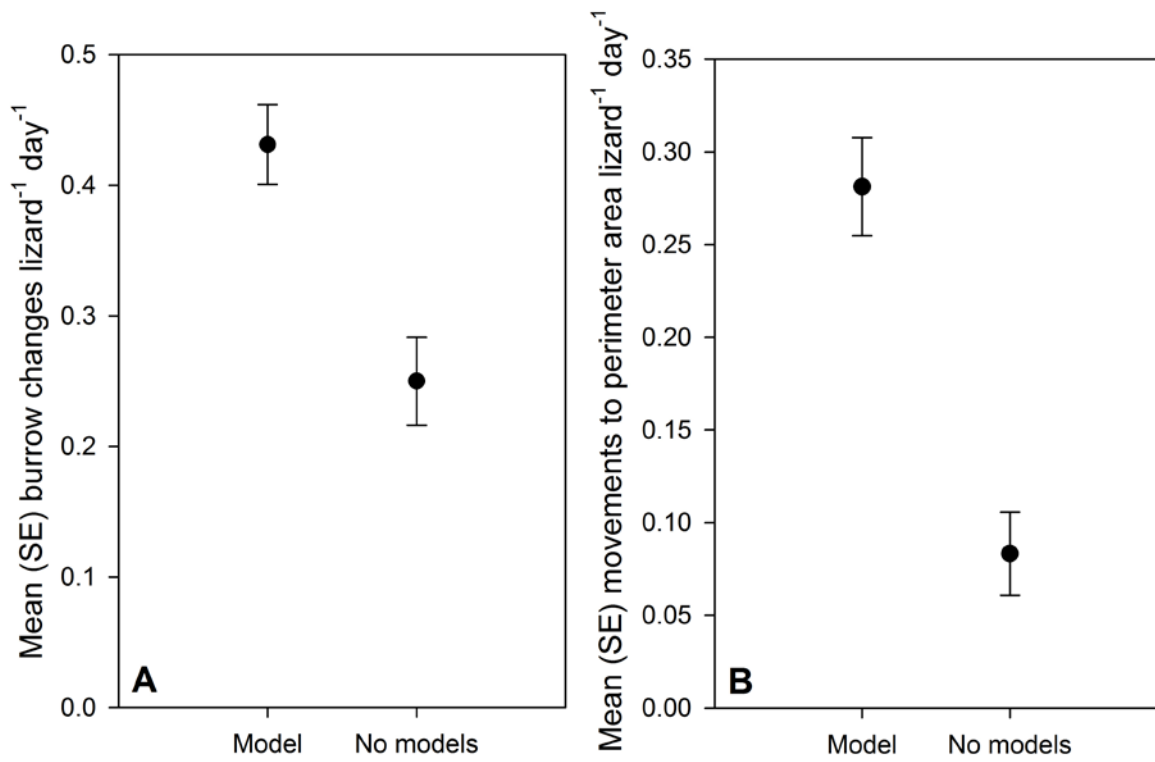
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505 Fig. 4. In cages with and without burrows: A) the mean number burrow changes per day; and B) the

506 mean number of movements to the perimeter area per day.

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