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ORIGINAL PAPER

The impacts of a toxic invasive prey species (the cane toad, *Rhinella marina*) on a vulnerable predator (the lace monitor, *Varanus varius*)

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Abstract The magnitude of impact of an invasive species on native taxa, and the time course of recovery, depend on the native's ability to adjust to the invader. Here, we examine the impact of a toxic invasive prey species (cane toad *Rhinella marina*) on a vulnerable top-predator (lace monitor *Varanus varius*) in southern Australia. Lace monitor populations crash as soon as toads invade, as occurs in related species in tropical Australia. The toad's impact falls primarily on larger lizards, such that mean body sizes decline precipitously after toad arrival. Feeding trials with free-ranging lizards clarified the reasons for that size-biased vulnerability. Large lizards attacked novel prey more rapidly than did smaller conspecifics, especially in toad-naïve populations. Small lizards were more cautious in investigating novel prey (more tongue flicks and bites prior to ingestion) and swallowed the item more slowly. These traits may allow smaller lizards to detect and avoid toad toxins. Seventy percent of monitors from toad-naïve populations readily consumed dead cane toads (with parotoid glands removed) and 85 % consumed frogs. In contrast, no conspecifics from toad-exposed populations consumed toads whereas 40 % ate frogs. Following a single meal of toxic toad (typically eliciting illness), all monitors refused toads but 40 % continued to eat frogs. Lace monitors thus can rapidly learn taste aversion to cane toads. This behavioral plasticity enables survival of smaller lizards (that approach and process prey more cautiously than their larger relatives), and may explain this species' recovery in long-term toad-colonized regions of northern Australia.

Keywords Behavioral plasticity · *Bufo marinus* · Invasive species impact · Taste aversion learning · Varanidae

Introduction

The ecological impacts of invasive species are a major conservation concern (Mack et al. 2000; McGeoch et al. 2010). Impacts of an invader, however, are complex (Melbourne et al. 2007) and are not likely to be evenly distributed across all individuals even within a single population of vulnerable natives (Brown et al. 2011; Somaweera and Shine 2012). Intraspecific differences in vulnerability arise from variation in behavioral, morphological and/or physiological traits that mediate an invader's impact (Rayner et al. 2007; Phillips et al. 2010; Shine 2012). Through time, such traits may shift via phenotypic plasticity (e.g., learning) and/or via genetically based adaptation, allowing a vulnerable native species to overcome the impact of an invader (Mooney

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and Cleland 2001; Carroll 2007, 2008). If we understand the mechanisms that confer resistance to invader impacts, we can better predict longer-term outcomes, and potentially improve management (e.g. O'Donnell et al. 2010).

The continuing advance of the cane toad (*Rhinella marina*) through Australia is an infamous example of animal invasion (Lowe et al. 2000; Shine 2010). Native to Central and South America, cane toads were introduced to northern Australia in 1935, to control agricultural pests (Lever 2001). Since their introduction, these highly toxic anurans have spread across much of tropical and subtropical Australia (Kearney et al. 2008; Kolbe et al. 2010). Due to its geographical isolation over evolutionary time, many of Australia's native species are poorly equipped to deal with invaders (Dickman 1996; Banks et al. 2000). Cane toads have caused severe declines in native frog-eating predators (via fatal ingestion: Shine 2010), thus disrupting ecological function (Brown et al. 2011, 2013; Doody et al. 2013).

Unlike the invasion of cane toads across the tropical north of Australia, where toads advance as a continuous and rapid front (>50 km/year: Phillips et al. 2006, 2007; Urban et al. 2007), the invasion of toads into southeastern Australia is progressing slowly (1–3 km/year: McCann et al. 2014) and is patchily distributed (Jolly et al. 2015). This provides a unique opportunity to compare adjacent populations of vulnerable predators that differ only in their exposure to toads. The lace monitor *Varanus varius* is a large, predatory lizard native to eastern Australia (Weavers 2004). Lace monitors are voracious generalist predators and scavengers, include native frogs in their diet (Losos and Greene 1988; Jessop et al. 2010) and are highly vulnerable to toad toxin (Ujvari et al. 2012). As a result, lace monitor populations have been significantly impacted by the invasion of cane toads into southern Australia (Jolly et al. 2015). Nonetheless, lace monitors are common in areas of northeastern Australia where toads have been established for almost 80 years (Lloyd 2006; Wilson 2012), suggesting that populations of this lizard can adjust to this toxic invader and recover.

