

THE ECOLOGICAL IMPACT OF INVASIVE CANE TOADS
(*BUFO MARINUS*) IN AUSTRALIA

RICHARD SHINE

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

E-MAIL: RICK.SHINE@SYDNEY.EDU.AU

TEL: +612-9351-3772

FAX: +612-9351-5609

Short title: ECOLOGICAL IMPACT OF INVASIVE TOADS

In press, *Quarterly Review of Biology*

KEYWORDS

alien species, food-webs, introduced species, invasive species, predator-prey,

Rhinella marina, toxicity

ABSTRACT

Although invasive species are viewed as major threats to ecosystems worldwide, few such species have been studied in enough detail to identify the pathways, magnitudes and timescales of their impact on the native fauna. One of the most intensively-studied invasive taxa in this respect is the cane toad (Bufo marinus), introduced to Australia in 1935. A review of these studies suggests that a single pathway (lethal toxic ingestion of toads by frog-eating predators) is the major single mechanism of impact, but that the magnitude of impact varies dramatically among predator taxa, and through space and time. Populations of large predators (varanid and scincid lizards, elapid snakes, freshwater crocodiles, and dasyurid marsupials) may be imperilled by toad invasion, but impacts vary spatially even within the same predator species. Some of the taxa severely impacted by toad invasion recover within a few decades, via aversion learning and longer-term adaptive changes. No native species have gone extinct as a result of toad invasion, and many native taxa widely imagined to be at risk are not affected. That lack of major impact results from physiological ability to tolerate toad toxins (e.g. in many birds and rodents), and the reluctance of many native anuran-eating predators to consume toads, either innately or as a learned response. Indirect effects of cane toads (as mediated through trophic webs) likely are as important as direct effects, but more difficult to study. Overall, some Australian native species (mostly large predators) have declined due to cane toads; others (especially species formerly consumed by those predators) have benefited; and for yet others, effects are minor or are mediated indirectly rather than through direct interactions with the invasive toads. Factors that increase a predator's vulnerability to toad invasion include habitat overlap with toads, anurophagy, large body size, inability to develop rapid behavioural aversion to toads as prey items, and physiological vulnerability to bufotoxins as a result of a lack of coevolutionary history of exposure to other bufonid taxa.

INTRODUCTION

Invasive species are widely viewed as major threats to biodiversity, and there are many examples of catastrophic ecological impacts from such taxa (Pimentel et al. 2000). Equally, there are abundant examples of introduced species that have had relatively minor ecological impact, despite spreading widely – or even positive effects on native fauna (Wonham et al. 2005; King et al. 2006). Understanding the nature of such interactions is critical for establishing conservation priorities: given limited resources, conservation efforts need to focus on species and areas where the invader's impact is most severe. Also, knowledge on pathways of impact may suggest novel approaches to impact reduction: for example, it might be possible to manipulate an invasive predator's responses to native prey through conditioned taste aversion learning (Nicolaus et al. 1983a,b; O'Donnell 2009; O'Donnell et al. 2009).

The current paper deals with the ecological impact of a large anuran amphibian in Australia: the cane toad, *Bufo marinus* (or *Rhinella marina*: Frost et al. 2006; Pramuk 2007; see Fig. 1). The cane toad is a member of the “true toads” (family Bufonidae), a group with a natural worldwide distribution in the Americas, Africa and Eurasia (Tyler 1975; Zug et al. 1975; Cogger 2000). The cane toad is one of the world's largest anurans (to 23 cm, 1.25 kg: Tyler 1975), with a natural range in Central and tropical South America extending from 27° N latitude in southern Texas and western Mexico to 10° S latitude in central Brazil (Zug and Zug 1979). As in other bufonids, the parotoid (shoulder) glands of cane toads contain potent bufogenins, bufotoxins, and other substances (Zug and Zug 1979). The active constituents of cane toad toxins (steroid-derived) differ from those of Australian native frogs (typically peptides: Daly and Witkop 1971; Tyler 1987). All life stages of the cane toad (eggs, tadpoles, metamorphs and adults) are toxic, although toxin

types and content change markedly during toad ontogeny: Hayes et al. 2009). Toxin levels (and thus, danger to vertebrate predators) are high in eggs, decrease through tadpole life, are lowest at around the time of metamorphosis, and increase rapidly thereafter (Hayes et al. 2009).

Brought from Hawaii in 1935 to control sugar cane pests in northeastern Queensland, cane toads have now spread throughout much of Queensland, northern NSW and the wet-dry tropics of the Northern Territory. In 2009, they crossed the border into Western Australia (Fig. 2). Because cane toads eat a wide variety of prey, have greater fecundity than native anurans, and develop rapidly in tropical regions, colonizing cane toads attain very high densities (Freeland 1986; Lever 2001). They tolerate a broad range of environmental and climatic conditions and occupy a wide range of habitats (Urban et al. 2007), albeit with a clear preference for anthropogenically degraded sites (Zug and Zug 1979). Ultimately, the cane toad's Australian range may encompass an area of approximately 2 million km² (Sutherst et al. 1995). Exact predictions of the toad's eventual range within Australia depend on the modelling approaches used, but all models agree that the Kimberley region of northwestern Australia will be suitable for toads (Urban et al. 2007, 2008; Kearney et al. 2008). The situation in southern Australia is more difficult to predict, especially given the uncertainty about future climatic conditions (see Fig. 2b).

Reflecting its relative recency and the ease with which cane toads can be distinguished from native frogs, the invasion of cane toads through Australia has been documented in enough detail to allow detailed analysis of speeds and trajectories of progress of the invasion front (Urban et al. 2007, 2008). Research on the ecological impact of cane toads in Australia also has been unusually detailed, compared to the sketchy information available on ecological impacts of most invasive species, including the cane

toad itself in the many other countries to which it has been introduced (Lever 2001). As a result, the toads' Australian invasion offers a robust opportunity to investigate exactly what happens when a highly toxic invasive species spreads through a complex tropical ecosystem far outside its native range.

The ecological impact of cane toads has aroused great concern not only among conservation biologists and wildlife managers, but also among members of the general public (see Beckmann and Shine 2009). In this paper, I summarise current understanding on the ecological impacts of invasive cane toads on native fauna in Australia. The topic has been reviewed several times before, notably by Freeland (1984, 2004), van Dam et al. (2002), and Webb and Glanznig (2004). However, these reviews were written prior to a recent major expansion of research on cane toad impacts (see below). As the toad invasion front moved closer to the city of Darwin, logistical obstacles to research decreased at the same time as public concern (and thus, funding opportunities) increased. This review focuses on threats to native fauna rather than to domestic pets or humans (for toad impact on those latter species, see Knowles 1964; Roberts et al. 2000; Sakate and Oliveira 2000; Reeves 2004).

Intuition suggests that evaluating the impact of cane toads on native fauna should be straightforward: we merely need to assess abundance of native taxa before *versus* after toad invasion at a site, or compare faunal abundances in sites containing *versus* lacking cane toads. Unfortunately, such population-level counts often are subject to wide error, and are difficult to interpret. For example, extensive surveys in the wet-dry tropics by Woinarski et al. (2004) showed that more than 1000 sample sites would be needed to be 90% certain of detecting a 20% change in abundance. As a result, even limited experimental studies about mechanisms of impact may reveal more than extensive survey work (Thomson 2006). Thus, I first review information about pathways of impact.

Although the invasion of cane toads may affect native species in several ways (e.g. predation on native animals, competition with native species, and poisoning of native predators), available evidence identifies one pathway of direct impact (lethal toxic ingestion) as the most important (see below for the basis for this conclusion), so I then consider this pathway in more detail. Finally, I review information on population-level and longer-term impacts of cane toads on biodiversity, and attempt to identify generalities emerging from the accumulated data. Table 1 summarizes the nature and magnitude of likely impacts of cane toads on the Australian fauna.

PATHWAYS OF CANE TOAD IMPACT

PREDATION ON INVERTEBRATES BY TOADS

The diet of cane toads in Australia consists mainly of arthropods, with ants, termites and beetles being the most important numerically (van Beurden 1980a; Freeland 1984, 1990; Cameron and Cogger 1992; Werren 1993). Although cane toads have been reported to consume 200 food items per night, far more than most native frogs (Tyler and Cappo 1983; Freeland et al. 1986a,b), typical feeding rates may be much lower, and more similar to those of sympatric frogs (e.g. Greenlees et al. 2007).

Because they attain high population densities and eat frequently, cane toads have the potential to cause declines in the abundance and diversity of some invertebrate taxa, particularly terrestrial beetles, termites and ants. Such effects might be particularly pronounced during the tropical dry-season, when desiccation risk concentrates cane toads around the shrinking margins of waterbodies (Alford et al. 1995; Freeland and Kerin 1988; Child et al. 2008a,b, 2009). Many native anurans are inactive over this period, so that the

invertebrate fauna may lack a history of evolutionary exposure to anuran predation during the dry-season. Reductions in the abundance of seed-harvesting ants could potentially alter plant community dynamics, leading to long-term vegetation changes (Andrew 1986; Andersen 1991; Andersen and Braithwaite 1996; van Dam et al. 2002). Many researchers have reported emaciated toads around dry-season waterbodies (e.g. Tyler 1994; R. A. Alford, pers. comm.). That emaciation suggests that toads have significantly reduced the abundance of invertebrate prey in such areas. Experimental work to evaluate this effect would be of great interest.

The only direct experimental analysis of the impact of toad predation was performed in outdoor enclosures on the Adelaide River floodplain of the tropical Northern Territory (Greenlees et al. 2006). The work was conducted during the wet-season, and reported significant declines in abundance of invertebrates in enclosures occupied by toads compared to anuran-free enclosures; however, native frogs had almost as much impact as did cane toads in this respect. Greenlees et al. (2006) also reported that cane toad predation caused shifts in the species composition of invertebrates, with a decline in the prey types (notably small-bodied invertebrates, such as ants) preferred by toads.

Although cane toads forage preferentially on taxa such as ants and beetles (Bailey 1976; Freeland et al. 1986b; Lever 2001), they are opportunistic feeders and hence, might impact significantly on some taxa that would normally comprise only a small part of the diet. For example, although anurans rarely prey upon molluscs (Drewes and Roth 1981), cane toads from invasive populations in other parts of the world feed readily on land snails, with terrestrial gastropods constituting more than 40% of the contents of toad stomachs in some samples (Hinckley 1963; Bailey 1976; Grant 1996). Toad predation thus might imperil threatened species of land snails (Camaenidae) endemic to small limestone outcrops of the Kimberley region. Laboratory trials indicate that under wet conditions

(which encourage activity both by snails and toads), cane toads readily consume a wide range of camaenid species (Pearson et al. 2009). Whether or not this vulnerability will translate into population-level impacts depends upon encounter rates between snails and toads. Field surveys reveal little habitat overlap between toads and camaenids, suggesting that the snail populations may withstand toad invasion (Pearson et al. 2009).

COMPETITION BETWEEN TOADS AND INVERTEBRATES

Cane toads also might influence invertebrates through processes other than predation. For example, the presence of toad larvae in artificial waterbodies suppressed the development of mosquito larvae, and discouraged oviposition by female mosquitoes (Hagman and Shine 2007). In both of these respects, the effects of cane toads resemble those of native frogs, and presumably involve competitive interactions between anuran and mosquito larvae that have favoured the ability of female mosquitoes to detect anuran tadpole presence and use that information when selecting oviposition sites (Mokany and Shine 2003a,b).

PREDATION ON TOADS BY INVERTEBRATES

Toad invasion may provide an additional food source for predatory native invertebrates, many (but not all) of which tolerate toad toxins better than do vertebrates. For example, meat ants of the genus *Iridomyrmex* take many metamorph toads (Clerke and Williamson 1992; Ward-Fear et al. 2009a,b,c). Laboratory and field studies show that cane toad metamorphs are more vulnerable to ant attack than are the metamorphs of native frog species (Ward-Fear et al. 2009a). That vulnerability reflects the facts that toad metamorphs are smaller and slower than frog metamorphs, are primarily diurnal in their activity (an adaptation to reduce vulnerability to intraspecific cannibalism: Pizzatto and Shine 2008; Pizzatto et al. 2008), and lack effective antipredator responses to ants (Ward-

Fear et al. 2009a,b). Increases in the abundance of ant species that feed upon metamorph toads (such as the dominant dolichodorine species within the genus *Iridomyrmex*) might have flow-on effects to predation rates on other animals, or to interactions among competing ant species.

Other native invertebrates that can feed upon cane toads without ill effects include crustaceans such as freshwater crayfish (*Cherax* spp., and *Euastacus hystricosus*, *E. suttoni*, and *E. valentulus*: Hutchings 1979; Crossland 1998a; Crossland and Alford 1998) and crabs (*Holthuisana* sp.: Crossland and Alford 1998; *Holthuisana transversa*: M. Crossland, unpubl. data) as well as adult dytiscid diving beetles (*Cybister godeffroyi*, *Hydaticus vittatus*, *Sandracottus bakewelli*: Crossland 1998a; Crossland and Alford 1998) and dragonfly larvae (*Trapezostigma* sp., *Hemianax papuensis*: Crossland and Alford 1998). Mosquitoes also feed on cane toads (van Beurden 1980b). Not all invertebrates are unaffected by toad toxins. Leeches (*Goddardobdella elegans*: Crossland and Alford 1998; unidentified NT species: G. P. Brown, pers. comm.) frequently die after feeding on larval or adult toads, and aquatic snails (*Austropeplea lessoni*) die after consuming toad eggs (Crossland and Alford 1998). Other invertebrates vary in their susceptibility to toads. Some dytiscid diving beetle larvae (*Cybister* sp., *Hydaticus* sp.) and notonectid backswimmers (*Anisops* sp.) consume toad hatchlings or tadpoles without ill effect while other individuals die (Crossland and Alford 1998). Belastomatid giant water bugs (*Lethocerus insulanus*) are highly sensitive to some developmental stages of toad tadpoles, but not others (Crossland 1998a; Crossland and Alford 1998).

PREDATION ON VERTEBRATES BY TOADS

Despite frequent speculation to the contrary, predation by cane toads on other vertebrates is unlikely to be important in terms of broad ecological impact. Cane toads do

consume vertebrates, but do so rarely (e.g. Stammer 1981). This is true in the aquatic as well as terrestrial phase of the toad life-history: toad tadpoles rarely consume the eggs of native frogs (Crossland 1998b; M. R. Crossland and R. Shine, unpubl. data). One exception may involve predation by toads on the eggs and nestlings of ground-nesting birds such as bee-eaters (*Merops ornatus*: Boland 2004). In studies to follow-up Boland's work, however, Beckmann and Shine (unpubl. data) found rather different results. In experimental trials in large outdoor enclosures, cane toads avoided (rather than selected) burrows containing scent cues from birds or their eggs. However, field nest-burrows of bee-eaters often contained toads or frogs, hinting that toads may usurp such burrows and reduce bee-eater reproductive success (C. Beckmann and R. Shine, unpubl. data).

COMPETITION BETWEEN TOADS AND AQUATIC VERTEBRATES

Cane toads are more fecund than are Australian frogs (Pengilley 1981; Tyler 1994) and toad tadpoles often form large aggregations (Wassersug 1971; Freeland 2000). Such factors may increase competitive effects of toad tadpoles on the larvae of native frogs (Freeland 1984). In an experiment designed to assess the effects of native tadpoles on toad tadpoles, Alford (1999) found that growth rates of toad tadpoles were unaffected by tadpoles of Peters' frog (*Litoria inermis*), but were greatly reduced (and survival was reduced to nil) in the presence of tadpoles of the ornate burrowing frog (*Limnodynastes [Opisthodon] ornatus*). Crossland et al. (2009) found that cane toad tadpoles significantly affected tadpoles of *O. ornatus* via size-based competitive effects, but that these effects were highly sensitive to the timing of breeding of the two species. *Opisthodon ornatus* tadpoles performed better and had increased survival and increased mass at metamorphosis when cane toad tadpoles were added late to ponds, and performed worse (zero survival) when cane toad tadpoles preceded them into ponds, compared with when both species

were added to ponds simultaneously. Because cane toad tadpoles are not significant predators of *O. ornatus* larvae (Crossland 1998b), these effects were probably due to competition. However, such competitive priority effects were reversed when *O. ornatus* tadpoles encountered toad eggs. In this situation, survival of toad eggs was reduced (via predation) while survival of *O. ornatus* tadpoles was also reduced (via poisoning from ingestion of toxic toad eggs). Thus, lethal ingestion and competition play complex and overlapping roles in this interaction; and under some circumstances, the additional mortality inflicted by cane toad presence may reduce overall tadpole densities enough to increase body sizes at metamorphosis – and hence, potentially, increase rates of *Opisthodon* recruitment from a waterbody (Crossland et al. 2009).

