

Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader

Stephanie O'Donnell, Jonathan K. Webb* and Richard Shine

School of Biological Sciences A08, University of Sydney, Sydney, NSW 2006 Australia

Summary

1. Even when we cannot eradicate an invasive species, we may be able to reduce its ecological impact. In Australia, a critically endangered predator, the northern quoll *Dasyurus hallucatus* is threatened by the invasion of the highly toxic cane toad *Bufo marinus*. Following toad invasion, quoll populations have become extinct across Northern Australia. Toads are continuing to spread, and will soon invade the Kimberley, one of the quoll's last strongholds. To prevent future local extinctions, we need a new approach for mitigating the impact of cane toads on this iconic predator.
2. We investigated whether conditioned taste aversion (CTA) could be used to modify quoll predatory behaviour and mitigate toad impacts. We successfully induced an aversion to live toads in juvenile northern quolls by feeding them a dead toad containing a nausea-inducing chemical (thiabendazole).
3. To investigate whether CTA enhanced quoll survival, we fitted radiocollars to 31 toad-smart and 31 toad-naïve quolls, and monitored their survival after reintroduction to the wild. We analysed telemetry data using the program MARK to investigate whether survival was influenced by sex or experimental treatment (toad-smart vs. toad-naïve).
4. Five of 17 (29%) toad-naïve male quolls died shortly after release, as soon as they encountered and attacked large cane toads. In toad-naïve quolls, apparent survival rates were higher for females (0.84) than for males (0.58), reflecting a sex difference in the propensity to attack toads. In both sexes, toad-smart quolls had higher apparent survival rates than did toad-naïve conspecifics (mean daily apparent survival rates for females, 0.94 vs. 0.84 respectively; for males, 0.88 vs. 0.58).
5. *Synthesis and applications.* Wildlife managers could aerially deploy taste aversion baits in the field, ahead of the toad invasion front, to teach toad-naïve quolls to avoid live cane toads before the toads invade such areas. This approach has wider applications, and could also be used to mitigate the impacts of invasive vertebrate predators on threatened fauna. When invasive predators cannot be eradicated, CTA may provide a feasible way to maintain populations of endangered fauna in the presence of the invader.

Key-words: conditioned taste aversion, invasive species, predator–prey, program MARK, reintroduction, survival

Introduction

One of the gravest threats to global biodiversity is the human-mediated movement of plants and animals beyond their natural distributions (Williamson 1996). Invasive species can substantially modify natural ecosystems, and have been implicated in the extinctions of numerous native animals (Fritts & Rodda 1998; Mack *et al.* 2000). In Australia, the impact of invasive species has been particularly severe. Half of all mammal species extinctions world-wide in the last two centuries

have occurred in Australia, and many more taxa persist only as remnant populations (Short & Smith 1994). These declines generally are attributed to introduced predators, such as cats *Felis catus* and foxes *Vulpes vulpes* (Dickman 1996; Risbey, Calver & Short 1997). For the past 80 years, management has focused on eradication and/or exclusion of the invasive predators. Although invasive species can be eradicated from small islands (Clout & Russell 2006), eradication is rarely possible on larger islands or continents, and long-term control programmes are labour-intensive and expensive (Reynolds & Tapper 1996; Harding, Doak & Albertson 2001). Even if captive-raised native fauna can be re-introduced, such

*Correspondence author. E-mail: jwebb@bio.usyd.edu.au

programmes experience little success if the threatening process is still in place and hence, the released animals suffer the same fate as their forebears (Armstrong & Seddon 2007). Because the control of many invasive species is difficult, we urgently need new approaches for reducing their ecological impact.

Conditioned taste aversion (CTA) could be used to ameliorate the impacts of some types of invasive species: those in which the mechanism of impact involves feeding behaviour. CTA occurs when an animal associates the taste of a food item with post-consumption illness, and thereafter avoids that food (Garcia, Hankins & Rusiniak 1974). A single negative experience can create a long-lasting aversion to prey in many animals (Gustavson 1977). We can use this response for conservation purposes, by adding an undetectable, nausea-inducing chemical to a previously appetising food item and thus modifying predator responses in subsequent encounters (Gustavson 1977). CTA has been used to reduce rates of predation on lambs by coyotes *Canis latrans* and wolves *Canis lupus* (Gustavson & Nicolaus 1987), predation by crows on the eggs of endangered birds (Nicolaus *et al.* 1983; Dimmik & Nicolaus 1990), and to discourage 'nuisance' bears from raiding food-stores (Ternent & Garshelis 1999). Because CTA produces the strongest aversions when the prey is novel (Gustavson 1977), the novelty of a native prey to an invasive predator (or *vice versa*) renders CTA ideally suited for use as a management tool in this context.

In Australia, the highly toxic cane toad *Bufo marinus* was introduced to Queensland in 1935 and has since spread across northern Australia (Lever 2001). Because toad toxins are very different to those found in native frogs, many native vertebrate predators die after attacking or consuming toads (Covacevich & Archer 1975; Webb, Shine & Christian 2005; Smith & Phillips 2006). In northern Australia, cane toads have caused severe population declines of varanid lizards (Griffiths & McKay 2007; Doody *et al.* 2009) and freshwater crocodiles (Letnic, Webb & Shine 2008), and have caused local extinctions of a marsupial carnivore, the northern quoll *Dasyurus hallucatus* (Burnett 1997; Woinarski *et al.* 2008). Shortly after cane toads colonised Kakadu National Park, the largest conservation reserve in northern Australia, quoll populations crashed, and several populations went extinct (Watson & Woinarski 2004; Oakwood 2008). These rapid extinctions led to the northern quoll being listed as endangered under the Australian *Environment Protection and Biodiversity Conservation Act* 1999.