To understand the mechanisms underlying the impact of cane toads on large predators, such as the lace monitor, and how those vulnerable populations adjust in ways that facilitate persistence, we need information on the shifts in predator numbers and relevant traits (e.g., body sizes, feeding responses) elicited by toad arrival; and the proximate determinants of an individual predator's vulnerability to the invader's arrival. We used a combination of field surveys and feeding trials to determine whether a predator's body size affected its vulnerability to toad invasion; and if so, what those patterns might tell us about long-term impacts and management options in this system. We predict that larger lizards (that are less cautious when feeding) are likely to be more susceptible to fatal toxic ingestion of toads. Additionally, we predict that the apparent recovery of lace monitors observed in areas long colonized by toads is explained by lizards developing an aversion to feeding on toads.

Methods

Study species

Lace monitors ("goannas", *V. varius*) are among the largest terrestrial carnivores in southeastern Australia (to >2 m total length, 14 kg mass: Guarino 2001). These opportunistic carnivores and scavengers consume birds, mammals, reptiles, amphibians, and arthropods (Losos and Greene 1988; Jessop et al. 2010). Lacking physiological resistance to toad toxins (Smith and Phillips 2006; Ujvari et al. 2012), Australian varanid lizards are vulnerable to lethal toxic ingestion of toads (Shine 2010). Lace monitors have suffered severe ecological impacts from toads (Jolly et al. 2015), as have their congeners in tropical Australia (Ujvari and Madsen 2009; Brown et al. 2013; Doody et al. 2013). Individual variation in the complex color pattern of these lizards allows recognition of specific animals, especially if photographs are available.

Study sites

We worked at 16 campgrounds in northeastern New South Wales (from 28°22′S, 153°14′E to 29°57′S, 153°15′E), between October 2013 and February 2014. Due to the patchy distribution and slow progression (McCann et al. 2014) of cane toads at the southern edge of their invasion, we were able to select study sites such that the presence of toads was not confounded by latitude, longitude, elevation, climate or vegetation (see Jolly et al. 2015 for analyses). Each site consisted of a cleared campground area plus an adjacent 5 km section of access road through native bushland. Goannas are habituated to human presence in these areas, enabling close approach without undue disturbance.

Body-size distributions and relative abundance of lace monitors and cane toads

During hour-long surveys in sunny weather (0900–1600 h, >23 °C), we slowly walked or drove each site on ten occasions during the 5-month survey period (for details see Jolly et al. 2015). To minimize stress, no goannas were handled, so we were unable to determine their sex. We estimated lizard snout–vent length (SVL; to the nearest 50 mm) by placing a tape measure near the animal or estimating size from a photograph plus later measurements of the relevant area. We also recorded the snout–urostyle length (SUL) of toads found at the campgrounds and bushland sites, during surveys conducted at night in suitable weather (1930–2330 h, >17 °C; see Jolly et al. 2015).

Effects of lizard body size on prey-handling behavior

Free-ranging lace monitors from six toad-naïve populations ($n = 10$ lizards; range 25–70 cm SVL) and four toad-exposed populations ($n = 10$ lizards; range 20–70 cm SVL), were each offered a novel food item (a chicken neck, thrown near the goanna). We then recorded the lace monitors' prey-handling behavior with a video camera (GoPro Hero 3; Woodman Labs, San Mateo, California, USA). Chicken necks are similar in size and shape to anurans, are novel prey, and were readily consumed by lace monitors of all sizes. From the video footage, we scored four prey-handling behaviors: the length of time (in seconds) to detect and bite the chicken neck; the number of tongue flicks prior to swallowing the chicken neck; the number of times the goanna bit the chicken neck prior to swallowing it; and the time (in seconds) from picking up the chicken neck to completely ingesting it. We estimated lizard SVL as described above.