More evidence that cane toad tadpoles can affect the growth of native tadpoles comes from the Darling Downs area of southern Queensland (Williamson 1999). Tadpoles of three of four native frog species (*Limnodynastes tasmaniensis*, *L. terrareginae*, *Notaden bennetti*) grew more slowly in the presence of cane toads, and survival was sometimes reduced in the two *Limnodynastes* (Williamson 1999). A fourth species, *Opisthodon ornatus*, showed higher not lower rates of growth if kept with *Bufo* tadpoles, reflecting lower survival rates (and thus, densities) (Williamson 1999). A range of aquatic vertebrates and invertebrates feed on algae, detritus and suspended organic matter (van Dam et al. 2002). Freeland (2004) reported that cane toad larvae can substantially reduce such algal mats, presumably thereby affecting both food supply and habitat for other anuran larvae as well as invertebrates (note the studies by Mokany and Shine 2003a,b, and Hagman and Shine 2007 for experimental evidence of such interactions between anuran larvae and mosquito larvae). Hagman and Shine (2008, 2009) reported that the tadpoles of native frog species showed little overt reaction to alarm pheromones from cane toads, suggesting that the toad's pheromones are unlikely to suppress activity of native tadpoles.

COMPETITION BETWEEN TOADS AND TERRESTRIAL VERTEBRATES

Cane toads attain high population densities (Cameron and Cogger 1992), consume many invertebrates (Freeland 1984, 2000) and use the same kinds of retreat-sites as do many native species (Cohen and Alford 1996; Schwarzkopf and Alford 1996). Therefore, they may compete with native species for food and shelter sites. Experimental studies to evaluate competition between toads and frogs have yielded complex results. In the tropical wet-season, weather-dependent shifts from one night to the next in invertebrate abundance and availability reduce the potential for effective competition between cane toads and other predators utilizing invertebrate prey (Greenlees et al. 2007). As a result, total food intake rates of native frogs (*Cyclorana australis* and *Litoria dahlii*) were not significantly reduced by the presence of cane toads in their outdoor enclosures (Greenlees et al. 2007).

Competitive effects may be more important during the dry-season, when high densities of toads persist long-term around waterbody margins. Most native anurans are inactive during this time of year, but other invertebrate-eating taxa such as lizards, birds, and small marsupials remain active and may experience reduced prey availability. Experimental studies to evaluate that possibility would be of great interest.

Focusing on dry-season interactions, Freeland and Kerin (1988) examined competitive interactions between cane toads and three species of native tree frogs (*Litoria pallida*, *L. rothii* and *L. rubella*) around waterholes in the Gulf of Carpentaria. Cane toads had no detectable impact on habitat or food use by the native frogs, or on the species composition and population sizes of native frog communities active during the dry season. The absence of competitive interactions may reflect the cane toad's heavy reliance on ants and termites, whereas native tree frogs ate other kinds of prey (Freeland and Kerin 1988). Also, the erratic climatic conditions of the region resulted in non-equilibrium frog

communities (Freeland 1990). Intuition suggests that cane toads are more likely to have an adverse impact on larger terrestrial frogs (e.g. *Cyclorana australis*, *Limnodynastes convexiusculus*). However, aestivation by *C. australis* during the dry season removes this species from competition during the period of the year when resources are most likely to be limiting (Janzen 1973).

Direct behavioural interference, rather than competition for food, may play a role. Pizzatto and Shine (2009) showed that nine of 10 native frog species that were tested avoided retreat-sites scented by cane toad chemical cues (the exception was *Litoria rubella*), and Greenlees et al. (2007) reported that the presence of cane toads reduced nocturnal activity levels of the native frog *Cyclorana australis*. Occasional observations of male toads clasping female frogs, and vice versa, suggest the potential for sexual harassment, as is known to occur between native and introduced taxa in other phylogenetic lineages (e.g. Valero et al. 2008). Female anurans may experience severe fitness costs (including drowning in some cases) from prolonged amplexus – a particularly likely situation if males and females are of different species, and hence do not react to the intraspecific cues that normally stimulate termination of amplexus (Bowcock et al. 2008, 2009).

Although most studies of competition have involved native anurans, other vertebrate species also might compete with toads for limited resources. Boland (2004) suggested that cane toads may usurp the nesting burrows of bee-eaters, *Merops ornatus*. Boland reported that 33% of all nesting attempts were ‘lost’ due to cane toads (via either nest predation or nest usurpation), and that average chick production per nest fell from about 1.2 to 0.8 after toad invasion.

TRANSFER OF PARASITES FROM CANE TOADS TO NATIVE VERTEBRATES

Invasive species can transfer pathogens to the native fauna. Zupanovic et al. (1998) reported antibodies against ranaviruses in Australian (and native-range) cane toads, and speculated that the toad invasion may bring harmful viral pathogens to native fauna. Delvinquier and Freeland (1988) concluded that three of the 14 protozoan species carried by cane toads in Australia were of neotropical origin. Cane toads in Australia also contain a nematode lungworm (*Rhabdias pseudosphaerocephala*) endemic to the Americas, and presumably brought to Australia in 1935 with the original founding toads (Dubey and Shine 2008). Although this nematode might cause significant impact if it infected native frogs, Dubey and Shine (2008) found no cases of *R. pseudosphaerocephala* infection in native frogs in northeastern Queensland. Preliminary trials by Pizzatto and Shine (unpubl. data) indicate that the toads' nematode can infect native frogs (at least under laboratory conditions), but that the infection generally does not persist in frogs, nor cause major viability decrements. Concern also has been expressed about the cane toad invasion carrying chytrid fungus to western parts of Australia, but our PCR tests of 100 adult cane toads (50 from Cairns, 50 from Normanton) provided no evidence of any chytrid infection (B. L. Phillips et al. unpubl. data). Any impact of parasite transfer, if it occurs, is likely to be some years post-invasion: typically, invasion-front populations of toads lack parasites (Phillips et al. 2009a).

PREDATION BY VERTEBRATES ON TOADS

Cane toads provide a novel additional food source for some vertebrates. Snakes such as the keelback (*Tropidonophis mairii*) can consume small cane toads without dying (but nonetheless show clear evidence of ill effects: see Ingram and Covacevich 1990; Llewelyn et al. 2009a,b). Slatey-grey snakes (*Stegonotus cucullatus*) also are relatively resistant to the toxins of cane toads (Phillips et al. 2003) and sometimes consume cane

toads in the field (Llewelyn et al. 2009a,b). Although snakes thus may take substantial numbers of small toads under some conditions, this seems to be uncommon. Given a choice, keelback snakes prefer native frogs to toads (Llewelyn et al. 2009b). Some birds also consume toads (e.g. corvids: Bekker 1985; Caswell 1987; Barraclough 1988; Donato and Potts 2004; egrets: McKilligan 1984; raptors: Mitchell et al. 1995). Raptors (*Milvus migrans*, *Haliastur sphenurus*) take many road-killed toads from highways on the Adelaide River floodplain, but (like the snakes) selectively take frogs rather than toads if given a choice (C. Beckmann and R. Shine, unpubl. data). Water rats (*Hydromys chrysogaster*) and introduced black rats (*Rattus rattus*) frequently consume cane toads (Cassels 1966; Fitzgerald 1990).

KILLING NATIVE WILDLIFE BY LETHAL TOXIC INGESTION

Because Australian predators have no evolutionary history of exposure to bufonid toxins, many of these animals (as well as domestic cats and dogs) die after mouthing or ingesting cane toads (Lever 2001). Despite occasional reports of toad toxins "polluting waterbodies with their poisons" (e.g. Freeland 1984), the only evidence of impact involves poisoning of predators via direct ingestion of toads. The strong allometry of toxin content in cane toads means that toad body size strongly influences the risk posed to a predator. As a result, the vertebrates most at risk from cane toads are animals that are large enough to consume an adult toad. In practice, this allometry results in vulnerability being greatest for large-bodied species of frog-eating snakes (especially elapids), lizards (especially varanids, but also the bluetongue skink), freshwater crocodiles, and northern quolls (Burnett 1997; van Dam et al. 2002; Phillips et al. 2003; and see below). Because these are the most dramatic direct impacts of cane toad invasion, I review data on vulnerability of species within each vertebrate lineage in more detail below.

LETHAL TOXIC INGESTION

Direct poisoning of predators is the most significant pathway by which cane toads impact the Australian native fauna. A broad range of native terrestrial vertebrate species are known to have died after mouthing or ingesting cane toads: for example, Lever (2001) notes 27 native species of terrestrial vertebrates (as well as domestic cats and dogs, and humans) in which individual predators are known to have died (Lever 2001).

Unfortunately, detailed quantification is lacking in most cases.

AQUATIC INVERTEBRATES

The toxic effects of cane toad eggs and tadpoles on Australian aquatic invertebrate predators are poorly studied. Because cane toads breed both in temporary and permanent waterbodies (Crossland and Alford 1998; Freeland 2000) many aquatic invertebrate predators will encounter the early life stages of cane toads. Crossland and Alford (1998) found that cane toad eggs, hatchlings and/or tadpoles were toxic to native snails (*Austropeplea lessoni*), water beetle larvae (Dytiscidae), backswimmers (Notonectidae) and leeches (Hirudinea), and individuals of these taxa died after consuming cane toads. Mortality of the snails (100%) and leeches (60%) was high, but the other taxa showed intraspecific variation in their susceptibility to cane toads. Other aquatic invertebrate predators including water scorpions (Nepidae), giant water bugs (Belastomatidae), dragonfly larvae (Odonata), freshwater prawns, crabs and crayfish (Decapoda) either consumed cane toad eggs or tadpoles without apparent ill effect, or killed cane toads but consumed none or little of the carcass. Similarly, fishing spiders (*Dolomedes* sp.) also kill

and partially consume toad tadpoles without apparent ill effect (M. R. Crossland, unpubl. data). Some water beetles and crustaceans (freshwater prawns, shrimps, crabs and crayfish) can live on cane toad eggs and tadpoles for at least four weeks without apparent ill effect, and they may be potential predators of cane toads in nature (M. R. Crossland, unpubl. data).

TERRESTRIAL INVERTEBRATES

Some terrestrial invertebrates are successful cane toad predators. Martin and Freeland (unpubl. data) observed a centipede preying on a 60 mm sub-adult cane toad without apparent ill effects, while van Beurden (1980a) reported predation by large wolf spiders and ants on cane toad metamorphlings. Clerke and Williamson (1992) recorded meat ants (*Iridomyrmex purpureus*) consuming small toads in Queensland. Ward-Fear et al. (2009b,c) reported high rates of predation by bearded meat ants (*Iridomyrmex reburrus*) on metamorph cane toads in the Darwin area.

FRESHWATER FISH

Experimental studies on Australian freshwater fish have found that most species either ignore cane toad early life stages or taste and reject them without apparent ill effects (Pearse 1980; Hearnden 1991; Crossland and Alford 1998). Alford et al. (1995) concluded that "no native fish species were adversely affected by aquatic stages of *B. marinus*". However, more detailed work showed that cane toad eggs or tadpoles are toxic when consumed by the fly-specked hardyhead (*Craterocephalus stercusmuscarum*: Crossland and Alford 1998), the banded grunter (*Amniataba percooides*), the spangled grunter (*Leiopotherapon unicolor*: Hearnden 1991), the purple-spotted gudgeon (*Morgurnda adpersa*: Pearse 1980), glassfish (Family Ambassidae), western rainbowfish (*Melanotaenia australis*), and black catfish (*Neosilurus ater*: Wilson 2005). Most fish

probably avoid cane toad early life stages because they can detect their noxiousness (Licht 1968; Lawler and Hero 1997; Crossland 2001). Barramundi (*Lates calcifer*) and sooty grunters (*Haphaestus fuliginosus*) that attacked tadpoles spat them out almost immediately, but displayed signs of distress by vigorously opening and closing their mouths and shaking their heads from side to side for up to a minute (Crossland 2001). Barramundi in particular were able to rapidly learn to avoid toad tadpoles, and some individuals continued to avoid toad tadpoles one day after their previous encounter (Crossland 2001). At least one other fish species (the northern trout gudgeon, *Mogurnda mogurnda*) also rapidly learns to avoid toad tadpoles (Nelson 2008; Nelson et al. 2010). Attributing sources of mortality is difficult under field conditions, but Grace and Sawyer (2008) reported a case of fish mortality associated with toad breeding. This involved approximately 70 spangled perch (*Leiopotherapon unicolor*) presumably killed by ingesting toad eggs or tadpoles; black-banded rainbowfish (*Melanotaenia nigrans*) were unaffected.

Experimental studies indicate that for most fishes, toad eggs are more likely to be lethal than are toad tadpoles (Greenlees and Shine 2009). The taxa tested included ambassids (*Ambassus macleayi*), eleotrids (*Mogurnda mogurnda*), melanotaenids (*Melanotaenia australis*, *M. splendida*), plotossids (*Neosilurus hyrtlui*), and pseudomugils (*Pseudomugil gertrudae*, *P. inconspicuus*, *P. tenellus*). Fortunately, the brief duration of the egg stage, and the restriction of eggs to shallow pond edges, reduces the rates at which eggs are encountered by native predators. Predators encounter toad tadpoles more often, but the tadpoles are less toxic (especially late in development: Hayes et al. 2009), and their toxicity is more easily detectable by predators (Greenlees and Shine 2009).

AMPHIBIANS

Crossland and Alford (1998) investigated the effects of cane toad eggs, hatchlings and tadpoles on tadpoles of native frog species from the Townsville and Cape York Peninsula areas. Consumption of cane toad eggs was always fatal to native tadpoles, but the number of tadpoles that fed on eggs varied among species: *Litoria bicolor* 100%, *L. rubella* 30%, *L. infrafrenata* 100%, *L. nigrofrenata* 60%, *L. alboguttata* 100% and *Opisthodon ornatus* 90%. Similarly, consumption of cane toad hatchlings was always fatal to native tadpoles and predation rates varied: *L. infrafrenata* 80%, *L. alboguttata* 20% and *O. ornatus* 10%. *Litoria rubella* and *L. nigrofrenata* did not consume cane toad hatchlings. No native frog tadpoles ate live cane toad tadpoles (Crossland and Alford 1998), but many frog tadpoles will feed on the carcasses of dead tadpoles; exposure to dead cane toad tadpoles killed 60% of *L. alboguttata*, 50% of *Cyclorana brevipes* and 90% of *O. ornatus* (Crossland and Azevedo-Ramos 1999). In contrast, *L. rubella* tadpoles (0% mortality) and *L. gracilentata* tadpoles (20% mortality) were less likely to feed on dead cane toad tadpoles, although they readily ate dead native tadpoles (Crossland and Azevedo-Ramos 1999). The fact that *L. rubella* rarely ate cane toad eggs, hatchlings or tadpoles suggests that either they have a greater ability than other native tadpoles to detect the noxiousness of cane toads, or *L. rubella* tadpoles do not eat the early life stages of other anuran species (Crossland 1998b; Crossland and Alford 1998; Crossland and Azevedo-Ramos 1999). Behavioural responses suggest that native frog tadpoles are unable to detect the toxicity of cane toad eggs. Tadpoles did not avoid cane toad eggs, but grazed on egg strings until they had penetrated the gelatinous string and consumed the fertilized eggs inside, after which they always died (Crossland and Alford 1998). However, the major predator of cane toad eggs and tadpoles is the cane toad tadpole itself (Hearnden 1991).

More recently, anuran species from the Northern Territory have been evaluated in this respect. Field and laboratory studies have clarified interactions between native frog

tadpoles and cane toad eggs on the Adelaide River floodplain. Of 14 species tested in the laboratory (*Opisthodon ornatus*, *Limnodynastes convexiusculus*, *Cyclorana australis*, *C. longipes*, *Litoria bicolor*, *L. caerulea*, *L. dahlii*, *L. microbelos*, *L. nasuta*, *L. pallida*, *L. rothii*, *L. rubella*, *L. tornieri*, *Uperoleia lithomoda*), most attempted to eat toad eggs; and all died if they did so (Crossland and Shine 2009). The exceptions may have been too small to physically penetrate the toad's egg capsule (Crossland and Shine 2009). The only tadpoles that survived were those that did not consume toad eggs; and these animals almost all consumed eggs (and died) when re-tested (Crossland and Shine 2009). In the field, toad spawning was followed by mass mortality of tadpoles belonging to several species of native frogs (Crossland et al. 2008). Counts of species abundance before *versus* after those kill events suggested non-random mortality rates: for example, *Litoria rothii* tadpoles appeared to be particularly vulnerable.