Cane toads have invaded 60% of the quoll's historic geographic range and will cover that range entirely within the next two decades (Urban *et al.* 2007). To prevent the quoll from becoming extinct, wild-caught northern quolls were translocated to two toad-free offshore islands in 2003 (Rankmore *et al.* 2008). At the same time, the Territory Wildlife Park established a captive breeding programme to maintain genetic diversity and to facilitate future reintroductions to the wild. Despite these safeguards, there is no guarantee that offshore islands will remain toad-free, and reintroductions to mainland Australia are likely to fail unless we develop new methods for mitigating toad impacts on native

predators. We took advantage of the Territory Wildlife Park captive breeding and reintroduction programme to investigate whether we could use CTA to educate juvenile northern quolls to avoid cane toads. We then fitted radiocollars to toad-smart and toad-naïve quolls, and monitored their survival after reintroduction to the wild.

Materials and methods

STUDY SPECIES

The northern quoll is a cat-sized carnivorous marsupial that consumes fruits, insects, mammals, lizards and frogs (Oakwood 1997; Pollock 1999). Both sexes mature at 11 months of age, and females breed during their first year, with mean litter sizes of seven young (Oakwood 2000). Quolls have one breeding season each year, and although females can live for several years, a high proportion of males die following reproduction (Begg 1981; Dickman & Braithwaite 1992; Oakwood 2000). Quolls are nocturnal, and during the day they shelter in dens inside tree hollows, logs, rock crevices, termite mounds, under dense grass and inside burrows (Oakwood 1997).

CONDITIONED TASTE AVERSION

Juvenile quolls were housed singly in enclosures (6 × 4.5 × 2.25 m) at the Territory Wildlife Park, near Darwin, Northern Territory. Prior to release, we allocated quolls to two experimental groups: a CTA group, henceforth 'toad-smart' ($N = 31$: 15 males, 16 females) and a control group, henceforth 'toad-naïve' ($N = 31$: 17 males, 14 females). Between 1 and 7 days prior to release (mean = 3 days), we offered each toad-smart quoll a small (< 2 g) non-lethal dead toad (O'Donnell 2009) to which we added 400 mg kg⁻¹ body mass of the nausea-inducing chemical thiabendazole (Sigma-Aldridge, Sydney, Australia) in powdered form. To test whether CTA resulted in toad aversion, we tested the response of quolls from both treatment groups to a live toad. One to 2 days post-treatment, toad-smart quolls were given a small (< 2 g) live toad in an open-topped plastic container so that they could potentially attack and/or eat it. Toad-naïve quolls were offered a small live toad (< 2 g) in a plastic container (5 cm high, 19 cm wide) with mesh covering both ends. The quolls could see and smell the toad, but could not taste or eat it. This design enabled us to evaluate the responses of all quolls without compromising the toad-naïve status of the control group before they were released into the field. We filmed encounters with hidden video cameras and scored the feeding responses of individual quolls as either 'reject', 'attack' or 'ignore'.

RELEASE AND RADIO MONITORING OF JUVENILE QUOLLS

Prior to release, we fitted each quoll with a radiocollar containing a mortality sensor (Sirtrack, Havelock North, New Zealand) and applied a topical anti-parasite agent (Frontline, Merial, Australia). Collars weighed < 5% of quoll body mass and were designed to fall off the animals within a month. We released quolls at five sites between November 2008 and February 2009 (Table 1). Quolls were transported to the release sites in individual calico bags wrapped in a towel inside a box to reduce stress. We released animals at dusk (17:00–19:00 h) near hollow logs or dense undergrowth, and monitored them throughout the night. We attempted to keep quolls within sight for the first hour, and to obtain visual contact at least once an

Table 1. Release sites at which juvenile northern quolls were radiotracked to assess their daily survival after reintroduction to toad-infested habitats

Site name	GPS location (WGS 84 UTM)	N	Toad-smart		Toad-naïve	
			Males	Females	Males	Females
Territory Wildlife Park	0715680 8595490	11	3	3	3	2
Lake Bennett	0735402 8567668	4	1	0	2	1
Beatrice Hill Farm	0751442 8608320	5	1	2	0	2
Fogg Dam	0751471 8608766	14	3	4	3	4
Mary River Park	0787534 8571446	28	7	7	9	5

Individuals were either toad-smart (i.e. had received the conditioned taste aversion treatment) or were toad-naïve.

hour during the night. To estimate how many cane toads quolls encountered whilst foraging, we recorded the number of cane toads that we observed along the travel routes of 11 toad-naïve and 10 toad-smart quolls. On the following days, we located individuals every morning (if possible, to the animal's den site) and night, and recorded their location with a GPS (GPS 12XL; Garmin, Olathe, KS, USA). Because the transmitters were fitted with a mortality sensor (activated by cessation of movement), we could assess each animal's fate (alive, dead, or unknown with lost collar).

To assess the short-term survival of quolls, we radiotracked each quoll for a minimum of 10 days. After this time, we attempted to trap quolls by placing traps (up to 25 Elliot aluminium folding traps, baited with a mixture of oats, honey and peanut butter or day-old quail) near quoll den sites. We scanned all quolls captured in traps with a microchip reader to determine their identity. Hence, trapping allowed us to retrieve collars for use on other animals and determine the fate of quolls that had lost their collars prematurely. To reduce the numbers of 'uncertain fate' cases, we radiotracked from a helicopter at each site 30–42 days after the initial release. This allowed us to determine the status (alive vs. dead) of some missing animals and estimate how far they had travelled from their initial release sites.