Effects of toad-exposure and lizard body size on feeding responses

To quantify feeding responses, we tested free-ranging lace monitors from six toad-naïve populations ($n = 23$ lizards; range 25–70 cm SVL) and four toad-exposed populations ($n = 12$ lizards; range 20–70 cm SVL) to a chicken neck, a nontoxic native frog species (*Mixophyes fasciolatus*), and a cane toad. Body sizes of *M. fasciolatus* and *R. marina* that we used for these trials did not differ significantly (mean mass ± SE = 51.46 ± 4.04 g vs. 59.31 ± 5.89 g respectively; one-factor ANOVA: $F_{1,24} = 1.21$, $P = 0.28$; mean SUL ± SE = 71.95 ± 2.14 mm vs. 76.87 ± 2.19 mm respectively; $F_{1,24} = 2.58$, $P = 0.12$). The frogs were collected as road-kill; the toads were culled and euthanized by a community group. Only frogs with minimal structural damage from road fatalities were used, to limit the likelihood that trauma-induced cues would affect the trials. All anurans were frozen until required. To minimize risk to goannas, we removed the parotoid glands from euthanized toads. Sufficient toxin remained to make goannas nauseous (see "Results" section) and potentially elicit a learnt aversion.

In each trial, we slowly approached a lizard and placed a plastic platter containing the three prey items (arranged in random order) within 1–5 m of the goanna's head. From cover, we videoed goanna responses to score the number of tongue flicks directed to each prey item, and whether or not each prey item was consumed. Each goanna was then observed for at least 15 min to record any signs of illness, and was photographed for later identification (for follow-up feeding trials, see below). No goannas consumed either the frog or the toad without also consuming the chicken neck; data from goannas that refused all prey types (including the chicken neck) were not included in statistical analyses. To prevent satiation confounding goanna prey choices, only data from lizards that consumed an additional chicken neck after completion of feeding trials were accepted.

To test for learnt toad-aversion, we repeated these trials 1–3 days later with the same lace monitors, from six toad-naïve populations ($n = 19$ lizards; range 25–70 cm SVL) and four toad-exposed populations ($n = 12$ lizards; range 20–70 cm SVL). Additional feeding trials with toad-naïve lizards were conducted after 30 days, but we could only locate five goannas from toad-naïve populations at that time. Because no toad-exposed lizards consumed toads in initial trials (see "Results" section) no further tests were conducted with this population.

Statistical analysis

All data were assessed for normality and homogeneity of variances (Levene's test). Using the statistical software JMP Pro Version 9.0 (SAS Institute, Cary, NC), we compared the relative abundance and mean body size (SVL) of lace monitors encountered in campgrounds and surrounding bushland, in both toad-exposed and toad-naïve populations. Relative abundance and lizard SVL were used as dependent variables, and toad-exposure (toad-exposed vs. toad-naïve) and location (campgrounds vs. bushland) were used as independent variables in two-way analyses of variance (ANOVA). Toad body-size distributions were visually compared between sites varying in time since invasion (<5 years, 5–10 years, and $\geq$10 years). Formal statistical analysis of these data was not required, because the only critical issue for impact on varanids was the presence or absence of small toads.

To clarify how the snout–vent lengths of goannas influenced feeding responses to chicken necks, we examined the relationship between four dependent variables: attack latency (ln[sec]); number of tongue flicks; number of bites; time taken to swallow food item (sec), and the independent variable toad-exposure status (toad-exposed vs. toad-naïve). Goanna SVL (cm) was included as a covariate. We used analyses of covariance (ANCOVA) to test for interactions between toad-exposure and the covariate (SVL).

Using the statistical software package R version 3.0.3 (R Development Core Team 2011), we examined the feeding responses of goannas to anuran prey. We used generalized linear mixed models (GLMM) to determine whether the feeding responses of goannas, ingestion (willingness to consume; binomial distribution) and interest (number of tongue flicks; Poisson distribution), differed between prey types. In this analysis, goanna response (consumed or refused; number of tongue flicks) was the dependent variable, toad exposure (toad-naïve or toad-exposed), prey type (frog or toad), trial day (day 1 or day 2) and goanna size (SVL cm, with interaction term removed) were independent variables, and goanna identity was included as a random effect to compare responses of individuals between days, and to control for repeated measures. Because most toad-exposed goannas refused to eat toads, and most toad-naïve goannas consumed toads, we experienced quasi-complete separation of the binomial data (Heinze 2006) such that the overall interaction between all independent variables (toad-exposure × prey type × trial day) was inconsistent with the trends observed ($z = 3.92$, $P = 1$; see "Results" section). This issue occurs when sample sizes are small and responses move to fixation after a single experience (e.g., Morosinotto et al. 2012; Llewelyn et al. 2013)—as is common with learnt taste aversion (Gustavson and Gustavson 1985; Nicolaus et al. 1989).

