

1 **Title:** Not such silly sausages: Northern quolls exhibit aversion to toads after training with  
2 toad sausages.

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26 **Abstract**

27 The invasion of toxic cane toads (*Rhinella marina*) is a major threat to northern  
28 quolls (*Dasyurus hallucatus*) which are poisoned when they attack this novel prey item.  
29 Quolls are now endangered as a consequence of the toad invasion. Conditioned taste aversion  
30 can be used to train individual quolls to avoid toads, but we currently lack a training  
31 technique that can be used at a landscape scale to buffer entire populations from toad impact.  
32 Broad scale deployment requires a bait that can be used for training, but there is no guarantee  
33 that such a bait will ultimately elicit aversion to toads. Here we test a manufactured bait—a  
34 ‘toad sausage’—for its ability to elicit aversion to toads in northern quolls. To do this, we  
35 exposed one group of quolls to a toad sausage and another to a control sausage and compared  
36 the quolls’ predatory responses when presented with a dead adult toad. Captive quolls that  
37 consumed a single toad sausage showed substantially reduced interest in cane toads,  
38 interacting with them for less than half the time of their untrained counterparts and showing  
39 substantially reduced attack behaviour. We also quantified bait uptake in the field, by both  
40 quolls and non-target species. These field trials showed that wild quolls were the most  
41 frequent species attracted to the baits, and that approximately 61% of quolls consumed toad-  
42 aversion baits when first encountered. Between 40-68% of these animals developed aversion  
43 to further bait consumption. Our results suggest that toad-aversion sausages can be used to  
44 train wild quolls to avoid cane toads. This opens the possibility for broad-scale quoll training  
45 with toad aversion sausages: a technique that may allow wildlife managers to prevent quoll  
46 extinctions at a landscape scale.

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## 50 **Introduction**

51 Invasive species are a major threat to biodiversity (Reaser *et al.* 2007; Woinarski, Burbidge  
52 & Harrison 2014). In Australia, species such as feral cats (*Felis catus*) (Legge *et al.* 2017),  
53 domestic dogs (*Canis familiaris*) (Doherty *et al.* 2017), foxes (*Vulpes vulpes*) (Short & Smith  
54 1994; Risbey *et al.* 2000) and cane toads (*Rhinella marina*) (Burnett 1997; Letnic, Webb &  
55 Shine 2008; Jolly, Shine & Greenlees 2015) all have serious impacts on native species.  
56 Controlling these species at a landscape scale, however, has proved extremely difficult  
57 (Ziembicki *et al.* 2015). Because of this, increasing attention is being paid to mitigating the  
58 impact of invasives, rather than suppressing their populations (Simberloff *et al.* 2013).

59 Cane toads are a case in point. These invasive amphibians now occupy more than 1.5  
60 million square kilometres of Australia, continue to spread (Urban *et al.* 2007), and have  
61 proved difficult to control. The cane toads' defensive chemicals (bufadienolides and related  
62 toxins) are highly cardioactive and are unlike toxins possessed by native Australian animals  
63 (Hayes *et al.* 2009). As a result, many vertebrate predators, including varanid lizards, snakes,  
64 and marsupial predators such as quolls, die after attacking or consuming toads (Covacevich  
65 & Archer 1975; Webb, Shine & Christian 2005; Smith & Phillips 2006; Hayes *et al.* 2009;  
66 Shine 2010). Some reptilian predator populations have adapted to the presence of toads by  
67 evolving innate aversion to toads (Phillips & Shine 2005; Llewelyn *et al.* 2011). In the short  
68 term, some marsupial predators rapidly learn to avoid toads as prey (Webb *et al.* 2008; Webb,  
69 Pearson & Shine 2011). An obvious avenue for mitigating the impact of toads, then, is to  
70 train predators to avoid toads (Webb *et al.* 2008).

71 Such training can be achieved through conditioned taste aversion (CTA).  
72 Conditioned taste aversion is a powerful innate response found across all vertebrates; an  
73 evolved defence mechanism against poisoning (Sinclair & Bird 1984; Conover 1995; Cohn &

74 MacPhail 1996; Bernstein 1999; Mappes, Marples & Endler 2005; Page & Ryan 2005;  
75 Glendinning 2007). With CTA, animals acquire an aversion to a referent food as a result of a  
76 nauseating experience (Gustavson & Nicolaus 1987). Agriculturalists and wildlife managers  
77 have used conditioned taste aversion to reduce wildlife damage to crops, industry, or  
78 livestock (Gustavson *et al.* 1974; Ellins & Catalano 1980; Avery 1985; Provenza *et al.* 1990;  
79 Ternent & Garshelis 1999; Smith *et al.* 2000). CTA has also been used successfully to reduce  
80 predation on native or introduced wildlife (Nicolaus & Nellis 1987; Conover 1989; Nicolaus  
81 *et al.* 1989; Semel & Nicolaus 1992; Avery *et al.* 1995; Bogliani & Fiorella 1998; Cox *et al.*  
82 2004).

