Indirect impacts of invasive cane toads (*Bufo marinus*) on nest predation in pig-nosed turtles (*Carettochelys insculpta*)

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Abstract. The cane toad (*Bufo marinus*) was introduced into Australia in 1935. Because this toxic frog is novel to the Australian fauna, its introduction has impacted native fauna in a variety of ways. We anticipated a severe decline in the yellow-spotted monitor lizard (*Varanus panoptes*) associated with the arrival of cane toads along the Daly River, Northern Territory, and predicted a simultaneous impact on nest predation in the pig-nosed turtle (*Carettochelys insculpta*) because the lizard is the chief predator of *C. insculpta* eggs at the site. We surveyed for monitors and cane toads for five years at two sites before and after the arrival of cane toads, and surveyed for turtle nest predation for three years before, and one year after, the arrival of the toads. Collectively, our data and observations, combined with unpublished reports, indicate that: (1) cane toads arrived at our study sites during the wet seasons of 2003–04 and 2004–05; (2) the lizard *V. panoptes* readily succumbs to cane toad toxins; (3) *V. panoptes* has experienced a marked decline in relative population numbers coincident with the arrival of the toads at the site; and (4) *V. panoptes* has been reduced to such low numbers that it is currently no longer a significant predator of pig-nosed turtle eggs.

Introduction

The South American marine or cane toad (*Bufo marinus*) has invaded over 50 countries (Easteal 1981; Lever 2001), including Australia, where the toads were introduced in 1935 in north Queensland as a biocontrol agent (Freeland 1985). Since then cane toads have spread south to New South Wales and west to the Northern Territory, and are moving rapidly towards Western Australia (reviewed in Phillips *et al.* 2003).

Several features of the cane toad render it likely to impact heavily on the Australian frog-eating fauna: (1) its success as a colonist allows it to obtain a wide distribution within Australia over time (Sutherst *et al.* 1995; Lever 2001); (2) it reaches population densities far beyond those within its native range (Covacevich and Archer 1975; Lampo and Bayliss 1996; Lampo and De Leo 1998); and (3) its toxins, typical of the Bufonidae, are not present in any native frog species (Daly and Witkop 1971; Tyler 1987) and so most of Australia's fauna has not evolved any resistance to (or avoidance of) its effects.

Quantitative evidence of such impacts is surprisingly rare (reviewed in Phillips *et al.* 2003; Smith and Phillips 2006; but see Catling *et al.* 1999), and is at least partly attributable to lack of study rather than the lack of impacts (Lever 2001; Smith and Phillips 2006). Nevertheless, anecdotes and local reports indicate that many predators succumb to toads following ingestion (reviewed in Lever 2001). Population declines resulting from toad ingestion are suspected for northern quolls (*Dasyurus hallucatus*), monitor lizards, dingoes, and possibly snakes (reviewed in Lever 2001; Phillips *et al.* 2003; Webb *et al.* 2005; Smith and Phillips 2006), and studies of the impacts of cane toads on selected predators are currently underway in the north of the Northern Territory (e.g. Doody, unpubl. data; NT Government 2003).

In cases where impacts of cane toads on predator populations are substantial to severe, we would expect concomitant impacts on other animals preyed upon by these predators, particularly when the predator represents the chief source of mortality on the prey (see Zavaleta *et al.* 2001). We anticipated a severe decline in the yellow-spotted monitor lizard (*Varanus panoptes*) associated with the arrival of cane toads along the Daly River, Northern Territory (Burnett 1997), and predicted a simultaneous impact on nest predation in the pig-nosed turtle (*Carettochelys insculpta*), because the lizard is the chief predator of *C. insculpta* eggs at the site (Doody *et al.* 2003*a*, 2004). Quantifying and understanding indirect or secondary impacts is important in achieving broad ecosystem restoration in invasive species eradication or control programs (Zavaleta *et al.* 2001).

Herein we present five years of monitor survey data spanning the arrival of cane toads at two sites as evidence that a marked population decline in the monitor *V. panoptes* was due to invading cane toads. We then examine the hypothesis that this decline secondarily impacted pig-nosed turtles by comparing egg predation rates of *C. insculpta* before (three years) and after (one year) the arrival of cane toads.

