

Richard Shine

13 Reducing the Ecological Impact of Invasive Cane Toads

13.1 Introduction

Many invaders cause ecological devastation and huge economic costs, stimulating the expenditure of vast amounts of time and effort in attempts to control the invader. Those efforts sometimes succeed — for example, eradication of feral rodents from offshore islands has enabled native taxa to recover (Howald *et al.*, 2007). In most cases, however, invaders have continued to spread despite intensive efforts to control them. Part of the problem is the inherent difficulty of the challenge; regrettably, many efforts to control invasive species have been undertaken without any clear understanding of the invader's biology (Saunders *et al.*, 2010). Although it is politically attractive to combat an alien's arrival by killing as many of the foreigners as possible, many invasive species reproduce at rates so high that simply culling adults has no significant long-term impact on invader abundance.

The key to effective invader control is to understand the enemy. By analogy, military strategists confronted with an invading army would try to understand why that army was invading, what resources it relied upon, what impacts it was having, and what lines of communication were important in facilitating its onward march. Killing enemy soldiers might be part of the military response, but it would not be the only component. To conquer an invading army, we need to understand that army's ways of functioning. Military history abounds with examples whereby deciphering the communication code used by the enemy was key to eventual victory.

In this chapter I explore recent research on the invasion of cane toads (*Bufo [Rhinella] marina*) through Australia, and review our attempts to control the numbers and spread of the invader, and mitigate its ecological impact. Much of the work is ongoing, and most of it has yet to proceed to the stage of landscape-scale deployment. Nonetheless, we have developed several novel approaches that work well in laboratory trials and in small-scale field studies, and can claim the first successes in enabling native biota to persist despite the invader's presence. An ecological approach, based on comprehensive basic research into toad biology and impact, has generated new methods that have already achieved clear-cut positive results in a system where the prior expenditure of vast resources has achieved very little. Scientific efforts to mitigate the ecological impact of invasive cane toads thus provide a valuable case history of the application of ecological, evolutionary, and behavioral research to achieve conservation outcomes.

13.2 Background of the Study System

Cane toads are large (up to > 2 kg, but typically around 200 to 400 g as adults; see Figure 13.1A) bufonid anurans, native to an extensive area of South America, Central America, and Mexico (Lever, 2001). Reflecting their large body size, and a phylogenetically conservative tendency for bufonids to produce larger clutches of small eggs, the fecundity of cane toads is extraordinary. Clutch sizes in excess of 30,000 eggs have been reported (Lever, 2001). The eggs are laid in long strings in shallow ponds, fertilized externally by an amplexing male, and hatch within one to two days (depending on water temperature). The small black tadpoles often form schools in shallow water, and grow rapidly. They metamorphose into tiny (approx. 0.1 g, 10 mm long) toadlets after a brief larval phase (thermally-dependent, but typically 1 to 2 months). Toadlets that emerge during the long dry season of the wet-dry tropics are restricted to the margins of their natal pond until seasonal rains allow them to disperse; during this phase, a few of the earlier-transforming metamorphs may grow large enough to ingest their smaller relatives, and the larger toads become specialist cannibals (Pizzatto & Shine, 2008). Toadlets are diurnally active, thereby reducing vulnerability to their cannibalistic nocturnal larger brethren (Pizzatto *et al.*, 2008).



Fig. 13.1: Cane toads (*Rhinella marina*) are large, heavy-bodied bufonids (A) that can reach startlingly high abundances at the invasion front (B). Photographs by Matt Greenlees (A) and Ruchira Somaweera (B), with permission.

Cane toads feed on a diverse array of prey types, but especially on small insects such as ants and beetles. They exploit local opportunities, such as the congregation of insects attracted to artificial lights at night (Zug & Zug, 1979; González-Bernal *et al.*, 2011). Growth rates can be high, with sexual maturation at a few months of age in

tropical Australia, and probably around a year of age in cooler climates (Brown *et al.*, 2013a). Reproductive frequency of females in the wild is not well documented.

In the era before pesticides were developed, toads of various species were widely translocated in attempts to control agricultural insect pests (Turvey, 2013). As commercial sugar plantations were established across the tropics, cane toads were brought in to consume insects such as scarab beetles (Anonymous, 1934; Turvey, 2013). In this way, cane toads were brought from their native range in French Guinea to plantations in Puerto Rico, and thence to Hawaii, and thence to Australia (Turvey, 2013). In 1935, 101 toads collected in the Honolulu region were shipped to an agricultural experimental station in a sugar-growing region of northeastern Australia (Mareeba, Queensland), where they were maintained and bred in captivity. Thousands of their offspring were released in the cane fields.

The toads gradually expanded their range westwards across Australia into drier country, at around 10 to 15 km per year (Urban *et al.*, 2007). The rate of invasion accelerated as the toads spread through tropical Queensland, into and through the Northern Territory, and into Western Australia (Urban *et al.*, 2007). By the time the toad invasion front reached the city of Darwin, the invasion was moving at around 50 km per annum. Although human-assisted translocations continue to play a role in extending the toad's distribution in Australia (van Beurden, 1981; White & Shine, 2009), the acceleration of the tropical front is due to evolved shifts in toad behavior and morphology (Phillips *et al.*, 2006; 2010a). Radio-tracking shows that toads at the invasion front disperse almost ten times faster than do their conspecifics in long-colonized areas (Alford *et al.*, 2009; Lindström *et al.*, 2013). Even when raised under standardized conditions, the progeny of these toads inherit their parents' dispersal rates (Phillips *et al.*, 2010a).