83         One of the Australian species most strongly impacted by cane toads is the northern  
84 quoll, *Dasyurus hallucatus*. As toads have spread, they have caused numerous local  
85 extinctions of this native marsupial predator (Burnett 1997; Oakwood & Foster 2008). CTA  
86 training using small toads infused with the nausea inducing chemical thiabendazole (TBZ)  
87 elicits aversion to live toads in northern quolls (O'Donnell, Webb & Shine 2010), suggesting  
88 the technique has promise as a management tool for mitigating toad impact. Capacity to  
89 elicit aversion is, however, only the first hurdle. To be effective as a management tool, CTA  
90 needs to meet two additional conditions. First, CTA training needs to be deliverable to a large  
91 number of individuals under field conditions. Second, prey aversion needs to occur in a large  
92 enough proportion of the population, and be behaviourally persistent for long enough (within  
93 and across generations), that population-level benefits are realised. In quolls, it is clear that  
94 CTA training in captivity can be used to elicit toad aversion, and that this aversion improves  
95 survival rates when animals are released into the field (O'Donnell, Webb & Shine 2010).  
96 More importantly, parentage analyses demonstrated that some offspring of surviving 'toad  
97 smart' females also survived and reproduced (Cremona *et al.* 2017), suggesting that training a

98 single generation could yield significant conservation benefits. The remaining challenge then  
99 is to effectively deliver CTA training to a large number of individuals under field conditions.

100 In captivity, CTA training was achieved by feeding quolls a small non-lethal-sized  
101 toad laced with the nausea-inducing chemical thiabendazole. Such a strategy is not feasible at  
102 a large scale in a field setting. To achieve in situ training at scale requires use of a  
103 manufactured training bait. Any bait, of course, needs to fulfil the criteria we have identified  
104 above: elicits aversion to toads, has a high uptake rate; and effectively trains a high enough  
105 proportion of the population that population persistence is assured. An additional  
106 consideration is whether the bait is taken by non-target species. This is a major concern in  
107 lethal baiting campaigns (Sinclair & Bird 1984; Avery *et al.* 1995; Fairbridge *et al.* 2003;  
108 Glen & Dickman 2003; Claridge & Mills 2007; Jolley *et al.* 2012), but a smaller  
109 consideration in non-lethal baiting such as we envisage here. Non-target uptake remains  
110 important, however, because it can reduce target species' access to bait and so significantly  
111 increase the cost and complexity of the baiting effort. Because of this, it is important to  
112 understand non-target species uptake rates.

113 In this study we assess the value of a manufactured bait ('toad aversion sausages').  
114 We ask whether quolls generalise their CTA from the bait to toads, whether the bait is taken  
115 up by wild quolls (and non-target species), and whether it appears to elicit CTA under field  
116 conditions.

## 117 **Methods**

### 118 *Cane toad sausages*

119 Cane toad sausages were made up of 15g of minced skinned adult cane toad legs, 1 whole  
120 cane toad metamorph weighing <2g, and 0.06g of Thiabendazole (per sausage; dose rate less  
121 than 300mg/kg adult quoll body weight, determined by the smallest – 200g – adult seen at

122 our study site) packed into a synthetic sausage skin. In our captive trials, we used the same  
123 sausage composition, to accurately reflect our field scenario. Thiabendazole is an  
124 inexpensive, broad-spectrum anthelmintic and antifungal agent (Robinson, Stoerk & Graessle  
125 1965). It is orally-effective and regarded as relatively safe, producing low mammalian  
126 mortality: oral LD<sub>50</sub> is 2.7g/kg body weight (Dilov *et al.* 1981). It is fast acting and peak  
127 concentration occurs in the plasma one hour after consumption (Tocco *et al.* 1966).  
128 Thiabendazole has produced strong aversions to treated foods in lab rats (Gill, Whiterow &  
129 Cowan 2000; Massei & Cowan 2002), wolves (*Canis lupus*) (Gustavson, Gustavson &  
130 Holzer 1983; Ziegler *et al.* 1983), and black bears (*Ursus americanus*) (Ternent & Garshelis  
131 1999). Thiabendazole induces a robust CTA after a single oral dose (Nachman & Ashe 1973;  
132 O'Donnell, Webb & Shine 2010) and is physically stable at ambient conditions in the bait  
133 substrate (Gill, Whiterow & Cowan 2000; Massei, Lyon & Cowan 2003).

