

# The (non) impact of invasive cane toads on freshwater crocodiles at Lake Argyle in tropical Australia

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## Keywords

alien species; *Bufo marinus*; ecological impact; invasive species; spatial heterogeneity.

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## Abstract

The most substantial (and to date, unexplained) heterogeneity in the impact of toxic cane toads (*Rhinella marina*) on the native fauna of tropical Australia involves freshwater crocodiles (*Crocodylus johnstoni*); some populations have experienced catastrophic mortality whereas others have been unaffected. A trend for higher impact in more arid areas suggests that Western Australian (Kimberley region) crocodile populations may be at high risk. We monitored crocodile densities and body sizes, and the spread of cane toads, at a large water body (Lake Argyle) in the eastern Kimberley. Toads arrived on the lakeshore in early 2009, and spread to cover > 300 km of lakeshore, and colonize all of the larger islands within a 24-month period. Physical removal of > 10 000 toads by a community group depressed toad abundances, but only briefly. Spool-tracking showed that toads moved extensively along the lakeshore (up to 90 m per night), often into floating vegetation in the lake. Crocodiles thus encountered toads (3–15% of crocodiles were < 2 m from a toad when sighted), and we recorded 36 cases of toads being seized by crocodiles. Nonetheless, crocodile mortality was rare, and crocodile numbers did not decrease through time, nor differ between toad-infested versus toad-free areas of the lake. Although ingestion of a single adult toad may be fatal to a freshwater crocodile, and the Lake Argyle crocodiles encounter and consume these toxic anurans, the population-level impact of toad invasion has been trivial. Hence, the Lake Argyle crocodile population may not warrant immediate active management to reduce the impact of cane toads.

## Introduction

Many species introductions into new geographic areas have had negative effects upon native biodiversity (e.g. Mack *et al.*, 2000; McGeoch *et al.*, 2010; Powell, Chase & Knight, 2011); however, a high proportion of all introduced species fail to become established, and even the alien taxa that succeed sometimes have little effect, or even a beneficial effect, on populations of native species (King, Ray & Stanford, 2006; Schlossberg & King, 2010). Interactions between invasive species and natives, and thus the impacts of invaders on native species, are complex and often spatially and temporally heterogeneous. In some cases, the same native species may be negatively affected by an invader in some parts of its range but not others (e.g. Melbourne *et al.*, 2007; Letnic, Webb & Shine, 2008). That heterogeneity makes it difficult to frame generalizations about invader impact, and means that we need studies at a wide range of locations before we can sensibly evaluate the overall impact of a biological invasion on a particular native taxon (Ujvari, Shine & Madsen, 2011).

The intensity of the impact of an invader may depend upon many factors, including traits of the native taxon, of the invader, and of the environment in which the interaction

occurs (Letnic *et al.*, 2008; Riley, Dybdahl & Hall, 2008; Brown, Phillips & Shine, 2011). One intensively studied invasion involves the cane toad *Rhinella marina* in tropical Australia (see review by Shine, 2010). Introduced into north-eastern Queensland in 1935, this highly toxic anuran native to South and Central America has spread across more than 1 million km<sup>2</sup> of tropical and subtropical Australia (Lever, 2001). Direct poisoning of large predators is the most significant mechanism by which cane toads impact the Australian native fauna (Shine, 2010), and it may be the only invasive amphibian species worldwide that affects native species through this mechanism (Global Invasive Species Database, 2005). Presumably because Australia lacks endemic bufonids, many native predators have little physiological tolerance of the bufadienolide chemical defences used by toads (e.g. Lever, 2001; Phillips & Shine, 2006), and often die as a result of consuming toads. The native predators at risk from direct poisoning by toads comprise a phylogenetically disparate assemblage of carnivores, including lizards (e.g. Doody *et al.*, 2009; Price-Rees, Brown & Shine, 2010), snakes (e.g. Phillips, Brown & Shine, 2010a), marsupials (Woinarski *et al.*, 2008; O'Donnell, 2009) and freshwater crocodiles (Letnic *et al.*, 2008).

Some native taxa appear to be affected by cane toad invasion to a consistent degree both spatially and temporally. For example, large varanid lizards and marsupial quolls have declined dramatically across the cane toads' entire Australian range (van Dam, Walden & Begg, 2002; Doody *et al.*, 2009; How, Spencer & Schmitt, 2009; Ujvari & Madsen, 2009; O'Donnell, Webb & Shine, 2010) whereas birds and anurans have been largely unaffected (Greenlees *et al.*, 2007; Beckmann & Shine, 2009; Greenlees, Phillips & Shine, 2010). In affected species, population declines occur immediately after the toads invade [e.g. yellow-spotted monitor (*Varanus panoptes* – Doody *et al.*, 2006), bluetongue lizard (*Tiliqua scincoides intermedia* – Price-Rees *et al.*, 2010) and death adder (*Acanthophis praelongus* – Phillips *et al.*, 2010b)].