The cane toad's march across tropical and subtropical Australia has had devastating impacts on native predators (such as lizards, snakes, crocodiles and carnivorous marsupials) that attempt to consume the newcomers (Shine, 2010). Like many bufonids, cane toads possess potent defensive chemicals (bufadienolides, bufotoxins) that can rapidly be fatal if ingested by a predator (Hayes *et al.*, 2009; Shine, 2010; Ujvari *et al.*, 2013). Minor genetic changes can increase the predator's physiological resistance to the toxins, and such modifications are common in the predator fauna of areas that contain native toads (Ujvari *et al.*, 2013). Because Australia contains no endemic bufonids, however, many Australian taxa are evolutionarily naïve to bufotoxins; and as a result, the invasion of cane toads has been accompanied by a wave of predator mortality (Shine, 2010). In several areas, researchers have documented >90% mortality of large varanid lizards within the first few months of toad invasion (Doody *et al.*, 2009; Brown *et al.*, 2013b). The same is true of freshwater crocodiles in some but not all populations (Letnic *et al.*, 2008; Somaweera *et al.*, 2013), and for large dasyurid marsupials (quolls) (O'Donnell *et al.*, 2010).

Although these cases of "death by toad" have aroused public outrage, and stimulated governments to fund attempts to control toads, recent research has provided a

more nuanced view of toad impact. First, many native predators (such as most birds) are capable of surviving the toad invasion, either because they are physiologically resistant to the toad's toxins (reflecting an evolutionary origin in parts of the world containing native bufonids) or because they rapidly learn not to eat the toxic toads. For example, a diverse array of fishes, frogs, lizards, crocodiles, and small marsupials all exhibit conditioned taste aversion. Initial consumption of a small toad results in non-lethal illness; thereafter, the predator deletes toads from its diet (O'Donnell *et al.*, 2010). Some individual predators die, but most survive and can coexist with toads thereafter (Shine, 2010). Taste aversion does not protect larger predator species because the toad invasion front consists entirely of large (and thus, highly mobile) toads; consuming one of these is fatal, giving the predator no opportunity to learn (because toxin content increases rapidly with increasing toad body size) (Phillips & Shine, 2006). High toad abundances at the invasion front (Fig. 13.1b) mean that most or all local predators soon encounter a large toad.

Cane toads may also affect Australian ecosystems by preying on native taxa (especially insects); by competing for food with other insectivores; and by modifying the behavior of other species. For example, some frogs reduce their activity levels when toads are present (Greenlees *et al.*, 2007), move away from toads (Mayer *et al.*, 2015), and change the structure of the male advertisement call in response to toad calls (Bleach *et al.*, 2014). Predators also modify their attack strategies as a result of conditioned taste aversion (Webb *et al.*, 2008) and may ignore palatable native prey that resembles the toxic invader (Nelson *et al.*, 2010). More important, however, are indirect ecological impacts of cane toads, mediated via changes in the abundance of apex predators. The virtual elimination of large varanid lizards due to lethal toxic ingestion of toads, for example, has powerful flow-on effects to the myriad taxa that were previously consumed by these giant reptiles (Brown *et al.*, 2013b). As a result, the invasion of cane toads is often followed — counter-intuitively — by increasing rather than decreasing abundance of many native species (Brown *et al.*, 2011). Such effects may be short-term, due to the eventual recovery of varanid populations. A goanna species whose populations crash dramatically when toads first arrive (*Varanus panoptes*, the floodplain monitor) is common in coastal Queensland, where toads have been present for almost 80 years. Lizards in this long-colonized area refuse to consume dead toads, but readily consume dead frogs (Llewelyn *et al.*, 2014). Thus, the primary ecological impacts of cane toads may be ephemeral, on a timescale of decades, and decrease as the native fauna evolves (or learns) toad-avoidance. Another significant impact is a positive one: native taxa capable of consuming toads without ill effect (notably, invertebrates such as ants and water-beetles) increase in number because of the enhanced food supply. Perhaps for that reason, high toad densities are achieved mostly in the years immediately following invasion; after that, numbers (and perhaps body sizes) fall appreciably (Freeland *et al.*, 1986; Phillips & Shine, 2005).

13.3 Classical Approaches to Toad Control

Widespread revulsion for cane toads among the general public, and an often-exaggerated notion of the breadth and duration of the toads' ecological impacts, have stimulated vigorous but largely ineffective attempts to curtail toad abundance. Collecting toads at night, with the aid of a flashlight, is a common activity for rural residents across the Australian tropics. In several regions, people have banded together to form “toad-busting” associations that undertake organized large-scale culls. The leaders of such groups often make media statements about the threats posed by toads, and the need for their groups to be suitably resourced to deal with that threat. As a result, millions of dollars of government as well as private funding, as well as many thousands of hours of volunteer effort, have been devoted to collecting adult toads and humanely euthanizing them.

The methods used by toad-busting groups (both volunteer and government-funded) have been straightforward. Most groups primarily focus on hand-collecting, but a few also use lighted traps that attract insects, and thus toads. Unfortunately, commercially available toad traps are very inefficient: they catch only a small proportion of the local toads, and inflict significant mortality on native species (R. Shine, unpubl. data). Current research at James Cook University is exploring ways to enhance trapping success by using more appropriate lighting (UV rather than visible spectrum) and including toad advertisement calls (L. Schwarzkopf, pers. comm.).