We determined the cause of quoll mortality whenever possible. We attributed mortality to cane toad ingestion if sick or dying quolls exhibited symptoms similar to those reported in canine victims of toad ingestion: i.e., reddening of the oral mucosa, profuse salivation, progressive muscle paralysis, abnormal cardiac rhythms and convulsions (Roberts *et al.* 2000; Sakate & Oliveira 2000; Reeves 2004) plus the absence of any external injuries. We autopsied all dead quolls to check for known signs of toad poisoning, including gastrointestinal inflammation or haemorrhagic process, lung congestion, and oedema and haemorrhage caused by cardiac failure (Sakate & Oliveira 2000).

STATISTICAL ANALYSES

Feeding responses of quolls in the two treatment groups were compared using logistic regression with treatment group as the independent variable, and 'reject, attack or ignore' as the dependent variable. The encounter rates of toads by quolls were compared with a two-factor ANOVA. Both treatment and sex were incorporated into the analyses.

We used radiotelemetry to estimate the short-term (10 days) survival of toad-naïve and toad-smart quolls following their release. Our main aim was to determine whether or not CTA enhanced the survival of quolls following reintroduction to the wild. When the fate of all radiotagged animals is known, the Kaplan–Meier procedure can be used to estimate survival (Pollock, Winterstein & Conroy 1989). However, we could not determine the fate of all radiocollared

animals. Some collars fell off the quolls prematurely, and some quolls emigrated from the study sites, where their fate (alive vs. dead) could not be ascertained.

To estimate the apparent survival of northern quolls, we used a combination of data on encounters with live animals plus recoveries of dead animals, using the method of Burnham (1993). This method estimates apparent survival more accurately than do methods involving only data on live recaptures (Burnham 1993; Sandercock 2006). The Burnham model estimates four parameters: survival (S), the probability that a quoll alive on day t is also alive on day $t + 1$; fidelity (F), the probability that a quoll released on the study site on day t has not permanently emigrated from the site on day $t + 1$; recapture (p), the probability that a quoll which is alive is either re-sighted or recaptured during the sampling period; and reporting rate (r), the probability that a quoll that dies during the interval between occasions t and $t + 1$ is found. Although true survival can be estimated in some situations, in most field studies some animals permanently emigrate with unknown fate, so that only 'apparent survival' can be estimated (Burnham 1993; Francis & Cooke 1993; Francis & Sauro 2002). In our study, some animals emigrated with unknown fate; thus, we estimated apparent survival rather than true survival.

We used Program MARK version 5.1 to analyse the telemetry data (White & Burnham 1999). Data were entered using the LD format (Cooch & White 2006). We included two factors (treatment and sex) in the input data file, by assigning each individual to one of four groups (toad-naïve males, toad-naïve females, toad-smart males, toad-smart females). This procedure allowed us to test models which included the effects of sex, treatment and interactions between these factors in MARK. We first ran a series of candidate models in MARK to test four predictions: (i) toad-smart quolls would have higher survival than toad-naïve quolls (independent of sex); (ii) in each sex, toad-smart quolls would have higher survival than toad-naïve quolls; (iii) toad-smart males would have higher rates of survival than toad-naïve males, but survival of toad-smart and toad-naïve females would be similar; and (iv) females would have higher rates of survival than males, irrespective of treatment group. These predictions followed from our laboratory experiments which showed that CTA successfully induced an aversion to live toads, and that male quolls were more likely to attack cane toads than were females. We also tested whether survival rates varied with time, sex, treatment group or interactions between these factors. We also included null models where survival rates were constant across sex and treatment groups.

We used the Akaike Information Criterion (AIC) for model selection (Burnham & Anderson 1998). Prior to model selection, we used the bootstrap goodness-of-fit (GOF) procedure to evaluate the GOF of the most saturated (general) model S (group \times time), p (group),

r (constant), F (constant) (Cooch & White 2006). Based on 1000 bootstrap replicates, there was no evidence of lack of fit of this model to the data ($P = 0.26$). We calculated the variance inflation factor \hat{c} from the GOF statistics, which revealed no significant over-dispersion ($\hat{c} = 1.07$). However, to ensure parameter estimates were robust, we used the variance inflation factor to adjust the AIC values (termed corrected quasi-likelihood AIC or QAIC_c) and standard errors of parameter estimates (Cooch & White 2006). For each model, we calculated ΔQAIC_c , the difference between the QAIC_c for that model and the smallest QAIC_c among the set of models fitted, and Akaike weights. The best-supported models were those with $\Delta\text{QAIC}_c < 2$, and their relative difference in performance was assessed by the normalized likelihood of the models (Akaike weights; Burnham & Anderson 1998). Model averaging procedures were then used to estimate daily rates of apparent survival (Cooch & White 2006).

Results

EFFECT OF CTA ON QUOLL PREDATORY BEHAVIOUR

We obtained feeding responses from 15 toad-naïve (10 males, 5 females) and 19 toad-smart quolls (11 males, 8 females). Quoll feeding responses to cane toads were affected by the application of CTA (likelihood ratio test from logistic regression: $\chi^2 = 11.300$, 2 d.f., $P < 0.004$) and by quoll sex (likelihood ratio test: $\chi^2 = 11.334$, 2 d.f., $P < 0.004$). Toad-smart quolls were less likely to attack toads, and females were less likely to attack than were males (Fig. 1). During pre-release feeding trials, the only animals to attack live toads were males: four toad-naïve animals attacked toads in wire mesh-cages, and one toad-smart male bit and immediately rejected a toad unharmed. The remaining males (10 toad-smart and 5 toad-naïve individuals) all sniffed and rejected the toads. Five toad-naïve and two toad-smart females ignored toads, one toad-naïve female sniffed the toad before moving away from the container, and six toad-smart females sniffed the toad and rejected it unharmed.