The toxicity of cane toads shifts rapidly during the course of the animal's early life-history, based on analyses of bufadienolide content as well as mortality rates of native tadpoles consuming those life-history stages (Hayes et al. 2009). Thus, virtually 100% of tadpoles (*Limnodynastes convexiusculus* and *Litoria rothii*) consuming toad eggs died, but later-stage tadpoles were less toxic (Hayes et al. 2009). The toxin is contained in the ovum not the jelly coat (Crossland and Shine 2009).

Anurans also are at risk after metamorphosis, if they attempt to consume small terrestrial-phase cane toads. Although van Dam et al. (2002) speculated that only the largest frog species would be at risk in this way, recent studies show vulnerability even in smaller taxa such as *Limnodynastes convexiusculus* (Greenlees et al. 2009). In laboratory trials, we have also recorded fatal toxic ingestion of toad metamorphs by *Cyclorana australis*, *C. alboguttata*, *C. novaehollandiae*, *Litoria caerulea*, and *L. dahlii*. Despite anecdotal reports to the contrary, *Litoria dahlii* was no more resistant to the toxins of cane

toads (in eggs, tadpoles or metamorphs) than were other local frog species (Shine et al. 2009). Supporting these conclusions, Grace and Sawyer (2008) reported mortality of 11 post-metamorphic *L. dahlii* and two *Limnodynastes convexiusculus* at a site where toads had bred. In the Fogg Dam area, we have found recently-killed specimens of *L. dahlii* ($n = 3$), *Cyclorana australis* ($n = 2$), and *Limnodynastes convexiusculus* ($n = 4$), apparently as a result of toad ingestion (Greenlees et al. 2009 and unpubl.). Some of these dead frogs contained single metamorph toads in the gut. The impact of toads on terrestrial-phase frogs is reduced by rapid aversion learning, as documented in *Limnodynastes convexiusculus*, *Cyclorana australis* and *Litoria dahlii* (Nelson 2008; Nelson et al. 2010; Greenlees et al. 2009). Nonetheless, the invasion of cane toads may exert selection on life-history traits such as breeding seasonality and size at metamorphosis in native anurans (Greenlees et al. 2009).

CROCODILES

Covacevich and Archer (1975) reported that saltwater crocodiles (*Crocodylus porosus*) could ingest cane toads with impunity. By contrast, there are reports of freshwater crocodiles (*Crocodylus johnstoni*) dying after mouthing or ingestion of cane toads (Begg et al. 2000; see Fig. 3). Freeland (1990) reported that *C. johnstoni* actively hunts and ingests cane toads, and Letnic and Ward (2005) provided photographs of this behaviour (see also Fig. 3). Smith and Phillips (2006) showed that physiological resistance to toad toxins is lower in freshwater crocodiles than in saltwater crocodiles. Doody et al. (2009) reported death of some freshwater crocodiles in the Daly River due to toad ingestion, but no overall effect on crocodile populations. In a study primarily focused on population-level impact, Letnic et al. (2008) reported 34 dead freshwater crocodiles in the Victoria River, and attributed these deaths to cane toad ingestion. The evidence included a

wave of crocodile deaths moving upriver coincident with the cane toad invasion front, and toads in the stomachs of some of the dead crocodiles (Letnic et al. 2008). Consistent with Doody et al.'s study, Letnic et al. reported much lower rates of toad-induced mortality of freshwater crocodiles in the Daly River.

TURTLES

Turtles sometimes ingest cane toads without ill effects, whereas other predation attempts (even by the same turtle species) can be fatal. Covacevich and Archer (1975) reported that a long-necked turtle (*Chelodina* sp.) ate a dead cane toad without becoming ill, and Crossland and Alford (1998) reported that saw-shelled turtles (*Elseya latisternum*) and Krefft's river turtles (*Emydura krefftii*) consumed cane toad tadpoles but were unaffected. Hamley and Georges (1985) found toads in the stomachs of four field-collected saw-shelled turtles from the Brisbane area. The same authors fed toads to this turtle species in captivity without noting any ill effects, and even maintained two specimens for four months or more on a diet composed exclusively of cane toads. By contrast, there are unsubstantiated reports from Aboriginal communities on Groote Eylandt and the Borroloola region that cane toads have killed 'goanna, bluetongue, long-necked turtle, geese and everything' (Evans 1999). Similarly, community members from Beswick and Burunga, south of Katherine, included barramundi and long- and short-necked turtles in their list of species affected by toads (Begg et al. 2000). Scientific studies of toad impacts on taxa such as barramundi (see above) and geese (see below) suggest that these statements may be in error, whereas the statements about goannas and bluetongue lizards are consistent with other evidence (see below). Hence, it is difficult to evaluate the reliability of the statements about turtle mortality. E. Kruger (pers. comm.) has reported dead long-neck turtles (*Chelodina rugosa*) in waterbodies used by cane toads for breeding.

In our experimental studies, long-necked turtles (*Chelodina rugosa*) seized but rejected toad tadpoles, and survived. However, consumption of toad eggs was fatal (Greenlees and Shine 2009). As is the case for other aquatic predators such as fish, the jelly coat of the egg (which lacks toxicity: Crossland and Shine 2009) may mask the poisons sequestered within the ovum, such that the predator swallows the entire egg mass before detecting its toxic nature.

LIZARDS

The area of Australia invaded by cane toads contains high densities and species diversities of lizards belonging to several phylogenetic lineages. The impact of cane toads across those lineages is highly non-random, with fatal poisoning an important pathway of impact only for species within three lineages: the Varanidae (goannas), the Scincidae (skinks), and the Agamidae (dragons). Varanids often grow to large body sizes, and readily attack large prey items (Losos and Greene 1988); hence, they may attack a large cane toad more readily than would a lizard from most other lineages. Even relatively small varanids thus may be at risk from cane toad invasion, whereas the impact appears to fall heavily only on a few large-bodied species within the Scincidae and Agamidae. Smith and Phillips (2006) directly measured toxin resistance of a range of lizard species; most were highly sensitive to the toxins.

Varanid lizards (goannas) often die after ingesting or mouthing cane toads (Lever 2001; van Dam et al. 2002; Phillips et al. 2003). There are many reports of goannas found dead in the field soon after the arrival of cane toads: the evidence for causation (a freshly-dead goanna with a toad in its mouth or stomach) is unambiguous. In the wet-dry tropics of the Northern Territory, most of these cases involve the large yellow-spotted monitor *Varanus panoptes* (e.g. Doody et al. 2009; Ujvari and Madsen 2009; G. P. Brown, pers.

comm.). Medium-sized varanid species also may be at risk, based on population-level declines reported for *Varanus gouldii* (Freeland 2004; T. Madsen, pers. comm.), *V. mitchelli* and *V. mertensi* (Doody et al. 2009), although *V. scalaris* remains common in areas of high toad abundance near Darwin (T. Madsen, pers. comm.). Laboratory trials have confirmed that small varanids such as *V. acanthurus*, *V. glauerti*, and *V. glebopalma* readily consume small toads, and are likely to die if they do so (R. Shine et al. unpubl. data); but the restriction of small toads to riparian habitats for much of the year may reduce their encounter rates with non-riparian varanid species.

Most species of scincid lizards exhibit relatively small adult body sizes. Given the strong allometry in toxin content of cane toads (Phillips and Shine 2006a,b), such small predators are unlikely to be at risk from consuming a cane toad large enough to kill them. Doubtless, occasional individuals of smaller species eat toads large enough to be fatal: we have recorded this outcome in one laboratory encounter between a cane toad and a striped skink (*Ctenotus robustus*: M. Greenlees et al. unpubl. data). One scincid species at considerable risk is the bluetongue skink (*Tiliqua scincoides intermedia*), a large omnivore that is widely distributed across tropical Australia. Captive individuals of this species from northwestern Australia readily consume small toads, and die (Price-Rees et al. 2010); and the same outcome has been observed in free-ranging animals (Sanson 2010).

Most dragon lizards (Agamidae) are unlikely to be directly affected by cane toads (Griffiths and Christian 1996; Cogger 2000). Several years after cane toads reached Lawn Hill National Park, rangers reported removing cane toads from the mouths of frillneck lizards that frequented the camping area (van Dam et al. 2002). These lizards were distressed but not dead; however, over the next few years they apparently disappeared from the area. In trials with field-collected animals in captivity, frillneck lizards did not eat small toads, but readily took insects (Ujvari et al. 2010).

SNAKES

In laboratory trials, individuals of many species of frog-eating snakes die after ingesting a tiny amount of toad toxin (Fearn 2003; Phillips et al. 2003; Phillips and Fitzgerald 2004). The snakes most at risk from cane toads are frog-eating species that cannot tolerate toad toxins; that frequently encounter toads; that can swallow toads large enough to be fatal; and whose geographic distribution overlaps greatly with that of the cane toad (Sutherst et al. 1995; Cogger 2000). A risk assessment based on these criteria identified 49 snake species potentially at risk from the toad invasion (Phillips et al. 2003). Of these, 26 were likely to have their range totally encompassed by that of the toad (under predicted 2030 climate change) and three have already had their range totally encompassed. Thus, the toad invasion constitutes a potential threat to 70% of the Australian colubrid snakes (7 of 10 species), 40% of the pythons (6 of 15), and 41% of the elapids (36 of 87). Nine of these "at risk" species are currently recognized as threatened on a federal or state level (Cogger et al. 1993).

More recent work on feeding responses of snakes offered edible-sized cane toads in captivity is more encouraging. Many species identified as potentially at risk by Phillips et al.'s (2003) study were reluctant to take cane toads as prey, or released the prey immediately after striking it and thus, survived the encounter (R. Shine et al. unpubl. data). Colubrids and pythons appear to be at less risk than elapid (venomous) snake species (M. Greenlees et al. unpubl. data). Most variation in survival rates reflected snake behaviour (tendency to attack *versus* ignore a toad), but two colubrid species have high physiological tolerance to toad toxins (*Stegonotus cucullatus* and *Tropidonophis mairii*: Phillips et al. 2003). Elapid snakes appear to be at more risk; in the laboratory, we have recorded high

mortality rates in death adders (*Acanthophis praelongus*), black whip snakes (*Demansia papuensis*) and king brown snakes (*Pseudechis australis*: M. Greenlees et al. unpubl. data).

Laboratory experiments provide detailed data on one of these ‘high risk’ species, the death adder *Acanthophis praelongus*. Individuals of all sizes and both sexes, and from woodland and floodplain habitats, consumed cane toads in the laboratory, and died after mouthing or ingesting toads (Webb et al. 2005; Phillips et al. 2009b). Death adders are especially vulnerable because they are ambush foragers that use caudal luring to attract prey to within striking range (Cogger 2000). The lure of adult northern death adders is black, and it resembles a small wriggling invertebrate (Webb et al. 2005). Because cane toads are attracted to black coloured wriggling objects (Ingle and McKinley 1978), encounter rates between death adders and cane toads are likely to be high after the toad invasion. Experimental trials confirm that cane toads are readily attracted to the lure of a death adder; indeed, more readily than are native frogs (Hagman et al. 2009a). Dead death adders with cane toads in their mouths have been reported from the Mary River region of Kakadu National Park (T. Flores, pers. comm.) and from the Adelaide River floodplain (Phillips et al. 2009b).

BIRDS

Covacevich and Archer (1975) reported that some individual crows (*Corvus* sp.) and kookaburras (*Dacelo novaeguineae*) died after mouthing cane toads, whereas other individuals of the same species consumed young toads or road-killed toads with no ill effects. van Beurden (1980a) recorded deaths of kookaburras, the little bittern (*Ixobrychus minutus*) and the black bittern (*Ixobrychus flavicollis*) after ingesting juvenile cane toads. At least seven native bird species can eat cane toads successfully, either because they eat

only the non-toxic parts of the toad or they are immune to the toxins (Covacevich and Archer 1975; Freeland 1987; Seabrook 1991; Mitchell et al. 1995).

Using data on bird foraging habits and diets, Dorfman (1997) predicted that 76 bird species from Kakadu National Park were potentially under threat from cane toads. Catling et al. (1999) listed several additional species that were potential consumers of cane toads, and a risk assessment by van Dam et al. (2002) suggested that 66 species of birds might be at risk from cane toads in Kakadu National Park. A more extensive review of available data suggests a less gloomy scenario for toad impacts on Australian birds via lethal toxic ingestion. Beckmann and Shine (2009) reviewed all available literature on this topic, and concluded that cane toads appear to have minimal impact on Australian birds. This ability to survive toad invasion appears to result from a widespread physiological tolerance of bufotoxins, perhaps reflecting close genetic ties between Australian birds and conspecifics or congeneric taxa in Asia, where many bufonid species possess toxins similar to those of cane toads (Meyer and Linde 1971).

MAMMALS

Webb and Glanznig (2004) listed nine species of native mammals and two species of introduced mammals as potentially at risk from ingesting cane toads. There are many reports of domestic dogs dying or becoming ill after mouthing or ingesting cane toads (Rabor 1952; Knowles 1964; Covacevich and Archer 1975; van Beurden 1980a), hinting that dingos could be at risk. Feral cats and pigs also may be negatively affected by cane toads (Begg et al. 2000); feral pigs frequently consume anurans (White 2008). Covacevich and Archer (1975) collated anecdotal reports of dogs, cats and quolls dying as a consequence of attempting to ingest toads. The ghost bat (*Macroderma gigas*) is thought to eat native frogs (ANPWS/DEST 1991) and therefore may eat cane toads. Although

other bat species may eat native frogs and potentially cane toads, there is little information on this topic.

In captivity, some native rodents (*Melomys burtoni*, *Rattus colletti*, *R. tunneyi*) readily attacked and killed small toads, and did not appear to suffer any ill effects from ingesting the anurans (J. Webb et al., unpubl. data). Other rodents (*Mus domesticus*, *Pseudomys nanus*, *Zyzyomys argurus*) showed no interest in cane toads as prey. Small dasyurid marsupial species such as planigales (*Planigale ingrami*, *P. maculata*) and dunnarts (*Sminthopsis virginiae*) attacked the first toad they encounter, became ill as a result, and were reluctant to attack toads thereafter (Webb et al. 2008 and unpubl. data). Relatively few of these dasyurids died as a result of attempting to ingest toads (Webb et al. 2008). Planigales (*P. maculata*) from northeastern Queensland, where toads have been abundant for several decades, reacted similarly to cane toads as did naïve animals from the Northern Territory, but appear to have evolved a higher physiological resistance to toad toxins (Llewelyn et al. 2009c).

The mammal species most often implicated as a victim of toad invasion is the northern quoll, *Dasyurus hallucatus*. Data on the fate of quolls radio-tracked in the field have been interpreted to suggest that lethal ingestion of cane toads is responsible for the local extinction of populations of northern quolls from the Mary River region of Kakadu National Park (Oakwood 2003a,b). However, only four of 14 quolls whose fate was known during Oakwood's studies were killed by ingesting toads, suggesting that other pressures also may threaten quoll populations. A more recent monitoring study of radio-tracked quolls confirms that many quolls die from ingesting toads (S. O'Donnell et al. 2009). In eight cases for which cause of mortality could be confirmed, seven were from ingestion of cane toads; the other quoll was killed by a feral cat. Quolls encountered (and were killed by) toads even in areas and at times when few toads were seen by observers

(O'Donnell et al. 2009). This result is a discouraging one, hinting that even low densities of cane toads may threaten quoll survival.

INDIRECT IMPACTS

The information above all relates to more-or-less direct impacts of cane toads – that is, outcomes of encounters between toads and native fauna. Toad invasion also may affect native species indirectly, via changes to sympatric species (Pace et al. 1999; Mack et al. 2000; Roemer et al. 2002). For example, if cane toads directly reduce the abundance of insects, they may thereby reduce feeding rates of native insectivores. This relatively simple case is included under the category of “competition” in the discussion above, but more complex scenarios are easy to envisage. For example, Waterhouse (1974) speculated that predation on dung beetles by cane toads could reduce rates of dung breakdown, with flow-on consequences to many aspects of ecosystem function. Freeland (2004) speculated that toad-induced shifts in host-parasite ecology could destabilize anuran community structure. More important, however, may be the mortality of top-order predators that are killed when they attempt to ingest these highly toxic anurans. In an experimental study, Crossland (2000) demonstrated that toxic effects of cane toad eggs on populations of predatory native frog tadpoles resulted in reduced predation on the eggs of other native frog species, and as a result, larval survival of these species was increased. As reviewed below, toad invasion can massively reduce numbers of predators such as varanid lizards, elapid snakes, freshwater crocodiles, and northern quolls. The consequent reduction of predator pressure on the usual prey of these species thus may change the abundance of particular species, and hence the composition of ecological assemblages (as may have occurred for small agamid lizards following toad-induced mortality of larger varanids:

Doody et al. 2009). A sudden release of predation pressure on specific life-history stages (such as turtle eggs: Doody et al. 2006) also might generate shifts in age structure within a species.