Despite collecting massive numbers of toads, the toad-busting groups have not conducted any research to evaluate the effectiveness of their activities. Available data are not encouraging. In the most detailed analysis, a major community-group toad-cull on the shores of Lake Argyle depressed toad abundances only briefly; with the next wet season, toad numbers soon surpassed those present prior to the culling operation (Somaweera & Shine, 2012). Mark-recapture studies, and observations during community toad-busts in north-eastern New South Wales, also show that volunteer collectors typically catch only a small proportion of the total toad population (M. Greenlees, pers. comm.).

The fundamental problem with direct culling of adult toads is the immense fecundity of this species. If a single pair of adults can produce 30,000 eggs in a clutch, even a few survivors of the control program can rapidly repopulate an area. Mathematical models show that it would be impossible to exterminate toads from an area, or even to seriously reduce their densities, without achieving unrealistically high monthly rates of capture (McCallum, 2006).

Sadly, the predictions from those models are borne out by the available data. The most clear-cut evidence for the ineffectiveness of current toad-culling operations is that the rate of toad invasion has continued unabated across the regions (near Darwin, NT and Kununurra, WA) that are home to the largest, best-funded, and most highly organized toad-busting groups (Peacock, 2007). In the course of routine collections around the city of Darwin over several years when toad-busts were frequently

carried out, my research team always encountered abundant toads even in sites that were “busted” on a regular basis (G. P. Brown, pers. comm.).

The largest expenditure of funds on toad control (more than 11 million Australian dollars) was given by the federal government to the CSIRO (Commonwealth Scientific and Industrial Research Organization) to search for biocontrol approaches. Those funds supported research both in Australia and in the toad’s native range in Venezuela. Potentially lethal viruses were found within South America, but also proved lethal to Australian frogs. The work then shifted towards an attempt to create a genetically-engineered virus that would kill toads at metamorphosis (Shanmugathan *et al.*, 2010). That program was eventually abandoned due to technical difficulties as well as the growing realization that such a virus, even if toad-specific, could wreak havoc on populations of bufonids in other parts of the world, where they are an important component of the native fauna.

In summary, despite vast effort and financial expenditure, attempts to control cane toads have managed only to reduce the densities of adult toads in selected areas for short periods of time. Control efforts have failed because they centered on a single aim (to reduce the number of toads in a local area) and a simple approach (killing as many toads as possible). Unfortunately, the methods developed in this respect (such as traps and hand-collecting) fail to account for the toads’ massive fecundity, which make simple removal of animals ineffective. More sophisticated biological control (including genetic-modification) methods can overcome these problems, but face immense technical hurdles as well as near-insuperable political and ethical obstacles to implementation. Is there an alternative approach that avoids these flaws? Recent research has identified several promising new directions, which I will explore below. Most of these new ideas arose from a broad-ranging research program (funded as basic, not applied, research by the Australian Research Council) that set out to understand the biology and impact of the invader before devising novel methods for toad control.

13.4 Manipulation of Habitat Suitability

In severely arid margins of the toad’s Australian range, these animals need to find a moist substrate (or standing water) to replenish their water balance every two or three nights during dry conditions. Thus, fencing off a farm dam in arid country can spell rapid death for any toads outside the fence (Florance *et al.*, 2011). However, the method is ineffective in wetter times of year, or in landscapes where alternative water sources are available (Florance *et al.*, 2011).

Eliminating the water source would have similar effects. A recent paper has suggested closing off water bodies as a way to curtail the toads’ further expansion into the arid Pilbara region of Western Australia (Tingley *et al.*, 2013). In this harsh landscape, stock watering-points (artificial dams and troughs) offer the only surface water for most of the year; thus, toads may be unable to move through such country without

access to those dams (Florance *et al.*, 2011). Tingley *et al.* (2013) identified a hyper-arid region where toad colonization would occur only through a narrow coastal corridor; shutting down the dams in that corridor might prevent cane toads from invading a large area of Western Australia. The feasibility of implementing that suggestion is still under discussion.

Other types of manipulations can create habitats that are avoided by toads. For example, removing domestic stock can enable dense regrowth of vegetation, unattractive to cane toads as foraging sites (Zug & Zug, 1979) or as calling sites for reproductive males (Hagman and Shine, 2006; Semeniuk *et al.*, 2007). Steep banks and deep water also discourage toad-breeding (Hagman & Shine, 2006; Semeniuk *et al.*, 2007). In some regions, local councils require residents who construct farm dams to surround them with dense vegetation to discourage toad breeding.

13.4.1 Manipulation of Biotic Interactions

The increasingly fast pace of the toad invasion has left behind some of their pathogens, including a lungworm (*Rhabdias pseudosphaerocephala*) that was brought to Australia from South America with the original toads (Dubey & Shine, 2008). The parasite is thus absent from the toad invasion front (Phillips *et al.*, 2010b). Infection with the lungworm can kill metamorph toads, and reduces growth rate in adult as well as juvenile toads (Kelehear *et al.*, 2009; 2011). Could we then translocate the parasite to the invasion front, shortening the pathogen-free interval? Unfortunately, further research revealed two flaws in this scheme (which has already been implemented unintentionally by community groups, who have spread the parasite to the invasion front through poor quarantine protocols: Kelehear *et al.*, 2012a). First, the parasite is readily transmitted to a native frog species (*Litoria splendida*), where it causes high mortality (Pizzatto & Shine, 2012). Second, low host densities at the toad invasion front reduce parasite transmission rates, so that the lungworms would be unlikely to flourish (Kelehear *et al.*, 2012b). To overcome the latter problem, we could provide additional hosts by experimentally infecting a “Typhoid Mary” species of native frog, *Litoria caerulea*, that can carry the parasite but is not harmed by it (Pizzatto & Shine, 2011, 2012).