RATES OF ENCOUNTERS WITH TOADS POST-RELEASE

The mean number of adult toads that quolls encountered after release neither differ significantly between toad-naïve and toad-smart animals (means of 3.5 vs. 5.3, $F_{1,17} = 0.79$, $P = 0.38$), nor between male and female quolls (means of 5.1 vs. 3.4, $F_{1,17} = 1.43$, $P = 0.25$, interaction $F_{1,17} = 1.20$, $P = 0.29$).

SOURCES OF QUOLL MORTALITY AFTER REINTRODUCTION

Most monitoring intervals were short (mean = 7 days, range: 0–24 days) for logistical reasons. Of 62 quolls released, 13 died soon after release, and we lost signals from another 8 animals due to equipment malfunction. Of eight cases where we could reliably identify the source of mortality, seven were caused by quolls attacking cane toads, and one was due to predation by a feral cat. Five of seven of the quolls killed by attacking toads were toad-naïve males (Table 2).

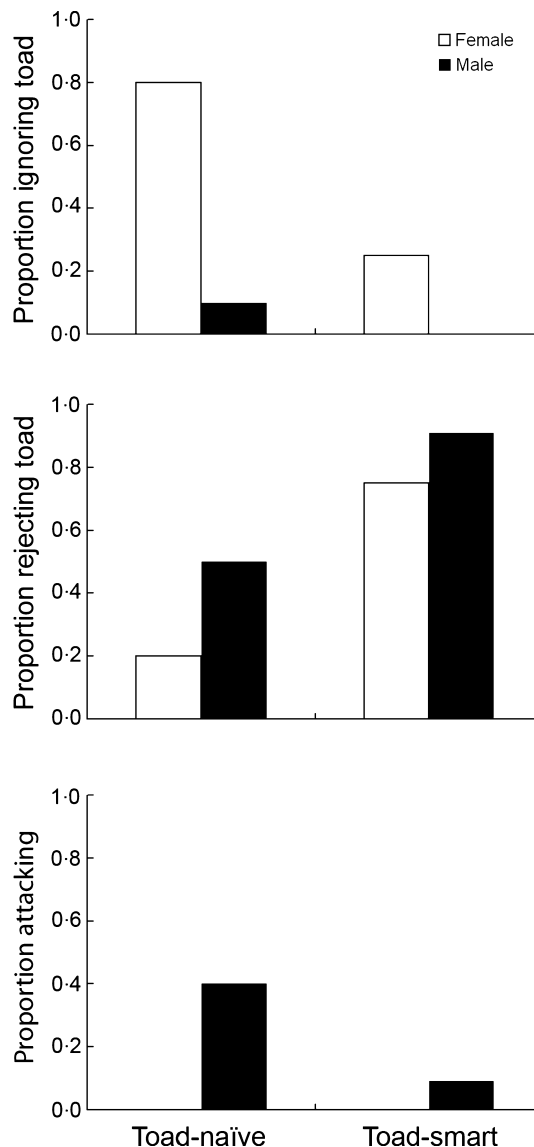


Fig. 1. Effects of sex and conditioned taste aversion on the feeding responses of captive-raised juvenile northern quolls *Dasyurus hallucatus* to cane toads *Bufo marinus* immediately prior to the quolls' release into the wild. Toad-smart quolls received a single dead toad laced with thiabendazole, a nausea-inducing chemical, whereas control quolls did not and were therefore considered as 'toad-naïve'.

EFFECT OF CTA ON SURVIVAL IN REINTRODUCED QUOLLS

On average, toad-smart quolls survived twice as long as toad-naïve females, and toad-smart males survived five times longer than toad-naïve males (Table 2, Fig. 2). Our evaluation of alternative models fitted to the mark-recapture and 'known death' data show that these treatment effects were highly significant. The best-supported model, $S(\text{group})$, $p(\text{group})$, $r(\text{constant})$ $F(\text{constant})$ was one in which toad-smart quolls had higher rates of apparent survival than did toad-naïve conspecifics of the same sex (Table 3). Model-averaged estimates of daily apparent survival were higher for toad-smart females ($S = 0.94$, $SE = 0.02$) and males ($S = 0.88$, $SE = 0.04$) than

Table 2. Fate of northern quolls released in the wild, as a function of the animal's sex and treatment (toad-smart vs. toad-naïve)

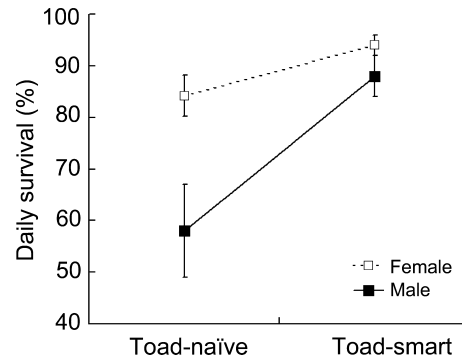
Group	Sex	<i>N</i>	Found dead	Number killed by toad poisoning	Mean time alive (days)	Range (days)
Toad-smart	Male	14	2	2	12.3	1–31
Toad-smart	Female	16	2*	0	10.17	0–20
Toad-naïve	Male	17	5	5	2.17	0–14
Toad-naïve	Female	15	4*	0	5.42	0–20

*Number killed by toad poisoning' indicates a minimum estimate, and includes only those cases where data were available to show causation, not all cases where this was a possible cause.

*The carcasses of two females released in the early stages of the study were recovered in follow-up telemetry fieldwork. These mortalities were not incorporated in statistical analyses of daily survival estimates because of uncertainty as to their times of death.

for toad-naïve females ($S = 0.84$, $SE = 0.04$) and males ($S = 0.58$, $SE = 0.09$). Thus, our second prediction, that training would enhance survival of quolls within each sex, was supported by the mark–recapture and dead encounter data.