Indirect effects occur in two distinct ways (Wootton 1994). ‘Interaction chains’ occur where one species, by changing the abundance of another, indirectly affects a third species that directly interacts with them both. For example, an introduced leafhopper caused a population expansion in a parasitoid wasp, increasing rates of predation on a native leafhopper (Settle and Wilson 1990). ‘Interaction modifications’, on the other hand, occur where one species affects the interaction between two other species, for example a shelter plant can modify a predator-prey interaction by providing the prey with cover and decreasing vulnerability to predation. An interaction modification also can occur where one species affects another via a change in the behaviour of a third species. Behavioural shifts like this might have major implications for conservation (Curio 1996; Buchholz 2007). For example, in response to introduced brown trout (*Salmo trutta*) in New Zealand streams, mayfly nymphs (*Nesameletus ornatus*) reduce the time spent grazing; this behavioural change subsequently increases algal biomass (McIntosh and Townsend 1996; Townsend 1996).

Predicting the indirect effects of invasive species on ecosystems is extremely difficult. For example, the introduction of pigs to the Californian Channel islands caused an increase in the abundance of golden eagles, which then preyed on a major predator – island foxes – and caused their population to decline dramatically (Roemer et al. 2002). Feral house-mice on offshore islands have complex effects on dasyurids and skinks; and suburban cats simultaneously increase mortality rates of adult birds, and decrease rates of predation by rodents on bird nests (Dickman 2007). Even more subtle effects can have significant consequences – for example, if the invasive species modifies behaviour of a

native taxon, that change can ramify through the system. Webb et al. (2008) showed that marsupial carnivores (*Planigale maculata*) exposed to metamorph toads rapidly began to avoid not only toad metamorphs, but also frog metamorphs. That aversion to native frogs decreased through time (i.e. the predators learnt to distinguish noxious from edible prey), but the toad-averse planigales investigated such potential prey more carefully prior to seizing it, plausibly increasing the chances of escape for frog metamorphs (Webb et al. 2008). Similarly, Nelson et al. (2010) reported that exposure to toad tadpoles induced native fishes (*Mogurnda mogurnda*) to shift their foraging effort towards non-tadpole prey, thereby reducing predation on native tadpoles, and increasing predation on alternative prey types.

Cane toads actively select human-modified (degraded) habitats (e.g. Zug and Zug 1979; Lever 2001), and thus their impacts are tightly intertwined with other anthropogenic modifications. For example, one of the major impacts of cane toads likely involves flow-on effects due to the death of native predators such as varanid lizards (Doody et al. 2006). The magnitude of such impacts will depend upon the pre-toad densities of such predators, which will be massively dependent upon human activities (e.g. provision of extra food at campgrounds; subsistence hunting; attacks by domestic dogs). As a result, toad impacts may depend sensitively upon the details of prior disturbance regimes imposed by human activities.

POPULATION-LEVEL IMPACTS

There is a substantial difference between observing mortality of individual predators, and inferring that such cases are common enough to affect population numbers

or viability (Doody et al. 2009). Many processes that kill native animals do not threaten population persistence; especially in stochastic environments, abundance and distribution are regulated by a host of factors (e.g. weather conditions, food supply, disease) and increases in mortality due to toad invasion may have little effect on overall population numbers. Indeed, both ecological theory and manipulative experiments suggest that in some cases, additional mortality may increase rather than decrease population numbers (Crossland et al. 2009). This paradoxical result reflects the role of density-dependent processes. For example, if tadpoles of native frogs occur at such high densities that competition for food resources greatly reduces growth rates and survival, then any extrinsic mortality source (such as cane toads) may actually benefit the surviving tadpoles by liberating them from the competitive effects (Alford et al. 1995). In keeping with this inference, experimental addition of cane toads to experimental ponds can increase the body sizes of metamorphosing frogs (Crossland et al. 2009). However, the magnitude and direction of such effects depend upon the numbers and times of breeding of toads and frogs, so generalities about the impact of toads in this situation may prove difficult to identify (Crossland et al. 2009).

Another important complication is that the direct impact of cane toads on any given native species is likely to be accompanied by a suite of indirect impacts, mediated via the toads' impact on other taxa with which the target species interacts (see above). For example, the invasion of cane toads kills (fatally poisons) many tadpoles of native frogs, and also a significant number of frog metamorphs (Crossland et al. 2008). We might thus expect frog populations to decline following toad invasion. However, cane toads also kill (fatally poison) many frog-eating predators: indeed, from a predator's perspective, a cane toad is simply a booby-trapped frog. Thus, frog populations will be increased by the death of these top-predators, at the same time as frogs are being killed by ingesting toads. The

change in population size of frogs will, thus, represent the balance between these two effects (plus others, such as competition-reduction). In such a situation, frog numbers might well increase after cane toad invasion, despite high levels of direct mortality inflicted upon the frogs by interactions with toads.

Given that we cannot infer population-level effects from data on mortality of individual predators, we are left with the challenge of actually measuring population-level effects directly. This is a difficult challenge; even with a relatively stable "closed" population, detecting (for example) a 20% increase or decrease from one year to the next requires very large sample sizes or high capture rates per individual (Caughley 1977; Woinarski et al. 2004). If individuals can disperse from one population to the next, the challenge becomes much harder because dispersal (immigration–emigration) may contribute more to changing densities than does any process acting within the population under study. If we further add in high reproductive rates, spatial heterogeneity and environmental stochasticity, the logistical difficulties of assigning causation to any year-to-year change in densities become incredibly challenging. Unfortunately, much of the area colonized by cane toads, and many of the species affected, have ecological attributes that preclude exact enumeration. Year-to-year variation in wet-season rainfall patterns has immense influence on reproductive rates, growth rates and survival rates of animals in the wet-dry tropics (e.g. Madsen and Shine 1999, 2000; Madsen et al. 2006; Brown and Shine 2007). Population densities of some species thus fluctuate enormously from one year to the next, especially in the case of taxa (such as frogs) with high reproductive rates. Thus, for example, annual numbers of some native frog species at an intensively-studied area of the Adelaide River floodplain frequently shifted by more than 50% from one year to the next, even before cane toads arrived at the site (Crossland et al. 2008). Some of the species most likely to be affected by cane toad ingestion are large predatory reptiles and

mammals, with much lower reproductive rates – and thus, we might expect greater temporal consistency in population densities. Unfortunately, such taxa also tend to be rare and to be highly mobile, so that robust population estimates are almost impossible to obtain.

Even if we surmounted these obstacles and documented a strong correlation between cane toad arrival and a reduction in abundance of some native species, that correlation provides only weak evidence of a causal connection. Changes in land-use patterns, fire regimes and the presence of invasive plants, animals and pathogens all affect native fauna, and such changes are occurring rapidly throughout much of the cane toads' Australian range. Thus, a decline in some species coincident with toad arrival might well be due to some third, unappreciated factor. Northern quolls provide a clear example of this ambiguity. There is no doubt that many of these marsupials die when they attempt to ingest cane toads; radio-tracking studies document this link clearly (O'Donnell 2009; O'Donnell et al. 2009). However, northern quoll populations have been in decline for many years, and their virtual disappearance from many areas long predates the arrival of cane toads (Braithwaite and Griffiths 1994). Separating out the impact of toads from the impact of other threatening processes is a Herculean task in these complex and dynamic systems.

One clear implication of these sources of ambiguity is that any scientific studies that wish to document impacts of cane toads on native fauna must include replication on a scale that allows cane toad impact to be differentiated from other sources of variation. Thus, for example, simply surveying faunal abundance in toad-colonized *versus* non-colonized sites is fraught with problems because (a) habitat variables may explain why some sites have been colonized by toads and others have not, and those same variables may well affect composition of the native fauna; and (b) species richness and abundance of

native taxa (and their ease of detection by the observer) vary in complex ways across the landscape, independent of any effects of toads, so that the sites to be compared must be closely matched for all variables that might influence those native species. In practice, this is a major challenge, especially when combined with temporal variation in faunal composition and/or detectability.

The end result of these factors is that we know relatively little about the population-level impacts of cane toads on native fauna. There are many anecdotal reports of declines in particular species at about the same time that cane toads have invaded, but typically few data are provided. For example, Schultze-Westrum (1970) reported that in Papua New Guinea, increases in cane toad populations in savannas coincided with declines in native reptile populations, including several species of gecko, skink and other terrestrial species that sheltered under logs and rocks. Following the invasion of cane toads, cane toads became the dominant animal found under logs and rocks, suggesting that competition for shelter sites was involved in the decline (Schultze-Westrum 1970). Many similar examples can be cited from Australia. For example, Breeden (1963) reported declines in snakes, monitor lizards, frillnecked lizards (*Chlamydosaurus kingii*) and quolls following the appearance of toads in north Queensland; and Pockley (1965) and Rayward (1974) claimed that populations of snakes, goannas and birds had declined following the arrival of toads in southeastern Queensland and northern New South Wales. Unfortunately, these reports provided no quantitative evidence. Many of the stories that one hears about cane toad impact are inconsistent with the available data, raising doubt about the value of such opinions. Strong public revulsion against cane toads may encourage reports of ill-effect even if the actual observations are, at best, equivocal. Even in cases where the data show a consistent decline following toad invasion, causation is rarely clearcut. Paradoxically, some of the most readily interpretable data involve cases where densities of native species

are not affected by cane toad invasion. In such cases (such as for native frogs: see below), parsimony suggests that we accept the null hypothesis that cane toads have no significant impact on these native taxa, at least at the timescale for which data are available (typically, quite short-term).

INVERTEBRATES

High densities and feeding rates of cane toads have suggested to many observers that toad invasion may significantly deplete invertebrate populations (e.g. Pippet 1975). However, data to support this prediction are weak or non-existent. Catling et al. (1999) reported that the abundance of beetles was lower in sites colonized by cane toads compared to toad-free sites, but variances were high (indeed, the highest density of beetles was recorded at a toad-colonized site). Overall, Catling et al. (1999) concluded that there was little evidence that cane toads caused a significant adverse effect on the diversity and abundance of many of the native fauna examined – and that apparent effects may well be statistical artefacts. Freeland (2004) highlighted further statistical problems associated with inferring effects based on this kind of abundance data, and pointed out numerous inconsistencies in the results of surveys by Catling et al. (1999) compared to those of Watson and Woinarski (2003a,b) in terms of which species were affected by toads. Freeland (2004) also noted the continued presence of some of the putatively “negatively impacted” species in areas long after toad invasion.

Freeland (1993, 2004) has suggested that cane toads may have contributed to a decline in the proteocephalid tapeworm of the python *Antaresia maculosa*. The incidence of this parasite in native frogs (an intermediate host) decreased after toads invaded, possibly because higher feeding rates allowed cane toads to acquire most of the tapeworm larvae, preventing their subsequent passage to the pythons (these pythons rarely consume

toads). The parasite's incidence was higher in invasion-front populations of cane toads than in populations from long-colonized areas, consistent with the inference of a decline (Freeland et al. 1986b).

FISHES

Grace (2008) presents data on numbers of barramundi and saratoga in a billabong of the Mary River, over an 18-year period encompassing the arrival of cane toads at this site. There is no hint in these data of any shifts in fish abundance coincident with cane toad invasion.

AMPHIBIANS

The close phylogenetic relatedness between cane toads and native frogs results in many broad similarities in ecology, physiology and behaviour; and hence, intuition suggests that cane toad invasion might imperil frogs via competition, predation and disease transfer (see above). Any such effects likely would be opposed by positive effects resulting from deaths of frog-eating predators (see above). Possibly reflecting the balance between these two impacts (and also, the difficulty of accurately enumerating anuran densities), research so far has failed to detect any effect of cane toad invasion on frog populations. A range of methods has been used to look for changes in frog population densities before *versus* after toad invasion. Importantly, all have incorporated some level of replication in space and/or time. Direct counts of anurans around waterholes in the Gulf of Carpentaria during the tropical dry-season showed that numbers of *Litoria pallida*, *L. rothii* and *L. rubella* did not change significantly when cane toads invaded the study sites (Freeland and Kerin 1988). The same was true for numbers of *Litoria rothii* on the Adelaide River floodplain (even though this species was a frequent victim of lethal toxic ingestion of toad eggs in the same study area: Crossland et al. 2008), and for total anuran

biomass and species richness in that latter area also (Greenlees et al. 2007). In an innovative and geographically extensive study, Grigg et al. (2006) used fixed listening-posts to record anuran calls over longer periods before and after toad colonization. They reported no significant effects of cane toads on the numbers of frog species calling.

Watson and Woinarski (2003a,b) compared sites in Kakadu National Park the year before *versus* after toad invasion. No native frog species showed any substantial decline in toad-invaded areas; instead, there was a tendency for a relative increase in species richness and abundance following toad invasion. This relative increase was most marked for *Litoria wotjulemensis*, *L. rothii* and *Uperoleia* sp. A broader comparative survey comparing declining *versus* non-declining anuran species across Australia found a weak overall association between anuran decline and geographic overlap with cane toads, but this association disappeared in more detailed analyses (Murray and Hose 2005).

CROCODILES

Freshwater crocodiles remain common (or have recovered) in areas of Queensland that have contained high densities of cane toads for several decades (Letnic et al. 2008). Catling et al. (1999) found no evidence that cane toads affected freshwater crocodile populations. However, there are numerous anecdotal reports of freshwater crocodiles dying following cane toad consumption (van Dam et al. 2002). Letnic et al. (2008) and Doody et al. (2009) reported no decline in freshwater crocodiles on the Daly River, despite some cases of mortality due to toad ingestion. Similarly, Freeland (2004) reported that spotlight surveys on the Elsey National Park and Nitmiluk National Park prior to and following the arrival of cane toads revealed deaths of some crocodiles (presumably due to toad ingestion) but no overall population-level impact. In the course of our intensive research at Fogg Dam on the Adelaide River floodplain, my research group has not noted

any decline in numbers of *Crocodylus johnstoni*. All of these cases suggest that mortality rates from toad ingestion are too low to have population-level effects.

The situation is very different on the Victoria River (Letnic et al. 2008). At this more arid site, the cane toad invasion has caused mass mortality of crocodiles, reducing population densities by up to 70%. The divergence in levels of impact across sites may reflect differing low rates of encounter between crocodiles and toads. In well-watered areas, toads have many potential rehydration sites away from the river; but in more arid sites, the toads are forced to enter the river to rehydrate and thus, encounter rates between toads and crocodiles are higher in more arid conditions (Letnic et al. 2008). The area currently being invaded by toads is relatively arid, and the habitats around Lake Argyle may intensify toad impacts on the very large population of *C. johnstoni* found in that lake.

TURTLES

To my knowledge, the only quantitative evidence of cane toad impacts on turtles involves positive effects. On the Daly River, cane toad invasion killed many yellow-spotted monitors and presumably as a result, rates of predation by varanid lizards on the nests of pignose turtles (*Carettochelys insculpta*) fell from an average of around 17 to 23% to zero after toad invasion (Doody et al. 2006). At Fogg Dam, nightly counts of long-necked turtles (*Chelodina rugosa*) on the dam wall have tended to increase since cane toad invasion (G. P. Brown, pers. comm.).

LIZARDS

Burnett (1997) reported significant population declines of varanid lizards in Cape York and Lawn Hill after the arrival of cane toads. Based on data collected in a six-to-seven year period before and after toad invasion on the Daly River, Doody et al. (2009) reported a 83–96% decline of yellow-spotted goannas (*Varanus panoptes*; see Fig. 4), a

reduction of 71–97% in Mitchell's water monitor (*V. mitchelli*) and a decline of 87–93% in Merten's water monitor (*V. mertensi*). Griffiths and McKay (2007) similarly reported a major decline in *V. mertensi* in the Darwin area following toad arrival: estimates of site occupancy by lizards fell from 95% to 14% over an 18-month period. Radio-tracking of *V. panoptes* in Kakadu National Park suggested a 50 to 70% mortality due to toad invasion (Holland 2004). Also based on radio-tracking this species, Ujvari and Madsen (2008) concluded that at least 90% of adult male *V. panoptes* on the Adelaide River floodplain were killed by toad ingestion. In conjunction with abundant evidence of goannas being fatally poisoned by toad ingestion (see above), the consistency of these reports provides overwhelming evidence that the invasion of cane toads has serious immediate impacts on goanna populations.

