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1 **Invasion of cane toads (*Rhinella marina*) affects the problem-solving**
2 **performance of vulnerable predators (monitor lizards, *Varanus varius*)**

3

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16 **Keywords.** – prey acquisition task; behavioural flexibility; *Bufo*; reptile cognition

17

18 **Abstract**

19 Variation in morphological, genetic, or behavioural traits within and among native species
20 can modify vulnerability to impacts from an invasive species. If an individual's vulnerability
21 depends upon its cognitive performance, we may see adaptive shifts in cognitive traits post-
22 invasion. Commonly, animals with enhanced cognitive abilities perform better in novel tasks,
23 often by prioritising decision accuracy over decision speed. In eastern Australia, giant
24 monitor lizards (*Varanus varius*) are fatally poisoned if they ingest invasive cane toads
25 (*Rhinella marina*), but vulnerability is lower for individuals that carefully evaluate the novel
26 prey type before swallowing it. To test if toad-imposed selection for neophobia and caution
27 affected cognitive performance, we tested free-ranging monitors with a device that required
28 lizards to manipulate the apparatus in order to obtain food. Success at accomplishing that
29 task, and the speed of that success, were lower in lizards from long-colonised sites than from
30 uninvaded sites. Our results suggest that toad invasion has modified cognitive phenotypes
31 within populations of this apex predator, a change that might have substantial effects on other
32 species.

33

34 **Significance statement**

35 Many studies of the impacts of biological invasions focus on the numerical effect of an
36 invader on the abundances of native taxa, neglecting other types of impacts. Colonising taxa
37 can also impose selection on behavioural traits of native species, generating shifts in
38 behaviour as native taxa adapt to intruders. Such shifts in behaviour are interesting not only
39 in their own right, but also because such shifts (especially in apex predators) may influence
40 other taxa within food-webs. Importantly, the nature and magnitude of such shifts may
41 change over time post-invasion.

42

43 **Introduction**

44 Biological invasions can pose novel challenges for native taxa, exerting powerful selective
45 forces on a wide range of behavioural as well as physiological and morphological traits
46 (Strauss et al. 2006; Berthon 2015). For example, the arrival of a novel invasive predator may
47 select for an ability of native prey to detect and avoid cues produced by that predator
48 (Bourdeau et al. 2013), whereas the arrival of a novel invasive prey may select for an ability
49 to detect and willingness to consume that prey type (Barber et al. 2008). Adaptive shifts in
50 antipredator or foraging tactics by native species, in turn, may influence interactions of the
51 affected species with other organisms within food webs (David et al. 2017). Such effects may
52 be especially strong if the native taxon that is affected is an apex predator, that imposes top-
53 down regulation of smaller species (Doody et al. 2012). For example, increased or decreased
54 neophobia of predators due to an invasive species might influence both feeding rates and prey
55 selection (Nersesian et al. 2011). More generally, an invader may induce adaptive shifts in
56 the cognitive skills and tactics of a predator (Caller and Brown 2013).

57

58 One type of threat posed by an invasive species is that of lethal toxic ingestion, if the new
59 arrival possesses chemical defences fatal to native predators lacking a history of sympatry
60 (and hence, coevolution) with the invader or its relatives (Marshall et al. 2018). One
61 intensively studied example of such an impact involves the continuing spread of cane toads
62 (*Rhinella marina*) through Australia (Shine 2010; Tingley et al. 2017). The bufadienolide
63 defensive chemicals of toads are fatal to predators that lack an evolutionary history of
64 sympatry with these anurans (Shine 2010; Pinch et al. 2017). In Australia, the arrival of toads
65 has caused dramatic population declines (sometimes > 90%) in populations of vulnerable
66 predators such as quolls, crocodiles, snakes, and lizards (Letnic et al. 2008; Shine 2010).
67 However, populations of some of the affected predators are buffered from that impact

68 through taste aversion, whereby they refuse to consume toads as prey as a result of learning
69 (O'Donnell et al. 2010) or adaptation (Phillips and Shine 2004). Importantly, that refusal to
70 consume toads may be part of a broader suite of behavioural changes, whereby a wide range
71 of stimuli elicit a more cautious predator approach than was previously the case. For
72 example, exposure to toad larvae induced predatory fish to cease consuming the larvae of
73 native anurans as well (Nelson et al. 2010), and exposure to metamorph toads induced
74 carnivorous marsupials (planigales) to assess other prey types more carefully before
75 launching an attack (Webb et al. 2008). Other predatory fish not only learned to avoid toxic
76 toad larvae, but showed rapid evolution of aversion learning capacity, performing better in
77 trials with novel aversive stimuli as well as with toads (Caller and Brown 2013).