Could we instead increase the abundance of native species that act as predators or competitors of cane toads? Contrary to oft-expressed opinions, many native Australian animals can consume cane toads without ill effect. For example, many birds and rodents are physiologically tolerant of the toads’ toxins, and often eat the invasive anurans (Beckmann & Shine, 2009; Shine, 2010). More importantly, many types of aquatic insects not only prey on cane toad larvae, but attack these small slow-swimming tadpoles more readily and effectively than they attack native anuran larvae (Cabrera-Guzmán *et al.*, 2012). By restoring pond habitats in the peri-urban areas where cane toads breed, we may be able to build up healthy populations of these miniature toad-enemies.

Native taxa can reduce toad recruitment by competition as well as by predation. The tadpoles of native frogs can outcompete cane toad tadpoles, in natural water bodies as well as in laboratory trials (Cabrera-Guzmán *et al.*, 2011), so that encouraging recolonization of native frogs in anthropogenically disturbed areas might substantially reduce toad tadpole survival (Cabrera-Guzmán *et al.*, 2011).

13.4.2 Manipulation of Toad Abundance

Previous attempts to control cane toads have focused almost entirely on culling adult animals – with no long-term effect, because of the high fecundity of the invader (above). We first need to eradicate recruitment by killing eggs or tadpoles; only then will a cull of adult toads have a long-term impact on toad abundance. This is a simple and obvious point, so why has almost all of the previous control effort been focused on the terrestrial stages of the toad's life-history? In terms of community activities, people simply are not aware of tadpoles in turbid water bodies; it is the large adult toads in their backyards that upset them, and that they want to remove. In contrast, the lack of scientific research on tadpole control is based on a key assumption: that strong density-dependence within the larval phase makes tadpole culling unproductive. Killing a few thousand tadpoles may just improve conditions for the survivors, and has no net effect on recruitment (Crossland *et al.*, 2009). If we accept the assumption of strong density-dependence in tadpole survival rates, mathematical models identify the adult phase as the best one to target for toad control (Lampo & DeLeo, 1998). The difficulty of precisely measuring the form of density-dependence is a problem, because this parameter strongly affects the output of models that predict population-level responses to given levels of mortality (Thresher & Bax, 2006).

Issues of density-dependence are irrelevant, however, if we are able to totally eradicate tadpoles from water bodies. Toads often select small shallow open ponds, close to human habitation, and breed in only a small proportion of ponds in an area (Williamson, 1999; Hagman & Shine, 2006); thus, the eggs and tadpoles are far more concentrated in space and time than are adult toads. As a result, an effective weapon against tadpoles would be relatively easy to implement. Studies by Michael Crossland and colleagues have revealed exciting opportunities in this respect, based upon exploiting intraspecific competitive mechanisms that facilitate targeted control. Like many invasive species, cane toads thrive in disturbed habitats where native fauna are already extirpated; thus, the toads compete most strongly against conspecifics. The mechanisms they have evolved to fulfill this function can be co-opted to provide novel and species-specific weapons for toad control. For example, cane toad tadpoles seek out and kill (consume) newly-laid eggs of their own species, thereby eliminating future competitors (Crossland & Shine, 2011).

They locate those clutches by detecting chemicals emitted by the eggs, specifically the bufagenin component of the toad's toxins (Crossland *et al.*, 2012). Funnel traps baited with those toxins (easily collected from the parotoid glands of adult cane toads) capture thousands of toad tadpoles with virtually no bycatch, and enable eradication of toad larvae from natural breeding ponds (Crossland *et al.*, 2012; Figure 13.2).



Fig. 13.2: Funnel traps baited with toad parotoid gland secretions attract thousands of toad tadpoles but repel the tadpoles of native frogs.

In current work, we are exploring an even more powerful weapon for toad control. Again reflecting the advantages of suppressing the viability of younger conspecifics, toad tadpoles produce chemicals that disrupt early development of eggs laid in their pond. Even a few hours' exposure to a low concentration of those chemicals generally induces 100% mortality (Crossland & Shine, 2012; Clarke *et al.*, 2015a,b). If we can identify the nature of that chemical, it has great promise as a simple, easily-deployable and highly species-specific method to prevent toad recruitment, and hence to achieve the key first step necessary to reduce toad abundance.

13.4.3 Manipulation of Toad Distribution and Population Structure

The high vagility, broad abiotic tolerances, powerful chemical defenses, and remarkable fecundity of cane toads mean that we will never eliminate them entirely from Australia. Given that we can achieve partial reductions in numbers by our new methods, should we aim for suppression of toads across their entire Australian range, or focus on specific areas where the toad's impact is highest (such as near the invasion front, and in regions that contain endangered fauna)? The latter tactic may have many benefits, by allowing persistence of predator populations in the toad-free sites, and by intensifying larval competition in the remaining areas where toads are allowed to breed unfettered by control efforts. If all of the toads in a local area breed in a single pond, either later clutches will be killed in the egg stage by existing tadpoles or (if several clutches are laid simultaneously) high levels of larval competition for food, followed by cannibalism in the metamorph stage, will result in toads largely controlling their own abundances.

Similarly, we may be able to manipulate the population structure of toads in ways that reduce recruitment. Habitat differences between adult males and females provide an opportunity for sex-biased capture. Male toads spend long periods beside water bodies calling to attract mates, whereas females move through the intervening habitat matrix acquiring food (Shine, 2010). Thus, culls conducted away from water may result in a preponderance of males among the survivors, and strong sexual conflict (Bowcock *et al.*, 2009) in a male-biased population may further reduce the survival rates of the remaining females (females that are amplexed by multiple males often drown during spawning attempts).