Encouragingly, some smaller varanid species (e.g., *V. scalaris*) remain common after toad invasion (T. Madsen, pers. comm.) and at least some of the larger species (e.g. *Varanus panoptes*) that decline abruptly with toad invasion, are abundant several decades post-toad invasion in places such as Townsville and Borroloola (e.g. J. Llewelyn, B. L. Phillips, and L. Schwarzkopf, pers comm.; R. Shine, pers. obs.). Individuals from these populations do not attack cane toads (Freeland 1990). These results suggest that either large varanids have learnt to avoid eating cane toads, or there has been strong selection against varanids that eat cane toads (Freeland 1990). Freeland (2004) provides data on the time taken for an expert hunter (with trained dogs) to locate *Varanus panoptes* before *versus* after cane toads arrived in a study area near Borroloola in the Northern Territory. The mean time to find a goanna averaged 35 minutes in control (non-toad-invaded) areas, and 32 minutes at the main site in the year prior to toad invasion. That time to locate a lizard increased to an average of 103 minutes in the year after toads arrived, but then

decreased again to means of 56 and 38 minutes over the two following years (Freeland 2004).

Although there have been many reports of a decline in the abundance of frillneck lizards, *Chlamydosaurus kingii* (see above), studies by Ujvari et al. (2010) report that one of three study populations of frillnecks declined when toads arrived, another population remained stable, and third population increased. Those authors concluded that toad invasion was unlikely to be responsible for any of these changes in frillneck abundance.

Our laboratory studies have shown high mortality rates (through fatal poisoning) of bluetongue skink *Siliqua scincoides intermedia* (see Fig. 4) from northwestern Australia when tested in captivity (see above). Field rates with bluetongue lizards on the Adelaide River floodplain over the period 1999 to 2008 averaged approximately 0.025 lizards per night over the period 1999 to 2005 (year after toad arrival), falling to less than 0.01 lizards per night since that time (Price-Rees et al. 2010).

Watson and Woinarski (2003a,b) compared lizards in Kakadu National Park the year before versus after toad invasion, and reported declines in populations of varanid lizards (presumably due to fatal toxic ingestion of toads), as well as in the terrestrial gecko *Gehyra nana* and the skink *Carlia gracilis*. The causes for declines of these latter species are unclear. The same surveys revealed an increase in abundance of the dragon *Dragonia bilineata* (perhaps reflecting decreased predation by varanids). A similar phenomenon may explain population increase following toad invasion in another small agamid, *Amphibolurus gilberti*, in the Daly River region (Doody et al. 2009).

SNAKES

It is notoriously difficult to obtain robust population-density estimates for snakes, because these animals typically are rare, secretive, highly mobile, and infrequently active

(Seigel 1993). Hence, despite much anecdotal evidence that cane toads have been responsible for declines in population numbers of elapid snakes (Covacevich 1974; Covacevich and Archer 1975; van Beurden 1980; Mirtschin and Davis 1982; Easteal et al. 1985; Seabrook 1993), actual data are rare. Shine and Covacevich (1983) documented a decrease through time in the number of specimens of toad-vulnerable snake species relative to non-vulnerable snake species registered in the Queensland Museum, but pointed out that the data were consistent with habitat changes as well as with the impact of cane toads. Freeland (2004) pointed to a lack of extinctions of snake populations, even at a local level, by examining data from small islands where any negative effect of cane toads on such snakes likely would result in local extirpation. His tabulation of data on the occurrence of snake species on islands off Queensland does not reveal any trend for frog-eating species to be absent from islands that contain cane toads.

Quantitative population-abundance information is available for death adders (*Acanthophis praelongus*) on the Adelaide River floodplain. Laboratory studies and field-based radio-tracking of death adders at this site showed a toad-induced 48% mortality, and counts of road-killed snakes in the same area indicate a mean reduction in snake numbers of 89% concurrent with cane toad invasion (Phillips et al. 2009b).

In the same general area, we have extensive unpublished data on other snake species. Nocturnal counts of active snakes were made on the wall of Fogg Dam (Adelaide River floodplain) by G. P. Brown over a 12-year period (1998 to 2009; more than 3,600 standardized survey nights, comprising 83% of all nights over that 12-year period), bracketing the cane toad's arrival in 2006. Of the nine most common snake species, three (keelback *Tropidonophis mairii*, small-eyed snake *Cryptophis pallidiceps*, death adder *Acanthophis praelongus*) were encountered more frequently since the arrival of toads than had been the case beforehand. Counts of two other species (brown tree snake *Boiga*

irregularis, slatey-grey snake *Stegonotus cucullatus*) showed no evidence of significant impact, albeit with a trend to increasing encounter rates following toad invasion.

Encounter rates with Children's pythons (*Antaresia childreni*) and carpet pythons (*Morelia spilota*) both increased concurrent with the arrival toads, and then declined. Encounter rates with water pythons (*Liasis fuscus*) had been increasing prior to the arrival of toads, but began to decrease at about the time of toad arrival. The remaining species (king brown *Pseudechis australis*; see Fig. 4) had been declining in encounter rates prior to toad arrival, and continued this pattern after the arrival of toads. No king brown snakes were recorded in the final 23 months of this study, suggesting possible local extinction of this taxon.

Highlighting the difficulties of inferring causation from correlational data, some of the species that declined were the ones least likely to experience any direct impact from cane toads. Instead, the usual prey of water pythons (native rats) were in atypically low abundance because of a flood in 2006, so python numbers were reduced by starvation. A lack of rats also forced water pythons to begin consuming other snakes, especially keelbacks (a species whose decline cannot be directly attributed to toads, because these snakes are physiologically capable of consuming cane toads: Phillips et al. 2003; Llewelyn et al. 2009). The increase in numbers of death adders – a species at high risk from toads, and whose population was recorded to decline precipitously at a nearby site (by 89%: see above) remains puzzling. The only species that seems to have experienced a dramatic decline in numbers at this site as a direct result of lethal toxic ingestion of toads is the king brown snake. What is clear is that (a) major changes have occurred in the composition of the snake community, concurrent with cane toad invasion, and (b) few of those changes are likely to have been causally linked to cane toads, but instead reflect other year-to-year variation in this dynamic system. Our data thus paint a cautionary tale for any attempt to interpret population-level impacts of cane toads in the absence of detailed information on

the ecology, behaviour and physiology of the species involved. Even with thousands of nights of survey data at a single site, standardized for search effort and techniques, it is difficult to detect any unambiguous impacts of cane toad invasion on the overall snake fauna at Fogg Dam (G. P. Brown, pers. comm.).

BIRDS

Catling et al. (1999) reported that nectarivorous/granivorous birds were less common following cane toad invasion, but interpreted this result as a statistical artefact. In comparisons of sites in Kakadu the year before *versus* after toad invasion, Watson and Woinarski (2003a,b) noted a general trend for relative increases in the abundance and species richness of birds. Species that were more common in the toad-invaded areas included the mistletoebird *Dicaeum hirundinaceum*, red-backed fairy-wren *Malurus melanocephalus*, white-winged triller *Lalage sueurii*, golden-headed cisticola *Cisticola exilis* and magpie lark *Grallina cyanoleuca*. In contrast, numbers declined for the banded honeyeater *Cissomela pectoralis*, helmeted friarbird *Philemon buceroides*, olive-backed oriole *Oriolus sagittatus* and lemon-bellied flycatcher *Microeca flavigaster*. Watson and Woinarski (2003a,b) did not survey waterbirds, the group most likely to encounter toads.

I am unaware of any other quantitative studies on the impact of cane toads on bird populations; given strong public interest in birds, this lack of reports hints that toad impacts may not generally be severe. Information on the outcomes of encounters between birds and toads suggests that despite occasional mortality from fatal poisoning, cane toad invasion is unlikely to severely affect most bird populations (Beckmann and Shine 2009). An alternative pathway of impact involves usurpation of nesting burrows of birds such as bee-eaters (*Merops ornatus*: Boland 2004); data on the abundance of this species as a function of toad presence would be of interest. Similarly, given that toad invasion kills

many varanid lizards, predation on the eggs and nestlings of ground-nesting birds (such as plovers) might be reduced. Information on abundances of ground-nesting birds could clarify this possibility.

MAMMALS

Based on track counts, Catling et al. (1999) suggested that toad invasion may have reduced dingo populations in the Borroloola region. However, more robust data from Kakadu sites provided no evidence of any such impact (Watson and Woinarski 2003a,b). Following toad invasion, Watson and Woinarski (2003a,b) recorded fewer northern quolls (*Dasyurus hallucatus*), western chestnut mice (*Pseudomys nanus*) and pale field-rats (*Rattus tunneyi*), and more agile wallabies (*Macropus agilis*) and feral pigs (*Sus scrofa*). Numbers of fawn antechinus (*Antechinus bellus*) increased also, but the increase fell short of statistical significance. The other mammal species that were surveyed (common rock rat *Zyomys argurus*; northern brown bandicoot *Isoodon macrourus*; feral buffalo *Bubalus bubalus*; Kakadu pebble-mound mouse *Pseudomys calabyi*; grassland melomys *Melomys burtoni*; delicate mouse *Pseudomys delicatulus*; black-footed tree rat *Mesembriomys gouldi*; dingo *Canis familiaris dingo*; feral horse *Equus caballus*; red-cheeked dunnart *Sminthopsis virginiae*) showed no overall increase or decrease in toad-colonized sites.

Reflecting its iconic status and rapid decline, the northern quoll (*Dasyurus hallucatus*; see Fig. 4) has attracted most research attention in this respect. Burnett (1997) reported serious population declines in northern quolls in Cape York and Lawn Hill within a few months after the arrival of cane toads. Unfortunately, it is difficult to tease apart the effects of cane toads from other threatening processes. Populations of some small mammals such as the northern quoll and northern bandicoot have declined rapidly over recent decades, prior to the invasion of cane toads (Braithwaite and Griffiths 1994;

Woinarski et al. 2001). The toad may exacerbate these declines, and Oakwood (2003) reported the extirpation of one study population coincident with toad arrival in Kakadu National Park. Watson and Woinarski (2003) found no northern quolls in 110 quadrats of Kakadu that cane toads had invaded, whereas 41 individuals had been found in 17 of these quadrats in the previous year. In conjunction with the results of radio-tracking studies (Oakwood 2003a,b; O'Donnell 2009; O'Donnell et al. 2009), these data leave no doubt that cane toad invasion severely threatens the viability of northern quoll populations.

LONG-TERM IMPACTS OF CANE TOADS

There are massive logistical obstacles to quantifying the numerical impact of cane toads on the Australian fauna over a timescale of decades or beyond. First, we lack quantitative data on population sizes of native species prior to the toad's invasion through Queensland. Second, abundances of most species fluctuate so much through time and space, and are so heavily impacted by a suite of other anthropogenically-imposed challenges (e.g. land-clearing, pesticides, changes to water flows, other invasive species) that it would be difficult to interpret those data in the light of cane toad impact even were we to obtain precise numbers on prior abundance. All that can be stated is that: (a) so far as we know, no species has gone extinct as a result of cane toad invasion; and (b) some of the species known to decline dramatically soon after toad invasion are abundant in areas well behind the current invasion front. Although these data are anecdotal, even superficial observation confirms that "toad-sensitive" species such as yellow-spotted monitors (*Varanus panoptes*) are common in northeastern Queensland, where they thrive in areas containing high densities of cane toads (e.g. Fearn 2003; J. Llewelyn, D. Nelson, L.

Schwarzkopf, pers. comm.; R. Shine, pers. obs.). Woinarski et al. (2008) surveyed populations of northern quolls in Queensland, in areas long colonized by cane toads. They found co-occurring quolls and toads at several sites, and inferred that coexistence between quolls and toads seemed to be stable in this system.

Given that these same species apparently declined precipitously with cane toad invasion in Queensland (Burnett 1997) and in the Northern Territory (see above), the current situation suggests recovery post-invasion. How has this happened? Longer-term, at least some Australian predators adapt to the presence of cane toads. The most extensive data come from studies of the red-bellied blacksnake (*Pseudechis porphyriacus*) by Phillips and collaborators. Comparisons between snakes from toad-colonized areas *versus* areas not yet invaded by toads revealed differences in a set of traits predicted to enhance a snake's probability of surviving an encounter with a toad. Snakes from toad-colonized areas refused to attempt to ingest toads, and were more resistant to the toads' toxin than were conspecific animals from areas lacking cane toads (Phillips and Shine 2006c). Other data suggest that these shifts in behaviour and physiology reflect genetically-based (adaptive) shifts rather than learning or physiological acclimation (Phillips et al. 2004, 2006c). Blacksnakes from toad-colonized areas exhibited smaller head sizes relative to body size, a pattern also seen in the anuran-eating *Dendrelaphis punctulatus*, but not in two sympatric snake species not predicted to be at risk from cane toads (*Hemiaspis signata*, *Tropidonophis mairii*: Phillips and Shine 2004). Smaller relative head size renders a snake less vulnerable to lethal toxic ingestion, because small-headed snakes can ingest only small toads (Phillips and Shine 2004). Hence, cane toad invasion appears to have favoured rapid evolutionary shifts in behaviour, physiology and morphology of snake predators, in ways that facilitate snake survival in the presence of toads.

Such shifts may occur quickly. Phillips et al. (2009) demonstrated that cane toad invasion imposes strong selection on feeding responses (propensity to attack toads) and morphology (relative head size) in a population of floodplain death adders (*Acanthophis praelongus*) near Darwin. In this study, feeding responses of adders were monitored in captivity, and then the snakes were released and radio-tracked in an area recently invaded by cane toads. Snakes that refused to attack toads in the laboratory were more likely to survive after release; and snakes with relatively small heads were more likely to survive than were larger-headed conspecifics (Phillips et al. 2009). Encouragingly, then, Australian snakes can adapt to cane toad invasion; but nonetheless, populations of these predators may require long periods before they return to pre-toad levels (if indeed they ever do). Freeland (2004) suggested that large varanids might return to pre-toad abundances within a few years, but anecdotal reports suggest that some previously-common predator species are still relatively rare in toad-infested areas of northeastern Queensland (e.g. *Pseudechis porphyriacus*: B. L. Phillips, pers. comm.).

Potentially, very low population levels *per se* (due to toad invasion) might affect the probability of extinction as well as rates of subsequent recovery. Reduced genetic variability due to "bottleneck" effects can imperil population recovery (Madsen et al. 1999), and low population sizes render such systems more vulnerable to stochastic threats (Caughley 1994). In practice, such issues are unlikely to be significant for most Australian native fauna affected by cane toad invasion. Most of the animals involved (e.g. varanid lizards, large elapid snakes) are highly vagile, enabling significant gene flow to persist even at low population densities. Relatively high population numbers at a landscape scale mean that even severe reductions are unlikely to pose real threats of extirpation. Detailed population-genetics analyses to address these questions would be of value.

WHAT FACTORS INFLUENCE THE ECOLOGICAL IMPACT OF THIS INVASIVE SPECIES?

The intense research on ecological impacts of invasive cane toads in Australia provides an unusually detailed case study of how the arrival of a single toxic species can affect a speciose tropical fauna. Accordingly, we can ask what general lessons emerge from the accumulated data on toad impact. I identify several such emergent themes below.

1. Community perceptions of invasive-species impacts are often in error. The general public holds diverse views about cane toads, most of which are very negative. A widespread abhorrence of the animal (apparently reflecting its size and appearance) has led some community spokespeople to promulgate catastrophe scenarios, whereby the cane toad invasion is predicted to massively affect virtually all native species (this opinion is especially common in communities where toads are yet to arrive: Clarke et al. 2009). Indeed, surveys of public opinion often rank cane toads among the greatest ecological threats to Australian ecosystems (Fitzgerald et al. 2007). That widespread concern has stimulated massive levels of expenditure by state and federal governments (more than \$9,500,000 over the period 1986 to 1996: Shine et al. 2006) and enormous effort by volunteers to eradicate local toad populations by direct collection. In reality, the direct impact of cane toads falls most heavily on a small number of native taxa, rather than across a wide spectrum of native fauna.