#### 134 *Captive trials*

135 The uptake of toad aversion sausages by *D.hallucatus* and their subsequent response to toads  
136 was observed in captive northern quolls previously collected from toad-free areas of Astell  
137 Island, and then housed at the Territory Wildlife Park, Northern Territory. Animals (9 male  
138 and 9 female) were randomly allocated treatment ( $n= 9$ ) or control ( $n=9$ ) sausage groups.  
139 Treatment sausages were exactly as described previously. Control sausages were comprised  
140 of store purchased beef sausages. These were selected as a control sausage as it was an item  
141 that animals are also not familiar with to control for hunger differences and any possible  
142 neophobic responses.

143 To measure individual responses to cane toads following ingestion of sausage, each  
144 individual was presented with a dead adult cane toad the following evening. The dead adult  
145 toad was secured in a wire cage, so that animals could see and smell the prey item but not

146 access it. The experiment was run over 3 nights. Experiments began at sunset and ran for on  
147 average 2 hours. The response was filmed using a GoPro Hero 3 White camera (GoPro Inc,  
148 San Mateo, California, USA).

## 149 **Field trials**

### 150 *Study area*

151 The field study was conducted between May 2016- February 2017 at Mornington Wildlife  
152 Sanctuary, a 300,000 ha property in the central Kimberley region of western Australia  
153 managed for conservation by the Australian Wildlife Conservancy (17°01'S, 126°01'E; Fig.  
154 1). The area is characterized by savanna woodland dissected by sandstone gorges of varying  
155 topographic complexity. On average, this area receives 788 mm of rain annually, most of  
156 which falls during the wet season from November to April.

157 We worked at four sites on the property; Site 1 (SJ) was at Sir John Gorge  
158 (17°31.780S, 126°13.080E) along the Fitzroy River. Site 2 (KP) (17°31'43.032,  
159 126°13'11.050) was approximately 2 km upstream from Site 1 in the same gorge. Site 3 (TC)  
160 (17° 30' 37.213,126°14'4.092) was 5 km upstream from Site 2 in a narrow rocky gorge that  
161 feeds into Sir John Gorge. Site 4 (RP) (17°35'12.119, 126°19'21.959) was a narrowly incised  
162 sandstone gorge following a watercourse within rocky range country approximately 9 km  
163 north-east of Site 1. Sites were selected based on the detection of quolls in the Australian  
164 Wildlife Conservancy's fauna surveys (AWC unpub. data). At the time of the study, toads  
165 were yet to arrive at our sites; they subsequently arrived by March 2017.

### 166 *CTA sausage field trials*

167 In this study, "site" is the location where an experiment took place. "Bait station" is a  
168 location within a site where sausage bait was offered. A "session", is a time interval when  
169 bait stations were active. A total of four sessions were conducted approximately five months

170 apart. Sessions recorded up to four “bait events”. Bait Events are defined as an occasion  
171 when new bait was placed at a bait station and (if still existing) the old bait removed.

172 Each site contained 20 bait stations placed 50-80m apart in a linear transect along a  
173 gorge wall where the presence of *D. hallucatus* was previously confirmed (AWC, unpub.  
174 data). Bait stations consisted of one cane toad sausage placed under a single camera trap  
175 (White flash and Infrared Reconyx Motion Activated, (HP800, U.S.A). Cameras were  
176 secured to trees or rocky ledges approximately 1m from the ground and aligned to face  
177 directly downwards (Diete *et al.* 2016). Cameras were set to take five consecutive  
178 photographs for each trigger with no delay between triggers. Each cane toad sausage was  
179 placed inside a ring of powdered insecticide (Coopex) to protect from ant spoilage. Each  
180 session’s bait stations were rebaited up to three times (for a maximum of 4 bait events within  
181 any given session) whereby bait stations were rebaited with a fresh CTA bait and the old bait  
182 removed (Table 1). A total of 513 individual cane toad sausages were deployed over the  
183 period of study.

