

Behavioural responses of reptile predators to invasive cane toads in tropical Australia

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Abstract The ecological impact of an invasive species can depend on the behavioural responses of native fauna to the invader. For example, the greatest risk posed by invasive cane toads (*Rhinella marina* Bufonidae) in tropical Australia is lethal poisoning of predators that attempt to eat a toad; and thus, a predator's response to a toad determines its vulnerability. We conducted standardized laboratory trials on recently captured (toad-naïve) predatory snakes and lizards, in advance of the toad invasion front as it progressed through tropical Australia. Responses to a live edible-sized toad differed strongly among squamate species. We recorded attacks (and hence, predator mortality) in scincid, agamid and varanid lizards, and in elapid, colubrid and pythonid snakes. Larger-bodied predators were at greater risk, and some groups (elapid snakes and varanid lizards) were especially vulnerable. However, feeding responses differed among species within families and within genera. Some taxa (notably, many scincid and agamid lizards) do not attack toads; and many colubrid snakes either do not consume toads, or are physiologically resistant to the toad's toxins. Intraspecific variation in responses means that even in taxa that apparently are unaffected by toad invasion at the population level, some individual predators nonetheless may be fatally poisoned by invasive cane toads.

Key words: *Bufo marinus*, ecological impact, foraging tactics, invasive species, predator-prey interaction.

INTRODUCTION

Invasive species affect native taxa via a diverse array of mechanisms, and the nature and magnitude of impact can vary not only among species, but even differ dramatically through space and time, as a result of local environmental conditions (Pimentel *et al.* 2000). Depending on the mechanism of impact, the arrival of an invader can differentially affect size-classes or sexes even within a single population of vulnerable native animals (Webb *et al.* 2005). As a result, predicting invader impact is fraught with difficulty, even in relatively straightforward cases where the mechanism is well understood. That challenge is exacerbated by the possibility of indirect effects, whereby an invader-induced change in abundance or behaviour of a native taxon cascades through into impacts on another native, potentially overwhelming any direct impact of the invader on the latter native species (Wootton 1994; Nelson *et al.* 2010). The complexity of invader effects means that we need to evaluate mechanisms indepen-

dently of overall (population-level) impact. For example, an invader may have negligible overall impact on populations of a native species either because it has no direct effect, or because strong positive and negative effects cancel each other out (Brown *et al.* 2011). Distinguishing between these two scenarios may help us to understand the reasons for geographic and temporal variation in invader impacts on threatened native taxa. Thus, we need empirical data on mechanisms of impact, as well as overall population-level responses (i.e. comparisons of faunal abundance pre- and post-invasion).

The invasion of cane toads (*Rhinella marina* Bufonidae) through tropical Australia has attracted detailed study. The major mechanism of toad impact is lethal toxic ingestion (Shine 2010). Because Australia lacks native bufonids, the distinctive chemical defences (bufadienolides) of toads are rapidly fatal if ingested by many native Australian predators. Thus, invasion of toads has caused massive population-level declines of some predators (Shine 2010; Brown *et al.* 2011). However, other predator taxa have been unaffected at the population level, perhaps because they do not attempt to consume toads, or rapidly learn not to do

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so, or are physiologically tolerant of the toad toxins (reflecting pre-adaptation through ancestry in a region that contains toads: [Llewelyn *et al.* 2011](#)). Wildlife managers need to predict (or at least, understand) the differential vulnerability of native species, so they can focus conservation efforts on the most highly threatened taxa. This has stimulated several attempts to predict toad impact on native reptile predators. The first such attempt was by [Phillips *et al.* \(2003\)](#), who relied on the (pre-toad-invasion) dietary habits of native snakes to infer whether or not a snake was likely to attempt to eat toads. Because many snake species eat frogs, they predicted that those that also try to eat toads would be at high risk. Field surveys in the Darwin area several years later suggested that these predictions were in error; several snake species expected to decline had in fact increased in abundance after toad arrival ([Brown *et al.* 2013](#)). One plausible explanation is that survival rates of predators may have been enhanced more by indirect effects (such as toad-induced mortality of apex predators, especially large varanid lizards) than they were reduced by direct (fatal poisoning) effects ([Brown *et al.* 2011](#)). Another possibility is that anuran-eating snakes can distinguish between toads and frogs, and that many frog-eating snakes (and lizards) do not attempt to eat toads even when they are available. The only way to evaluate that alternative hypothesis is to actually expose predators to toads, and see how they react.