Results

Body-size distributions of lace monitors and cane toads

We obtained data on 199 lace monitors. Goanna counts did not differ between campgrounds and adjacent bushland (two-way ANOVA: $F_{1,28} = 0.85, P = 0.32$; interaction between toad-exposure and location $F_{1,28} = 0.42, P = 0.52$). However, goannas were more abundant when toads were absent (two-way ANOVA: $F_{1,28} = 24.42, P < 0.001$; Fig. 1b). Goannas in campgrounds were larger than those in surrounding bushland, and toad-naïve goannas were larger than those in toad-exposed sites (Fig. 1a). The divergence in mean body sizes between campground and bushland goannas was greater in sites without toads, than in sites where toads were present (two-factor ANOVA interaction: $F_{1,195} = 57.30, P = 0.004$). Our measurements of 229 cane toads showed that both small (<5 cm) and large (>10 cm) cane toads were present in all sites, regardless of time since colonization.

Effects of lizard body size on prey-handling behavior

The latency before a goanna attacked a novel food item was dependent on an interaction between the lizard's size and its prior exposure to cane toads (ANCOVA interaction: $F_{1,16} = 21.54$, $P = 0.001$; Fig. 2a). Among toad-naïve goannas, larger animals attacked sooner. This relationship was weaker in toad-exposed goannas (ANCOVA: $F_{1,16} = 6.93$, $P = 0.018$; Fig. 2a). Larger goannas also tongue-flicked less often prior to feeding (ANCOVA: $F_{1,17} = 13.36$, $P = 0.002$; Fig. 2b), consumed the chicken neck with fewer bites (ANCOVA: $F_{1,17} = 45.52$, $P < 0.0001$; Fig. 2c) and swallowed it more rapidly (ANCOVA: $F_{1,16} = 19.2$, $P = 0.0001$;

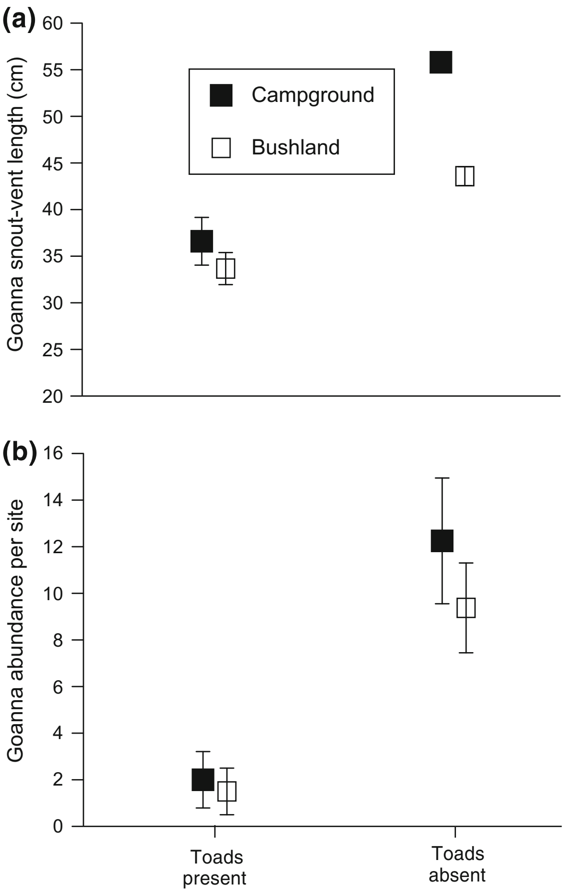

Fig. 1 Impacts of cane toad presence and habitat type on body sizes (**a**) and abundances (**b**) of lace monitors (*Varanus varius*) encountered in campgrounds and surrounding bushland areas in northeastern New South Wales, Australia. These lizards were more abundant in areas lacking cane toads ($P < 0.001$) and also larger, especially in campgrounds (interaction $P = 0.004$, main effect of toad presence $P < 0.001$)

Fig. 2d) than did smaller conspecifics. For the three latter behaviors, a goanna's response was not significantly affected by whether or not the area contained cane toads, nor was it affected by an interaction between toad presence and lizard body size (all $P > 0.05$).