Our first prediction, that toad-smart quolls would have higher overall survival than toad-naïve quolls, independent of sex, also received some support from the data. However, this model was 5.7 times less well supported than the best-supported model (incorporating sex, above; Table 3). Our third prediction, that toad-smart males would have higher survival rates than toad-naïve males, but survival of toad-smart and toad-naïve females would be similar, also received some support from the data. However, the model consistent with this prediction (model 2 in Table 3) was 3.3 times less well supported than the best-supported model. Our fourth prediction, that females would have higher rates of survival than males, irrespective of treatment group, was not well supported by the

**Fig. 2.** Estimated daily apparent survival rates of northern quolls after reintroduction to toad-infested areas, as a function of sex and taste aversion status (toad-smart vs. toad-naïve).

data (Table 3). Two models which incorporated sex-specific survival received little support from the data, and were 124 times less well supported than the best-supported model. Although our focus was on survival of quolls, the analysis also suggested that recapture rates were affected by sex and treatment. The three best-supported models incorporated group-specific recapture rates, but involved constant return rates and site fidelity (Table 3).

Discussion

Our results provide unequivocal evidence that invasive cane toads pose a significant threat to northern quolls, and support previous studies which inferred that cane toads were the major cause of local extinctions (Watson & Woinarski 2003, 2004; Oakwood 2008). Within hours of their release, we saw four toad-naïve quolls attacking large toads, and then convulsing and dying. Clearly, cane toads pose a considerable impediment to population recovery in northern quolls. Even on nights when we saw little toad activity, some radiotracked toad-naïve

Table 3. Model selection results for analysis of apparent survival (*S*), recapture (*p*), return (*r*) and site fidelity (*F*) for northern quolls

Survival (<i>S</i>)	Recapture (<i>p</i>)	Return (<i>r</i>)	Fidelity (<i>F</i>)	Delta QAICc	AIC weight	Model likelihood
Group	Group	Constant	Constant	0.0000	0.5824	1
F (constant) M (CTA)	Group	Constant	Constant	2.4037	0.1751	0.3006
CTA	Group	Constant	Constant	3.4713	0.1027	0.1763
Group	Constant	Constant	Constant	4.4173	0.0640	0.1098
Group	Group	Group	Constant	5.9387	0.0299	0.0513
Group	Group	Constant	Group	6.4803	0.0228	0.0392
Sex	Group	Constant	Group	9.6377	0.0047	0.0081
Sex	Sex	Constant	Constant	9.6927	0.0046	0.0079
Group	Constant	Group	Constant	10.2478	0.0035	0.0060
Group	Constant	Constant	Group	10.7716	0.0027	0.0046
Time	Group	Constant	Group	11.1628	0.0022	0.0038
Time	Group	Constant	Constant	11.9408	0.0015	0.0026
Constant	Group	Constant	Constant	11.9677	0.0015	0.0025

The most parsimonious model is shown in boldface font. The best-supported model was one where within each sex survival differed between toad-smart and toad-naïve quolls. The term 'group' shows that the parameters varied between the four groups (toad-smart males, toad-naïve males, toad-smart females and toad-naïve females), whereas the term 'constant' shows that parameters were constant across groups. The term 'CTA' refers to the treatment (conditioned taste aversion), and 'time' shows that parameters varied with each sampling period.

quolls found toads within several hours, and were killed by attacking them. Because a single encounter with a toad can kill a quoll, simply reducing toad densities will not mitigate the impact of cane toads on quoll populations. Either we need to eliminate every toad (an unrealistic aim: McCallum 2006), or else we need a different approach.

Our results suggest that CTA could offer a viable alternative way to enhance predator survival. Importantly, our work demonstrates *proof of concept* of this approach, in that two major requirements for the application of CTA were met. First, a single dose of a nausea-inducing (thiabendazole-laced) dead toad altered the feeding behaviour of juvenile northern quolls, causing them to ignore or sniff and reject a live toxic prey type (cane toads) that they would otherwise try to eat. Secondly, this CTA induced aversion to live toads increased the short-term survival rates of quolls after release in the wild. The top four survival models all included a positive effect of CTA on quoll survival, and the best-supported model was one which toad-smart females and males had higher daily apparent survival rates than their toad-naïve conspecifics (Fig. 2). Nonetheless, our study has two caveats. First, although we applied an anti-parasite agent to all quolls, the ingestion of thiabendazole (an anti-helminth drug) by toad-smart quolls may have influenced their parasite load, and possibly, their longer term survival. Secondly, our CTA method was not 100% effective, and following reintroduction two toad-smart males attacked large toads. This problem could be due to dose rates (the quolls may not have become nauseous), or because the cues from large toads overshadowed the aversion to small toads. Although most toad-smart quolls sniffed and rejected small toads in captivity, following reintroduction the quolls encountered large toads, and additional cues (prey size, sound and movement) may have influenced their willingness to attack the toad. Additional studies to fine tune our CTA methodology would be worthwhile.

A quoll's sex also influenced its propensity to attack toads in captivity and subsequent survival rates in the field. Encounter rates between quolls and toads after release did not differ between sexes or treatments, so the difference in survival rates was likely to be related to a difference in predator behaviour. Male quolls are much bolder than females in responding to novel stimuli, including large anurans (O'Donnell 2009). Depending on the local environment, bolder animals may obtain a fitness benefit (Dall 2004) or cost (Bremner-Harrison, Prodohl & Elwood 2004). In quolls, the strong sexual divergence in foraging responses appears to result in differential survival rates. Male quolls are more active than females, and probably encounter toads earlier and more often than females. Males are less cautious with large novel frogs, and do not sniff prior to attacking them, and they are more likely to bite the toad's deadly parotoid glands (O'Donnell 2009). Hence, most encounters between a male quoll and a large toad probably will be lethal for the quoll. Because female quolls are more cautious when they encounter a large, novel prey, they may experience a learning event rather than a lethal encounter.