Materials and methods

Study area and study period

We studied predator–prey relationships during the dry season along an ~100-km stretch of the Daly River, between Claravale Crossing and the Douglas River ($14^{\circ}04'40''S$, $131^{\circ}15'00''E$). The area is in the northwestern Northern Territory, Australia, and is situated within the wet–dry tropics. We quantified predation of pig-nosed turtle nests by *V* panoptes for three years before the arrival of cane toads (1996–98), and for one year after the toads arrived (2004). Surveys for *V* panoptes and cane toads were conducted from 2001 to 2005, and spanned the arrival of cane toads at two sites.

Study species

The pig-nosed turtle is a monotypic freshwater species inhabiting southern New Guinea and northern Australia (Georges and Wombey 1993); within Australia it occurs in rivers and associated billabongs (Georges *et al.* 2005). Two clutches are laid about five weeks apart in excavated chambers on sandy banks and beaches during the dry season between July and October (Doody *et al.* 2003*a*, 2003*b*, 2003*c*). The chief predator of pig-nosed turtle eggs on the Daly River, the stronghold for the species, is *V. panoptes* (Doody *et al.* 2004).

Varanus panoptes is a large carnivorous lizard inhabiting woodlands and floodplains in New Guinea and northern Australia. The species is a generalist feeder, preying upon both invertebrates and vertebrates (Shine 1986; James *et al.* 1992; Blamires 2004). Populations of *V. panoptes* along river floodplains are active year round, while those in woodland become inactive during the dry season, indicating that the availability of food and water in the floodplain dramatically influences activity patterns (Christian *et al.* 1995; Christian and Weavers 1996).

Turtle nest surveys

In 1996 pig-nosed turtle nest surveys were conducted along an ~20-km stretch of river roughly centred on Oolloo Crossing. In 1997 and 1998 nest surveys spanned the same stretch plus an additional, adjacent ~60-km stretch upriver (to Claravale Crossing). In 2004 nest surveys encompassed the above ~80 km plus an additional ~10-km stretch adjacent and downriver. In each year nest surveys overlapped the monitor survey stretches at the Oolloo site (see below). In some cases nest surveys were conducted daily or nearly so (1996), while in other cases surveys were less frequent and separated by 7–10 days. In all cases surveys included the nesting season.

Nest surveys were conducted by boat, and involved searching for suitable nesting beaches, as determined by noting tracks in the sand, and by visually assessing beach characteristics preferred by nesting turtles (Georges 1992; Doody *et al.* 2003*c*). Nest-finding involved using a probe to locate the nest chamber, which is softer than the surrounding substrate. We were confident that this technique enabled us to find most nests laid (Doody *et al.* 2000). We confirmed the presence of eggs for each nest by excavating the nest by hand, revealing the hard-shelled spherical eggs.

Nests preyed upon by monitors were conspicuous, characterised by eggshells and empty, dug-out nest chambers (Doody *et al.* 2003*c*). Because turtle egg predation generally occurs within the first 24 h of laying (Spencer 2002; Doody *et al.* 2003*a*), and because we visited each beach several days to several weeks after laying, all other nests without these signs were considered to have escaped predation. Although occasionally the monitor *V. mertensi* preys upon turtle nests at the site, most nest predation is attributable to *V. panoptes* (Doody *et al.* 2003*a*; Doody, unpublished data).

Monitor surveys

Monitor surveys were conducted by boat along two 30-km stretches of river that were \sim 30 km apart (temporary treatment and control sites). The Oolloo site spanned from \sim 15 km downstream of Oolloo Crossing

to the junction of the Douglas River, while the Daly River Township (DRT) site spanned from the township itself to 30 km upstream. Site designation was based on our prediction that cane toads would invade the Oolloo site at least one year before invading the DRT site.

Although the focus of this paper is on *V. panoptes*, we also counted *V. mertensi*, *V. mitchelli* and freshwater crocodiles (*Crocodylus johnstoni*), because we anticipated potential impacts of cane toads on those species (concurrent, ongoing study; see also Burnett 1997). Our search image for *V. panoptes* was that of a large (1–1.5 m) stationary lizard, and these animals seldom moved quickly upon noticing us. This species tended to bask in the early morning hours, forage during late morning, either become inactive or forage in more shaded areas above the riverbanks during midday, become active again late in the day, and roost in self-excavated holes before dusk (authors' observations).

Five surveys were conducted at each site each year between 20 May and 9 June. Surveys were conducted only on sunny days. Each survey consisted of visual searches along one bank for the 30 km, and a return search along the opposite bank of the same 30-km stretch. Because we were interested in consistent counts rather than unbiased activity patterns (e.g. associated with aspect and sunlit banks), we started each survey at the same location, and surveyed in the same direction. The duration of each survey was ~9 h. Surveys started at 0830 hours and ended at ~1730 hours; two 15-min breaks were taken at ~1015 hours and ~1445 hours, and a 45-min break was taken at ~1330 hours.