13.4.4 Manipulation of Toad Behavior

Evolutionary processes at work during the toads' Australian invasion have dramatically increased the rate at which the toad invasion is spreading through Australia and the invader's ability to cross barriers of unsuitable (e.g., dry) habitat, as well as the breadth of habitats into which toads will move (Shine *et al.*, 2011). Two evolutionary processes are at work. First, natural selection may favor genes for faster dispersal (reflecting trophic advantages to toads in the vanguard, where prey is plentiful and competition from conspecifics is low: Brown *et al.*, 2013a). Second, non-adaptive "spatial sorting" of dispersal-enhancing genes has also played a role (Shine *et al.*, 2011; Lindström *et al.*, 2013). Under spatial sorting, genes for more rapid dispersal accumulate at the invasion front simply because faster individuals can find their way to the invasion vanguard and, when they breed, they inevitably do so with other fast-dispersers. The end result is a sorting of genes; any gene that codes for low dispersal rates is left behind in the already-colonized range, and the invasion front accelerates because it is increasingly dominated by individuals with genes that enable

rapid dispersal, even if that behavior takes the individual into a habitat where it is unlikely to survive (Shine *et al.*, 2011).

Breeding experiments have shown that this dispersal acceleration is heritable (Phillips *et al.*, 2010a). Thus, we could reset the clock on this process by simply releasing progeny of toads from long-colonized areas in Queensland in advance of the invasion front. The newly-arriving fast-dispersers would encounter an established population of sedentary toads, interbreed with them, and dilute the spatially-sorted concentration of “fast-dispersal” genes. That simple intervention could achieve three aims: (1) slow down the toad invasion (perhaps back to around 10 km per annum, instead of > 50 km per annum as currently occurs); (2) curtail the toad’s ability to pass through barriers of unsuitable habitat, thus preventing further spread into isolated pockets of suitable conditions; and (3) restrict toads to the kinds of habitats they generally prefer, rather than moving out into a broader range of habitats where they will impact vulnerable native taxa. Additionally, it would enable native predators to learn toad-avoidance by encountering small (and thus, non-lethal) toads before the advent of the large toads at the invasion front (see below). Unfortunately, any proposal to release cane toads ahead of the invasion front attracts howls of outrage from community toad-busting groups, who advocate manual collection as the “solution” to the toad invasion.

13.4.5 Reduction of Predator Exposure to Lethally Large Toads

The major impact of cane toads on Australian native fauna occurs immediately after the toads arrive in a new area. Naïve predators encounter large adult toads, try to eat them, and are fatally poisoned. Smaller toads would have provided an opportunity for those predators to learn toad aversion, but that opportunity does not arise because the front is dominated by large toads. The lack of reproduction in invasion-vanguard toads may be a result of spatial sorting for dispersal-enhancing genes: a toad that foregoes reproduction, and devotes its time and energy to dispersal instead, may thereby enhance its ability to remain at the forefront of the invasion wave (Shine *et al.*, 2011; Brown *et al.*, 2013a).

The importance of the toad population structure (presence of juvenile toads, small enough to induce aversion learning without killing the predator) is highlighted by the lower and briefer impact of cane toads at the southern front, where invasion is slower because of suboptimal temperatures (Urban *et al.*, 2007). Here, toads breed soon after arriving in a new area and, as an apparent result, many predators learn to coexist with toads rather than dying (Jolly *et al.*, 2015). Studies on large varanid lizards show that vulnerable species adjust their foraging tactics to exclude toads from the menu; hence, species whose populations have been decimated as the toad wave has spread across the tropics are thriving once again in long-colonized areas of eastern Australia (Llewelyn *et al.*, 2014).

If the major impact of cane toads occurs only at the invasion front, and decreases as soon as toads begin breeding (providing aversion-inducing smaller toads), we could potentially maintain predator populations simply by protecting them from that initial onslaught. Large numbers of predators could be captured just prior to toad arrival, maintained in captivity for a year or two, then released at their sites of capture. Alternatively, the animals could be immediately re-released in an area that was invaded by toads two or three years previously, where toads have already begun to breed.

13.4.6 Increase in Predator Exposure to Non-lethal (Small) Toads

Another way to expose predators to small as well as large toads, and thus stimulate aversion learning, is to introduce small (juvenile) toads to newly-invaded areas and/or train individual predators (perhaps captive-bred, or recently captured in advance of the toad invasion front). Some proportion of predators will have the opportunity to learn taste aversion, facilitating population persistence. As in the tactic described above, the key insight is that toad impact depends upon predator behavior; predators are at risk only if they attempt to consume a toad. Thus, we can protect vulnerable predators by changing their behavior, even if we are unable to eradicate toads. We cannot possibly protect all of the predators in all areas, but even pockets of surviving (toad-averse) predators could provide nuclei for recolonization.

My proposal to release “teacher toads” for this purpose was opposed by community toad-busting groups, on the grounds that these additional toads would just add to the ecological impact of the invader rather than reduce it. However, the arguments were simplistic, without reference to the underlying rationale for the proposal. The idea of aversion-training captive-bred predators and then releasing them is less controversial, and has been adopted with great success in the case of a carnivorous marsupial, the northern quoll (*Dasyurus hallucatus*). Aversion-trained quolls survived after release, whereas their non-trained siblings did not (O’Donnell *et al.*, 2010). Capturing, aversion-training, and then releasing individuals also enhanced survival in another vulnerable predator, the northern bluetongue lizard (*Tiliqua scincoides intermedia*) (Price-Rees *et al.*, 2013). A larger-scale field test of the idea with goannas (*Varanus panoptes*) is currently underway.