Based on this reasoning, we conducted trials where we captured predatory reptiles in advance of the toad invasion, maintained them in captivity, and offered them live (ingestible-size) cane toads. We recorded whether or not the predator attacked the toad, whether or not it ate the toad, and whether or not the predator was killed by toad toxins. For ethical reasons, we performed the work on only small sample sizes, except in cases where the study was part of a larger project on responses of specific taxa (e.g. to quantify selection on behaviour and morphology in death adders, *Acanthophis praelongus*: [Phillips *et al.* 2010](#)). To further reduce the numbers of animals killed for this component of the work, we primarily used animals that had been collected as voucher specimens during faunal surveys, and were destined for euthanasia and preservation anyway. The resultant small sample sizes reduce our ability to make robust comparisons, but still reveal several interesting patterns that clarify modes of impact of invasive cane toads on reptile predators in tropical Australia.

MATERIALS AND METHODS

The data in this paper were gathered over several years (2005 to 2009), on animals collected from a range of localities i.e. from Darwin in the Northern Territory (NT) to the Mitchell

Plateau in Western Australia (WA). Collection localities moved westwards as the toad front advanced, such that all specimens were taken from areas not yet invaded by cane toads (and hence, the responses of the predators had not been affected by prior exposure to toads). The basic protocol was to collect reptiles of any species that might attack and consume a cane toad, and bring them back to our husbandry facilities in Darwin (2005 only), or to the Middle Point research station near Darwin (2006 to 2009; 131°18'50"E, 12°33'26"S) where the animals were maintained individually in opaque plastic containers with access to water and shelter. Enclosure sizes depended upon the species concerned, and ranged from 105 × 105 × 80 cm (for the largest lizards and snakes) to 21 × 12 × 7 cm (for the smallest lizards and snakes). The enclosures were kept in an outdoor, shaded building exposed to ambient air temperature and light levels.

Because some reptiles refuse to feed in captivity, we only offered toads to reptiles that were feeding consistently on alternative prey (e.g. native frogs, crickets). An ingestible-sized toad (i.e. body size appropriate for the predator in question) was placed into the predator's enclosure and left for 24 h, after which we recorded the fate (dead or alive) of both toad and potential predator. The toad was then removed, and an alternative prey item provided. Surviving predators were offered toads (and other prey types, alternately) on up to six occasions, after which the animals were humanely euthanized and preserved. Details of our experimental protocols differed through time and among species, depending on factors such as the availability of toad metamorphs of different sizes, and alternative prey, and whether or not the parotoid glands of toads were emptied (by manual pressure) prior to the anurans being offered to the predators.

Statistical analyses of these data were conducted in Statview 5.0 and JMP 9.0 (SAS Institute, Cary, NC, USA). We compared species in terms of the relative numbers of predators ignoring, attacking, consuming and being killed by toads using contingency-table tests. We evaluated interspecific relationships between predator behaviour (% of specimens showing each behaviour) and mean body size (mass) per species, using linear regression.

Ethical note

Conducting trials in which predators are exposed to live prey items raises serious ethical issues, because of the potential suffering involved both by the prey if attacked, and by predators if poisoned by the toxic prey. In this case, the relevant animal ethics committee (University of Sydney Animal Care and Ethics Committee) decided that this suffering was justified by the potential value of the results for conservation and management. As noted above, we minimized the ethical problems by restricting the study to small sample sizes, to animals collected immediately in advance of the toad invasion front (i.e. from populations that would have soon encountered live toads in the field), and by using animals that had been taken as voucher specimens in pre-toad-invasion faunal surveys, as part of population-level monitoring studies of toad impact (and hence, were scheduled to be euthanized immediately). In practice, suffering was minor; prey animals seized by predators typically were killed almost instantly, and

predators poisoned by cane toads died of cardiac failure as soon as they ingested (or in some cases, mouthed) the toad. Although we monitored enclosures to detect and humanely euthanize any animals that were severely affected but not killed by encounters, no such events were recorded and thus, we did not need to intervene.

RESULTS

We obtained data on the behavioural responses of 252 snakes (136 elapids, belonging to 10 species; 81 colubrids, belonging to 4 species; and 35 pythons, belonging to 3 species) and 206 lizards (120 scincids, belonging to 12 species; 23 agamids, belonging to 8 species; 1 pygopodid; and 62 varanids, belonging to 9 species). Overall, reptile predators attacked toads in about half of the trials, both in snakes (elapids 52%, colubrids 52%, pythons 57%) and lizards (skinks 10%, agamids 11%, pygopodid 0%, varanids 74%). Predators were killed by ingesting toad toxins in 21% of trials (elapids 31%, colubrids 14%, pythons 32%, skinks 3%, agamids 2%, pygopodid 0%, varanids 41%).