## 184 **Data analysis**

### 185 *Captive trials*

186 Videos were scored by the same observer who was blind to the quoll’s treatment or control  
187 group. Following Kelly and Phillips (2017) we separated the time that quolls spent  
188 exhibiting various predatory behaviours into three categories: “Sniff”, “Investigate” and  
189 “Attack”. Sniff was defined as when quolls were visibly twitching their nose in the direction  
190 of the toad, “Investigating” behaviour was defined as the quoll being engaged with the cage  
191 containing the toad, exhibiting scent marking or digging around the outside of cane toad  
192 enclosure and “attack” behaviour was defined as quolls exhibited pawing or licking or biting  
193 behaviour to toads cages. We summed all of these to measure the total time spent interacting



194 with a toad. We converted each of these variables to a proportion of time spent in each of  
195 these activities, where the denominator was the total time that the animal was observable on  
196 camera. These response variables were not normally distributed, and could not be made to  
197 conform to normality through transformation. Because of this we used bootstrapping to  
198 obtain confidence intervals for the mean time engaged in each behaviour, and to test the null  
199 hypothesis that there was no difference between treatments in mean time spent in each  
200 activity. The perception that animals exhibit a lower propensity towards attacking a prey item  
201 following ingestion and subsequent malaise during CTA training is non-controversial  
202 (Gustavson *et al.* 1974; Gustavson *et al.* 1976; Gustavson 1982; Gustavson & Basche 1983;  
203 Gustavson, Gustavson & Holzer 1983; Ziegler *et al.* 1983; Gustavson & Nicolaus 1987;  
204 Nicolaus 1987; Nicolaus & Nellis 1987; Nicolaus *et al.* 1989; Schneider & Pinnow 1994;  
205 Smith *et al.* 2000; Riley & Freeman 2004; Sevelinges *et al.* 2009; O'Donnell, Webb & Shine  
206 2010; Thornton & Raihani 2010; Thornton & Clutton-Brock 2011). More relevant to this  
207 study is the outcomes of previous trials by O'Donnell, Webb and Shine (2010) and Kelly and  
208 Phillips (2017) where quolls exhibited less interest in prey items after consuming a toad  
209 metamorph laced with thiabendazole. Based on these previous results, we had a strong *a*  
210 *priori* expectation that animals could either be unaffected or only become less interested in  
211 toads after ingestion of cane toad sausages. Thus, we employed a one-tailed test, with the  
212 alternative hypothesis that the mean time spent investigating and attacking toads will be  
213 lower in the treatment group. This analysis was performed using R (R Core Team, 2016).

#### 214 *Field trials*

215 Images from bait stations were collated and tagged by pass, session, site, bait-event, species  
216 and activity. A 'pass' was defined as when a new species entered the frame or when images  
217 that were at least 5 minutes between when the previous detection of the same species passed.  
218 This reduced any likelihood of individuals of the same species being overlooked during

219 analysis. “Activity” was hierarchical, with the highest activity being ‘Bait taken’; this was  
220 defined as either photographic evidence of animal eating bait or bait being taken from the bait  
221 station. ‘Bait investigated’ was defined as when bait was sniffed but not consumed or taken.  
222 ‘Bait area investigated with no bait available’ was defined as when no bait was available at a  
223 bait station, but the animal was still visiting or investigating the bait station.

224 We analysed data using two levels of observation to determine 1) which species were  
225 attracted to bait, and 2) which species took bait. A frequency distribution ( $n$  times each  
226 species was recorded) was calculated and the proportion of bait takers in each species was  
227 estimated. Passes in which we were unable to identify the species were pooled and removed  
228 from further analysis. Additionally, if a species total number of visits was less than 10 we  
229 removed that species from the analysis. Additionally *Varanus tristis*, *V. panoptes*, *V. mitchelli*  
230 and *V. mertensi* were pooled into ‘*Varanus* other species’ due to small sample sizes.

231 We identified individual *D. hallucatus* that visited bait stations by their unique spot patterns  
232 (Hohnen *et al.* 2013) to determine visitation rate and bait uptake of individuals. To do this we  
233 employed Wild ID (Version 1.0, January 2011) (Bolger *et al.* 2011) to extract distinctive  
234 image features in animals spot patterns, the program calculates a matching score that  
235 characterizes the goodness of fit between two images. These matching scores were then used  
236 to rank and select matches to each focal image. We also conducted manual checks with all  
237 photographs and compared them to those already identified to determine whether a new  
238 individual had been recorded. Quolls were identified to individual within each session, and  
239 we treat each session (separated by a minimum of four months) as independent with regard to  
240 quoll ID and behaviour. This decision was made for logistical reasons (difficulty of  
241 identifying individuals using spot ID), but is supported by exploratory analysis of first pass  
242 uptake rates showing that these do not vary systematically with session (see Results). It is

243 likely, therefore, that any training is forgotten within the 4-5 month window between  
244 sessions.