78

79 Although learnt avoidance of prey is a common behavioural response to the arrival of a toxic
80 invasive species, are other behavioural traits modified also? In the case of apex predators,
81 does the arrival of a toxic invasive species alter attack strategies and/or cognitive skills?

82 Lizards of the family Varanidae (monitor lizards, “goannas”) are apex predators across much
83 of Australia (Sutherland et al. 2011) and appear to have more advanced cognitive skills than
84 do most other reptiles, with captive specimens rapidly learning complex tasks (e.g., Manrod
85 et al. 2008; Cooper et al. 2019). Also, a single population of varanids may contain individuals
86 with a wide variety of “personality” types that differ along continua such as boldness-
87 shyness, activity levels and neophobia (Ward-Fear et al. 2018) that affect a variety of
88 ecological traits including an individual’s vulnerability to invasive toads (Ward-Fear et al.
89 2020). Hence, selection imposed by the toad invasion might alter the distribution of
90 behavioural phenotypes, and hence ability to solve a standardised cognitive challenge.

91

92 Previous studies have identified a correlation between cognitive ability and improved
93 performance in novel tasks in a range of taxa (Sol et al. 2005) including reptiles (Amiel et al.
94 2011; Szabo et al. 2020). Commonly, higher cognitive performance translates into an
95 enhanced ability to solve novel problems. For varanid lizards at the toad invasion front, the
96 challenge is to detect the novel invader when it is first encountered, determine that it is toxic,
97 and respond appropriately by avoiding consuming it and all conspecifics on future
98 encounters. If cognitive ability is linked to lizard survival following the invasion of cane
99 toads, we would expect to see lizards that can detect and avoid cane toads persisting through
100 time, while lizards lacking the cognitive capacity to discriminate and avoid the toxic prey
101 item would be removed from the population.

102

103 To explore this possibility, we designed a novel testing apparatus to assess problem-solving
104 skills in these giant lizards, and we monitored the interactions between lizards and this
105 apparatus in a wide range of sites encompassing areas with and without invasive cane toads.
106 We predicted that the arrival of cane toads would select for lizards that had higher cognitive
107 ability, such that lizards in toad-present areas would be more likely to solve the puzzle, and
108 would do so faster than lizards from areas without toads.

109

110 **Methods**

111 **Study animals**

112 Cane toads (*Rhinella marina*) are large bufonid anurans native to a wide area of South
113 America (Zug and Zug 1979). Released in north eastern Australia in 1935 as a biological
114 control, toads have now expanded their range across many tropical and subtropical areas of
115 that continent (Urban et al. 2007). Many native predators are physiologically unable to deal
116 with the toad's potent toxins (Phillips et al. 2003; Pinch et al. 2017), and experience high

117 levels of mortality following the arrival of toads (Ujvari and Madsen 2009; Ward-Fear et al.
118 2016).

119
120 The lace monitor (*Varanus varius*) is one of the world's largest lizards (exceeding 200 cm
121 total length, 14 kg mass: (Weavers 1988) and is abundant in open woodland habitats along
122 eastern Australia (Vincent and Wilson 1999; Cogger 2014). This semi-arboreal apex predator
123 and scavenger has a generalist diet, including anurans (Vincent and Wilson 1999; Cogger
124 2014). Lace monitors actively hunt using a range of sensory stimuli to locate food items, and
125 commonly forage by dexterously clawing at burrows, logs, or crevices to extract prey (De
126 Lisle 1996). Lace monitors are capable of learning to avoid toxic prey after a single
127 encounter (Jolly et al. 2016), and in populations with a long history of sympatry with toads,
128 the monitors exhibit a strong avoidance response to the toxic anuran (Pettit et al. 2020).