Some broad patterns emerge from the data in Table 1:

1. In all the families that we studied except the sole pygopodid, at least some individuals attacked cane toads, and died as a result. In some cases, predators died soon after they seized a toad, before swallowing it.
2. The frequency of such attacks varied among species (contingency table, $\chi^2 = 133.29$, $P < 0.0001$), with attacks more frequent by species within some families than others. For example, all elapid species except the ornate snake (*Furina ornata*) and all of the varanid species except *Varanus storri* were recorded to attack and kill toads, whereas we recorded attacks on toads by only three of the 13 scincid species and two of the seven agamid species.
3. Species differed not only in whether or not they would attack toads, but also in whether or not such attacks were followed by ingestion of the toad (looking only at predators that attacked toads; $\chi^2 = 60.31$, 27 d.f., $P < 0.0002$; Table 1). For example, most snakes that attacked toads went on to consume them (e.g. *Acanthophis*, *Enhydryis*, *Pseudechis*, *Pseudonaja*, *Stegonotus*), but we never recorded consumption of toads by three snake species that often attacked toads (*Boiga*, *Dendrelaphis*, *Furina*: see Table 1).
4. Ingestion of a toad was more likely to be followed by predator mortality in some species than others ($\chi^2 = 90.94$, $P < 0.0001$). For example, slatey-grey snakes (*Stegonotus cucullatus*) often consumed toads, but never showed ill effects from doing so.

In contrast, all of the bluetongue skinks (*Tiliqua scincoides intermedia*) that ate toads, died as a result (Table 1).

5. In an interspecific comparison, larger-bodied species were more likely to attack toads (Fig. 1a; $n = 47$ taxa, mean body mass vs. % attack toads, $r^2 = 0.28$, $P < 0.0001$). However, a predator species mean body mass was not significantly related to its probability of eating the toad after attacking it (based on the 28 species where attacks were recorded, $r^2 = 0.05$, $P = 0.24$) or for it to die from toad-poisoning if it attacked a toad ($n = 28$, $r^2 = 0.01$, $P = 0.66$). Nonetheless, the body-mass effect on propensity to attack was strong enough to result in overall significant correlations between body mass and the probability of eating a toad (based on the full 47 species, $r^2 = 0.29$, $P < 0.0001$; see Fig. 1b) and dying as a result ($n = 47$, $r^2 = 0.18$, $P < 0.003$; see Fig. 1c). Thus, larger-bodied species may be at more risk from toad invasion, simply because they are more likely to attack toads.

DISCUSSION

Our data from encounters between reptile predators and invasive cane toads fill a significant gap in our knowledge about mechanisms of toad impact and possible population effects. Previous studies have reported the results of similar trials on other vertebrates, including native fishes (Nelson *et al.* 2010, 2011a,b), freshwater crocodiles (Somaweera *et al.* 2011), frogs (Shine *et al.* 2009; Greenlees *et al.* 2010; Nelson *et al.* 2010, 2011a,b), birds (Beckmann & Shine 2011, Beckmann *et al.* 2011) and mammals (Webb *et al.* 2008, 2011; O'Donnell *et al.* 2010; Llewelyn *et al.* 2010a; Kaemper *et al.* 2013). However, relatively few squamate taxa have been studied in this respect (see Appendix S1 for a summary of published reports on responses of reptiles to invasive cane toads).

Any conclusions from our trials must be made with caution. First, sample sizes were small for almost all of the taxa (for ethical reasons), and there was substantial individual variation in predatory responses to toads even within a single predator taxon (Table 1). Within several of the taxa that we tested, some individuals seized the first toad that was offered (and died as a result) whereas conspecifics (often, collected from the same population) consistently refused toads in six successive trials, despite feeding enthusiastically on alternative prey types during intervening trials. Also, minor variation in the sizes of toads that were offered (driven by availability) may have influenced feeding responses; predators may selectively take some size-classes of toads rather than others (as has been shown in the toxin-tolerant *Tropidonophis mairii*: Llewelyn *et al.*

Table 1. Results of trials in which recently captured lizards and snakes were offered edible-sized cane toads (*Rhinella marina*)