Effects of toad-exposure and body size on feeding responses of lizards

Whether or not a goanna consumed the frog and toad it was offered depended on whether the lizard occurred in an area that contained cane toads (GLMM toad-exposure: $z = 3.53$, $P = 0.015$), and whether it had been previously offered a toad (GLMM day: $z = 7.20$, $P = 0.008$; Fig. 3). Toad-naïve lizards consumed both the frog and toad when they were first offered, whereas goannas from toad-exposed sites consumed the frog but not the toad (GLMM toad-exposure × prey type interaction: $z = 6.79$, $P = 0.013$). On the subsequent trial (1–3 days later), all goannas refused the toad but many consumed the frog (GLMM toad-exposure × prey type × day interaction: $z = -12.37$, $P = 1$). Thirty days later, these goannas continued to accept frogs but not toads (Fig. 3). Goanna size did not affect responses to prey items, regardless of toad-exposure (GLMM SVL: $z = 25.12$, $P = 0.36$), but that test is weakened by the fact that most goannas tested were sexually mature adults (juvenile goannas were rarely seen in sites without cane toads; see Fig. 1).

On the first trial, goannas from toad-exposed areas tended to investigate the novel prey type (chicken neck) and the familiar prey type (frog) more carefully (i.e., with more tongue flicks) than did goannas from areas without toads; however, they soon lost interest in the toad (Fig. 4). In contrast, toad-naïve goannas exhibited lower tongue-flick rates to the chicken neck and frog than to the toad (Fig. 4). When re-tested 3 days later, all goannas tongue-flicked the toad only briefly before abandoning it, whereas the chicken neck and (especially) the frog, attracted more attention (GLMM main interaction: $z = 2.91$, $P = 0.0036$; Fig. 4). Those patterns persisted through to Day 30 (Fig. 4).

Behavior of goannas after consuming cane toads

The goannas that consumed a cane toad (17 of the 23 toad-naïve lizards tested) were observed for 15 min post-consumption to assess signs of ill-health. Although we rendered "feeder" toads less toxic by removing their parotoid glands, and all of the goannas that consumed toads were large (45–70 cm SVL), three-quarters of the lizards were severely ill. Within 1–5 min post-consumption, they began swaying or stumbling, and/or rubbed their snouts into the substrate. Within 2 min of these first symptoms, most goannas convulsed, and six regurgitated.

Discussion

In southern Australia, cane toads not only have caused a decline in abundance of lace monitors (Jolly et al.