## 245 **Results**

### 246 *Captive trials*

247 Of the treatment animals, seven (77%) consumed all or part of a cane toad sausage and eight  
248 (88%) control animals consumed beef sausages. Treatment had no significant effect on  
249 whether the initial sausage was consumed, ( $\chi^2 = 0.0$ ,  $df = 1$ ,  $p = 1$ ). In our video trials, quolls  
250 spent an average of only 0.6% of the total time on camera interacting with the toad. Control  
251 animals, however, spent more than twice as much time interacting with the toad than  
252 treatment animals (control = 0.95%; treatment = 0.42%, bootstrap p-value = 0.022). When  
253 we break this down by specific types of interaction, control animals spend approximately  
254 sixty times longer investigating (control = 0.15%; treatment = 0.00024%, bootstrap p-value =  
255 0.051); twice as much time sniffing (control = 0.70%; treatment = 0.35%, bootstrap p-value =  
256 0.044); and twenty times more time attacking (control = 0.03%; treatment = 0.0015%,  
257 bootstrap p-value = 0.036) toads when compared with the control (Figure 2).

### 258 *Field trials*

#### 259 *Target and non-target uptake*

260 A total of 26 species were captured on camera traps visiting bait stations. For eleven of these  
261 species, there were sufficient data to compare their response to bait uptake. The most  
262 frequent visitors to the bait stations were quolls, with  $n = 345$  passes (Figure 3). Almost all  
263 bait removal was executed by quolls that took 65 baits of the 90 baits removed. Other species  
264 took far fewer: *Zyomys argurus*, 9; *Ctenotus spp.*, 2; *Pseudantechinus ningbing*, 2; *Varanus*  
265 *glauerti*, 2; and *Varanus glebopalma*, 2.

#### 266 *Target uptake and training rates*

267 First pass uptake responses to the bait did not vary systematically across sessions ( $\chi^2=1.7$ ,  
268  $df=4$ ,  $p=0.79$ ; Fig. 4). We thus treated individuals as independent across sessions with regard  
269 to behaviour.

270 Following identification of individual quolls within sessions, it became apparent that  
271 bait stations were visited by a total of 70 “individual” quolls over the period of the study. Of  
272 these individuals, and considering only their first bait encounter, the bait was taken by 28  
273 individuals and rejected (bait investigated but not taken) by 18 individuals. Thus the total  
274 bait uptake rate at first encounter was 61% ( $SE=7.2\%$ ). A further 24 individuals only visited  
275 bait stations when there was no bait available.

276 Across all passes, a total of 31 quolls consumed a bait. Ten of these animals ultimately  
277 consumed baits on more than one occasion within a session (32%,  $SE=8.3\%$ ). Clearly, these  
278 individuals were not effectively trained, failing to even exhibit aversion to the bait. We have  
279 two ways of estimating the conversion rate (from untrained to trained, given bait  
280 consumption). Placing an upper bound, we could consider all individuals that took a bait but  
281 were not observed to take a second bait (20 of 31 = 68%) as trained. For a lower bound, we  
282 could take the conservative approach and consider only those known to have consumed a bait  
283 and then seen to approach and reject a bait as trained (7 of 17 = 41%). Thus, somewhere  
284 between 41 and 68% of animals consuming a bait appear to have been trained.

## 285 **Discussion**

286 Our captive trials clearly indicate that training a quoll using a thiabendazole-laced toad  
287 sausage changes their behaviour towards toads. Although our sample sizes were modest and  
288 not all of our treatment animals fully consumed the bait, it is clear that sausage-trained  
289 animals spent substantially less time interacting with a toad —between one half to one  
290 sixtieth of the time as control animals. This behavioural shift is reflected across all prey

291 acquisition behaviours: investigating, sniffing, and attacking. Quolls clearly generalise their  
292 acquired aversion from the bait to a real toad.

293         The field trials show that the toad sausages are attractive to quolls. Although 26  
294 species encountered the baits, quolls were the most frequent visitors to the bait at our study  
295 sites, and were far and away the most likely species to consume the bait. Thus, non-target  
296 uptake is relatively modest, compared with the high level of uptake of baits by non-target  
297 animals observed in other lethal-baiting studies (Cowled *et al.* 2006; Dundas, Adams &  
298 Fleming 2014) It is more difficult to estimate the rate of successful training in the field, but it  
299 is likely that between 41-68% of animals consuming a bait in the field have been successfully  
300 trained. The apparent independence of quoll behaviour to bait uptake across sessions also  
301 suggests that, in the absence of further reinforcing stimulus (i.e., cane toads), CTA training  
302 potentially only elicits aversion for a limited time (<4 months).