Estimates of daily apparent survival rates for toad-smart males (0.84) were lower than those of toad-smart females

(0.94), but this does not necessarily preclude the use of CTA for conservation. In terms of population viability, males are more expendable than females in any polygynous system lacking male parental care (as is the case with quolls: Oakwood, Bradley & Cockburn 2001). Even a few surviving males could inseminate many females, given the high dispersal rates of males in this species. More worryingly, estimates of daily apparent survival rates were low for toad-smart quolls (above). However, we estimated apparent survival, so true survival rates are likely to be higher, for two reasons. First, apparent survival includes emigration from the study sites, which occurred in both sexes. Secondly, we expect high rates of mortality immediately after release, when the quolls first encountered challenges (such as predators) with which they had no prior experience. A quoll that survives one such encounter may well survive subsequent encounters also. Thus, survival rates are likely to be lower immediately post-release than a few weeks later. We will need long-term monitoring data to test this inference, but our opportunistic surveys are encouraging, with at least two male and two female quolls known to be alive 4 months after release.

Captive breeding programmes and reintroductions are popular approaches for the management of endangered species, but many attempts fail because the factors responsible for the species decline have not been adequately addressed (Kleiman 1989; Short *et al.* 1992). In our study, we addressed one causal factor – the invasive cane toad – responsible for the recent decline of the northern quoll. However, prior to toad invasion, the geographic range of the quoll had already contracted (Braithwaite & Griffiths 1994), due to changes in land use, fire frequency and predation (Begg 1981; Braithwaite 1996; Woinarski, Milne & Wanganeen 2001). Frequent burning removes the grassy understorey and renders quolls more vulnerable to predation (Oakwood 1997). At our reintroduction sites, fire has not been excluded, and several quolls were killed by predators shortly after their release. Hence, predation is a significant source of mortality for juvenile quolls (Oakwood 1997), especially for captive-reared animals which are likely to be predator-naïve (Griffin, Blumstein & Evans 2000). To maximize their chances of success, future reintroductions of the northern quoll should be carried out at sites where fire has been excluded, and should incorporate fire management as part of the recovery programme.

Our results suggest that CTA could help to mitigate the impacts of cane toads on the critically endangered northern quoll. Because wild quolls will consume carrion and baits (Oakwood 1997; Glen, Gentle & Dickman 2007), wildlife agencies could aerially deploy 'toad baits' ahead of the cane toad invasion front, to educate quolls to avoid attacking cane toads before the toads invade (Webb *et al.* 2008). Alternatively, wildlife managers could utilise existing quoll monitoring programmes (mark-recapture), and could modify quoll predatory behaviour by placing toad baits inside cage traps. Before toad baits could be developed, more research is needed to establish that CTA produces a long-term aversion to live cane toads. Encouragingly, some of our toad-smart quolls have survived 4 months since their reintroduction to toad-infested areas.

In conclusion, our research also has implications for the management of invasive predators, which are responsible for numerous extinctions, yet are often difficult to eradicate (Mack *et al.* 2000; Courchamp, Chapuis & Pascal 2003). Because naïveté of native prey is central to the problems caused by invasive predators (Cox & Lima 2006), CTA could be used to modify feeding behaviour of invasive predators (Nicolaus & Nellis 1987). When used in conjunction with existing control methods, deployment of CTA baits could help to reduce predation rates on native fauna, and may allow threatened fauna to persist in areas where invasive predators cannot be eradicated. With further research, CTA may provide a powerful tool to mitigate the ecological impact of invasive species.

Acknowledgements

We thank volunteers for helping to track quolls, the members of Team Bufo for logistical assistance, Keith Christian and Tony Griffiths for loaning equipment, and Daryl and Lyn Frost for providing access to their property. We particularly thank Dion Wedd, Sarah Hirst and Lynda Veheret from the Territory Wildlife Park for their assistance and support throughout the project. Two anonymous reviewers provided comments and suggestions that helped to improve the manuscript. Funding was provided by the Australian Research Council, the Australian Government (Caring for our Country Grant) and the Northern Territory Government (NT Environment Grant). All procedures were carried out under approvals from the University of Sydney Animal Care and Ethics Committee and the Northern Territory Parks and Wildlife.