129

130 **Site descriptions**

131 We tested lace monitors from 17 populations along the east coast of Australia between
132 October 2017 and April 2018, and again in March 2020. Six of these sites are yet to be
133 invaded by cane toads, while the eleven other sites had been invaded for between one and 80
134 years at the time of our experiments (Fig. 1). Collectively, these sites encompass the
135 complete cane toad invasion chronosequence in Australia.

136

137 **Chronology of the cane toad invasion**

138 Extensive monitoring of the cane toads' recent southerly advance in New South Wales allows
139 precise estimation of invasion chronology in southern sites (Jolly et al. (2015). We used
140 ARCGIS (version 10.5) to establish the year in which toads earlier invaded sites in
141 Queensland. Records of the occurrence of cane toads were retrieved from the Atlas of Living

142 Australia database. A 20 km radial buffer zone was established around each site and the
143 earliest occurrence record within each buffer zone was extracted to provide a conservative
144 estimate of toad arrival.

145

146 **Problem-solving trial**

147 We measured lizard responses to a novel prey acquisition task focused on a trial apparatus
148 (puzzle) consisting of a PVC tube (28 cm high, diameter 16 cm) with a 9 x 12 cm window on
149 the side of the tube. A PVC cylindrical sleeve on the outside of this tube could be rotated
150 freely in either direction. The sleeve had two windows of the same size as the tube but
151 positioned 180° apart. One sleeve window was covered with wire mesh while the other was
152 unobstructed (Fig. 2).

153

154 We placed 10 chicken necks (approx. 220g) inside the tube and aligned the mesh-covered
155 window of the outer sleeve with the open window of the tube. The mesh allowed visual and
156 scent cues, but physical access to the bait could be achieved only by rotating the outer sleeve
157 180° to align the open sleeve window with the open tube window. A motion-sensing camera
158 (Scoutguard SG560k) was trained on the puzzle to record goanna responses in a series of 1-
159 minute videos.

160

161 We deployed one or three puzzles for 48 h -72 h at 17 sites (6 toad-absent and 11 toad-
162 present). Over the course of the study we increased the number of puzzles deployed (spaced
163 approximately 50 m apart) in an attempt to target multiple individuals in high-density areas.
164 A trial was initiated when a lizard triggered the remote camera and approached to within 30
165 cm of the puzzle and concluded when 30 minutes had elapsed. As some lizards interacted
166 with the puzzle sporadically (i.e., multiple short-duration visitations), we calculated the

167 cumulative time that each lizard spent at puzzles for our measures of puzzle success. The
168 puzzle was periodically checked (~ every three hours), and if solved it was refreshed with
169 bait and reset.

170

171 We reviewed the videos to identify individual lizards (based on body size, patterning and tail
172 condition), estimate the size of each animal (snout-vent length, = SVL; measured to the
173 nearest 50 mm), score if the problem was solved (yes/no), and record the time from initial
174 engagement with the puzzle until it was solved. It was not possible to record data blind
175 because our study involved focal animals in the field.

176

177 **Analyses**

178

179 We used generalised linear models (GLM) with a binomial distribution and logit link
180 function to investigate if the number of years since toads invaded (continuous variable), the
181 body size (SVL) of a lizard (continuous variable), and their interactions, predicted if a lizard
182 could solve the puzzle. Years since toad invasion and lizard SVL were used as the predictor
183 variables, with the outcome of the trial (solved or did not solve) as the response variable.

184

185 We used a GLM with a normal distribution and log link to test if the latency of lizards to
186 solve the problem changed with the duration of toad invasion. Years since toad invasion,
187 lizard body size, and their interaction were used as predictors, with the latency to solve the
188 puzzle as the response variable.

189

190 All analyses were conducted in JMP Pro (v14.2). Where appropriate, Levenes' test was used
191 to test for equality of variances, while normality was assessed visually.

