Hatchling Australian freshwater crocodiles rapidly learn to avoid toxic invasive cane toads

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Summary

Predicting the ecological impacts of invasive species on native fauna is a formidable challenge for conservation biologists. One way to deal with that challenge is to stage encounters between the invader and native species in the laboratory, to illuminate likely outcomes of encounters in the wild. The invasion of the highly toxic cane toad *Rhinella marina* across tropical Australia threatens many frog-eating predators, including freshwater crocodiles (*Crocodylus johnstoni*). To predict the impact of cane toads on crocodiles, we need to know whether crocodiles will attack cane toads, and whether predators that survive the toads' poisons will learn to avoid toads. We quantified these traits under laboratory conditions in hatchling freshwater crocodiles from Lake Argyle in Western Australia. All toad-naïve hatchling crocodiles attacked toads during their first encounter, and none showed signs of overt illness after consuming toads. However, crocodiles rapidly learnt to avoid toads as prey, and only four out of the 10 crocodiles attacked toads during subsequent encounters. Compared to control (toad-naïve) conspecifics, toad-smart crocodiles inflicted fewer bites on toads, held toads in their mouths for shorter time periods, and were more likely to reject toads as prey. In the field, toads were consumed more rarely than native frogs. Our results show that hatchling freshwater crocodiles can rapidly learn to avoid cane toads as prey. Hence, even if toads cause mortality of larger crocodiles (as happens in some areas), populations may recover via hatchling recruitment.

Keywords: aversion learning, Bufonidae, *Bufo marinus*, invasive, predator–prey.

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1. Introduction

Invasive organisms threaten biodiversity worldwide (IUCN, 2000; Mack et al., 2000). Due to their ecological and economic costs, invasive species have been the focus of considerable efforts in research and management (Mack et al., 2000). Eradication of the invader offers the best management option for mitigating impacts (United Nations Environment Programme, 1992), but is rarely possible at a large spatial scale; and long-term control programmes are expensive and labour-intensive (Reynolds & Tapper, 1996; Harding et al., 2001). In practice, scarce resources for conservation need to be allocated to control the invasive species most likely to have major ecological impacts; taxa that have minimal or transitory ecological impact warrant less investment. Accordingly, predicting the nature, magnitude and duration of ecological impact of an invasive taxon is a high priority for wildlife managers (Ricciardi et al., 2000).

Invasive species can alter natural ecosystems via several pathways: for example, via competition (Human & Gordon, 1996), predation (Fritts & Rodda, 1998), disease transmission (Dogiel et al., 1970) or indirect cascading effects on food webs (Roemer et al., 2002; Shine, 2010). Predator–prey interactions are major drivers of the dynamics of populations, communities, and ecosystems (Sergio et al., 2006), as well as the evolution of phenotypic traits (Johnson & Agrawal, 2003). Although considerable attention has been devoted to understanding how native prey adapt to exotic predators (e.g., Freeman & Byers, 2006; King et al., 2006), the reciprocal issue — responses of native predators to exotic prey — is less well understood (Carlsson et al., 2009). Furthermore, the exotic prey/native predator system offers powerful opportunities to study selection and contemporary evolution of adaptive traits in predator populations (Phillips & Shine, 2004; Carlsson et al., 2009).

The highly toxic cane toad *Rhinella marina* was introduced to Queensland in 1935 and has since spread across northern Australia (Lever, 2001). The defensive toxins of toads are very different to those found in Australian native frogs, and are fatal to many native vertebrate predators that attempt to consume toads (Covacevich & Archer, 1975; Smith & Phillips, 2006; Webb et al., 2005; Shine, 2010). Several apex predators have suffered massive population declines following the invasion of cane toads (Griffiths & McKay, 2007; Doody et al., 2009; Shine, 2010; Woinarski et al., 2010). One such predator is the Australian freshwater crocodile *Crocodylus johnstoni* (Letnic et