Species	No. predators	No. attacked toad	No. ate toad	No. died	Proportion attacked toad	Proportion ate toad	Proportion died
Snakes							
Elapidae							
<i>Acanthophis praelongus</i>	74	51	42	17	0.69	0.57	0.23
<i>Cryptophis pallidiceps</i>	1	0	0	0	0.00	0.00	0.00
<i>Demansia olivacea</i>	5	0	0	0	0.00	0.00	0.00
<i>Demansia papuensis</i>	10	8	5	7	0.80	0.50	0.70
<i>Demansia vestigiata</i>	6	5	3	0	0.83	0.50	0.00
<i>Furina ornata</i>	8	5	0	0	0.63	0.00	0.00
<i>Pseudechis australis</i>	11	8	7	6	0.73	0.64	0.55
<i>Pseudechis weigeli</i>	5	1	1	1	0.20	0.20	0.20
<i>Pseudonaja nuchalis</i>	15	10	8	6	0.67	0.53	0.40
<i>Suta punctata</i>	1	1	1	1	1.00	1.00	1.00
Colubridae							
<i>Boiga irregularis</i>	20	11	3	2	0.55	0.15	0.10
<i>Dendrelaphis punctulata</i>	20	10	3	0	0.50	0.15	0.00
<i>Enhydryis polylepis</i>	20	9	8	9	0.45	0.40	0.45
<i>Stegonotus cucullatus</i>	21	12	12	0	0.57	0.57	0.00
Pythonidae							
<i>Antaresia childreni</i>	27	10	6	4	0.37	0.22	0.15
<i>Liasis olivaceus</i>	3	1	1	0	0.33	0.33	0.00
<i>Morelia spilota</i>	5	5	4	4	1.00	0.80	0.80
Lizards							
Scincidae							
<i>Carlia triacantha</i>	4	0	0	0	0.00	0.00	0.00
<i>Carlia munda</i>	2	0	0	0	0.00	0.00	0.00
<i>Ctenotus burbidgei</i>	2	0	0	0	0.00	0.00	0.00
<i>Ctenotus inornatus</i>	9	0	0	0	0.00	0.00	0.00
<i>Ctenotus robustus</i>	37	9	7	1	0.24	0.19	0.03
<i>Ctenotus saxatilis</i>	6	0	0	0	0.00	0.00	0.00
<i>Ctenotus tantillus</i>	5	0	0	0	0.00	0.00	0.00
<i>Ctenotus pantherinus</i>	2	0	0	0	0.00	0.00	0.00
<i>Cyclodomorphus melanops</i>	1	0	0	0	0.00	0.00	0.00
<i>Glaphyromorphus brongersmai</i>	3	0	0	0	0.00	0.00	0.00
<i>Glaphyromorphus isolepis</i>	20	11	3	2	0.55	0.15	0.10
<i>Tiliqua scincoides intermedia</i>	29	11	7	7	0.38	0.24	0.24
Agamidae							
<i>Amphibolurus gilberti</i>	1	0	0	0	0.00	0.00	0.00
<i>Chelosania brunnea</i>	1	0	0	0	0.00	0.00	0.00
<i>Diporiphora</i> sp.	4	3	1	0	0.75	0.25	0.00
<i>Diporiphora albilabris</i>	1	0	0	0	0.00	0.00	0.00
<i>Diporiphora bennetti</i>	7	1	1	1	0.14	0.14	0.14
<i>Diporiphora superba</i>	1	0	0	0	0.00	0.00	0.00
<i>Diporiphora magna</i>	6	0	0	0	0.00	0.00	0.00
<i>Tympanocryptis centralis</i>	2	0	0	0	0.00	0.00	0.00
Pygopodidae							
<i>Lialis burtonis</i>	1	0	0	0	0.00	0.00	0.00
Varanidae							
<i>Varanus acanthurus</i>	14	7	5	2	0.50	0.36	0.14
<i>Varanus glauerti</i>	10	8	4	2	0.80	0.40	0.20
<i>Varanus glebopalma</i>	5	4	4	3	0.80	0.80	0.60
<i>Varanus gouldii</i>	5	4	3	1	0.80	0.60	0.20
<i>Varanus mertensi</i>	4	4	2	4	1.00	0.50	1.00
<i>Varanus mitchelli</i>	11	11	4	10	1.00	0.36	0.91
<i>Varanus scalaris</i>	5	4	3	2	0.80	0.60	0.40
<i>Varanus storri</i>	4	0	0	0	0.00	0.00	0.00
<i>Varanus tristis</i>	4	4	3	1	1.00	0.75	0.25

The table shows numbers of predators tested, and numbers that attacked and ate toads, and that died as a result. The final columns show those same numbers as proportions of the total number of predators tested per species.