192

193 **Results**

194 Thirty individual lace monitors (16 from toad-free sites, and 14 from toad-present sites
195 ranging from 5 to 62 years invaded) from 10 sites (5 uninvaded, 5 invaded) engaged with the
196 puzzle. Of the 30 lizards that interacted with the puzzle, 16 successfully manipulated the
197 puzzle and retrieved baits (see supplementary material for videos of lizards interacting with
198 puzzles). Of these 16 animals, 14 succeeded on their first attempt. The proportion of lizards
199 that successfully solved the puzzle declined with the number of years since toads invaded
200 (GLM $\chi^2_1=6.05$, $P=0.014$; Fig. 3). There was a significant main effect of lizard body size
201 (larger lizards had higher success rates; $\chi^2_1=5.12$, $P=0.024$), but the interaction between years
202 since toad invasion and body size was not significant ($\chi^2_1=0.80$, $P=0.37$).

203

204 Three lizards successfully solved the puzzle within one minute, whereas the slowest lizard to
205 solve the puzzle spent over 20 minutes to reach the bait. Among the 16 successful lizards, the
206 time taken to complete the puzzle differed significantly with time since toad invasion (GLM
207 $\chi^2_1=10.03$, $P=0.0015$; Fig. 4) but was not affected significantly by lizard body size ($\chi^2_1=0.60$,
208 $P=0.81$), nor by the interaction between the number of years since toads invaded and body
209 size ($\chi^2_1=1.28$, $P=0.26$).

210

211 **Discussion**

212 Our study is one of the first to measure problem-solving ability of reptiles in a field context
213 (but see; Storks and Leal 2020). Although field-based studies introduce many confounding
214 factors (e.g., variable site-specific differences), they can also provide a more realistic study
215 system by eliminating many of the artifacts, stresses and biases associated with laboratory
216 studies. Our results indicated an effect of toad invasion on problem-solving success, but not

217 in the direction that we had expected. In the rainbowfish studied by Caller and Brown (2013),
218 sympatry with invasive cane toads was associated with an increase in the capacity for
219 aversion learning. In strong contrast, the lizards that we studied exhibited a decline, not an
220 increase in the ability to solve a novel problem. That decline was evident both in the
221 proportion of lizards that solved the problem, and in the time taken to do so for the successful
222 lizards.

223

224 The reduction in success rates of lizards interacting with our puzzle likely reflects intense
225 selection on behavioural phenotypes as a consequence of cane toad invasion. The individual
226 varanids most at risk of lethal toxic ingestion are large bold lizards, that do not carefully
227 assess prey items prior to ingestion (Jolly et al. 2016; Ward-Fear et al. 2018). As these
228 individuals are fatally poisoned, an increasing proportion of the varanid population post-
229 invasion consists of smaller and shyer animals (as inferred from approach distances; Pettit et
230 al. in press). Such animals may not be as willing to engage vigorously with the test apparatus
231 as were their toad-vulnerable conspecifics. Thus, the primary driver of our results may not be
232 that toad-sympatric varanids have weaker cognitive skills; instead, it may be that they adopt a
233 more cautious approach. Such a shift would be consistent with the “pace of life” (POL)
234 hypothesis, whereby selection has favoured individuals that are less bold, impulsive and risk-
235 prone, and prioritise safety and eventual accuracy against the speed at which a task is
236 completed (Réale et al. 2010). The shift we see thus may be in tactics rather than cognitive
237 skills.

238

239 Regardless of the proximate mechanisms responsible for the shift that we have documented,
240 such a change in foraging-associated behaviour of an apex predator may have substantial
241 cascading effects on other species. Thus, for example, a population of shyer lizards may

242 spend less time in exposed habitats (Carter et al. 2010), or may be less willing to attack novel
243 prey types (Ward-Fear et al. 2018). Consequent shifts in the composition of the diet and the
244 rate of feeding might affect smaller species in a variety of ways, and could either increase or
245 decrease their numbers (Royauté and Pruitt 2015). More generally, a biological invasion can
246 affect an ecosystem not simply by changing the numerical abundance of an apex predator, but
247 also by modifying the ways in which those animals seek their food. In the system that we
248 studied, the invasion of cane toads appears to have profoundly affected the behaviour of lace
249 monitors (e.g., boldness, habitat use, engagement with a novel puzzle; (Pettit et al. in press;
250 LP et al. unpubl. data), but with little overall effect on the abundance of the monitor species
251 (LP et al. unpubl. data). As a result, a lack of numerical impact of an invader on a native
252 taxon may not mean a lack of biologically significant effects.