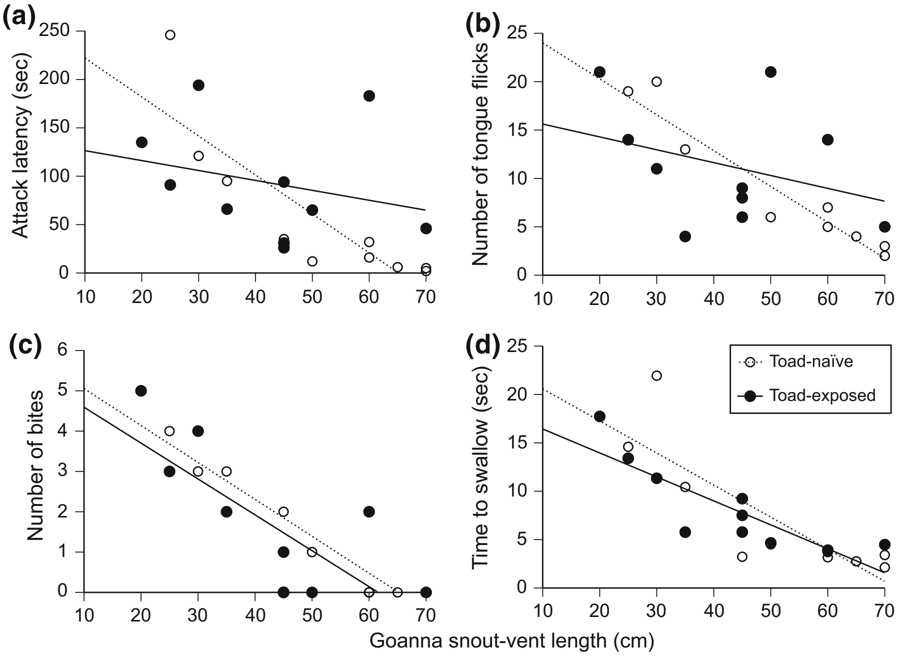

Fig. 2 Relationships between snout–vent length (SVL, cm) and prey-handling behavior of lace monitors (*Varanus varius*) from toad-naïve ($n = 10$) and toad-exposed ($n = 10$) populations. The graphs display: **a** attack latency (in seconds), **b** number of tongue flicks, **c** number of bites, and **d** time taken to swallow (in seconds) a single chicken neck thrown to free-ranging, campground lizards. Larger lizards consumed prey faster, with fewer tongue-flicks (all $P < 0.01$); latency to feed was also affected by an interaction between monitor body size and prior exposure to cane toads ($P = 0.001$; Fig. 2a)

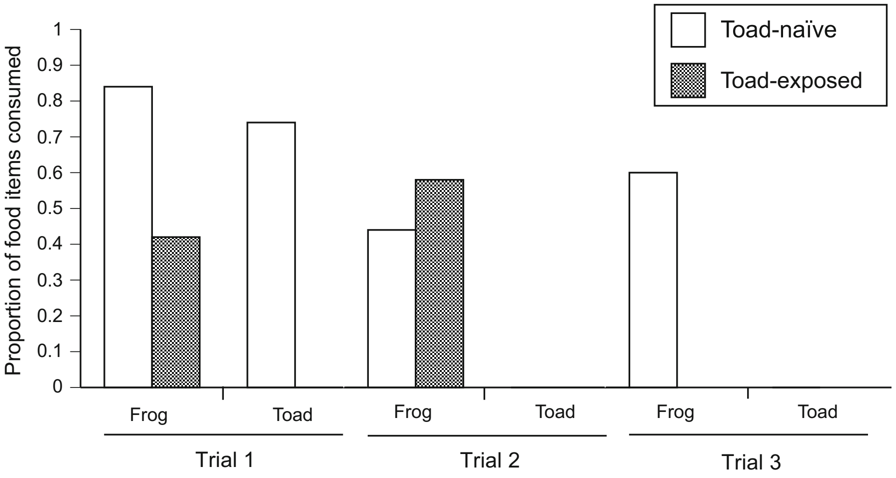

Fig. 3 The proportion of lace monitors (*Varanus varius*) from toad-naïve (Day 1: $n = 23$; Day 2–4: $n = 19$; Day 30: $n = 5$) and toad-exposed (Day 1: $n = 12$; Day 2–4: $n = 12$; Day 30: $n = 0$) populations that consumed a road-killed native nontoxic frog (*Mixophyes fasciolatus*) or a euthanized mildly toxic cane toad (*Rhinella marina*) in experimental trials. Lizards from toad-colonized areas were less likely to consume a cane toad; and exposure to a toad resulted in subsequent aversion to this prey type (interaction location × prior exposure $P = 0.013$)

2015), but also have modified the size structure of goanna populations, and the foraging behavior of the surviving lizards. Although toad-naïve lace monitors lack physiological resistance to bufadienolide toxins (Ujvari et al. 2012), lace monitors thrive in some areas where cane toads have been present for almost