al., 2008). Freshwater crocodiles feed on a diversity of prey, including frogs (Webb et al., 1982; Tucker et al., 1996), and have been observed eating cane toads (Letnic & Ward, 2005). Freshwater crocodiles have less physiological resistance to toad toxins than do sympatric saltwater crocodiles (*C. porosus*), and can die after mouthing or ingesting cane toads (Smith & Phillips, 2006). Intriguingly, this vulnerability has translated into massive spatial heterogeneity in the population-level impacts of toad invasion on freshwater crocodiles: from no discernible impact in the Daly River and Borroloola region (Catling et al., 1999; Doody et al., 2006) to very high impact in the Victoria River and Boodjamulla National Park in north-western Queensland (White, 2003; Letnic et al., 2008). In the arid Victoria River region, cane toads caused 77% mortality of crocodiles, mostly relatively large animals (>0.6 m long: Letnic et al., 2008). High mortality of freshwater crocodiles also occurred in the semi-arid Boodjamulla National Park (White, 2003). Potentially, such a massive mortality event could cause serious declines in crocodile numbers — especially in arid regions where scarcity of water increases encounter rates between crocodiles and toads (Letnic et al., 2008).

The longer-term impact of toads on freshwater crocodile populations will depend on the toads' effects on hatchling crocodiles. Freshwater crocodiles have high fecundity and populations can increase rapidly, as demonstrated by their recovery following the cessation of the commercial skin trade in 1963 (Smith & Webb, 1985). Thus, if cane toads do not negatively affect hatchlings, populations may recover rapidly after toad invasion. Importantly, hatching success of crocodile eggs may increase following toad invasion due to reduced rates of nest predation (Webb & Manolis, 2010), in turn due to toad-induced mortality of the primary nest predator (varanid lizards), thereby facilitating rapid population recovery. However, hatchling survival will be low if these animals attempt to eat cane toads, and die in the process. Hatchling crocodiles feed on insects, frogs and fish (Webb et al., 1982; Tucker et al., 1996; Somaweera, pers. obs.), and are likely to encounter and consume cane toads. However, because they are gape-limited predators, hatchling crocodiles can only consume small toads, which are less toxic than larger toads (Phillips & Shine, 2006; Hayes et al., 2009). Hence, hatchling crocodiles that ingest metamorph toads may survive the encounter, become ill, and subsequently avoid toads as prey. This 'taste aversion learning' occurs when an animal associates the taste of a food item with post-consumption illness, and thereafter avoids that food (Garcia et al., 1974);

a single negative experience can create a long-lasting aversion to prey in many animals (Gustavson et al., 1974). Clearly, whether or not hatchling crocodiles are capable of learning to avoid toads will influence how toads affect crocodile populations.

Cane toads recently invaded Lake Argyle, a large freshwater impoundment (surface area 880 km^2) in semi-arid northwestern Australia (16°22′S, 128°46′E). This lake harbours one of the largest populations of freshwater crocodiles, potentially at risk from the cane toad invasion because the arid surrounding landscape will increase rates of encounter between crocodiles and hydrating toads (Freeland, 2004; Letnic et al., 2008). In this paper, we investigate the feeding responses of hatchling freshwater crocodiles to cane toads (and, especially, whether crocodiles are able to learn to avoid the toxic toads) in order to predict impacts of cane toads on freshwater crocodiles in Lake Argyle and similar water bodies.

2. Materials and methods

2.1. Laboratory studies

In February 2010 we hand-collected 20 freshwater crocodile hatchlings (sex undetermined, 3–4 months old) from areas in Lake Argyle not yet invaded by cane toads. Hatchlings were individually marked by scute-clipping the tail, then airfreighted to the University of Sydney Tropical Ecology Research Facility 60 km from Darwin, Northern Territory. We housed hatchlings individually in plastic bins ($45 \times 25 \times 30$ cm) with mesh tops, in an animal house with a natural light/dark cycle. The bins were tilted so that one end remained dry and the other end had a pool of 5-cm-deep water. Ambient temperature was regulated at 29–32°C, and relative humidity at 80%. We fed animals 5 g (approximately 5% of average body mass) of lean beef with calcium and multi-vitamin supplements every other day and removed any uneaten food the morning after feeding. We replaced the water in holding tanks twice a week. Animals were acclimated to their environment for a month and were feeding regularly when trials commenced.