253

254 Although our results are encouraging in respect to the feasibility of studying cognitive skills
255 of free-living lizards, future studies could quantify problem-solving success on a wide variety
256 of tasks, and do so repeatedly with the same individuals to explore the influence of learning
257 (Szabo et al. 2018). Future work could also more carefully control issues such as ambient
258 conditions (weather) and motivation (hunger), and explore additional questions such as the
259 possibility of cultural learning (by observing conspecifics solving a problem; Kis et al. 2015).

260

261 Individuals with a higher capacity to learn, or those that make fast and accurate decisions,
262 generally are thought to deal better with novel threats than do conspecifics exhibiting slow
263 decision-making or inflexible behaviour (Amiel et al. 2011; Szabo et al. 2020). This may be
264 true in dynamic contexts where decision speed is favoured over decision accuracy (e.g.,
265 where an animal must respond quickly to multiple threats in rapidly-changing urban
266 environments; Batabyal and Thaker 2019). However, slow-moving cane toads represent a

267 different class of threat, where the advantages of decision accuracy (or being so inflexible as
268 to avoid the threat altogether) may outweigh the benefits of making a rapid decision. In our
269 system, we detected a significant decrease in the problem-solving performance of
270 anurophagous lizards following toad invasion, suggesting that behavioural traits that facilitate
271 problem-solving (at least on the task that we provided) reduce rather than enhance individual
272 fitness when toads invade.

273

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279

280 **Author contributions statement.** - LP designed the study, performed all fieldwork,
281 conducted the statistical analyses, and drafted the manuscript. GWF designed the study, and
282 critically revised the manuscript. RS conceived and designed the study, and critically revised
283 the manuscript. All authors gave final approval for publication.

284

285 **Animal Ethics.** - All procedures were approved by the University of Sydney ethics
286 committee (approval 2017/1202) and were carried out in accordance with relevant guidelines
287 and regulations under licence from state and federal wildlife agencies.

288

289 **Data accessibility statement.** - Data are available from the Figshare repository:
290 10.6084/m9.figshare.12863993

291

292 **Conflict of interest.** – All authors acknowledge no conflict of interest.

293

294

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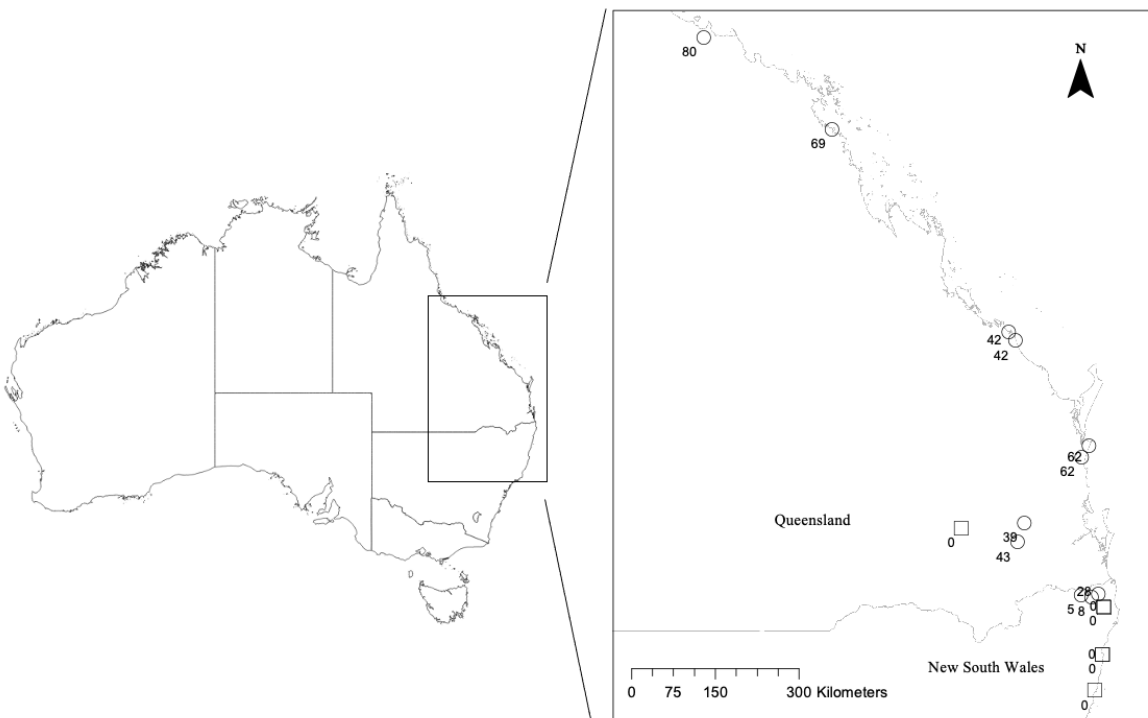
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401