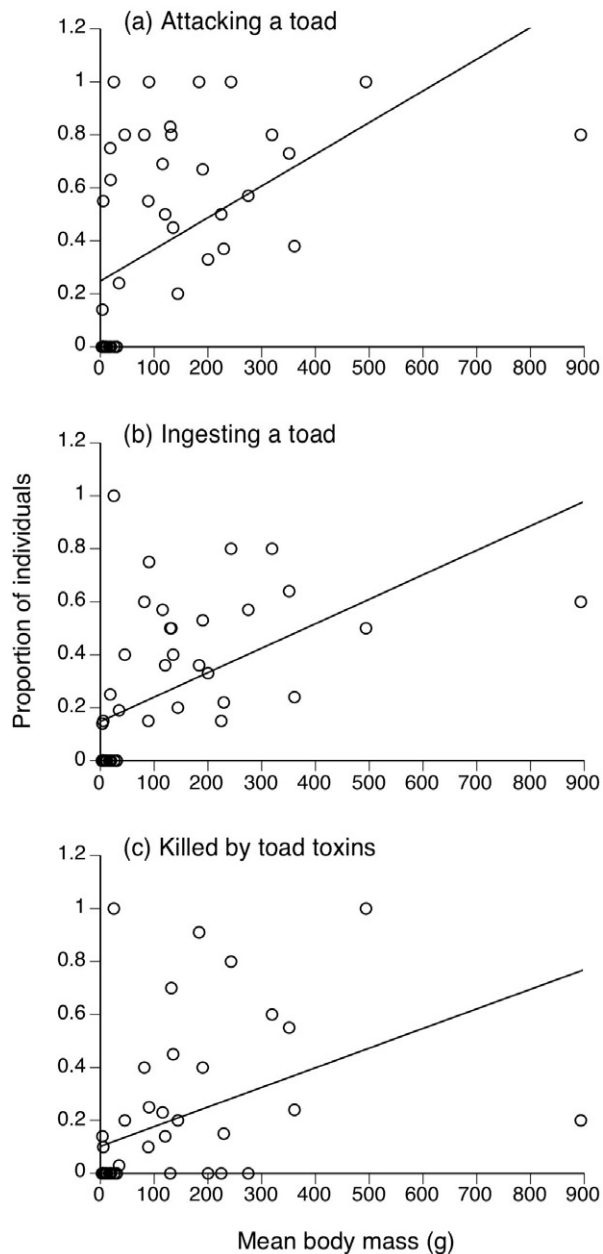


Fig. 1. Interspecific relationships between mean adult body mass of a predatory reptile species, and the proportion of individuals that attacked and consumed cane toads in laboratory trials, and that died as a result of ingesting the toxic toads. The lines show linear regressions fitted to these data.

2012). Thirdly, captivity may have influenced predator responses, either by changing hunger levels (for specimens that did not feed readily in captivity), curtailing usual predatory responses (e.g. through captivity-induced stress) or encouraging defensive rather than feeding strikes (if captivity, or the continued close proximity of toads, stimulated defensive behaviour).

Nonetheless, our results have some robust implications for toad impact. First, some individual predators

are likely to be killed by toad-toxin ingestion even in species that usually do not attack or ingest toads. In our study, this was true even for occasional specimens of relatively small-bodied lizard species that would be unlikely to ingest vertebrate prey items in the wild (e.g. *Ctenotus*, *Diporiphora*; see Table 1). Hence, anecdotal observations of dead predators in the wild after toad invasion may tell us very little about population-level impacts of this invasive anuran (see also Doody *et al.* 2009; Shine 2010). For example, although dietary analyses (Shine & Lambeck 1989) and feeding studies on captive frillneck lizards (*Chlamydosaurus kingii*) suggested that these iconic lizards will not eat anurans (including toads), and population studies showed no consistent decline in lizard numbers after toad invasion (Ujvari *et al.* 2011), we found a freshly dead adult male lizard of this species in Kununurra, WA, shortly after toads arrived in this region. The lizard contained a freshly ingested cane toad (Appendix S2) but was otherwise uninjured, strongly suggesting that the toad's toxins were responsible for the predator's death. Similarly, there are occasional reports of fatal toad-poisoning even in snake species that are physiologically resistant to bufotoxins, presumably because that tolerance is not absolute (Llewellyn *et al.* 2009) and individual predators occasionally ingest toads whose toxin content exceeds the predator's tolerance (e.g. *S. cucullatus* – Brown *et al.* 2011; *T. mairii* – Ingram & Covacevich 1990). Natural selection thus may favour 'toad-smart' traits even in taxa that are not affected at the population level by toad invasion.