We randomly assigned the animals to treatment (T) and control (C) groups. At dusk (1900 h), we offered the animals in the treatment group either a cricket or a metamorph cane toad (mean mass = 0.86 g, range = 0.25–1.46 g, SE = 0.067; collected near the research station) alternately for

five feeding sessions (5 nights; such that each animal encountered a cricket the first night, a toad the second night, a cricket the third night, etc.). All crocodiles were offered a toad during the final feeding session (on the 6th night). The control group received only crickets for the first five feeding sessions but each was offered a toad during the last session (6th night). After 14 h we recorded the outcome of the trial (prey item alive versus eaten, versus killed but not eaten). To avoid confounding, we used each individual prey item in only a single trial, and began half the trials a day after the other half (such that on any given night, half the treatment crocodiles received crickets and the other half received toads). Partway through the trials (morning of the third day) we fed crocodiles with their staple diet (beef) to maintain food intake and standardise hunger levels.

We videotaped the first set of encounters between crocodiles and crickets (day one for controls) and the first and the last sets of encounters between crocodiles and toads (day six for controls; day two and six for treatments). From the footage, we scored the crocodile's: (1) latency between noticing the prey and attacking it; (2) bite location; (3) total duration of time prey was held in the mouth; (4) number of bites; and (5) outcome (prey eaten or rejected).

All procedures were approved by the University of Sydney Animal Ethics Committee (Protocol No. L04/1-2010/2/5228), who judged that any suffering experienced by toads during these trials was outweighed by the potential importance of the data for conservation and management planning. Data were analysed using the statistical software JMP 5.01 (SAS Institute, Cary, NC, USA). We used contingency table analyses to compare the relative frequencies of attack responses to cane toads among three groups (controls during the first encounter, treatments during the first encounter and treatments during the last encounter). Variables that were scored from the videos (latency to attack; number of bites; ln-transformed time in mouth) were compared among the same three groups using ANOVA tests followed by Fisher's PLSD post-hoc tests.

2.2. Field studies

To assess whether free-ranging crocodiles have learnt to avoid toads as food, we stomach-flushed 34 crocodiles (SVL mean $\pm$ SE $= 193.6 \pm 12.2$ mm; mass mean $\pm$ SE $= 214.6 \pm 47.7$ g) captured in areas where cane toads

have bred in Lake Argyle (i.e., in places where the crocodiles would en-
counter metamorph and juvenile toads). Soon after a crocodile was caught,
we held its mouth open with a rubber ring while a water-lubricated sili-
cone tube (inner diameter 4 mm) was inserted through the mouth and into
the stomach. Water was pumped in using a 60-ml syringe, and the tube
was moved back and forth to stir the contents and then was gradually ex-
tracted while the crocodile was inverted and its abdomen massaged to-
wards the mouth. The procedure was repeated until the water was devoid
of food particles (2–4 times); regurgitated stomach-content samples were
seined through cheesecloth, and screened for body parts of frogs and toads.
To evaluate the availability of anurans as prey, we counted the number of
frogs (1900–2100 h) and cane toads (adults at 1900–2100 h and metamorphs
at 1100–1300 h the next day in the same location) in 1.5×1.5 m quadrants
along the shoreline close to where the crocodiles were collected. We used
Fisher's Exact Test to compare the relative numbers of frogs versus toads in
stomach contents versus quadrants.

3. Results

3.1. *Responses to crickets in the lab*

Crocodiles in both treatment and control groups attacked and consumed both
crickets and cane toads. Most crocodiles began moving towards the prey
soon after the prey animals moved. In many instances, crocodiles approached
to within 2–3 cm of the prey, watched the prey for up to 25 min without
moving, and then suddenly attacked. All crocodiles that approached a prey
item eventually attacked it. However at first encounter, toads were seized
sooner than crickets (toads after 7.98 ± 7.54 min versus 19.33 ± 15.87 min
for crickets, $t = 2.68$, $p = 0.012$).