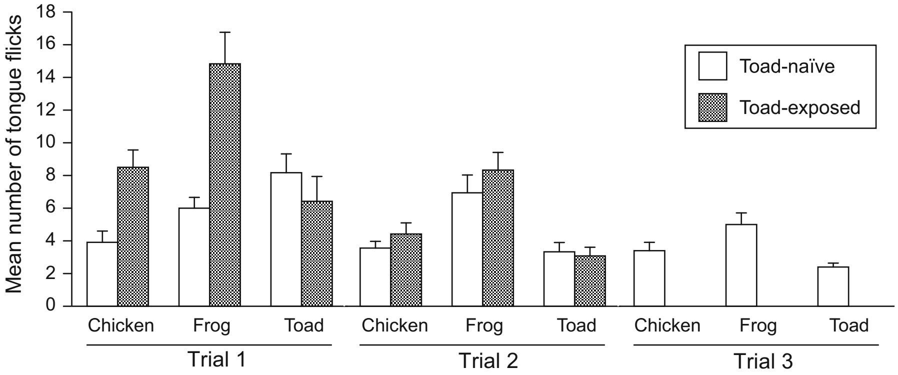

Fig. 4 Foraging responses of lace monitors (*Varanus varius*) from toad-naïve (Day 1: $n = 23$; Day 2–4: $n = 19$; Day 30: $n = 5$) and toad-exposed (Day 1: $n = 12$; Day 2–4: $n = 12$; Day 30: $n = 0$) populations. The graph shows mean number (±SE) of tongue flicks directed at: (1) a chicken neck; (2) a native nontoxic frog; and (3) a mildly toxic toad. Lizards from toad-colonized areas directed fewer tongue-flicks toward a cane toad; and exposure to a toad resulted in a decrease in tongue-flicks to this prey type (interaction location × prior exposure $P = 0.004$)

80 years (Lloyd 2006; Wilson 2012). The ability to rapidly learn not to feed on cane toads may ameliorate this invader's impact on vulnerable predators. Below, we first discuss the shifts in body sizes of goannas following toad invasion, and then consider mechanisms that enable smaller lizards to persist despite the invader's presence.

The effects of toad invasion on body-size distributions of lace monitors were striking: the goannas were smaller in toad-infested areas, both in campgrounds and the bushland. In areas without toads, in contrast, lace monitors in campgrounds were larger than those in the surrounding bushland. That size differential reflects human-supplied food resources in campgrounds (Jessop et al. 2012), coupled with behavioral exclusion of smaller lizards by larger conspecifics (Imansyah et al. 2008; Jessop et al. 2012).

Toad-induced shifts in numbers, body sizes, and the distribution of lizards across campground versus bushland habitat, all suggest that the impact of toad invasion falls most heavily on larger lizards. Large goannas disappear (presumably due to fatal poisoning) and their place is taken by smaller conspecifics that hitherto were relegated to less productive bushland sites. Smaller goannas also are more arboreal (Jessop et al. 2012; Wilson 2012), and so are unlikely to encounter toads. The size-specific impact of toads on goannas thus reflects an interaction between human food subsidies, ontogenetic shifts in varanid foraging tactics, habitat selection and territorial defense, and the allometry of toxin content within cane toads (Phillips and Shine 2006a; Hayes et al. 2009). An increase in maximal prey size with predator size (Losos and Greene 1988) places larger lace monitors at greater risk than their smaller conspecifics.

Lace monitors consume a wide variety of prey (Jessop et al. 2010, 2012; Metcalfe and Jones 2012) including dead toads (present study). Future work could usefully explore sex differences in toad impact. Male lace monitors grow much larger than females (Weavers 2004), and thus may bear a disproportionate impact (with obvious demographic consequences). In northern quolls (*Dasyurus hallucatus*), males are larger, more mobile and more adventurous in feeding behavior, and hence more likely to die from eating toads (O'Donnell et al. 2010).

Smaller goannas are cautious and take longer to consume novel prey items, plausibly facilitating detection of toxins prior to ingestion. The individuals persisting in toad-exposed populations may have survived the invasion of cane toads, at least in part, because of their cautious feeding behavior. Toad-naïve and toad-exposed goannas did not differ in regard to number of tongue flicks, number of bites, or time taken to swallow food items, but smaller lizards took longer to investigate, manipulate and swallow the novel food item. Visual inspection, tongue-flicking and biting allow goannas to assess the suitability of prey (Garrett and Card 1993; Cooper and Habegger 2001). The vomeronasal organs provide substantial information on a prey item prior to ingestion (Auffenberg 1984; Kaufman et al. 1996; Cooper 1997).

Smaller goannas investigated prey more thoroughly, a difference that may have enabled these animals to detect the meal's toxicity if the novel prey item had been a cane toad rather than a chicken neck.

Attributes of the invading toads, as well as those of predators, affect the impact of cane toads on native predators (Ashley et al. 2003; Phillips et al. 2010). In the Australian tropics, large adult toads dominate the toad invasion front (Phillips et al. 2006; Shine et al. 2011). Thus, every toad at the invasion front is large enough to be a lethal meal for a predator, causing declines of up to 96 % in some tropical varanid populations (Ujvari and Madsen 2009; Brown et al. 2013; Doody et al. 2013). Our data from the toad's southern invasion front paint a different picture. Even close to the colonization front, we found small (40 mm SUL) as well as large toads (140 mm SUL; C. Jolly, unpublished data). As a result, native predators are likely to encounter a small toad (large enough to induce taste aversion, but small enough to be non-lethal). Also, unlike snakes (Phillips and Shine 2004, 2006b), goannas are not gape-limited predators (Losos and Greene 1988). As a result, even a small goanna may be able to consume a large toad—but would take a long time to do so, perhaps adding to the opportunity for detection of toxins prior to fatal exposure.