Similarly, members of the general public envisage a wide range of mechanisms of impact, ranging from toads “poisoning the waterholes” via toxin release, through to encouraging drug abuse in people who become addicted to licking the toads or smoking their dried skins (Clarke et al. 2009). There are no data to suggest that either of these

issues is a major problem. More realistically, competition between toads and native frogs often is suggested to be a major mechanism of impact (Shine et al. 2006). Experimental studies and surveys do not support that hypothesis (Freeland and Kerin 1988; Catling et al. 1999; Grigg et al. 2006; Greenlees et al. 2006, 2007), although more research is warranted on effects of dense dry-season aggregations of toads on local prey abundances. Available data suggest that a single proximate mechanism – fatal poisoning of predators that attempt to ingest toads – is by far the most important mechanism of direct impact of cane toads on native fauna.

2. *Impacts are affected by several attributes of toad biology.* The biology of the invasive species necessarily influences the type, extent and magnitude of ecological interactions with native fauna, even if attention is restricted to a single mechanism of impact (i.e., lethal toxic ingestion). Importantly, cane toads have a multiphasic life history, with eggs and tadpoles in waterbodies, metamorphs restricted to riparian areas, and larger juveniles and adults spreading out through the drier landscape (e.g., Alford et al. 1995; Freeland and Kerin 1988; Child et al. 2008a). The types and amounts of toxins, as well as body sizes and habitat use, change considerably through toad ontogeny (Hayes et al. 2009). Specific features of toad biology also affect impact: for example, the presence of a non-toxic jelly coat around the (highly toxic) eggs is fatal to aquatic predators that otherwise would be able to detect and reject bufotoxin-containing prey items (Greenlees and Shine 2009). The end result of the complex life history and wide range in absolute body sizes and habitats used is to increase the range of predator species likely to ingest toads. The breadth of impact would be lower in the case of an invasive anuran species with larger metamorphs relative to adult size, or without an aquatic phase in the life history (as for the coqui, *Eleutherodactylus coqui*, currently invading the Hawaiian islands: Kraus 2009).

Superimposed on the wide body-size range of terrestrial-phase toads (from < 1 g to > 1 kg: see Fig. 1) is a strong positive allometry in toxin content (Phillips and Shine 2006a). Thus, a large adult toad contains orders of magnitude more toxin than a juvenile conspecific. That allometry appears to explain one of the strongest patterns to emerge from research on cane toad impact: the disproportionate mortality of predators that attain large body sizes themselves, and thus are prepared to attack large toads (see Fig. 4). The anurophagous predators involved belong to a diverse array of phylogenetic lineages, with large absolute body size the single common denominator.

Consistent (albeit, anecdotal) reports of eventual post-invasion reductions in toad abundance and recovery of predator populations suggest that impact-determining properties of the toad population may change with time since invasion also. In keeping with that inference, the toxin-containing parotoid gland is largest (relative to body size) in toads from the invasion front (Phillips and Shine 2006b). It is unclear whether this is an adaptive shift, or a phenotypically plastic response to larval environments (Hagman et al. 2009b). Toad abundance also may decrease in long-colonized areas, perhaps reflecting reduced food availability (Freeland et al. 1986a; Tyler 1994). Lastly, toad population structure may alter. Toads at the invasion front rarely reproduce, apparently because of strong spatial selection for traits that enhance dispersal abilities at the cost of investment into other processes (Brown et al. 2007; Phillips et al. 2009a). Thus, one reason for the intense ecological impact of toads at the colonization front may be the scarcity of toads small enough to comprise a non-fatal meal. If small toads are common, predators may have the opportunity for aversion learning (e.g., Webb et al. 2008; Greenlees et al. 2009). A shift in toad recruitment rates (and hence, in the availability of toads small enough to induce aversion but not cause predator death) might render predators more likely to survive in long-colonized areas than at the toad invasion front.

3. *Impacts are affected by several attributes of predator biology.* As noted above, any characteristic that increases the size of toads that a predator will attack is likely to greatly increase predator vulnerability, because of the strong positive allometry in toxin content of cane toads. Predator body size is the most obvious such trait, but in some species there may also be significant divergences in predatory tactics between the sexes. For example, male northern quolls (*Dasyurus hallucatus*) are bolder as well as larger than females, more willing to attack large toads, and thus much more likely to die as a result of such encounters (O'Donnell 2009). Divergences in prey types and foraging tactics may be widespread in species that exhibit marked sex divergences in mean adult body size, potentially modifying vulnerability to toad invasion (e.g., floodplain death adders, *Acanthophis praelongus*: Webb et al. 2005).

Interspecific (and occasionally, intraspecific) variation in physiological tolerance to bufotoxins also plays a role in determining predator vulnerability. Red-bellied blacksnakes (*Pseudechis porphyriacus*) and small marsupial carnivores (*Planigale maculata*) exposed to several decades of sympatry with cane toads show greater tolerance to toad toxins than do toad-naive conspecifics (Phillips and Shine 2006c; Llewelyn et al. 2009c). Given this rapidity of evolutionary response, we would expect that Australian predators with strong genetic ties to Asia (i.e., the descendants of relatively recent invasions from the north) will be able to tolerate bufotoxins better than can species with a long history of endemism in Australia (Beckmann and Shine 2009; Llewelyn et al. 2009b,c). Asia contains many toad species, with toxins broadly similar in chemical composition to the bufodienolides produced by cane toads (Meyer and Linde 1971). Within groups such as mammals, birds, snakes and crocodiles, taxa with recent links to Asia are indeed less vulnerable to toad invasion than are related taxa with a longer history of Australian endemism.

Aversion learning protects many native predators from the ill-effects of cane toad ingestion (Webb et al. 2008; Greenlees et al. 2009; Shine et al. 2009) and hence, variation in learning ability may influence magnitudes of impact. There is likely to be a complex interplay among the multiple selective forces induced by toad arrival. For example, a predator species capable of rapid aversion learning will be under little selection for increased physiological tolerance to toxin, because immediate rejection of the toxic prey removes the physiological challenge of dealing with the toad's poisons. Thus, we might expect some species to evolve physiological tolerance to toxins, others to evolve enhanced learning ability, and yet others to be under little effective selection because they already are able to cope with the novel challenge posed by cane toad invasion (Llewelyn et al. 2009b).

4. Impacts are affected by attributes of the local environment. Rates of encounter between cane toads and potential predators will be affected by the local habitat. For example, a relatively dry landscape matrix will keep most toads close to water (because they need to hydrate every few days: Alford et al. 1995), thus increasing rates of encounter with aquatic predators like freshwater crocodiles (Letnic et al. 2008) but decreasing rates of encounter with predator taxa that forage in drier habitats. At the extreme arid-zone edges of the toad invasion, this situation may generate great heterogeneity in toad impact both through space (riparian vs other sites) and time (dry weather vs rainy periods that allow toad dispersal across the landscape).

5. Impacts are affected by attributes of local foodwebs. The invasion of cane toads can result in mortality of a high proportion of large anurophagous reptiles and mammals. Because the species most strongly affected in this respect have broad diets (e.g., Shine et

al. 2006; Letnic et al. 2008; O'Donnell et al. 2009), their deaths reduce mortality rates for their usual prey taxa (e.g., see Doody et al. 2006 for reduced rates of varanid predation on turtle eggs following toad invasion). Presumably, such effects may flow through multiple trophic levels. As well as killing predators, however, cane toads can modify predatory tactics of the survivors; toad-averse predators switch their behaviours to target prey that do not resemble toads (Nelson 2008; Nelson et al. 2010) or more carefully evaluate potential prey before seizing them (Webb et al. 2008). Native species thus may benefit from “accidental mimicry” of the invasive toads; for example, a frog species that closely resembles a toad may be relatively safe, at least until predators learn to distinguish between the toxic invader and the non-toxic native (Webb et al. 2008; Nelson et al. 2010).

6. Impacts of invasive species are difficult to demonstrate. In the current review, I have relied on two types of information: survey data that show reduction in abundance of a native taxon before *versus* after toad arrival, and laboratory trials to document the outcomes of staged encounters between predators and toads. Both have major flaws. Survey data face two problems: (a) especially for rare species, count data are so variable that it is difficult to obtain statistically robust evidence of decline even for major changes in abundance (Watson and Woinarski 2003a); and (b) the inference of causation is based on a temporal correlation (i.e., faunal decline occurred at the same time that toads arrived), that could equally as well be explained by many other factors (e.g., weather conditions). Laboratory trials face the difficulty of extrapolation to the field. For example, if local ecological circumstances render encounter rates between predators and toads vanishingly unlikely, then whether or not that predator will attack a toad in the laboratory tells us very little about impact in the field. In practice, the combination of survey data and laboratory trials (plus reliable anecdotal reports of field encounters and their outcomes, or dissection

of stomach contents of predators found dead in the field: e.g., Fearn 2003; Letnic et al. 2008; Doody et al. 2009) is stronger than either survey or laboratory-trial data alone.

CONCLUSION

Cane toads have direct impacts on some species of Australian native animals, mostly involving the death of large predators (quolls, crocodiles, snakes, varanid and scincid lizards) through lethal toxic ingestion. Direct impacts on other species likely are not severe enough to have any major effects at the population level. However, high mortality rates of top predators will have flow-on effects, with populations of some native species increasing as a result, and others decreasing. A capacity for rapid learning of toad-avoidance by some predators, and for rapid adaptive shifts in others, mean that the ecological impact of cane toads is likely to decrease through time. Good land management practices can help to ensure healthy predator populations that can recover more rapidly and completely from the impact of toads. However, there is no room for complacency: myriad other threats act on native biodiversity, changing habitats and climate can potentially destabilize these systems, and toads are currently moving into areas of Australia with faunistic assemblages different from any that they have yet encountered. More than 70 years after cane toads were brought to Australia, it is only within the last five years that a clear picture is beginning to emerge about the consequences of that unfortunate introduction for the Australian fauna. Direct impacts of cane toads are now fairly well understood, but more research is needed to clarify the indirect (food-web-mediated) effects of this invasive species on native biodiversity.

ACKNOWLEDGEMENTS

Much of the information reviewed above comes from the work of my research group, “Team Bufo”. I thank them for their hard work, their insights, and their generosity in sharing ideas and data. In particular, our understanding of the ecological impacts of cane toads has been substantially enhanced by the work of my postdoctoral fellows (Greg Brown, Michael Crossland, Sylvain Dubey, Mattias Hagman, Ben Phillips, Ligia Pizzatto, Jonathan Webb), research students (Christa Beckmann, Haley Bowcock, Travis Child, Matt Greenlees, Crystal Kelehear, John Llewelyn, David Nelson, Stephanie O’Donnell, Sam Price-Rees, Ruchira Somaweera, Georgia Ward-Fear), laboratory staff (Melanie Elphick, Adele Haythornthwaite, Christine Rioux) and collaborators (Ross Alford, Di Barton, Rob Capon, Andrew Hayes, David Pearson, Lin Schwarzkopf, Cathy Shilton, Dion Wedd). Our research has been funded primarily by the Australian Research Council, through the University of Sydney. Additional funding has come from the Federal Department of Environment, Water, Heritage and the Arts, and in collaboration with the Western Australian Department of Environment and Conservation, the Territory Wildlife Park and the Australian Reptile Park. Preparation of this review was funded by the Commonwealth of Australia, under the Caring for Our Country initiative. I thank Tony Peacock (CRC for Invasive Species) for encouragement, and the reviewers and editor for helpful suggestions.

REFERENCES

- Alford R. A. 1999. Ecology: resource use, competition, and predation. Pages 240–278 in *Tadpoles: The Biology of Anuran Larvae*, edited by R. W. McDiarmid and R. Altig. Chicago: University of Chicago Press.
- Alford R. A., Cohen M. P., Crossland M. R., Hearnden M. N., Schwarzkopf L. 1995. Population biology of *Bufo marinus* in northern Australia. Pages 173–181 in *Wetland Research in the Wet-Dry Tropics of Australia*, edited by C. M. Finlayson. Supervising Scientist Report 101. Canberra: Supervising Scientist.

- Andersen A. N. 1991. Seed harvesting by ants in Australia. Pages 493–503 in *Ant-Plant Interactions*, edited by C. R. Huxley and D. F. Cutler. New York: Linnean Society of London, Oxford University Press.
- Andersen A. N., Braithwaite R. W. 1996. Plant-animal interactions. Pages 137–154 in *Landscape and Vegetation Ecology of the Kakadu Region Northern Australia*, edited by C. M. Finlayson and I. von Oertzen. Geobotany Series 23. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Andrew M. H. 1986. Granivory of the annual grass *Sorghum intrans* by the harvester ant *Meranoplus* sp. in tropical Australia. *Biotropica* 18:344–399.
- ANPWS (Australian National Parks and Wildlife Service)/DEST (Department of the Environment, Sport and Territories). 1991. *Nomination of Kakadu National Park by the Government of Australia for inscription in the World Heritage List*.
- Bailey P. 1976. Food of the marine toad, *Bufo marinus*, and six species of skink in a cacao plantation in New Britain, Papua New Guinea. *Australian Wildlife Research* 3:185–188.
- Barraclough N. 1988. Dead cane toads. *The Bird Observer* 672:21.
- Beckmann C., Shine R. 2009. Are Australia's birds at risk due to the invasive cane toad? *Conservation Biology*: in press.
- Begg G. W., Walden D., Rovis-Hermann J. 2000. *Report on the joint ERISS/PAN cane toad risk assessment field trip to the Katherine/Mataranka and Borroloola regions*. Unpublished Report. Darwin: Supervising Scientist.
- Bekker R. 1985. Predation on cane toads (*Bufo marinus*). *Herpetofauna* 16:52–53.
- Boland C. R. J. 2004. Introduced cane toads are active nest predators and competitors of rainbow bee-eaters: observational and experimental evidence. *Biological Conservation* 120:53–62.
- Bowcock H., Brown G. P., Shine R. 2008. Sexual communication in cane toads (*Bufo marinus*): what cues influence the duration of amplexus? *Animal Behaviour* 75:1571–1579.
- Bowcock H., Brown G. P., Shine R. 2009. Beastly bondage: the costs of amplexus in cane toads (*Bufo marinus*). *Copeia* 2009:29–36.

- Braithwaite R. W., Griffiths A. 1994. Demographic variation and range contraction in the northern quoll *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Wildlife Research* 21:203–217.
- Breeden K. 1963. Cane toad (*Bufo marinus*). *Wildlife in Australia* 1:31.
- Brown G. P., Shine R. 2007. Rain, prey and predators: climatically-driven shifts in frog abundance modify reproductive allometry in a tropical snake. *Oecologia* 154:361–368.
- Brown G. P., Shilton C. M., Phillips B. L., Shine R. 2007. Invasion, stress, and spinal arthritis in cane toads. *Proceedings of the National Academy (USA)* 104:17698–17700.
- Buchholz R. 2007. Behavioural biology: an effective and relevant conservation tool. *Trends in Ecology and Evolution* 22:401–407.
- Burnett S. 1997. Colonising cane toads cause population declines in native predators: reliable anecdotal information and management implications. *Pacific Conservation Biology* 3:65–72.
- Cameron E. E., Cogger H. G. 1992. *The herpetofauna of the Weipa region, Cape York Peninsula*. Technical Report No. 7. Sydney: Australian Museum.
- Cassels A. J. 1966. Disembowelled toads near water. *North Queensland Naturalist* 34:6.
- Caswell D. 1987. Australian raven eats cane toad. *The Bird Observer* 663:47.
- Catling P. C., Hertog A., Burt R. J., Wombey J. C., 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.
- Caughley G. 1977. *Analysis of Vertebrate Populations*. New York: Wiley.
- Caughley G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- Child T., Phillips B. L., Brown G. P., Shine R. 2008a. The spatial ecology of cane toads (*Bufo marinus*) in tropical Australia: why do metamorph toads stay near the water? *Austral Ecology* 33:630–640.
- Child T., Phillips B. L., Shine R. 2008b. Abiotic and biotic influences on the dispersal behaviour of metamorph cane toads (*Bufo marinus*) in tropical Australia. *Journal of Experimental Zoology* 309A:215–224.
- Child T., Phillips B. L., Shine R. 2009. Does desiccation risk drive the distribution of metamorph cane toads (*Bufo marinus*) in tropical Australia? *Journal of Tropical Ecology* 25:193–200.