303         The TBZ dose of <300mg/kg animal body weight in our cane toad sausages was  
304 relatively low compared to earlier work (400mg/kg in (Jolly *et al.* unpublished data;  
305 O'Donnell, Webb & Shine 2010; Cremona *et al.* 2017; Kelly & Phillips 2017) but was set  
306 low by regulators (Australian Pesticides and Veterinary Medicines Authority- (APVMA)) to  
307 allow for potential multiple bait uptake, sub-adult target, and non-target species. Given the  
308 LD<sub>50</sub> of TBZ is more than nine times higher than our dose rate; the delivered dose is very  
309 conservative. Our results suggest, however, that it is still effective. Regulators (APVMA)  
310 also limited the number of treatment baits available at a site at any one time to 30 baits per  
311 hectare. It is clear from our study that, at this density of baits, many quolls are simply not  
312 encountering the bait; arriving at the bait station after baits have been taken; this in a  
313 relatively low density quoll population, and despite multiple bait events at each site. Thus, to  
314 effectively bait a large proportion of the quolls at a site (particularly a high density site), a  
315 greater density of baits will be required.

316 In addition to the high visitation rate of individual quolls to bait stations, some  
317 individual quolls took baits on multiple occasions. Of the 70 “individual” quolls that visited  
318 bait stations throughout study period, ten individuals consumed a cane toad sausage on more  
319 than one occasion within a session. Why did these individuals manifestly fail to train? One  
320 possibility is the low dose rate, 0.06g of TBZ in each sausage was calculated to provide  
321 300mg/kg to the smallest adult quoll at our site; a 200g female. Long-term trapping at the  
322 site (AWC, unpub. data) suggests that adult quolls in this population can reach more than  
323 815g in weight. Thus, large animals could receive less than one quarter of the dose ingested  
324 by small animals. As a consequence, we could expect larger animals (typically males) to be  
325 harder to train with a fixed-dose bait. Another possibility is that these individuals were  
326 unhealthy for other reasons (e.g., males in the process of annual die-off) and so were willing  
327 to risk poisoning in order to acquire food, although such a mechanism would presumably  
328 cause changes in uptake rate across sessions, so seems unlikely.

329 Our results also hint strongly that individuals lose their acquired aversion over the 4-5  
330 month window between our baiting sessions. There was no evidence that first pass rates of  
331 bait uptake declined over time across sessions. Whether this aversion would decline in the  
332 presence of ongoing stimulus (i.e., continuous baiting, or the presence of toads) is unknown,  
333 but long-term mark-recapture studies of CTA-trained quolls released into toad-infested  
334 landscapes suggest that aversion can be long-held in the presence of reinforcing stimulus  
335 (Cremona *et al.* 2017). Nonetheless, our finding should sound a note of caution with regard  
336 to deployment of CTA. Training prior to toad arrival will need to be delicately timed: too  
337 early, and trained animals may lose their aversion before toads arrive. This need for  
338 precision timing is complicated by inevitable uncertainty with regard to where the toad  
339 invasion front is, and when it will arrive at the site (with spread rate also being contingent on

340 the unpredictable timing of the wet season in northern Australia). Thus, any baiting  
341 campaign will need to dedicate effort to predicting the date of toad arrival at the site.

342 Overall, however, our study is encouraging with regard to the use of toad sausages as  
343 a vehicle for large-scale CTA training of quolls. Our results suggest that quolls will consume  
344 cane toad sausages in the field and will, as a consequence, be less inclined to attack cane  
345 toads. This opens the possibility for broad scale application of CTA as a management  
346 technique for mitigating the impact of toads on quolls.

347 While many questions remain about optimal bait design, delivery, and timing, it is  
348 clear that CTA training using toad sausages is likely a viable tool for land managers seeking  
349 to protect quoll populations. Given that quoll populations in the Kimberley will likely be  
350 completely overrun by toads within the next five years, this is a tool that is urgently needed.  
351 More generally, however, our work joins a growing list of studies demonstrating that the  
352 impact of invasive species can be mitigated not only by controlling the invasive species, but  
353 also – or instead - by manipulating its mechanism of impact.

#### 354 **Authors' Contributions**

355 All persons who meet authorship criteria are listed as authors, and all authors certify that they  
356 have participated sufficiently in the work to take public responsibility for the content,  
357 including participation in the concept, design, analysis, writing, or revision of the manuscript.

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### 369 **Data accessibility**

370 Data and scripts are available upon request.

### 371 **Compliance with Ethical Standards**

372 The study was conducted within Mornington Wildlife Sanctuary in accordance with Wildlife  
373 Conservation Regulation 17 (Permit number: SFO10584). The area is jointly managed by  
374 traditional land-owners and the Australian Wildlife Conservancy. The research was approved  
375 by the University of Melbourne Animal Ethics Committee (Protocol: 1413369.2) and the  
376 University of Technology Sydney Animal Care and Ethics Committee (Protocol: 2012-432A)  
377 and Department of Parks and Wildlife Animal Ethics Committee (Protocol: DPaW AEC  
378 2016\_50 and Protocol 2013\_37). Additionally this study was conducted in accordance with  
379 the approved outline submitted to the AVPMA by the investigating team (Permit to allow the  
380 possession and supply for research use of an unregistered Agvet chemical product. Permit  
381 number: PER92262).