3.2. *Responses to toads in the lab*

All 10 crocodiles in the treatment group attacked metamorph toads during
the first encounter, but only four did so on the last day (third encounter).
Hence, the proportion of crocodiles in the treatment group that attacked toads
decreased between the first encounter and the last encounter ($\chi^2 = 10.97$,
df $= 1$, $p < 0.001$). In contrast, 8 of 10 animals in the control group attacked
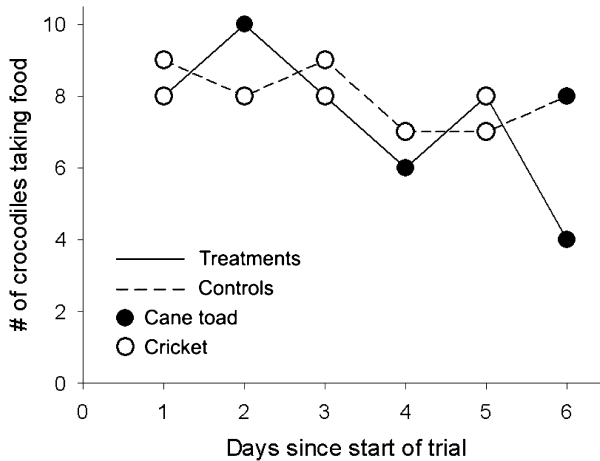
Figure 1. The number of crocodiles (treatment animals shown in solid line and controls in dotted line) that attacked prey items on the six days of trials (crickets in white dots and cane toads (*Rhinella marina*) in black dots). Treatment animals were offered cane toads and crickets on alternate nights, whereas controls were only offered crickets until the last night, when they were offered a toad.

the metamorph toads during their first encounter (comparing controls versus 'trained animals' in treatment group: $\chi^2 = 3.45$, df $= 1$, $p = 0.063$; Figure 1).

When the three toad encounters (control group encountering their first toad, treatment group encountering their first toad and the same treatment group encountering their last (third) toad) are considered, the mean latency to attack a toad did not differ significantly among the three groups (ANOVA, $F_{2,27} = 0.266$, $p = 0.786$; Figure 2a). However, the three groups differed in the mean amount of time they held a toad in the mouth ($F_{2,27} = 3.567$, $p = 0.0422$; Figure 2b); retention times were shorter for 'trained' crocodiles (i.e., those in the treatment group encountering their third toad) than for either the same animals on their first encounter with a toad, or the control animals (Fisher's PLSD test, $p < 0.05$ for both of these comparisons). We did not observe crocodiles gaping or head-shaking after they released the toads, but no released toad was attacked again during the remainder of that trial.

The number of bites inflicted on toads increased with the total time the prey was kept in the mouth (bites $= 3.027 + 0.650$, $r^2 = 0.604 \pm 7.473$, $F_{1,28} = 42.726$, $p < 0.001$). The three groups differed significantly in the
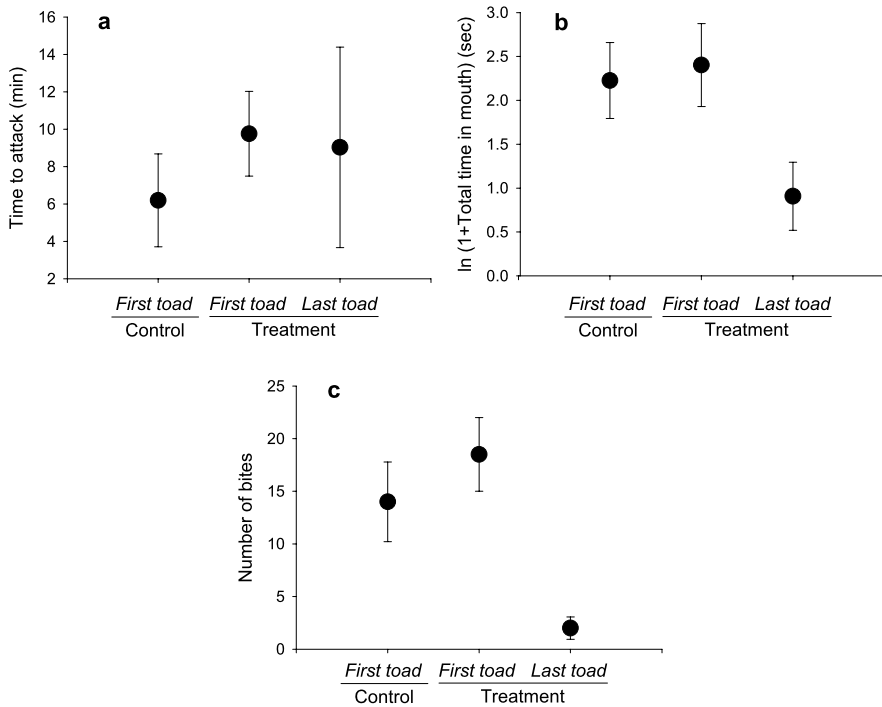
Figure 2. Responses of hatchling freshwater crocodiles (*Crocodylus johnstoni*) to invasive cane toads (*Rhinella marina*). The graphs compare behaviour of a crocodile during its first encounter with a toad, to responses to the animal's third encounter. Panel (a) shows latency to attack; panel (b) shows the duration of time the toad was held in the mouth before ingestion or release; and panel (c) shows the number of bites inflicted on toads while they were held in the crocodile's mouth. All graphs show mean values with standard errors.