The most substantial (and to date, unexplained) heterogeneity in toad impact involves freshwater crocodiles (*Crocodylus johnstoni*) (Letnic *et al.*, 2008; Shine, 2010). Toad invasion has caused major population declines of these crocodiles in at least two sites (Victoria River: Letnic *et al.*, 2008 and Boodjamulla National Park: White, 2003) whereas other populations have been largely unaffected by the arrival of the toxic anurans (Roper and MacArthur Rivers: Catling *et al.*, 1999; Daly River Catchment: Freeland, 2004; Doody *et al.*, 2009; Adelaide River floodplain; R. Shine, pers. obs.). Letnic *et al.* (2008) suggested that differing levels of landscape aridity may explain this heterogeneity, with impacts highest in dry landscapes that keep 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.

This hypothesis predicts increasingly severe impacts of cane toad invasion on freshwater crocodiles as the toads move even further west into the east Kimberley region of northern Western Australia. This hot and highly arid region is characterized by a mean maximum temperature of 35°C, with 183.4 days a year exceeding temperatures > 35°C, and a mean annual rainfall of 839.1 mm (Kununurra Aero, 25-year average data, 2011). Freshwater crocodiles are abundant in this region, and thus may be severely impacted by the toads' current spread (Freeland, 1990; Letnic *et al.*, 2008; Webb & Manolis, 2010).

To evaluate the severity of this threat, we monitored freshwater crocodile populations and the toad invasion process at Lake Argyle in the East Kimberley region. We conducted field surveys to document concurrent patterns of population change in cane toads and crocodiles, and to compare crocodile abundance and population structure in sites yet to be invaded versus nearby sites recently invaded by cane toads.

## Methods

### Study species

Freshwater crocodiles (*C. johnstoni*) are widespread across tropical Australia (Cogger, 2000). Adult males attain lengths of up to 3 m, larger than adult females (to 2 m:

Webb & Manolis, 1998). These riparian predators have generalized diets, with an ontogenetic shift from invertebrates to vertebrates with increasing body size: smaller crocodiles [< 60 cm snout-vent length (SVL)] mainly ingest insects, spiders, crustaceans and anurans, but larger crocodiles take increasing proportions of fish (and occasional reptiles, birds and small mammals: Webb, Manolis & Buckworth, 1982; Tucker *et al.*, 1996). Anurans are a common component of the diet of all size classes of crocodiles (Webb *et al.*, 1982; Somaweera *et al.*, 2011a). The low physiological tolerance of this species to cane toad toxins means that an adult crocodile is likely to die if it ingests a single large cane toad (Freeland, 1990; Smith & Phillips, 2006), whereas allometries of toad toxin content mean that a hatchling *C. johnstoni* may be unable to ingest a cane toad large enough to kill it (Somaweera *et al.*, 2011a).