- Clarke R., Carr A., White S., Rapohael B., Baker J. 2009. *Cane Toads in Communities*. Executive Report to the Australian Government, Bureau of Rural Sciences, Canberra, ACT
- Clerke R. B., Williamson I. 1992. A note on the predation of *Bufo marinus* juveniles by the ant *Iridomyrmex purpureus*. *Australian Zoologist* 28:64–67.
- Cogger H. G. 2000. *Reptiles and Amphibians of Australia. Sixth Edition*. Sydney: Reed Books.
- Cogger H. G., Cameron E. E., Sadlier R., and Egger P. 1993. *The Action Plan for Australian Reptiles*. Canberra: Australian Nature Conservation Agency.
- Cohen M. P., Alford R. A. 1996. Factors affecting diurnal shelter use by the cane toad, *Bufo marinus*. *Herpetologica* 52:172–181
- Covacevich J. 1974. An unusual aggregation of snakes following major flooding in the Ipswich-Brisbane area, south-eastern Queensland. *Herpetofauna* 7:21–24.
- Covacevich J., Archer M. 1975. The distribution of the cane toad, *Bufo marinus*, in Australia and its effects on indigenous vertebrates. *Memoirs of the Queensland Museum* 17:305–310.
- Crossland M. R. 1997. *Impact of eggs, hatchlings and tadpoles of the introduced cane toad Bufo marinus (Anura: Bufonidae) on native aquatic fauna in northern Queensland, Australia*. PhD thesis. Townsville: James Cook University of North Queensland.
- Crossland M. R. 1998a. Ontogenetic variation in toxicity of tadpoles of the introduced toad *Bufo marinus* to native Australian aquatic invertebrate predators. *Herpetologica* 54:364–369.
- Crossland M. R. 1998b. A comparison of cane toad and native tadpoles as predators of native anuran eggs, hatchlings and larvae. *Wildlife Research* 25:373–381.
- Crossland M. R. 2000. Direct and indirect effects of the introduced toad *Bufo marinus* (Anura: Bufonidae) on populations of native anuran larvae in Australia. *Ecography* 23:283–290.
- Crossland M. R. 2001. Ability of predatory native Australian fishes to learn to avoid toxic larvae of the introduced toad *Bufo marinus*. *Journal of Fish Biology* 59:319–329.
- Crossland M. R., Alford R. A. 1998. Evaluation of the toxicity of eggs, hatchlings and tadpoles of the introduced toad *Bufo marinus* (Anura: Bufonidae) to native Australian aquatic predators. *Australian Journal of Ecology* 23:129–137.

- Crossland M. R., Azevedo-Ramos C. 1999. Effects of *Bufo* (Anura: Bufonidae) toxins on tadpoles from native and exotic *Bufo* habitats. *Herpetologica* 55:192–199.
- Crossland M. R., Shine R. 2009. Vulnerability of an Australian anuran tadpole assemblage to the toxic eggs of the invasive cane toad (*Bufo marinus*). *Austral Ecology*: in press.
- Crossland M. R., Brown G. P., Anstis M., Shilton C., Shine R. 2008. Mass mortality of native anuran tadpoles in tropical Australia due to the invasive cane toad (*Bufo marinus*). *Biological Conservation* 141:2387–2394.
- Crossland M. R., Alford R. A., Shine R. 2009. Impact of the invasive cane toad (*Bufo marinus*) on an Australian frog (*Opisthodon ornatus*) depends on reproductive timing. *Oecologia* 158:625–632.
- Curio E. 1996. Conservation needs ethology. *Trends in Ecology and Evolution* 11:260–263.
- Daly J. W., Witkop B. 1971. Chemistry and pharmacology of frog venoms. Pages 497–519 in *Venomous Animals and their Venoms*, edited by W. Bucherl and E. E. Buckley. New York: Academic Press.
- Delvinquier B. L. J., Freeland W. J. 1988. Protozoan parasites of the cane toad, *Bufo marinus*, in Australia. *Australian Journal of Zoology* 36:301–316.
- Dickman C. R. 2007. The complex pest: interaction webs between pests and native species. Pages 208–215 in *Pest or Guest: The Zoology of Overabundance*, edited by D. Lunney, P. Eby, P. Hutchings and S. Burgin. Mosman: Royal Zoological Society of NSW.
- Donato D. B., Potts R. T. 2004. Culturally transmitted predation and consumption techniques by Torresian crows *Corvus orru* on cane toads *Bufo marinus*. *Australian Field Ornithology* 21:125–126.
- Doody J. S., Green B., Sims R., Rhind D., West P., Steer D. 2006. Indirect impacts of invasive cane toads (*Bufo marinus*) on nest predation in pignosed turtles (*Carettochelys insculpta*). *Wildlife Research* 33:49–54.
- Doody J.S., Green B., Rhind D., Castellano C. M., Sims R., Robinson T. 2009. Population-level declines in Australian predators caused by an invasive species. *Animal Conservation* 12:46-53.

- Dorfman E. 1997. *Possible threats to birds from cane toads in Kakadu National Park*. Unpublished List supplied to Parks Australia.
- Drewes R. C., Roth B. 1981. Snail-eating frogs from the Ethiopian highlands: a new anuran specialization. *Zoological Journal of the Linnean Society* 73:267–287.
- Dubey S., Shine R. 2008. Origin of the parasites of an invading species, the Australian cane toad (*Bufo marinus*): are the lungworms Australian or American? *Molecular Ecology* 17:4418–4424.
- Easteal S., van Beurden E. K., Floyd R. B., Sabath M. D. 1985. Continuing geographical spread of *Bufo marinus* in Australia: range expansion between 1974 and 1980. *Journal of Herpetology* 19:185–188.
- Evans S. 1999. Fisheries issues in the Borroloola region. Page 16 in *Wise Use of Wetlands in Northern Australia: Indigenous Use*, edited by P. Whitehead, M. Storrs, M. McKaige, R. Kennett and M. Douglas. Northern Territory University, Darwin: Centre for Tropical Wetlands Management and Centre for Indigenous Natural and Cultural Resource Management.
- Fearn S. 2003. *Pseudechis porphyriacus* (Red-Bellied Black Snake). Diet. *Herpetological Review* 34:253–254.
- Fitzgerald G., Fitzgerald N., Davidson C. 2007. Public attitudes towards invasive animals and their impacts. Report to the Invasive Animals Cooperative Research Centre, Canberra, ACT.
- Fitzgerald M. 1990. *Rattus rattus*: the introduced black rat, a successful predator on the introduced cane toad *Bufo marinus* in northern New South Wales. *Herpetofauna* 20:9–13.
- Freeland W. J. 1984. *Cane toads: a review of their biology and impact on Australia*. Technical Report 19. Darwin: Parks and Wildlife Unit, Conservation Commission of the Northern Territory.
- Freeland W. J. 1986. Populations of cane toad, *Bufo marinus*, in relation to time since colonisation. *Australian Wildlife Research* 13:321–329.
- Freeland W. J. 1987. Cane toads and the balance of nature. *Wildlife Australia* 24:12–15.

- Freeland W. J. 1990. *Effects of the cane toad *Bufo marinus* on native Australian wildlife: a review of past and current research*. Unpublished Report. Darwin: Conservation Commission of the Northern Territory.
- Freeland W. J. 1993. Parasites, pathogens and the impact of introduced organisms on the balance of nature in Australia. Pages 171–180 in *Conservation Biology in Australia and Oceania*, edited by C. Moritz and J. Kikkawa. Chipping Norton: Surrey Beatty and Sons.
- Freeland W. J. 2000. Unpublished Report to Parks and Wildlife Commission of the Northern Territory: Palmerston, NT.
- Freeland W. J. 2004. *An assessment of the introduced cane toad's (Bufo marinus Linnaeus) impacts on the native Australian fauna, with particular reference to the Eastern Kimberley region*. Unpublished Report to the WA Department of Industry and Resources. Palmerston, NT: HLA-Envirosciences Pty Ltd.
- Freeland W. J., Kerin S. H. 1988. Within habitat relationships between invading *Bufo marinus* and Australian species of frog during the tropical dry season. *Australian Wildlife Research* 15:293–305.
- Freeland W. J., Delvinquier B. L. J., Bonnin B. 1986a. Decline of cane toad, *Bufo marinus*, populations: status of urban toads. *Australian Wildlife Research* 13:597–601.
- Freeland W. J., Delvinquier B. L. J., Bonnin B. 1986b. Food and parasitism of the cane toad, *Bufo marinus*, in relation to time since colonisation. *Australian Wildlife Research* 13:489–499.
- Frost D. R., Grant T., Faivovich J., Bain R. H., Haas A., Haddad C. F. B., De Sá R. O., Channing A., Wilkinson M., Donnellan S. C., Raxworthy C. J., Campbell J. A., Blotto B. L., Moler P., Drewes R. C., Nussbaum R. A., Lynch J. D., Green D. M., Wheeler W. C. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297:1–370.
- Grace B. 2008. Cane toads and Top End fish. *Fishnote* 42:1–3. Berrimah: NT Department of Primary Industry, Fisheries and Mines.
- Grace B., Sawyer G. 2008. Dead fish and frogs associated with cane toads near Darwin. *NT Naturalist* 20:222–225.

- Grant G. S. 1996. Prey of introduced *Bufo marinus* on American Samoa. *Herpetological Review* 27:67–69.
- Greenlees, M. J., Shine R. 2009. Impacts of eggs and tadpoles of the invasive cane toad (*Bufo marinus*) on aquatic predators in tropical Australia. *Austral Ecology*, in press.
- Greenlees M. J., Brown G. P., Webb J. K., Phillips B. L., Shine R. 2006. Effects of an invasive anuran (the cane toad, *Bufo marinus*) on the invertebrate fauna of a tropical Australian floodplain. *Animal Conservation* 9:431–438.
- Greenlees M. J., Brown G. P., Webb J. K., Phillips B. L., Shine R. 2007. Do invasive cane toads (*Chaunus marinus*) compete with Australian frogs (*Cyclorana australis*)? *Austral Ecology* 32:900–907.
- Greenlees, M. J., Phillips B. L., Shine R. 2009. An invasive species imposes selection on life-history traits of a native frog. *Biological Journal of the Linnean Society*, in press.
- Griffiths A. D., Christian K. A. 1996. Diet and habitat use of frillneck lizards in a seasonal tropical environment. *Oecologia* 106:39–48.
- Griffiths A. D., McKay J. L. 2007. Cane toads reduce the abundance and site occupancy of freshwater goannas *Varanus mertensi*. *Wildlife Research* 34:609–615.
- Grigg G., Taylor A., McCallum H., Fletcher L. 2006. Monitoring the impact of cane toads (*Bufo marinus*) on Northern Territory frogs: a progress report. Pages 47–54 in *Science of Cane Toad Invasion and Control. Proceedings of the Invasive Animals CRC/CSIRO/Qld NRM&W Cane Toad Workshop, Brisbane, June 2006*, edited by K. L. Molloy and W. R. Henderson. Canberra: Invasive Animals Cooperative Research Centre.
- Hagman M., Shine R. 2006. Spawning-site selection by feral cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Austral Ecology* 31:551–558.
- Hagman M., Shine R. 2007. Effects of invasive cane toads on Australian mosquitoes: does the dark cloud have a silver lining? *Biological Invasions* 9:445–452.
- Hagman M., Shine R. 2008. Australian tadpoles do not avoid chemical cues from invasive cane toads (*Bufo marinus*). *Wildlife Research* 35:59–64.

- Hagman M., Shine R. 2009. Species specific communication systems in invasive toads *versus* Australian frogs. *Aquatic Conservation*: in press.
- Hagman M., Phillips B. L., Shine R. 2009a. Fatal attraction: adaptations to prey on native frogs imperil snakes after invasion of toxic toads. *Proceedings of the Royal Society B*: in press.
- Hagman M., Hayes R. A., Capon R. J., Shine R. 2009b. Alarm cues experienced by cane toad tadpoles affect post-metamorphic morphology and chemical defences. *Functional Ecology* 23:126-132.
- Hamley J., Georges A. 1985. The Australian snapping tortoise *Elseya latisternum*: a successful predator on the introduced cane toad? *Australian Zoologist* 21:607–610.
- Hayes R. A., Crossland M. R., Hagman M., Capon R. J., Shine R. 2009. Ontogenetic variation in the chemical defences of cane toads (*Bufo marinus*): toxin profiles and effects on predators. *Journal of Chemical Ecology* 35:391–399.
- Hearnden M. N. 1991. *Reproductive and larval ecology of Bufo marinus (Anura: Bufonidae)*. PhD thesis. Townsville: James Cook University of North Queensland.
- Hinckley A. D. 1963. Diet of the giant toad, *Bufo marinus* (L) in Fiji. *Herpetologica* 18:253–259.
- Holland D. C. 2004. *Interim report for study of impacts of cane toads, Bufo marinus, on two goanna species, Varanus panoptes and Varanus gouldii. Issues associated with the progressive entry into the Northern Territory of cane toads. Volume 1. Report No.1 October 2003.* Darwin: Legislative Assembly of the Northern Territory, Sessional Committee on Environment and Sustainable Development.
- Hutchings R. W. 1979. A native predator of the cane toad (*Bufo marinus*). *North Queensland Naturalist* 45:4–5.
- Ingle D., McKinley D. 1978. Effects of stimulus configuration on solicited prey catching by the marine toad *Bufo marinus*. *Animal Behaviour* 26:885–891.
- Ingram G. J., Covacevich J. 1990. *Tropidonophis mairii* vs. *Bufo marinus*. *Memoirs of the Queensland Museum* 29:396.
- Janzen D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687–708.

- Kearney M. R., Phillips B. L., Tracy C. R., Christian K. A., Betts G., Porter W. P. 2008. Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography* 31:423–434.
- King R. B., Ray J. M., Stanford K. M. 2006. Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. *Canadian Journal of Zoology* 84:108–115.
- Knowles R. P. 1964. The poisonous toad and the canine. *Veterinary Medicine* 59:38–42.
- Kraus F. 2009. *Alien reptiles and amphibians: a scientific compendium and analysis*. Springer, Netherlands.
- Lawler K. L., Hero J. M. 1997. Palatability of *Bufo marinus* tadpoles to a predatory fish decreases with development. *Wildlife Research* 24:327–334.
- Letnic M., Ward S. 2005. Observations of freshwater crocodiles (*Crocodylus johnstoni*) preying upon cane toads (*Bufo marinus*) in the Northern Territory. *Herpetofauna* 35:98–100.
- Letnic M., Webb J. K., Shine R. 2008. Invasive cane toads (*Bufo marinus*) cause mass mortality of freshwater crocodiles (*Crocodylus johnstoni*) in tropical Australia. *Biological Conservation* 141:1773–1782.
- Lever C. 2001. *The Cane Toad: The History and Ecology of a Successful Colonist*. Otley, West Yorkshire: Westbury Academic and Scientific Publishing.
- Licht L. E. 1968. Unpalatability and toxicity of toad eggs. *Herpetologica* 24:93–98.
- Llewelyn J., Phillips B. L., Shine R. 2009a. Sublethal costs associated with the consumption of toxic prey by snakes. *Austral Ecology* 34:179–184.
- Llewelyn, J., Schwarzkopf L., Alford R., Shine R. 2009b. Something different for dinner? Responses of a native Australian predator (the keelback snake) to an invasive prey species (the cane toad). *Biological Invasions*, in press.
- Llewelyn, J., Webb J.K.W., Schwarzkopf L., Alford R., Shine R. 2009c. Behavioural responses of carnivorous marsupials (*Planigale maculata*) to toxic invasive cane toads (*Bufo marinus*). *Austral Ecology*, in press.
- Losos J. B., Greene H. W. 1988. Ecological and evolutionary implications of diet in monitor lizards. *Biological Journal of the Linnean Society* 35:379–407.