General patterns in responses of reptile predators to toads (Table 1) are consistent with previous analyses (e.g. Shine 2010) in revealing variation at the familial and species level, as well as among individuals within species. In general, elapid snakes and varanid lizards appear to be more vulnerable to toads than are species within the other families studied. The primary reason for that disparity is that elapids and varanids were more likely to attack toads than were species from most of the other squamate families tested, and typically consumed toads after they killed them. In contrast, most scincid and agamid lizards did not attack toads; and most colubrid snakes either did not eat toads they had killed (*Boiga*, *Dendrelaphis*) or were able to tolerate the toad's toxins (*Stegonotus*). Extensive data on another colubrid, *T. mairii*, show that it is even more resistant to toad toxin than are *Stegonotus* (see Appendix S1). The apparent susceptibility of the aquatic homalopsine colubrid *Enhydryis polylepis* (Table 1) warrants further study. To our knowledge, there are no published data on population-level impacts of cane toads on this species.

A species body size as well as its familial identity affected the likelihood of a predator killing and eating a toad, and of dying as a result (Fig. 1). Larger species were at more risk, because they were more

likely to attack a toad (Fig. 1a). The consequences of launching such an attack presumably vary with many factors; for example, an adult estuarine crocodile (*Crocodylus porosus*) is so large that it is unlikely to be at risk even if it consumes a large toad, because the prey size (and thus, toxin content) is so low relative to predator size (Smith & Phillips 2006). Outcomes of encounters are further complicated by species-specific differences in maximal ingestible prey sizes of predators, and in the allometry of toxin content relative to toad body size in toads (Phillips & Shine 2006b). Broadly, the predators most at risk from toad invasion appear to be those that are prepared to attack relatively large prey, do not distinguish between toads and native frogs, are not physiologically pre-adapted to tolerate bufotoxins, and do not readily learn conditioned taste aversion.

Unfortunately, these mechanistic influences on predator vulnerability do not translate in any straightforward way into the magnitude of ecological (population-level) impacts of toad invasion. Thus, for example, detailed radio-tracking studies documented high mortality of death adders (*A. praelongus*) due to toad ingestion, whereas surveys at an adjacent site revealed a significant increase rather than decrease in adder abundance over the same period (Phillips *et al.* 2010; Brown *et al.* 2011). These conflicting trends reflect the importance of indirect effects, mediated via toad-induced poisoning of apex predators (large varanid lizards) that facilitated mesopredator release (Brown *et al.* 2011). However, our data clarify the mechanisms underlying persistence of toxin-vulnerable arboreal colubrid snakes (*Boiga* and *Dendrelaphis*) in tropical Australia; these snakes can readily distinguish between toads and frogs, and do not attempt to consume toads. Thus, lethal toxic ingestion is unlikely to be a high risk for these species. Based on our limited sample sizes, the same may be true for at least one species of elapid snake (*F. ornata*).

In conclusion, our laboratory trials show that a surprisingly wide taxonomic range of squamate reptile predators are vulnerable to the invasion of cane toads, although for most species the risk is minor. That ability to co-exist with toads is driven by a diverse array of traits, that differs among species. A frog-eating reptile species may be largely unaffected by toad invasion because of a reluctance to consume toads, an innate ability to rapidly distinguish between toads and frogs, an ability to learn taste aversion and/or an ability to tolerate toad toxins. Even in species that are at high risk due to toad-poisoning, however, the population-level consequences of that vulnerability may be reduced by offsetting indirect effects (Brown *et al.* 2011). The end result is that even in this intensively studied system, an understanding of toad impacts requires information on predator behaviour as well as population-level effects of toad arrival.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. The results of published studies on the responses of naïve Australian reptile predators to cane toads (*Rhinella marina*).

Appendix S2. Dissection of an adult male frillneck lizard (*Chlamydosaurus kingii*) found dead in Kununurra, WA in April 2011.