References

- Armstrong, D.P. & Seddon, P.J. (2007) Directions in reintroduction biology. *Trends in Ecology and Evolution*, **23**, 20–25.
- Begg, R.J. (1981) The small mammals of Little Nourlangie Rock, N. T. III. Ecology of *Dasyurus hallucatus*, the Northern Quoll (Marsupialia: Dasyuridae). *Australian Wildlife Research*, **8**, 73–85.
- Braithwaite, R.W. (1996) Biodiversity and fire in the savanna landscape. *Biodiversity and Savanna Ecosystem Processes: A Global Perspective* (eds O.T. Solbrig, E. Medina & J.F. Silva), pp. 121–140. Springer-Verlag, Berlin.
- Braithwaite, R.W. & Griffiths, A.D. (1994) Demographic variation and range contraction in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Wildlife Research*, **21**, 203–217.
- Bremner-Harrison, S., Prodohl, P.A. & Elwood, R.W. (2004) Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation*, **7**, 313–320.
- Burnett, S. (1997) Colonizing cane toads cause population declines in native predators: reliable anecdotal information and management implications. *Pacific Conservation Biology*, **3**, 65–72.
- Burnham, K.P. (1993) A theory for the combined analysis of ringed recovery and recapture data in marked individuals. *Marked Individuals in the Study of Bird Populations* (eds J.D. Lebreton & P.M. North), pp. 199–213. Birkhauser Verlag, Basel, Switzerland.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Clout, M.N. & Russell, J.C. (2006) The eradication of mammals from New Zealand islands. *Assessment and Control of Biological Invasion Risks* (eds F. Koike, M.N. Clout, M. Kawamichi, M. De Poorter & K. Iwatsuki), pp. 127–141. Shokadoh Book Sellers, Kyoto.
- Cooch, E.G. & White, G.C. (2006) *MARK – a Gentle Introduction*, 5th edn. <http://www.phidot.org/software/mark/docs/book/>, accessed 21 March 2009.
- Courchamp, F., Chapuis, J.L. & Pascal, M. (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, **78**, 347–383.
- Covacevich, J. & Archer, M. (1975) The distribution of the cane toad, *Bufo marinus*, in Australia and its effects on indigenous vertebrates. *Memoirs of the Queensland Museum*, **17**, 305–310.
- Cox, J.G. & Lima, S.L. (2006) Naïveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution*, **21**, 674–680.
- Dall, S.R.X. (2004) Behavioural biology: fortune favours bold and shy personalities. *Current Biology*, **14**, 470–472.
- Dickman, C.R. (1996) *Overview of the Impacts of Feral Cats on Australian Native Fauna*, pp. 1–97. Australian Nature Conservation Agency, Canberra, ACT.
- Dickman, C.R. & Braithwaite, R.W. (1992) Postmating mortality of males in the dasyurid marsupials *Dasyurus* and *Parantechinus*. *Journal of Mammalogy*, **73**, 143–147.
- Dimmik, C.R. & Nicolaus, L.K. (1990) Efficiency of conditioned aversion in reducing predation by crows. *Journal of Applied Ecology*, **27**, 200–209.
- Doody, J.S., Green, B., Rhind, D., Castellano, C.M., Sims, R. & Robinson, T. (2009) Population-level declines in Australian predators caused by an invasive species. *Animal Conservation*, **12**, 46–53.
- Francis, C.M. & Cooke, F. (1993) A comparison of survival rate estimates from live recaptures and dead recoveries of lesser snow geese. *Marked Individuals in the Study of Bird Populations* (eds J.D. Lebreton & P.M. North), pp. 169–183. Birkhauser Verlag, Basel, Switzerland.
- Francis, C.M. & Sauro, P. (2002) Estimating age-specific survival rates of tawny owls-recaptures versus recoveries. *Journal of Applied Statistics*, **29**, 637–647.
- Fritts, T.H. & Rodda, G.H. (1998) The role of introduced species in the degradation of island ecosystems: a case study of Guam. *Annual Review of Ecology and Systematics*, **29**, 113–140.
- Garcia, J., Hankins, W.G. & Rusiniak, K.W. (1974) Behavioural regulation of the Milieu Interne in man and rat. *Science*, **185**, 824–831.
- Glen, A.S., Gentle, M.N. & Dickman, C.R. (2007) Non-target impacts of poison baiting for predator control in Australia. *Mammal Review*, **37**, 191–205.
- Griffin, A.S., Blumstein, D.T. & Evans, C.S. (2000) Training captive-bred or translocated animals to avoid predators. *Conservation Biology*, **14**, 1317–1326.
- Griffiths, A.D. & McKay, J.L. (2007) Cane toads reduce the abundance and site occupancy of Merten's water monitor (*Varanus mertensi*). *Wildlife Research*, **34**, 609–615.
- Gustavson, C.R. (1977) Comparative and field aspects of learned food aversions. *Learning Mechanisms in Food Selection* (eds L.M. Barker, M.R. Best & M. Domjan), pp. 632. Baylor University Press, Waco, TX.
- Gustavson, C.R. & Nicolaus, L.K. (1987) Taste aversion conditioning in wolves, coyotes, and other canids: retrospect and prospect. *Man and Wolf: Advances, Issues, and Problems in Captive Wolf Research* (ed H. Frank), pp. 169–203. Junk, Boston.
- Harding, E.K., Doak, D.F. & Albertson, J.D. (2001) Evaluating the effectiveness of predator control: the non-native red fox as a case study. *Conservation Biology*, **15**, 1114–1122.
- Kleiman, D.G. (1989) Reintroduction of captive mammals for conservation. *BioScience*, **39**, 152–161.
- Letnic, M., Webb, J.K. & Shine, R. (2008) Invasive cane toads (*Bufo marinus*) cause mass mortality of freshwater crocodiles (*Crocodylus johnstoni*) in tropical Australia. *Biological Conservation*, **141**, 1773–1782.
- Lever, C. (2001) *The Cane Toad. The History and Ecology of a Successful Colonist*. Westbury Academic and Scientific Publishing, Yorkshire.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- McCallum, H.I. (2006) Modelling potential control strategies for cane toads. *Proceedings of the Invasive Animals CRC/CSIRO/QLD NRM&W Cane Toad Workshop* (eds K.L. Molloy & W.R. Henderson), pp. 123–133. Invasive Animals Cooperative Research Centre, Brisbane.
- Nicolaus, L.K. & Nellis, D.W. (1987) The first evaluation of the use of conditioned taste aversion to control predation by mongooses upon eggs. *Applied Animal Behaviour Science*, **17**, 329–346.
- Nicolaus, L.K., Cassel, J.F., Carlson, R.B. & Gustavson, C.R. (1983) Taste-aversion conditioning of crows to control predation on eggs. *Science*, **220**, 212–214.
- Oakwood, M. (1997) *The Ecology of the Northern Quoll, Dasyurus Hallucatus*. Australian National University, Canberra.
- Oakwood, M. (2000) Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology*, **48**, 519–539.
- Oakwood, M. (2008) *Monitoring Extinction of the Northern Quoll*. Report to the Australian Academy of Science, Canberra, Australia.
- Oakwood, M., Bradley, A.J. & Cockburn, A. (2001) Semelparity in a large marsupial. *Proceedings of the Royal Society B-Biological Sciences*, **268**, 407–411.
- O'Donnell, S. (2009) *Alien Versus Predator: Taste Aversion Learning as a way of Enhancing Survival in Northern Quolls (Dasyurus Hallucatus)*. University of Sydney, Sydney, Australia.