- Mack R. N., Simberloff D., Lonsdale W. M., Evans H., Clout M., Bazzaz F. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Issues in Ecology* 5:1–20.
- Madsen T., Shine R. 1999. Rainfall and rats: climatically-driven dynamics of a tropical rodent population. *Australian Journal of Ecology* 24:80–89.
- Madsen T., Shine R. 2000. Rain, fish and snakes: climatically-driven population dynamics of Arafura filesnakes in tropical Australia. *Oecologia* 124:208–215.
- Madsen T., Shine R., Olsson M., Wittzell H. 1999. Restoration of an inbred adder population. *Nature* 402:34–35.
- Madsen T., Ujvari B., Shine R., Olsson M. 2006. Rain, rats and pythons: climate-driven population dynamics of predators and prey in tropical Australia. *Austral Ecology* 31:30–37.
- McIntosh A. R., Townsend C. R. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? *Oecologia* 108:174–181.
- McKilligan N. G. 1984. The food and feeding ecology of the cattle egret, *Ardeola ibis*, when nesting in south-east Queensland. *Australian Wildlife Research* 11:133–144.
- Meyer K., Linde H. 1971. Collection of toad venoms and chemistry of toad venom steroids, in: Bucherl, W., Buckley, E.E., (eds) *Venomous animals and their Venoms*. Academic Press, New York, pp. 521-556.
- Mirtschin, P. J., Davis R. 1982. *Dangerous Snakes of Australia*. Adelaide: Rigby.
- Mitchell D., Jones A., Hero J. M. 1995. Predation on the cane toad (*Bufo marinus*) by the black kite (*Milvus nigrans*). *Memoirs of the Queensland Museum* 38:512.
- Mokany A., Shine R. 2003a. Biological warfare in the garden pond: tadpoles suppress the growth of mosquito larvae. *Ecological Entomology* 28:102–108.
- Mokany A., Shine R. 2003b. Oviposition site selection by mosquitoes is affected by cues from conspecific larvae and anuran tadpoles. *Austral Ecology* 28:33–37.
- Murray B. R., Hose G. C. 2005. Life-history and ecological correlates of decline and extinction in the endemic Australian frog fauna. *Austral Ecology* 30:564–571.

- Nelson D. W. M. 2008. *Bufo for breakfast: how cane toads affect native predators and their prey*. Honours thesis. Sydney: School of Biological Sciences, University of Sydney.
- Nelson D., Crossland M. R., Shine R. 2010. Indirect ecological impacts of an invasive toad on predator-prey interactions among native species. **Biological Invasions**, in press.
- Nicolaus, L. K., Cassel, J. F., Carlson, R. B., Gustavoson, C. R. 1983a. Taste-aversion conditioning of crows to control predation on eggs. *Science* 220: 212-214.
- Nicolaus, L. K., Hoffman, T. E., Gustavoson, C. R. 1983b. Taste aversion conditioning in free ranging raccoons (*Procyon lotor*). *Northwest Science* 56: 165-169.
- Oakwood M. 2003a. *The effect of cane toads on a marsupial carnivore, the northern quoll, Dasyurus hallucatus*. Unpublished Progress Report February 2003. Darwin: Parks Australia North.
- Oakwood M. 2003b. *The effect of cane toads on a marsupial carnivore, the northern quoll, Dasyurus hallucatus*. Unpublished Progress Report August 2003. Darwin: Parks Australia North.
- O'Donnell S. 2009. *Alien versus predator: taste aversion learning as a way of enhancing survival in Northern Quolls (Dasyurus hallucatus)*. Honours thesis. Sydney: School of Biological Sciences, University of Sydney.
- O'Donnell, S., J. K. Webb, and R. Shine. 2009. Conditioned taste aversion enhances the survival of an endangered predator imperiled by a toxic invader. *Journal of Applied Ecology*, in press.
- Pace M. L., Cole J. J., Carpenter S. R., Kitchell J. F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14:483-488.
- Pearse B. W. 1980. *Effects of feeding on Bufo marinus by native and exotic fishes*. Report to AES. Brisbane: Griffith University.
- Pearson D. J., Greenlees M., Ward-Fear G., Shine R. 2009. Predicting the ecological impact of cane toads (*Bufo marinus*) on camaenid land snails in north-western Australia. *Wildlife Research*: in press.

- Pengilley R. 1981. *Observations on the cane toad (Bufo marinus) in the southern Gulf Country, Queensland*. Internal Report. Darwin: Conservation Commission of the Northern Territory.
- Phillips B., Fitzgerald M. 2004. Encounters between eastern brown snakes (*Pseudonaja textilis*) and cane toads (*Bufo marinus*) in northern New South Wales. *Herpetofauna* 34:23–25.
- Phillips B. L., Shine R. 2004. Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proceedings of the National Academy of Sciences of the United States of America* 101:17150–17155.
- Phillips B. L., Shine R. 2006a. Allometry and selection in a novel predator-prey system: Australian snakes and the invading cane toad. *Oikos* 112:122–130.
- Phillips B. L., Shine R. 2006b. Spatial and temporal variation in the morphology (and thus, predicted impact) of an invasive species in Australia. *Ecography* 29:205–212.
- Phillips B. L., Shine R. 2006c. An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia. *Proceedings of the Royal Society B* 273:1545–1550.
- Phillips B. L., Brown G. P., Shine R. 2003. Assessing the potential impact of cane toads *Bufo marinus* on Australian snakes. *Conservation Biology* 17:1738–1747.
- Phillips B., Brown G. P., Shine R. 2004. Assessing the potential for an evolutionary response to rapid environmental change: invasive toads and an Australian snake. *Evolutionary Ecology Research* 6:799–811.
- Phillips B. L., Kelehear C., Pizzatto L., Brown G. P., Barton D., Shine R. 2009a. Parasites and pathogens lag behind their host during periods of host range-advance. *Ecology*: in press.
- Phillips B. L., Greenlees M. J., Brown G. P., Shine R. 2009b. Predator behaviour and morphology mediates the impact of an invasive species: cane toads and death adders in Australia. *Animal Conservation*: in press.
- Pimentel D., Lach L., Zuniga R., Morrison D. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50:53–65.
- Pippet J. R. 1975. The marine toad, *Bufo marinus*, in Papua New Guinea. *Papua New Guinea Agricultural Journal* 26:23–30.

- Pizzatto L., Shine R. 2008. The behavioral ecology of cannibalism in cane toads (*Bufo marinus*). *Behavioral Ecology and Sociobiology* 63:123–133.
- Pizzatto L., Shine R. 2009. Native Australian frogs avoid the scent of invasive cane toads. *Austral Ecology* 34:77–82.
- Pizzatto L., Child T., Shine R. 2008. Why be diurnal? Shifts in activity time enable young cane toads to evade cannibalistic conspecifics. *Behavioral Ecology* 19:990–997.
- Pockley D. 1965. The free and the caged. *Blackwoods Magazine* 1965:439–466.
- Pramuk J. 2007. Phylogeny of South American *Bufo* (Anura: Bufonidae) inferred from combined evidence. *Zoological Journal of the Linnean Society* 146:407–452.
- Price-Rees SJ, Brown GP, Shine R. 2010. Are bluetongue lizards (*Tiliqua scincoides intermedia*, Scincidae) threatened by the invasion of toxic cane toads (*Bufo marinus*) through tropical Australia? *Wildlife Research*, in press.
- Rabor D. S. 1952. Preliminary notes on the giant toad *Bufo marinus* (Linn.) in the Philippine Islands. *Copeia* 1952:281–282.
- Rayward A. 1974. Giant toads: a threat to Australian wildlife. *Wildlife* 17:506–507.
- Reeves M. P. 2004. A retrospective report of 90 dogs with suspected cane toad (*Bufo marinus*) toxicity. *Australian Veterinary Journal* 82:608–611.
- Roberts B. K., Aronsohn M. G., Moses B. L., Burk R. L., Toll J., Weeren R. 2000. *Bufo marinus* intoxication in dogs: 94 cases (1997-1998). *Journal of the American Veterinary Medical Association* 216:1941–1944.
- Roemer G. W., Donlan C. J., Courchamp F. 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences of the United States of America* 99:791–796.
- Sakate M., Oliveira P. C. L. D. 2000. Toad envenoming in dogs: effects and treatment. *Journal of Venomous Animals and Toxins* 6:52–62.
- Sanson, A. 2010. No winners in death match. *Northern Territory News* Feb 15, 2010:8.
- Schultze-Westrum T. G. 1970. *Conservation in Papua and New Guinea*. Final Report on the 1970 World Wildlife Fund Mission.

- Schwarzkopf L., Alford R. A. 1996. Desiccation and shelter-site use in tropical amphibians: comparing toads with physical models. *Functional Ecology* 10:193–200.
- Seabrook W. A. 1991. Range expansion of the introduced cane toad *Bufo marinus* in New South Wales. *Australian Zoologist* 27:57–62.
- Seabrook W. A. 1993. *Habitat use of the cane toad Bufo marinus: implications for assessment of impact and control strategies*. PhD thesis. Sydney: University of Sydney.
- Seigel R. A. 1993. Summary: future research on snakes, or how to combat "lizard envy". Pages 395–402 in *Snakes: Ecology and Behavior*, edited by R. A. Seigel and J. T. Collins. New York: McGraw-Hill.
- Settle W. H., Wilson L. T. 1990. Invasion by the variegated leafhopper and biotic interactions: parasitism, competition, and apparent competition. *Ecology* 71:1461–1470.
- Shine R., Covacevich J. 1983. Ecology of highly venomous snakes of the Australian genus *Oxyuranus*. *Journal of Herpetology* 17:60–69.
- Shine R., Brown G. P., Phillips B. L., Webb J. K., Hagman M. 2006. The biology, impact and control of cane toads: an overview of the University of Sydney's research program. Pp. 18–32 in *Proceedings of the Cane Toad Workshop*, CRC for Invasive Animals, Brisbane June 2006.
- Shine R., Greenlees M., Crossland M. R., Nelson D. 2009. The myth of the toad-eating frog. *Frontiers in Ecology and the Environment*: in press.
- Smith J., Phillips B. 2006. Toxic tucker: the potential impact of cane toads on Australian reptiles. *Pacific Conservation Biology* 12:40–49.
- Stammer D. 1981. Some notes on the cane toad (*Bufo marinus*). *Australian Journal of Herpetology* 1:61.
- Sutherst R. W., Floyd R. B., Maywald G. F. 1995. The potential geographical distribution of the cane toad, *Bufo marinus* L. in Australia. *Conservation Biology* 9:294–299.
- Thomson D. M. 2006. Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *Oikos* 114:407–418.

- Townsend C. R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation* 78:13–22.
- Tyler M. J. 1975. *The cane toad Bufo marinus: an historical account and modern assessment*. The Vermin and Noxious Weeds Destruction Board of Victoria and the Agriculture Protection Board of Western Australia.
- Tyler M. J. 1987. Frog and cane toad skin secretions. Pages 329–339 in *Toxic Plants and Animals: A Guide for Australia*, edited by J. Covacevich, P. Davies and J. Pearn. Brisbane: Queensland Museum.
- Tyler M. J. 1994. *Australian Frogs: A Natural History*. Sydney: Reed Publishers.
- Tyler M. J., Cappo M. 1983. *Diet and feeding habits of frogs of the Magela Creek system*. Unpublished Open File Record 10. Canberra: Supervising Scientist for the Alligator Rivers Region.
- Ujvari B., Madsen T. 2009. Invasion of cane toads associates with a significant increase in mortality in a naïve Australian varanid lizard. *Herpetological Conservation*: in press.
- Ujvari B., Shine R., Madsen T. 2010. Detecting the impact of invasive species on native fauna: cane toads (*Bufo marinus*), frillneck lizards (*Chlamydosaurus kingii*), and the importance of spatial replication. **Austral Ecology**, in press.
- Urban M., Phillips B. L., Skelly D. K., Shine R. 2007. The cane toad's (*Bufo marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society B* 274:1413–1419.
- Urban M., Phillips B. L., Skelly D. K., Shine R. 2008. A toad more traveled: the heterogeneous invasion dynamics of cane toads in Australia. *American Naturalist* 171:E134–E148.
- Valero A., Garcia C. M., Magurran A. E. 2008. Heterospecific harassment of native endangered fishes by invasive guppies in Mexico. *Biology Letters* 4:149–152.
- van Beurden E. K. 1980a. *Report on the results of stage 3 of an ecological and physiological study of the Queensland cane toad, Bufo marinus*. Canberra: Report to ANPWS.

- van Beurden E. K. 1980b. Mosquitoes (*Mimomyia elegans* [Taylor]) feeding on the introduced cane toad *Bufo marinus* (Linnaeus): implications for control of a toad pest. *Australian Zoologist* 20:501–504.
- van Dam R., Walden D., Begg G. 2002. *A preliminary risk assessment of cane toads in Kakadu National Park*. Supervising Scientist Report 164. Darwin: Supervising Scientist.
- Ward-Fear G., Brown G. P., Greenlees M., Shine R. 2009a. Maladaptive traits in invasive species: in Australia, cane toads are more vulnerable to predatory ants than are native frogs. *Functional Ecology* 23:559–568.
- Ward-Fear, G., Brown G. P., Shine R. 2009b. Factors affecting the vulnerability of cane toads (*Bufo marinus*) to predation by ants. *Biological Journal of the Linnean Society*, in press.
- Ward-Fear, G., Brown G. P., Shine, R. 2009. Using a native predator (the meat ant, *Iridomyrmex reburrus*) to reduce the abundance of an invasive species (the cane toad, *Bufo marinus*) in tropical Australia. *Journal of Applied Ecology*, in press.
- Wassersug R. 1971. On the comparative palatability of some dry-season tadpoles from Costa Rica. *American Midland Naturalist* 86:101–109.
- Waterhouse D. F. 1974. The biological control of dung. *Scientific American* 230:101–109.
- Watson M., Woinarski J. 2003a. *A preliminary assessment of impacts of cane toads on terrestrial vertebrate fauna in Kakadu National Park*. Unpublished Report February 2003. Jabiru: Kakadu Research Advisory Committee.
- Watson M., Woinarski J. 2003b. *Vertebrate monitoring and re-sampling in Kakadu National Park, 2002*. Project RS10. Unpublished Report March 2003. Jabiru: Parks Australia.
- Webb J. K., Glanznig A. 2004. *Predation, competition and lethal toxic ingestion caused by cane toads (Bufo marinus)*. Key Threatening Process Nomination to Commonwealth Government from WWF.
- Webb J. K., Shine R., Christian K. A. 2005. Intraspecific niche partitioning in a native predator may influence its response to invasion by a toxic prey species. *Austral Ecology* 30:201–209.

- Webb J. K., Brown G. P., Child T., Greenlees M. J., Phillips B. L., Shine R. 2008. A native dasyurid predator (common planigale, *Planigale maculata*) rapidly learns to avoid toxic cane toads. *Austral Ecology* 33:821–829.
- Werren G. L. 1993. Size and diet of *Bufo marinus* in rainforest of north-eastern Queensland. *Memoirs of the Queensland Museum* 34:240.
- Western Australian Department of Environment and Conservation. 2009. *Draft Cane Toad Strategy for Western Australia 2009–2019*. Perth: Government of Western Australia.
- White A. 2008. Predation of frogs in northern Australia by feral pigs. *Herpetofauna* 38:35–38.
- Wilson D. 2005. Toads and native fish. *Australia New Guinea Fishes Association News* 25:8–9.
- Williamson I. 1999. Competition between the larvae of the introduced cane toad *Bufo marinus* (Anura: Bufonidae) and native anurans from the Darling Downs area of southern Queensland. *Australian Journal of Ecology* 24:636–643.
- Woinarski J. C. Z., Milne D. J., Wanganeen G. 2001. Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecology* 26:360–370.
- Woinarski J. C. Z., Armstrong A., Price O., McCartney J., Griffiths A. D., Fisher A. 2004. The terrestrial vertebrate fauna of Litchfield National Park, Northern Territory: monitoring over a 6-year period and response to fire history. *Wildlife Research* 31:587–596.
- Woinarski J. C. Z., Oakwood M., Winter J., Burnett S., Milne D., Foster P., Myles H., Holmes B. 2008. *Surviving the toads: patterns of persistence of the northern quoll Dasyurus hallucatus in Queensland*. Report to the Natural Heritage Trust Strategic Reserve Program, March 2008.
- Wonham M. J., O'Connor M., Harley C. D. G. 2005. Positive effects of a dominant invader on introduced and native mudflat species. *Marine Ecology Progress Series* 289:109–116.
- Wootton J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443–466.
- Zug G. R., Zug P. B. 1979. The marine toad, *Bufo marinus*: a natural history resumé of native populations. *Smithsonian Contributions to Zoology* 284:1–54.

Zug G. R., Lindgren E., Pippet J. R. 1975. Distribution and ecology of the marine toad, *Bufo marinus*, in Papua New Guinea. *Pacific Science* 29:31–50.

Zupanovic Z., Lopez G., Hyatt A. D., Green B., Batrtran G., Parkes H., Whittington R. J., Speare R. 1998. Giant toads *Bufo marinus* in Australia and Venezuela have antibodies against 'ranaviruses'. *Diseases of Aquatic Organisms* 32:1-8.