382

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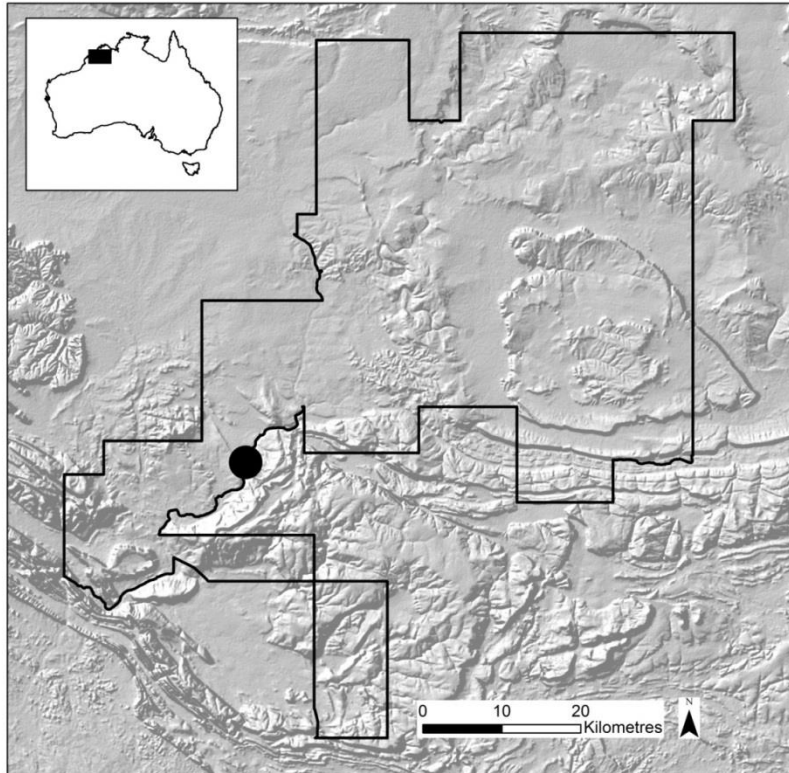


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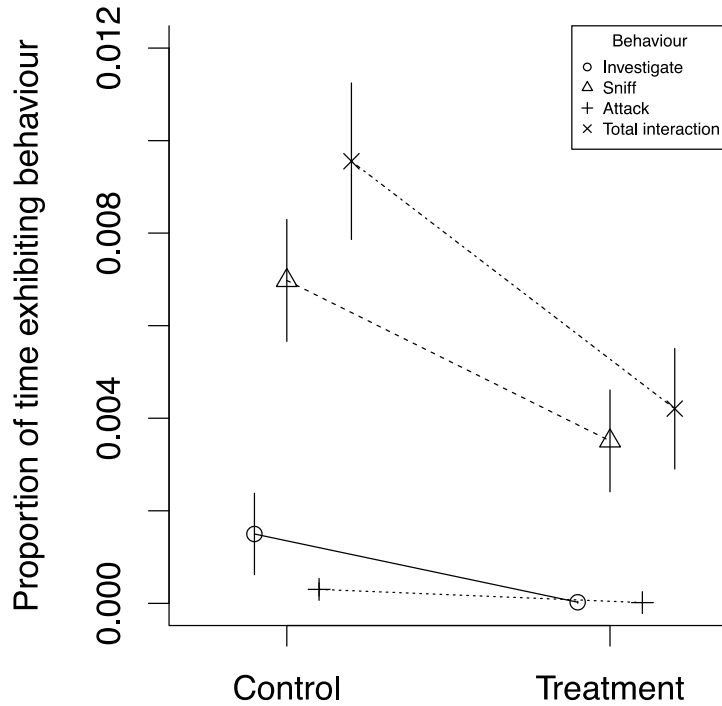
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## 591 **Figures**