Surveys involved four persons (two observers, one driver/observer, and one recorder that did not observe). We visually searched the entire riverbank. Boat speed was kept constant at ~8 km h⁻¹, and the distance of the boat from the bank was ~7–10 m.

Cane toad surveys

We surveyed for cane toads by vehicle along road transects. One transect was near the upstream end of the Oolloo site, and a second transect was near the downstream end of the DRT site. Both road transects were ~8 km long. We conducted three surveys at each site each year between 20 May and 9 June (we did not conduct toad surveys in 2001–02 because cane toads were >50 km from the sites). Surveys began at ~1930 hours. Each survey consisted of driving 40 km h⁻¹ along a dirt track with high-beam headlights on and counting toads on the road and shoulder. For each survey there were two observers and a recorder. Surveys were conducted only on nights following sunny days.

Results

Turtle nest predation

Prior to the arrival of cane toads (1996–98), the proportion of turtle nests taken by predators did not differ among years $(\chi^2 = 0.67, d.f. = 2, P = 0.717)$ and ranged from 17% to 23% (Fig. 1; N = 66 nests in 1996, N = 86 nests in 1997, N = 138nests in 1998). In contrast, 109 turtle nests experienced no predation by *V. panoptes* in 2004 (Fig. 1). This lack of predation resulted in the proportion of nests taken by predators differing among years when including 2004 ($\chi^2 = 26.37$, d.f. = 3, P < 0.001). We did find one nest that was preyed upon in 2004, but we determined the predator to be a dingo (*Canis lupus*), because we found pig-nosed turtle eggshells in dingo scats on the beach.

Monitor surveys

Due to the unbalanced design (different number of data years at each site) we analysed monitor counts separately for each site using repeated-measures MANOVA. We found significant differences in mean *V. panoptes* counts among years at both the Oolloo site ($F_{1,4} = 256.90$, P = 0.047) and the DRT site ($F_{1,2} = 22.30$, P = 0.016). At the Oolloo site, mean *V. panoptes* counts before the arrival of cane toads (2001–03) were significantly higher than counts after cane toad arrival (2004–05) (Fig. 2; Bonferroni-adjusted multiple comparisons, all P < 0.05). In contrast, among-year differences before toad arrival and among-year differences after toad arrival were not significantly different (Fig. 2; all P > 0.05). At the DRT site, the mean *V. panoptes* count in 2005 was significantly lower than the other two mean counts (2003–04) (Fig. 2; Bonferroni-adjusted multiple comparisons, all P < 0.01), whereas there were no significant differences in mean counts between 2003 and 2004 (Fig. 2; P = 0.190).

We found six dead *V. panoptes* in the Oolloo stretch during the 2004 surveys and in the following three months during a separate study (Fig. 3), indicating that monitors were still being impacted. A toad was found in the stomach of one dead monitor.

Toad surveys

Our survey data indicate that cane toads arrived and moved through the Oolloo site during the 2003–04 wet season. Toads were not present during the dry-season survey of 2003, but were common throughout that site during the dryseason surveys of 2004 (Fig. 2). This conclusion was supported by reports of toads arriving at the nearby Douglas Daly Research Farm and Douglas Daly Tourist Park during the wet season of 2003–04 (P. O'Brien, personal communication). We did not survey for toads in 2001–02 because no sightings were reported from the area and because unpub-

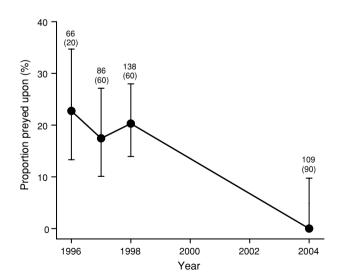


Fig. 1. Changes in predation of pig-nosed turtle nests by the monitor *V* panoptes, showing annual predation near 20% in 1996–98, but no predation during 2004. Vertical bars indicate 95% confidence intervals. Numbers of nests and length of river surveyed (km, in parentheses) are given above bars.

lished information indicated that the toad 'front' had not yet reached the sites (>50 km from the sites).