mean number of bites they inflicted on toads ($F_{2,27} = 7.874$, $p = 0.002$; Figure 2c). Crocodiles in the treatment group inflicted fewer bites on the toad in their last encounter than in their first encounter and also less than those in the control group during their first encounter (Fisher's PLSD test, both of these comparisons have $p < 0.05$). In cases where the toad was killed but not consumed, bite marks were observed on the toad's head (73% of trials) and body (27%). In all but one encounter (in which a toad was mutilated), the dead toads were punctured with teeth marks but intact. After killing toad metamorphs, all crocodiles consumed them headfirst, as occurs during attacks on native anurans in the wild (Somaweera, pers. obs.). No crocodile showed any sign of poisoning or distress after biting or eating toads, and all survived the rest of their stay in captivity (23 days).

Four of the 10 crocodiles that avoided toads showed one-trial learning and two showed two-trial learning. Of crocodiles that attacked toads during the first encounter, 80% consumed crickets the next day; all animals that attacked toads on the second encounter ate crickets the following day. Hence an encounter with a toad did not reduce the probability that a crocodile would attack a cricket. All animals consumed the staple diet (beef) offered on the third day.

3.3. Prey selection in the natural habitat

Of the 34 small crocodiles that we stomach-flushed, one had eaten a cane toad and another six animals had consumed native frogs (four *Litoria inermis* and two *L. rubella*). The crocodile that consumed a cane toad was larger than any of those that ate frogs (logistic regression with crocodile snout–vent length as independent variable and prey type as dependent variable, $\chi^2 = 5.74$, 1 df, $p = 0.02$). Frogs and toads were seen in approximately equal numbers in the quadrants (147 frogs, 135 toads) whereas frogs were consumed more often than toads (6 frogs, 1 toad). This bias towards eating frogs rather than toads was not statistically significant if all crocodiles were included (Fisher's Exact test, $p = 0.13$). However, if learning depends upon crocodile body size, with more rapid learning in smaller animals (because they are more affected by toad ingestion), then we might see toad avoidance only in small animals. If we restrict analysis to crocodiles <375 mm snout–vent length, the bias for toads to be consumed less often (relative to native frogs) than would be expected based on their relative abundances in quadrat counts is borderline for statistical significance (Fisher's Exact test, $p = 0.063$; $p = 0.03$ with a one-tailed test (since the direction of effect was predicted a priori)).