13.5 The Way Forward: Integrated Pest Control

Cane toads are formidable invasion machines, and it is unlikely that any single method will ever eradicate them. Even with a combination of methods, landscape-scale extirpation is vanishingly unlikely. However, the new weapons developed out of recent ecological research on this high-profile invasive anuran provide great encourage-

ment. We have already demonstrated that we can eradicate toad breeding in natural spawning sites (Crossland *et al.*, 2012) and that taste-aversion training can enable vulnerable predator species to persist (O'Donnell *et al.*, 2010; Price-Rees *et al.*, 2013). Current studies are assessing other (potentially more powerful) pheromone-based methods, both to disrupt embryogenesis (Crossland & Shine, 2011) and to discourage oviposition, thus concentrating toad breeding (M. R. Crossland, pers. comm.). Community groups across the toad's range in tropical Australia have adopted our tadpole-trapping methods, and have reported excellent results. The prospects for cane toad control are far brighter than was the case a few years ago, when all of the effort was targeted at killing toads rather than understanding them.

The most promising scenario includes an integrated approach, where we use a combination of methods deployed by private (community-based) conservation groups as well as employees of government at all levels (local, state, federal). Local knowledge will be invaluable to identify toad breeding sites and to evaluate the applicability of the available techniques. Part of the effort will go into collecting adult toads (as is currently the main focus), but that will increasingly be accompanied by techniques such as habitat manipulation, and prevention of toad recruitment by either suppression or collection of the toad's aquatic life-history stages. Some of my other suggestions — notably, the idea of releasing juvenile toads at the invasion front — face political obstacles, but these obstacles are fading as the futility of current toad-control methods (centered on hand-collecting adult toads) becomes increasingly apparent.

It is still far too early to claim success in the battle against the invasive cane toad in Australia. The toads have flourished despite decades of intensive effort designed to curb their numbers. We now have an arsenal of new and more effective methods to mitigate toad impact as well as reduce toad abundance, but these have yet to be deployed on a landscape scale. If that new approach succeeds, it will provide a striking example of the benefits of allocating research effort to understanding an invader before trying to eradicate it.

13.6 Acknowledgements

I thank my research group, Team Bufo, for their hard work, their innovative thinking, and their encouragement; working with them has been inspirational for me. The work was funded by the Australian Research Council.

In a nutshell

- Native to South and Central America, the large and highly toxic cane toad (*Bufo* [*Rhinella*] *marina*) has been translocated to many countries in futile attempts to control insect pests.
- Brought to Northeastern Australia in 1935, the toad has now spread across much of that continent, with devastating impacts on anuran-eating predators (lizards, snakes, marsupials, crocodiles) that are fatally poisoned when they try to consume the toxic newcomer.
- Physically removing toads has failed to reduce their numbers, or to curtail the invader's spread.
- Recent research into toad biology has provided two new approaches. The first is to release juvenile (and thus, non-lethal) toads at the current invasion front, to train native predators to avoid toads as prey. Taste aversion training can blunt the toad's impact even if we cannot eradicate the toxic invader. If sourced from long-colonized areas, these toads might also slow down toad advance by diluting invasion-front genes that code for dispersal-enhancing traits.
- The second tactic involves exploiting aspects of toad biology: for example, toad tadpoles are attracted to the toxins in newly-laid eggs, which they follow to locate and destroy future competitors. Funnel-traps baited with toad toxins can eradicate toad tadpoles from natural water bodies. Toad tadpoles also produce chemicals that disrupt embryonic development of toad eggs, providing another avenue for control.
- Cane toads in Australia provide a clear example that you need to understand an invasive species if you want to control it.

13.7 Bibliography

- Alford, R. A., Brown, G. P., Schwarzkopf, L., *et al.* (2009). Comparisons through time and space suggest rapid evolution of dispersal behaviour in an invasive species. *Wildlife Research*, 36, 23-28.
- Anonymous (1934). Toads save sugar crop. *Nature*, 134, 877-887.
- Beckmann, C., Shine, R. (2009). Are Australia's birds at risk due to the invasive cane toad? *Conservation Biology*, 23, 1544-1549.
- Bleach, I., Beckmann, C., Brown, G. P., *et al.* (2014). Effects of an invasive species on refuge-site selection by native fauna: the impact of cane toads on native frogs in the Australian tropics. *Austral Ecology*, 39, 50-59.
- Bowcock, H., Brown, G. P., and Shine, R. (2009). Beastly bondage: the costs of amplexus in cane toads (*Bufo marinus*). *Copeia*, 2009, 29-36.
- Brown, G. P., Kelehear, C., and Shine, R. (2013a). The early toad gets the worm: cane toads at an invasion front benefit from higher prey availability. *Journal of Animal Ecology*, 82, 854-862.
- Brown, G. P., Phillips, B. L., and Shine, R. (2011). The ecological impact of invasive cane toads on tropical snakes: field data do not support predictions from laboratory studies. *Ecology*, 92, 422-431.