We found no toads during surveys of the DRT site in 2004. However, because these surveys were conducted at the end of the DRT stretch farthest from the direction from which the toads were approaching, we needed to confirm that the toads had not reached the DRT site by other means (there are no roads near the rest of the DRT stretch). To achieve this we attempted to find the cane toad 'front' along the river during a single-night call survey through the 35-km DRT stretch. On this survey we heard no toads calling from 10 billabongs along this river stretch. However, we did hear toads calling from a billabong just 200 m upstream of the DRT stretch (the end closest to the approaching toads). Closer inspection revealed 25 calling males around a small semi-permanent billabong, ~150 m from the river. Subsequent searches on foot at the edge of the DRT stretch revealed one toad in 3 h of searching. This contrasted with casual observations of several toads active each night near our camp at the Oolloo site. Thus, the toads had either not penetrated the site in 2004, or had only just penetrated it.

Discussion

Collectively, our data and observations, combined with unpublished reports, indicate that (1) cane toads arrived at the Oolloo site during the wet season of 2003–04, and the DRT site the following wet season; (2) *V. panoptes* readily succumbs to cane toad toxins; (3) *V. panoptes* has experienced a marked decline associated with the arrival of the toads at both sites; and therefore (4) it has been reduced to such low numbers that it is currently no longer a significant predator of pig-nosed turtle eggs, leading to a 'positive' impact of ~20%.

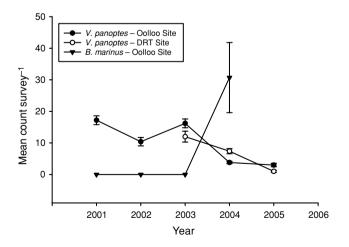


Fig. 2. Mean annual counts for the monitor *V. panoptes* at the two sites, and the cane toad *B. marinus* at the Oolloo site during 2001–04, showing an apparent decline in *V. panoptes* coinciding with the arrival of cane toads at the site during the wet season of 2003–04. Means were calculated from five surveys per year. Vertical bars are ± 1 s.e.

The sharp declines in *V. panoptes* counts at the Oolloo site between 2003 and 2004 (77%) and at the DRT site between 2003 and 2005 (92%) were synchronous with the arrival of cane toads at those sites (Fig. 2). These apparent declines may have continued beyond our study because we found a dead *V. panoptes* with a cane toad in its stomach in 2005 (Fig. 3). Although this species can die after ingesting toads (Burnett 1997), many apparently die from simply mouthing the toads (reviewed in Lever 2001). Because we have not observed a single dead *V. panoptes* in over 8 years at the site before toad arrival, we assume that the other five dead individuals we found died from mouthing cane toads.

Cane toads have been implicated in declines of some frogeating predators (reviewed in Lever 2001), most notably the northern quoll (*Dasyurus hallicatus*) and monitor lizards. Declines may also be occurring in some frog-eating snakes (Phillips *et al.* 2003) and dingoes (Catling *et al.* 1999), and current studies are quantifying short-term impacts on monitor lizards, snakes, quolls, and crocodiles (NT Government 2003; Doody, unpublished data). *V. panoptes* is considered to be at risk upon the arrival of the toads (Burnett 1997; Smith and Phillips 2006). Although our study of the impact of cane toads on monitors is continuing, our data on



Fig. 3. Two dead *V. panoptes*, apparently victims of cane toad ingestion, found during the study in May 2004.

the indirect impacts on pig-nosed turtle eggs was limited to one year.

Although we did not document egg predation during 1999–2003, the annual loss of pig-nosed turtle eggs of 17–23%, measured in 1996–98, was reduced to nil in 2004 (Fig. 1). The usual evidence of *V. panoptes* preying upon *C. insculpta* nests (eggshells and an opened and enlarged nest chamber) was not evident in 2004, despite *C. insculpta* nesting beach densities of 0.6–1.0 km⁻¹ (Doody *et al.* 2003*c*; Georges *et al.* 2003). Because we sampled a large number of nests (>100) over a large stretch of river (~100 km) we feel that our data are both robust and general to the area.

An increase of 20% of *C. insculpta* hatchlings into the population could have strong effects on population structure and/or size, particularly if this increase persists. However, more research is needed to determine whether or not these impacts are short- or long-term, and whether the boost in hatching success bolsters the number of adults in the population, or represents a transient effect due to low hatchling and/or juvenile survival. Turtles are long-lived (Gibbons 1987) and are generally characterised by low survival before adulthood (Congdon *et al.* 1994). From a conservation perspective, an increase in turtle recruitment would be welcomed in the population, because this species is currently of conservation concern (listed as: 'vulnerable' internationally: IUCN 2003; 'near threatened' at the state level: Northern Territory Parks and Wildlife Service.