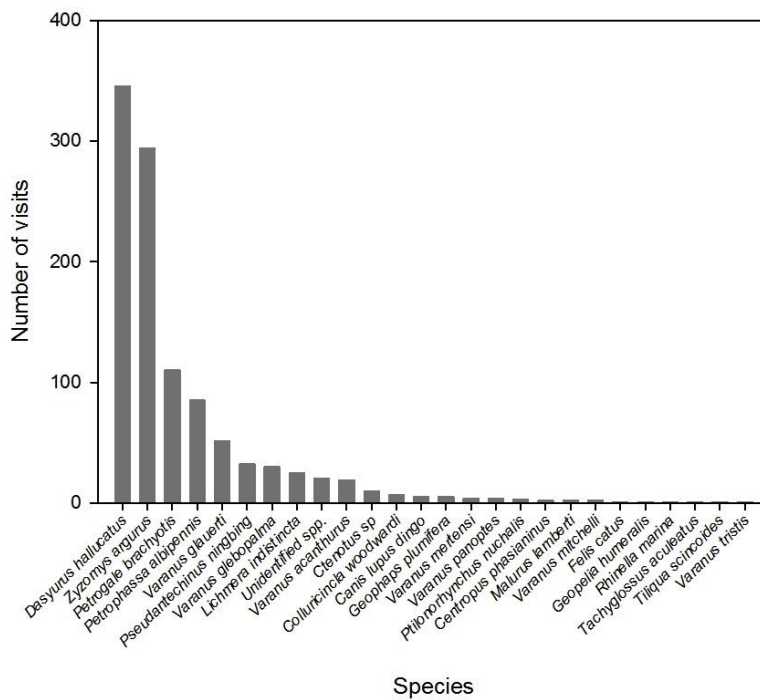
**Figure 1:** Location of the study area within Australian Wildlife Conservancy's Mornington Wildlife Sanctuary, in the central Kimberley, Western Australia.

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**Figure 2:** Mean proportion of active time that quolls spent directed towards toads. Behaviours are split into categories and across control and treatment groups. Error bars represent bootstrap standard errors.

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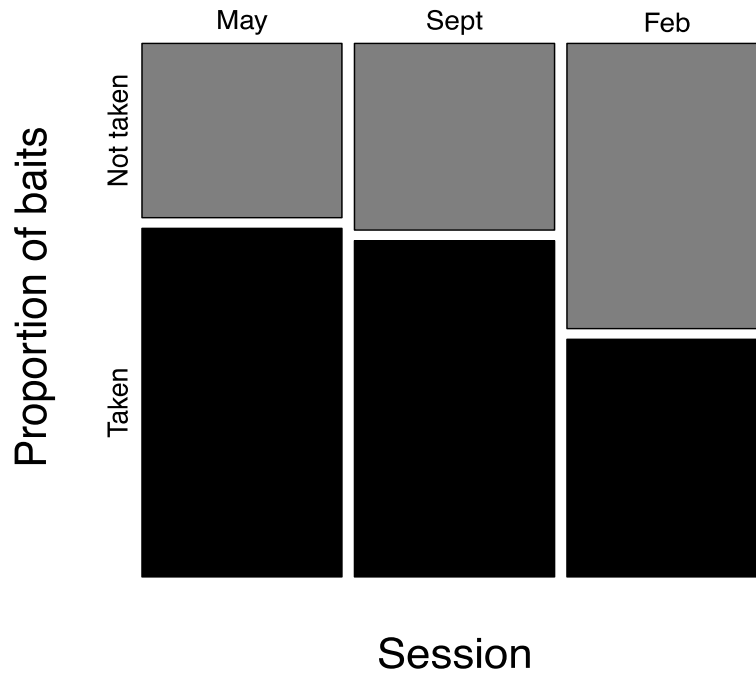
**Figure 3:** Frequency of visits to CTA bait stations by each species. Unidentified species group comprises unidentified rodents, birds, and frogs.

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**Figure 4:** First pass behavioural responses of northern quolls to the bait each session. “Sept” includes the one November session also.

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599 **Tables**

Site Name	Session Year	Session Month	No. Bait Events (BE)	BE 1-date	BE 2-date	BE 3-date	BE 4-date	No. of bait stations <sup>600</sup> <sub>601</sub>
KP	2016	Nov	1	31/10/16	1/11/16	2/11/16	*	20
RP	2017	Feb	1	3/2/2017	*	*	*	20
RP	2016	May	3	10/5/16	13/5/16	21/5/16	*	20
RP	2016	Sept	3	15/9/16	16/9/16	17/9/16	*	20
SJ	2017	Feb	1	3/2/2017	*	*	*	20
SJ	2016	May	3	10/5/16	13/5/16	21/5/16	*	20
SJ	2016	Sept	4	15/9/16	16/9/16	17/9/16	19/9/16	20
TC	2017	Feb	1	3/2/2017	*	*	*	33
TC	2016	May	3	10/5/16	13/5/16	21/5/16	*	20
TC	2016	Sept	3	15/9/16	16/9/16	17/9/16	*	20

**Table 1:** CTA sessions and bait events, \* denotes empty cells. Bait events occurred at the same time within each site. KP was baited only once in November to expand the sample size and CTA train quolls prior to cane toad arrival.