Taste aversion learning is widespread and may be especially advantageous in dietary generalists (Mery and Burns 2010; Robbins and Langkilde 2012; Caller and Brown 2013). Road-killed frogs are a common and easily available source of carrion in our study areas, exploited by the local goannas. Some of these anurans produce powerful skin toxins (e.g., *Limnodynastes terraereginae*, *Litoria caerulea*: Daly et al. 1984; Williams et al. 2000) and lace monitors may learn to avoid such distasteful prey. That aversion could readily be broadened to include toxic cane toads. Lace monitors are, however, easily excited by moving prey (C. Jolly, pers. obs.). We cannot comment on whether learnt aversion to dead toads was strong or persistent enough in this study to prevent future attacks on live toads once they invade toad-free populations of goannas.

Previous studies on the responses of native predators to invasive cane toads have explored the feeding behaviors of marsupials (planigales: Webb et al. 2008; Llewelyn et al. 2010a; quolls: O'Donnell et al. 2010), birds (Beckmann and Shine 2011; Beckmann et al. 2011), crocodiles (Somaweera et al. 2011), turtles (Greenlees and Shine 2010), snakes (Phillips and Shine 2006b; Llewelyn et al. 2010b; Phillips et al. 2010; Pearson et al. 2014), lizards (Price-Rees et al. 2011; Llewelyn et al. 2013), frogs (Greenlees et al. 2010; Nelson et al. 2011a, b; Shine 2014), fishes (Crossland 2001; Nelson et al. 2011a, b; Somaweera et al. 2011; Caller and Brown 2013) and invertebrates (Cabrera-Guzman et al. 2012). Some predators can detect toad toxins, some can tolerate those toxins, and some can rapidly learn taste aversion (Shine 2010). That diversity of responses has generated heterogeneity in direct impacts of cane toads (Shine 2010, 2014).

Although varanid lizards have suffered severe impacts from the invasion of cane toads across Australia, the mechanisms that determine their vulnerability remain unclear. Learnt behavioral aversion of toads may allow vulnerable varanids to persist in toad-invaded areas (Llewelyn et al. 2013). Some monitor species learn more quickly than others (Burghardt et al. 2002; Pianka and Vitt 2003; Manrod et al. 2008), and it is interesting to note that our toad-naïve lace monitors rapidly learned aversion, whereas the yellow-spotted monitors (*Varanus panoptes*) studied by Llewelyn et al. (2013) did not. This difference may be explained by the northern invasion front being dominated by large, fatally toxic toads, eliminating any possibility of learnt aversion by predators. Alternatively, interspecific differences in behavioral plasticity, ecology and/or cognition might play a role in this divergence.

In most cases, toad-vulnerable predators have adjusted to toad invasion by eliminating toads from their diets (Phillips and Shine 2004, 2006b; Shine 2010; Llewelyn et al. 2013). What is the long-term impact of cane toad invasion on goanna populations? As in tropical varanids (Shine 2010), the likely outcome appears to be a dramatic but temporary reduction in lizard numbers (and mean body sizes, in the lace monitor). The primary evidence for eventual recovery is the lizard's capacity for rapidly learnt taste aversion (present study) coupled with high abundance of lace monitors in areas where toads have been present for decades (Lloyd 2006; Wilson 2012). However, the timescale of that recovery, and the shifts in goanna behavior or physiology that enable it, remain obscure.

Behavioral adjustments that enable species to tolerate novel environmental challenges (such as invasive species and climate change: Kokko and

Sutherland 2001; Shine 2012) can arise from phenotypic plasticity and/or evolutionary adaptation. Adjustments that mitigate such impacts via rapid changes to an individual's phenotype (such as aversion learning) may enable the threatened population to persist until "evolutionary rescue" (due to selection on genetically-coded traits) ensures its long-term persistence. Understanding the interaction between these two processes, to enable us to predict the magnitude, direction and outcome of invasive species impacts, remains an exciting challenge for future research.

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