- Brown, G. P., Ujvari, B., Madsen, T., *et al.* (2013b). Invader impact clarifies the roles of top-down and bottom-up effects on tropical snake populations. *Functional Ecology*, 27, 351-361.
- Cabrera-Guzmán, E., Crossland, M. R., and Shine, R. (2011). Can we use the tadpoles of Australian frogs to reduce recruitment of invasive cane toads? *Journal of Applied Ecology*, 48, 462-470.
- Cabrera-Guzmán, E., Crossland, M. R., and Shine, R. (2012). Predation on the eggs and larvae of invasive cane toads (*Rhinella marina*) by native aquatic invertebrates in tropical Australia. *Biological Conservation*, 153, 1-9.
- Clarke, G., Crossland, M., Shilton, C., Shine, R. (2015a). Chemical suppression of embryonic cane toads (*Rhinella marina*) by larval conspecifics. *Journal of Applied Ecology*, in press. DOI: 10.1111/1365-2664.12528
- Clarke, G. S., Crossland, M. R., Shine, R. (2015b). Can we control the invasive cane toad using chemicals that have evolved under intraspecific competition? *Ecological Applications*, in press.
- Crossland, M. R., Alford, R. A., and 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.
- Crossland, M. R., and Shine, R. (2011). Cues for cannibalism: cane toad tadpoles use chemical signals to locate and consume conspecific eggs. *Oikos*, 120, 327-332.
- Crossland, M. R., and Shine, R. (2012). Embryonic exposure to conspecific chemicals suppresses cane toad growth and survival. *Biology Letters*, 8, 226-229.
- Crossland, M. R., Haramura, T., Salim, A. A., *et al.* (2012). Exploiting intraspecific competitive mechanisms to control invasive cane toads (*Rhinella marina*). *Proceedings of the Royal Society B*, 279, 3436-3442.
- Doody, J. S., Green, B., Rhind, D., *et al.* (2009). Population-level declines in Australian predators caused by an invasive species. *Animal Conservation*, 12, 46-53.
- Dubey, S., and 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.
- Florance, D., Webb, J. K., Dempster, T., *et al.* (2011). Excluding access to invasion hubs can contain the spread of an invasive vertebrate. *Proceedings of the Royal Society B*, 278, 2900-2908.
- Freeland, W. J., Delvinquier, B. L. J., and Bonnin, B. (1986). Decline of cane toad, *Bufo marinus*, populations: status of urban toads. *Australian Wildlife Research*, 13, 597-601.
- González-Bernal, E., Brown, G. P., Cabrera-Guzmán, E., *et al.* (2011). Foraging tactics of an ambush predator: the effects of substrate attributes on prey availability and predator feeding success. *Behavioral Ecology and Sociobiology*, 65, 1367-1375.
- Greenlees, M. J., Brown, G. P., Webb, J. K., *et al.* (2007). Do invasive cane toads (*Chaunus marinus*) compete with Australian frogs (*Cyclorana australis*)? *Austral Ecology*, 32, 900-907.
- Hagman, M., and Shine, R. (2006). Spawning-site selection by feral cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Austral Ecology*, 31, 551-558.
- Hayes, R. A., Crossland, M. R., Hagman, M., *et al.* (2009). Ontogenetic variation in the chemical defenses of cane toads (*Bufo marinus*): toxin profiles and effects on predators. *Journal of Chemical Ecology*, 35, 391-399.
- Howald, G., Donlan, C. J., Galván, J. P., *et al.* (2007). Invasive rodent eradication on islands. *Conservation Biology*, 21, 1258-1268.
- Jolly, C. J., Shine, R., Greenlees, M. J. (2015). The impact of invasive cane toads on native wildlife in southern Australia. *Ecology and Evolution*, 5, 3879-3894.
- Kelehear, C., Brown, G. P., and Shine, R. (2011). Influence of lung parasites on growth rates of free-ranging and captive adult cane toads. *Oecologia*, 165, 585-592.
- Kelehear, C., Brown, G. P., and Shine, R. (2012b). Rapid evolution of parasite life-history traits on an expanding range-edge. *Ecology Letters*, 15, 329-337.

- Kelehear, C., Cabrera-Guzmán, E., and Shine, R. (2012a). Inadvertent consequences of community-based efforts to control invasive species. *Conservation Letters*, 5, 360-365.
- Kelehear, C., Webb, J. K., and Shine, R. (2009). *Rhabdias pseudosphaerocephala* infection in *Bufo marinus*: lung nematodes reduce viability of metamorph cane toads. *Parasitology*, 136, 919-927.
- Lampo, M., and De Leo, G. A. (1998). The invasion ecology of the toad *Bufo marinus*: from South America to Australia. *Ecological Applications*, 8, 388-396.
- Letnic, M., Webb, J. K., and 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.
- Lindström, T., Brown, G. P., Sisson, S. A., *et al.* (2013). Rapid shifts in dispersal behavior on an expanding range edge. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 13452-13456.
- Llewelyn, J., Schwarzkopf, L., Phillips, B. L., *et al.* (2014). After the crash: how do predators adjust following the invasion of a novel toxic prey type? *Austral Ecology*, 39, 190-197.
- Mayer, M., Brown, G. P., Zimmerman, B., Greenlees, M. J., Shine, R. (2015). Habitat use of the introduced cane toad (*Rhinella marina*) and native frog species in tropical Australia. *Journal of Tropical Ecology*, 31, 531-540. DOI: 10.1017/S0266467415000474
- McCallum, H. (2006). Modelling potential control strategies for cane toads. In K. L. Molloy and W. R. Henderson (Eds.), *Science of Cane Toad Invasion and Control*. Proceedings of the Invasive Animals CRC/CSIRO/QLD NRM&W Cane Toad Workshop, Brisbane, June 2006 (pp. 123-133). Canberra, ACT: Invasive Animals Cooperative Research Centre.
- Nelson, D., Crossland, M. R., and Shine, R. (2010). Indirect ecological impacts of an invasive toad on predator-prey interactions among native species. *Biological Invasions*, 12, 3363-3369.
- O'Donnell, S., Webb, J. K., and Shine, R. (2010). Conditioned taste aversion enhances the survival of an endangered predator imperiled by a toxic invader. *Journal of Applied Ecology*, 47, 558-565.
- Peacock, T. (2007). *Community On-Ground Cane Toad Control in the Kimberley*. Review for Western Australia Department of Environment and Conservation. Canberra, ACT: Invasive Animals Cooperative Research Centre.
- Phillips, B. L., and Shine, R. (2006). Allometry and selection in a novel predator-prey system: Australian snakes and the invading cane toad. *Oikos*, 112, 122-130.
- Phillips, B. L., Brown, G. P., and Shine, R. (2010a). Evolutionarily accelerated invasions: the rate of dispersal evolves upwards during the range advance of cane toads. *Journal of Evolutionary Biology*, 23, 2595-2601.
- Phillips, B. L., Brown, G. P., Webb, J., *et al.* (2006). Invasion and the evolution of speed in toads. *Nature*, 439, 803.
- Phillips, B. L., Kelehear, C., Pizzatto, L., *et al.* (2010b). Parasites and pathogens lag behind their host during periods of host range-advance. *Ecology*, 91, 872-881.
- Phillips, B., and Shine, R. (2005). The morphology, and hence impact, of an invasive species (the cane toad, *Bufo marinus*) changes with time since colonization. *Animal Conservation*, 8, 407-413.
- Pizzatto, L., and Shine, R. (2008). The behavioral ecology of cannibalism in cane toads (*Bufo marinus*). *Behavioral Ecology and Sociobiology*, 63, 123-133.
- Pizzatto, L., and Shine, R. (2011). The effects of experimentally infecting Australian tree frogs with lungworms from invasive cane toads. *International Journal for Parasitology*, 41, 943-949.
- Pizzatto, L., and Shine, R. (2012). Typhoid Mary in the frogpond: can we use native frogs to disseminate a lungworm biocontrol for invasive cane toads? *Animal Conservation*, 15, 545-552.
- Pizzatto, L., Child, T., and Shine, R. (2008). Why be diurnal? Shifts in activity time enable young cane toads to evade cannibalistic conspecifics. *Behavioral Ecology*, 19, 990-997.