4. Discussion

Predicting the impact of cane toads on predator populations is a logistically difficult task, due to the plethora of potential influences on severity of the impact (Shine, 2010). Because crocodiles are wary and secretive, feeding is difficult to observe in the field. Staged encounters between predator and prey in the laboratory, thus, may be useful in predicting the impact of cane toad invasion on crocodiles. In this study, we estimated vulnerability of

hatchlings in advance of actual impact, by exploring the feeding (and learn-ing) behaviour of the predator. Contrary to a previous study that predicted massive impact of toads on crocodiles in arid-zone locations like Lake Ar-gyle (Letnic et al., 2008), our study suggests that crocodiles of at least one size class (hatchlings) can rapidly learn to avoid cane toads as prey, and may not experience high levels of mortality as a consequence of toad inva-sion. We found that toad-naïve hatchling freshwater crocodiles readily con-sumed metamorph cane toads and survived the encounter. Importantly, 60% of crocodiles that ingested toads subsequently avoided toads as food for up to two weeks (the duration of the study). Most crocodiles learnt to avoid toads as food after ingesting one or two meals.

Although abundant laboratory and field evidence shows that cane toads are highly toxic to freshwater crocodiles (Smith & Phillips, 2006; Letnic et al., 2008), all of our crocodiles that attacked metamorph cane toads survived the encounter. Toxin content is lower in metamorph toads than in any other stage of the life-history (Hayes et al., 2009); metamorphic toads have active parotoid glands (Flier et al., 1980; Freeland & Kerin, 1991) but produce too little toxin to be fatal to most predators (Buzzacott, 1938; Covacevich & Archer, 1975; van Beurden, 1980). Thus, the lack of any overt ill-effects from toad consumption may reflect the body sizes of toads consumed. More generally, the degree of risk posed by ingesting a cane toad depends upon the size of the toad (and, hence, its toxin content) relative to the size of the predator (and, hence, its ability to tolerate any given dose of toxin) (Phillips & Shine, 2006). Toxin content increases with toad body size at an allometric rate (i.e., toxicity increases very rapidly as toad body size increases), and maximal ingestible prey size also increases with predator body size in a gape-limited predator (Phillips & Shine, 2004). The end result of these two allometries is that a small increase in predator body size may enable the animal to ingest a toad with a much greater amount of toxin.

Crocodiles are gape-limited predators (Schmidt & Holbrook, 1984), and hatchlings cannot tear prey apart into pieces small enough to be swallowed. Because their maximum prey size, thus, is determined by their gape size, hatchling crocodiles can consume only small metamorph toads. The balance between the allometries of toxin content of toads vs maximal ingestible prey size of crocodiles will determine the predator's vulnerability. Our study sug-gests that hatchling crocodiles will not be killed by the size class of toads

they are capable of ingesting, but might experience nausea; and hence, aversion learning could induce a crocodile to delete toads from the diet. In the wild, this aversion learning might reduce over time, or be reinforced by additional encounters with toads. Larger crocodiles may be in a more perilous situation than are hatchlings, consistent with high mortality rates of larger crocodiles when toads first arrive (as documented by White, 2003 and Letnic et al., 2008). That is, the potential for a crocodile to consume a toad large enough to be lethal may increase rapidly with crocodile body size, because a slightly larger gape size allows ingestion of a toad with a much higher toxin content. If the predator's physiological tolerance of toxins is directly proportional to its body mass (as appears to be the case for most predators that consume toads: Phillips & Shine, 2004; Smith & Phillips, 2006), then the maximal toxin dose from an ingestible-sized toad may increase with crocodile body size faster than the predator's physiological tolerance; and hence, larger body size may render a crocodile more vulnerable to lethal toxic ingestion.

Although we did not see any overt signs of poisoning during the monitoring period in our captive crocodiles that consumed toads, we restricted intake to a single toad per crocodile per day. During the dry season, metamorph toads form dense aggregations near water (Cohen & Alford, 1996; Child et al., 2008a,b), and hatchling crocodiles may have the opportunity to consume several small toads in succession. In such cases, the cumulative effect of toxins from multiple toads might kill a hatchling. No dead hatchling crocodiles have been observed in toad-infested areas in the Victoria River (Letnic et al., 2008) or at Lake Argyle (Somaweera, pers. obs.) but small (<70 cm in total length) dead crocodiles with numerous metamorph toads in their stomachs have been recorded from Boodjamulla National Park in north-western Queensland (White, 2003; A. White, pers. commun., 2010).