402 **Figures**

403

404 **Figure 1**

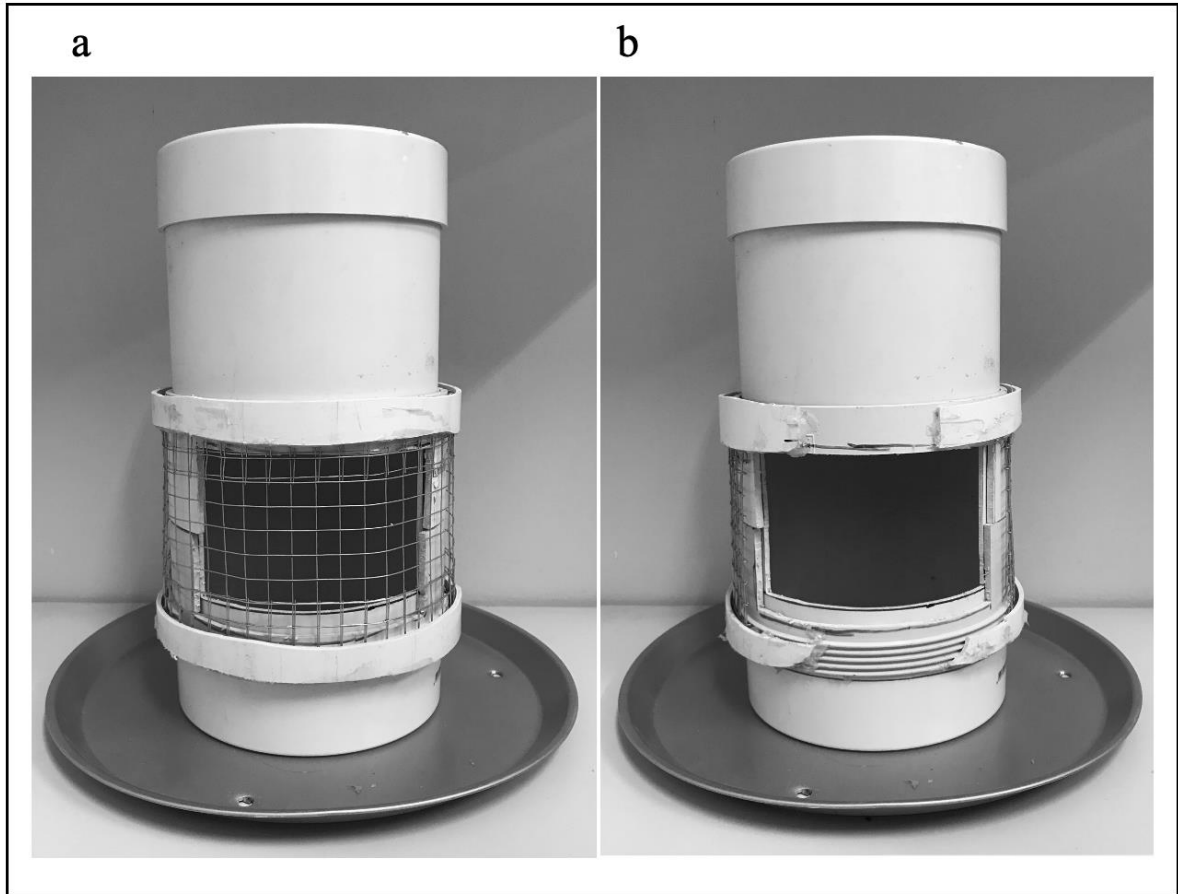


405

407 **Figure 2**

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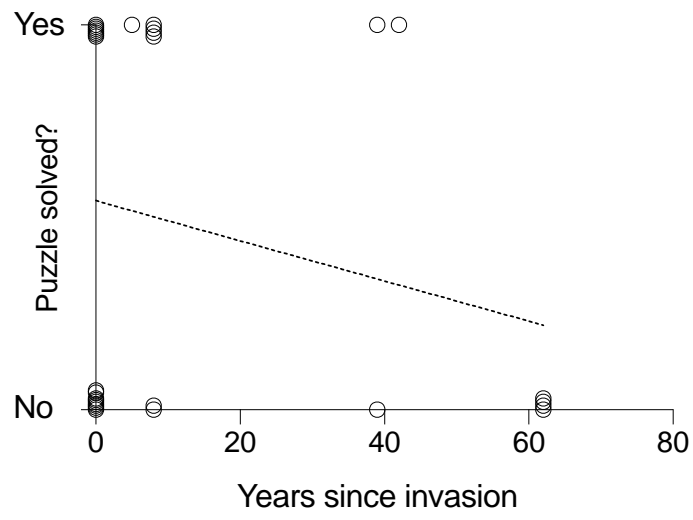


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412 **Figure 3**

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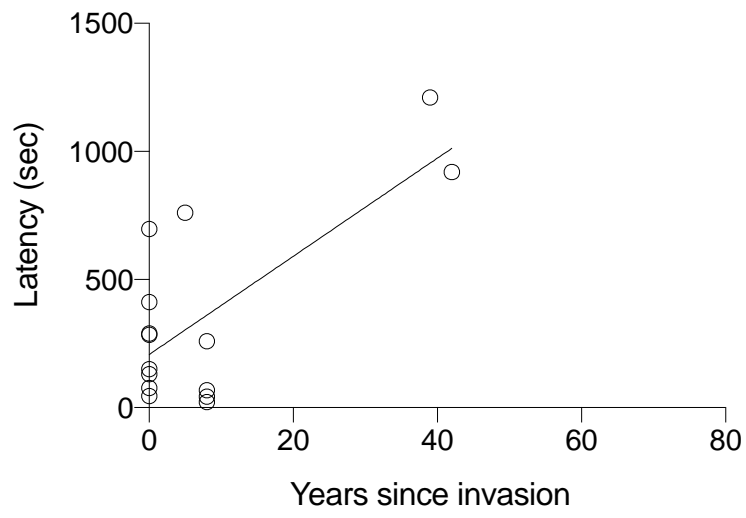


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416 **Figure 4**

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420 **Figure captions**

421

422 **Fig. 1** Study sites in which we assessed the behaviour and cognition of lace monitors
423 (*Varanus varius*) in areas with (circles) and without (squares) cane toads (*Rhinella marina*).
424 Numbers represent the number of years for which cane toads have been present at each site

425

426 **Fig. 2** Photos of the prey acquisition apparatus used in this study, showing the puzzle with
427 the (a) outer sleeve in the closed position, and (b) with the outer sleeve rotated 180° in the
428 solved position

429

430 **Fig. 3** The proportion of lace monitors (*Varanus varius*) that solved a novel prey acquisition
431 task as a function of the number of years since the site was invaded by cane toads (*Rhinella*
432 *marina*)

433

434 **Fig. 4** The mean time required by lace monitors (*Varanus varius*) to solve a novel prey
435 acquisition task as a function of time since invasion of the site by cane toads (*Rhinella*
436 *marina*)

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438