- Price-Rees, S. J., Webb, J. K., and Shine, R. (2013). Reducing the impact of a toxic invader by inducing taste-aversion in an imperilled native reptile predator. *Animal Conservation*, 16, 386-394.
- Saunders, G., Cooke, B., McColl, K., *et al.* (2010). Modern approaches for the biological control of vertebrate pests: an update on Australian research. *Biological Control*, 52, 288-295.
- Semeniuk, M., Lemckert, F., and Shine, R. (2007). Breeding-site selection by cane toads (*Bufo marinus*) and native frogs in northern New South Wales. *Wildlife Research*, 34, 59-66.
- Shanmuganathan, T., Pallister, J., Doody, S., *et al.* (2010). Biological control of the cane toad in Australia: a review. *Animal Conservation*, 13 (Suppl. 1), 16-23.
- Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Quarterly Review of Biology*, 85, 253-291.
- Shine, R., Brown, G. P., and Phillips, B. L. (2011). An evolutionary process that assembles phenotypes through space rather than time. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 5708-5711.
- Somaweera, R., and Shine, R. (2012). The (non) impact of invasive cane toads on freshwater crocodiles at Lake Argyle in tropical Australia. *Animal Conservation*, 15, 152-163.
- Somaweera, R., Shine, R., Webb, J., *et al.* (2013). Why does vulnerability to toxic invasive cane toads vary among populations of Australian freshwater crocodiles? *Animal Conservation*, 16, 86-96.
- Thresher, R. E., and Bax, N. (2006). Comparative analysis of genetic options for controlling invasive populations of the cane toad *Bufo marinus*. In K. L. Molloy and W. R. Henderson (Eds.), *Science of Cane Toad Invasion and Control. Proceedings of the Invasive Animals CRC/CSIRO/QLD NRMandW Cane Toad Workshop, Brisbane, June 2006* (pp. 117-122). Canberra, ACT: Invasive Animals Cooperative Research Centre.
- Tingley, R., Phillips, B. L., Letnic, M., *et al.* (2013). Identifying optimal barriers to halt the invasion of cane toads *Rhinella marina* in northern Australia. *Journal of Applied Ecology*, 50, 129-137.
- Turvey, N. (2013). *Cane Toads: A Tale of Sugar, Politics and Flawed Science*. Sydney: University of Sydney Press.
- Ujvari, B., Mun, H., Conigrave, A. D., *et al.* (2013). Isolation breeds naivety: island living robs Australian varanid lizards of toad-toxin immunity via four-base-pair mutation. *Evolution*, 67, 289-294.
- Urban, M., Phillips, B. L., Skelly, D. K., *et al.* (2007). The cane toad's (*Chaunus marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society B*, 274, 1413-1419.
- van Beurden, E. K. (1981). Bioclimatic limits to the spread of *Bufo marinus* in Australia: a baseline. *Proceedings of the Ecological Society of Australia*, 11, 143-149.
- Webb, J. K., Brown, G. P., Child, T., *et al.* (2008). A native dasyurid predator (common planigale, *Planigale maculata*) rapidly learns to avoid toxic cane toads. *Austral Ecology*, 33, 821-829.
- White, A. W., and Shine, R. (2009). The extra-limital spread of an invasive species via "stowaway" dispersal: toad to nowhere? *Animal Conservation*, 12, 38-45.
- 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.
- Zug, G. R., and Zug, P. B. (1979). The marine toad, *Bufo marinus*: a natural history resumé of native populations. *Smithsonian Contributions to Zoology*, 284, 1-54.