- Pollock, A.B. (1999) Notes on status, distribution and diet of northern quoll *Dasyurus hallucatus* in the Mackay-Bowen area, mideastern Queensland. *Australian Zoologist*, **31**, 388–395.
- Pollock, K.H., Winterstein, S.R. & Conroy, M.J. (1989) Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management*, **53**, 7–15.
- Rankmore, B.R., Griffiths, A.D., Woinarski, J.C.Z., Ganambarr, B.L., Taylor, R., Brennan, K., Firestone, K. & Cardoso, M. (2008) Island translocation of the northern quoll *Dasyurus hallucatus* as a conservation response to the spread of the cane toad *Chaunus [Bufo] marinus* in the Northern Territory, Australia. Report to The Australian Government's Natural Heritage Trust.
- Reeves, M.P. (2004) A retrospective report of 90 dogs with suspected cane toad (*Bufo marinus*) toxicity. *Australian Veterinary Journal*, **82**, 608–611.
- Reynolds, J.C. & Tapper, S.C. (1996) Control of mammalian predators in game management and conservation. *Mammal Review*, **26**, 127–156.
- Risbey, D.A., Calver, M.C. & Short, J. (1997) Control of feral cats for nature conservation. I. Field tests of four baiting methods. *Wildlife Research*, **24**, 319–326.
- Roberts, B.K., Aronsohn, M.G., Moses, B.L., Burk, R.L., Toll, J. & Weeren, R. (2000) *Bufo marinus* intoxication in dogs: 94 cases (1997–1998). *Journal of American Veterinary Medical Association*, **216**, 1941–1944.
- Sakate, M. & Oliveira, P.C.L.D. (2000) Toad envenoming in dogs: effects and treatment. *Journal of Venomous Animals and Toxins*, **6**, 52–62.
- Sandercock, B.K. (2006) Estimation of demographic parameters from live-encounter data: a summary review. *Journal of Wildlife Management*, **70**, 1504–1520.
- Short, J. & Smith, A.P. (1994) Mammal decline and recovery in Australia. *Journal of Mammalogy*, **75**, 288–297.
- Short, J., Bradshaw, S.D., Giles, J., Prince, R.I.T. & Wilson, G.R. (1992) Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia – a review. *Biological Conservation*, **62**, 189–204.
- Smith, J.G. & Phillips, B.L. (2006) Toxic tucker: the potential impact of cane toads on Australian reptiles. *Pacific Conservation Biology*, **12**, 40–49.
- Ternent, M.A. & Garshelis, D.L. (1999) Taste-aversion conditioning to reduce nuisance activity by black bears in a Minnesota military reservation. *Wildlife Society Bulletin*, **27**, 720–728.
- Urban, M.C., Phillips, B.L., Skelly, D.K. & Shine, R. (2007) The cane toad's (*Chaunus [Bufo] marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society Biological Sciences Series B*, **274**, 1413–1419.
- Watson, M. & Woinarski, J.C.Z. (2003) *Vertebrate Monitoring and re-Sampling in Kakadu National Park, 2002*. Report to Parks Australia. Tropical Savannas Cooperative Research Centre, Darwin.
- Watson, M. & Woinarski, J.C.Z. (2004) *Vertebrate Monitoring and re-Sampling in Kakadu National Park, Year 3, 2003–4*. Report to Parks Australia. Tropical Savannas Cooperative Research Centre, Darwin.
- Webb, J.K., Shine, R. & Christian, K.A. (2005) Does intraspecific niche partitioning in a native predator influence its response to an invasion by a toxic prey species? *Austral Ecology*, **30**, 201–209.
- Webb, J.K., Brown, G.P., Child, T., Greenlees, M.J., Phillips, B.L. & Shine, R. (2008) A native dasyurid predator (common planigale, *Planigale maculata*) rapidly learns to avoid a toxic invader. *Austral Ecology*, **33**, 821–829.
- White, G.C. & Burnham, K.P. (1999) Program Mark: survival estimation from populations of marked animals. *Bird Study (Supplement)*, **46**, S120–S139.
- Williamson, M. (1996) *Biological Invasions*. Chapman and Hall, London.
- Woinarski, J.C.Z., Milne, D.J. & Wanganeen, G. (2001) Changes in mammal populations in relatively intact landscapes in Kakadu National Park, Northern Territory, Australia. *Austral Ecology*, **26**, 360–370.
- Woinarski, J.C.Z., Oakwood, M., Winter, J., Burnett, S., Milne, D., Foster, P., Myles, H. & Holmes, B. (2008) Surviving the toads: patterns of persistence of the northern quoll *Dasyurus hallucatus* in Queensland. Report to The Australian Government's Natural Heritage Trust, March 2008.

Received 25 August 2009; accepted 4 March 2010
 Handling Editor: Mark Hebblewhite