The effect of cane toads on one species is likely to impact whole communities (Lever 2001). Our findings reflect one of many shifts in trophic links (reshuffling of predator and prey abundances) that are likely to occur with the cane toad invasion. Prior to the cane toad invasion, *V. panoptes* was a major predator of flatback sea turtle (*Natator depressus*) nests in northern Australia, with predation as high as 50% (Blamires and Guinea 2003; Blamires 2004). Although no data subsequent to the arrival of the toads are available, we would predict that numbers of adult *V. panoptes* have decreased and thus predation on *N. depressus* nests has also decreased.

In another example, Catling *et al.* (1999) found evidence that cane toads indirectly and negatively influenced small lizards that do not consume toads but may compete with them for food. Collectively these studies highlight the complexity of impacts (i.e. direct, indirect, positive, neutral, negative) on communities associated with introductions of exotic species (Zavaleta *et al.* 2001). Although the 'positive' impact of cane toads on pig-nosed turtles is outweighed by negative impacts of cane toads on other species and communities (reviewed in Lever 2001), the more comprehensive our understanding is of total impacts the more confidence we can have in initiating, supporting, and sustaining management strategies.

Ironically, some of the best experimental evidence for the complexity of communities or trophic links stem from efforts to eradicate invasive species. Removing an invasive species has been shown to have numerous secondary or indirect effects on other species or assemblages, in addition to 'positive' benefits for the impacted species of concern (Zavaleta *et al.* 2001). For example, removing feral cats on subantarctic Marion Island may have resulted in an increase in house mice, which in turn prey heavily on a moth (*Pringleophaga marioni*) that is important for nutrient cycling (Zavaleta *et al.* 2001). Because it is a generalist predator (Shine 1986; James *et al.* 1992; Blamires 2004), extinctions or severe population reductions of *V. panoptes* may result in similar top-down cascading effects.

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References

- Blamires, S. J. (2004). Habitat preferences of coastal goannas (*Varanus panoptes*): are they exploiters of sea turtles nests at Fog Bay, Australia? *Copeia* 2004, 370–377.
- Blamires, S. J., and Guinea, M. L. (2003). Emergence success of flatback sea turtles (*Natator depressus*) at Fog Bay, Northern Territory, Australia. *Chelonian Conservation and Biology* 4, 548–556.
- Burnett, S. (1997). Colonizing cane toads cause population declines in native predators: reliable anecdotal information and management implications. *Pacific Conservation Biology* 3, 65–72.
- Catling, P. C., Hertog, A., Burt, R. J., Wombey, J. C., and Forrester, R. I. (1999). The short-term effect of cane toads (*Bufo marinus*) on native fauna in the Gulf country of the Northern Territory. *Wildlife Research* 26, 161–185. doi:10.1071/WR98025
- Christian, K. A., and Weavers, B. W. (1996). Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecological Monographs* 66, 139–157. doi:10.2307/ 2963472
- Christian, K. A., Corbett, L. K., Green, B., and Weavers, B. W. (1995). Seasonal activity and energetics of two species of varanid lizards in tropical Australia. *Oecologia* 103, 349–357. doi:10.1007/ BF00328624
- Congdon, J. D., Dunham, A. E., and van Loben Sels, R. C. (1994). Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *American Zoologist* 34, 397–408.
- Covacevich, J., and 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.
- Daly, J. W., and Witkop, B. (1971). Chemistry and pharmacology of frog venoms. In 'Venomous Animals and their Venoms'. (Eds W. Bucherl and E. E. Buckley.) pp. 497–519. (Academic Press: New York.)