Crocodilians show several forms of learned behaviour (e.g., Davidson, 1964, 1966a,b; Williams, 1967, 1968; Bustard, 1968; Williams & Robertson, 1970; Northcutt & Heath, 1971; Williams & Albiniak, 1972; Webb & Messel, 1979; Pacheco, 1996; Ron et al., 1998; Sneddon et al., 1999, 2001) including food recognition (McIlhenny, 1935; Morpurgo et al., 1991; but see Weldon & McNease, 1991 for counter example). Our results show a previously unreported form of learning in crocodilians — taste aversion learning. Our data expand the growing understanding of the role of aversion learning in enabling predators to survive the invasion of a highly toxic prey type. Previous work suggests that some Australian predators (elapid snakes) are

unable to learn to avoid cane toads as prey and, hence, experience very high mortality rates when the toads arrive; that mortality rate eventually is reduced by adaptive (genetically-coded) shifts in traits such as feeding behaviour, toxin resistance and morphological determinants of maximal ingestible prey size (Phillips & Shine, 2006). Other species of predators experience relatively low levels of mortality following toad invasion, because most individuals survive their first experience of ingesting a toad, and avoid toads as prey thereafter (e.g., fishes, Nelson et al., 2011; frogs, Greenlees et al., 2010; marsupials, Webb et al., 2008; Llewelyn et al., 2010). In keeping with this scenario, teaching otherwise-vulnerable predators (northern quolls, *Dasyurus hallucatus*) to avoid toads as prey enables these animals to survive in toad-infested landscapes (O'Donnell et al., 2010).

Our data from stomach-flushing of free-ranging animals suggest that small crocodiles eat cane toads less often than frogs, despite the toads being commonly available. Continued predation on frogs, despite the presence of toads, shows that crocodiles in toad-infested areas have not developed an aversion to anurans in general. Laboratory studies on marsupials and fishes have demonstrated generalised aversion to anurans based on initial encounters with toads, but that aversion seems to be short-term (Webb et al., 2008; Nelson et al., 2011). Native anurans are an important component of the diet of small crocodiles (Webb et al., 1982; Tucker et al., 1996) and, thus, an aversion to all anurans would have important consequences for those predators. Although sample sizes are small, our results suggest that free-ranging freshwater crocodiles, like their counterparts in the laboratory, may be able to distinguish between toads and frogs, and avoid ingesting the toxic invasive species.

Our data on crocodiles reveal a combination of characteristics not previously documented: that is, a predator that is capable of aversion learning if it encounters cane toads, but nonetheless sometimes experiences high rates of mortality when toads invade. The likely resolution of this apparent paradox involves the great body-size range of individuals within a population of *C. johnstoni* (from <0.05 kg in hatchlings to >75 kg in adults: Webb & Manolis, 1989). Because of ontogenetic allometries in the toxin content of toads and the maximal ingestible prey size of crocodiles, smaller size classes of this predator species are unable to swallow a toad large enough to kill them (and hence, are able to survive via aversion learning) whereas larger conspecifics are at greater risk. Overall, our results are encouraging in terms

of the magnitude of threat that cane toads pose to populations of freshwater crocodiles. Even if larger animals are vulnerable to lethal toxic ingestion of toads, the hatchlings of surviving adults are likely to deal with toads through rapid aversion learning. Thus, even if the adult size-classes decline, the population may recover rapidly via recruitment of juveniles.

More generally, results from previous studies on interspecific variation in predator vulnerability to cane toads show that mortality falls disproportionately upon predator species that attain large body sizes, because such animals attack and ingest toads that are large enough to contain a fatal dose of toxin (Shine, 2010). Our data suggest the same pattern intraspecifically: that is, the severity of cane toad impact may differ with predator ontogeny, because of the allometries of maximal ingestible prey size and toad toxin content. Paradoxically, this is an encouraging result. It suggests that even for some predator species that experience high levels of mortality when toads first invade, the progeny of surviving adults may be better able to deal with the toxic invader (through aversion learning) than were the adults of their parents' generation. Size-related vulnerabilities of this kind may explain anecdotal reports of surprisingly rapid recovery of some predator populations following an initial period of high mortality when toads first invade an area (Shine, 2010).

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