- Doody, J. S., Georges, A., and Young, J. E. (2000). Monitoring plan for the pig-nosed turtle (*Carettochelys insculpta*) in the Daly River, Northern Territory. Final Report to NT Parks and Wildlife Commission, Northern Territory. Applied Ecology Research Group, University of Canberra.
- Doody, J. S., Sims, R., and Georges, A. (2003a). Gregarious nesting in pig-nosed turtles (*Carettochelys insculpta*) does not reduce predation risk. *Copeia* 2003, 894–898.
- Doody, J. S., Georges, A., and Young, J. E. (2003b). Twice every second year: reproduction in the pig-nosed turtle in the wet–dry tropics of Australia. *Journal of Zoology* 259, 179–188. doi:10.1017/ S0952836902003217
- Doody, J. S., West, P., and Georges, A. (2003c). Beach selection in pignosed turtles, *Carettochelys insculpta. Journal of Herpetology* 37, 178–182.
- Doody, J. S., Georges, A., and Young, J. E. (2004). Determinants of reproductive success and offspring sex in a turtle with environmental sex determination. *Biological Journal of the Linnean Society* 81, 1–16. doi:10.1111/j.1095-8312.2004.00250.x
- Easteal, S. (1981). The history of the introductions of *Bufo marinus* (Amphibia: Anura): a natural experiment in evolution. *Biological Journal of the Linnean Society* 16, 93–113.
- Freeland, W. J. (1985). The need to control cane toads. *Search* 16, 211–215.
- Georges, A. (1992). Thermal characteristics and sex determination in field nests of the pig-nosed turtle, *Carettochelys insculpta* (Chelonia: Carettochelydidae), from northern Australia. *Australian Journal of Zoology* **40**, 511–521. doi:10.1071/ZO9920511
- Georges, A., Wombey, J. (1993). Family Carettochelyidae. In 'Fauna of Australia, Vol. 2. Amphibia, Reptilia, Aves'. (Ed. J. Godsell.) pp. 153–156. (Australian Biological Resources Study, Dasett: Canberra.)
- Georges, A., Webster, E., Guarino, E., Thoms, M., Jolley, P., and Doody, J. S. (2003). Modeling dry season flows and predicting the impact of water extraction on a flagship species. Final Report to DLPE NT. Applied Ecology Research Group & CRC for Freshwater Ecology, University of Canberra.
- Georges, A., Rose, M., and Doody, J. S. (2005). Carettochelys insculpta, pig-nosed turtle. In 'The Conservation Biology of Freshwater Turtles'. (Eds P. C. H. Pritchard and A. Rhodin.) (IUCN Publications: Gland, Switzerland.)
- Gibbons, J. W. (1987). Why do turtles live so long? *Bioscience* **37**, 262–269. doi:10.2307/1310589
- IUCN (2003). 'IUCN Red List of Threatened Species.' www.redlist.org
- James, C. D., Losos, J., and King, D. R. (1992). Reproductive biology and diets of goannas (Reptilia: Varanidae) from Australia. *Journal* of Herpetology 26, 128–136. doi:10.2307/1564852
- Lampo, M., and Bayliss, P. (1996). Density estimates of cane toads from native populations based on mark-recapture data. *Wildlife Research* 23, 305–315. doi:10.1071/WR9960305
- Lampo, M., and De Leo, G. A. (1998). The invasion ecology of the toad Bufo marinus: from South America to Australia. Ecological Applications 8, 388–396. doi:10.2307/2641079
- Lever, C. (2001). 'The Cane Toad: The History and Ecology of a Successful Colonist.' (Westbury: Yorkshire.)
- Northern Territory Government (2003). Issues associated with the progressive entry into the Northern Territory of cane toads. Sessional Committee on Environment and Sustainable Development. Volume 1. Unpublished report.
- Phillips, B. L., Brown, G. P., and Shine, R. (2003). Assessing the potential impact of cane toads on Australian snakes. *Conservation Biology* 17, 1738–1747. doi:10.1111/j.1523-1739.2003.00353.x
- Shine, R. (1986). Food habits, habitats, and reproductive biology of four sympatric species of varanid lizards in tropical Australia. *Herpetologica* 42, 346–360.

- Smith, J., and Phillips, B. (2006). Toxic tucker: the potential impact of cane toads on Australian reptiles. *Pacific Conservation Biology*, in press.
- Spencer, R. (2002). Experimentally testing nest site selection: fitness trade-offs and predation risk in turtles. *Ecology* 83, 2136–2144.
- Sutherst, R. W., Floyd, R. B., and Maywald, G. F. (1995). The potential geographic distribution of the cane toad, *Bufo marinus* L. in Australia. *Conservation Biology* 9, 249–299.
- Tyler, M. J. (1987). Frog and toad skin secretions. In 'Toxic Plants and Animals: A Guide for Australia'. (Eds J. P. Covacevich and J. Pearn.) pp. 329–339. (Queensland Museum: Brisbane.)
- Webb, J. K., Shine, R., and 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. doi:10.1111/j.1442-9993.2005.01437.x
- Zavaleta, E. S., Hobbs, R. J., and Mooney, H. A. (2001). Viewing invasive species removal in a whole ecosystem context. *Trends in Ecology & Evolution* 16, 454–459. doi:10.1016/S0169-5347(01) 02194-2

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