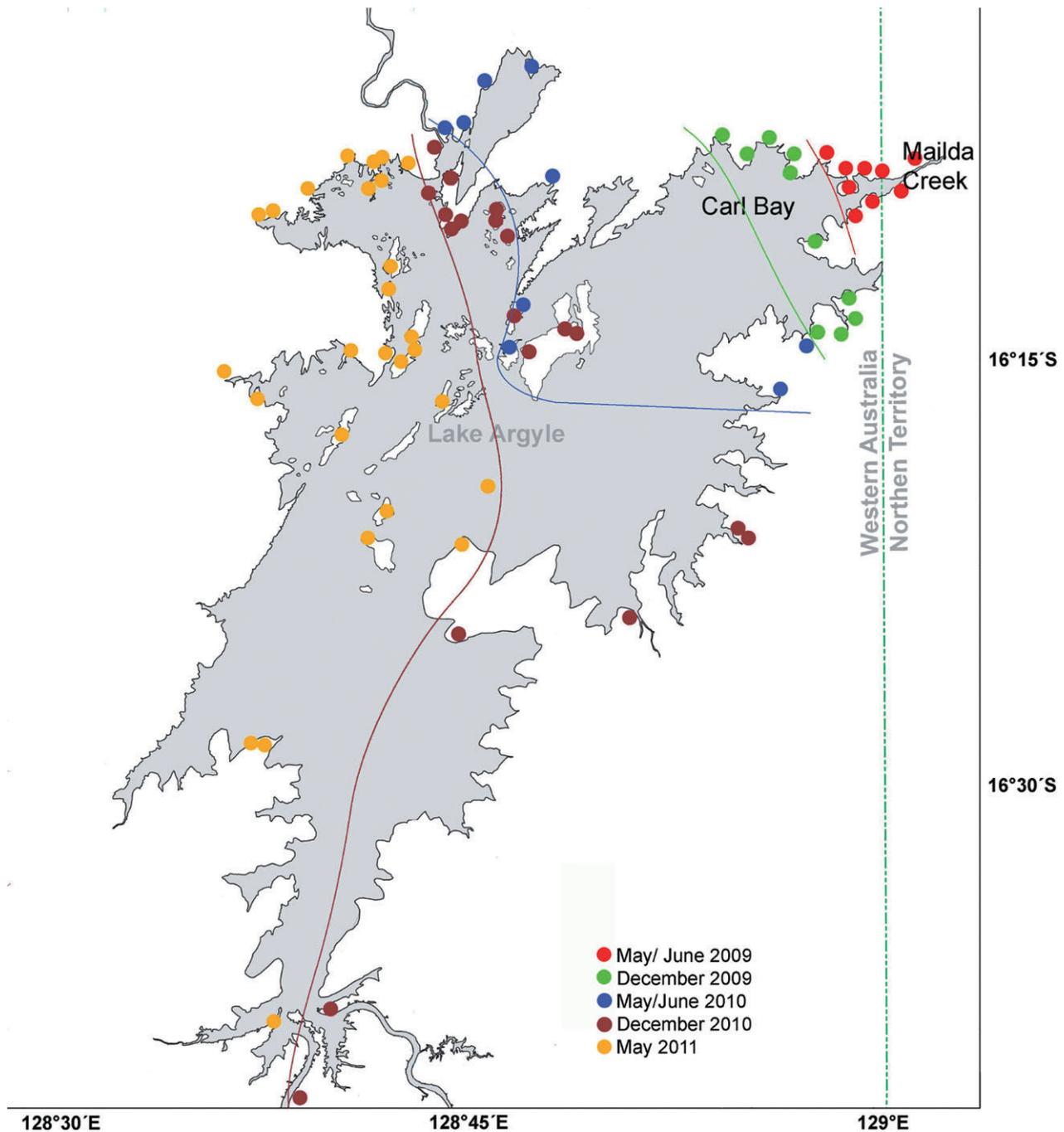
### Study site

Lake Argyle is a large man-made water body (surface area > 880 km<sup>2</sup>), constructed by damming the Ord River in 1972. Four rivers and many small creeks flow into the lake. Currently a total of 141 453 ha of the Ord River Floodplain and another 117 495 ha of Lakes Argyle and Kununurra are declared as Ramsar wetland sites of international importance (Kimberley TAFE & SWEK, 2008). As in other parts of monsoonal northern Australia (Webb, 1991) the lake experiences three main seasons, the wet season from November/December to April; the early dry season May to July/August and the build-up or the late dry season from September to December. Lake Argyle contains one of the largest populations of Australian freshwater crocodiles (*C. johnstoni*), with a resident non-hatchling population of > 30 000 animals (G. Webb Pty Ltd, 1989; WMI Pty Ltd, 2010).

### Crocodile surveys

From 2008 to 2010, we surveyed for freshwater crocodiles along three 3-km sections on each of the two banks (a total of six 3 km sites) of Carl Bay in Lake Argyle (16°09'S and 128°58'E). The 23.3-km long Matilda Creek flows into Carl Bay in the northeast corner of Lake Argyle (Fig. 1) and cane toads were first reported in the Western Australian side of Matilda Creek in March 2009 (R. Somaweera, pers. obs.). Toads colonized the sites in sequence (North 1 and South 1 first, North 3 and South 3 last); were reported from all six sites within 6 months of invading and were restricted to this section of the lake for the first several months after their arrival at Lake Argyle. Our surveys were conducted in November (2008, 2009 and 2010), April (2009, 2010) and August (2009, 2010). These dates coincide with the build-up (November), wet season (April) and dry season (August) in tropical northern Australia (Webb, 1991; Brown & Shine, 2006).

Shallow water and floating vegetation made it difficult to survey the eastern side of the lake from a boat. Thus we used a 660-cc all-terrain vehicle (ATV) to drive along the banks at



**Figure 1** Spread of cane toads along the shoreline of Lake Argyle. Toads were first seen in Matilda Creek flowing to Carl Bay in March 2009.

night, to scan the water’s edge and banks using a 100-W handheld halogen spotlight. The surveys were standardized with respect to driver, spotter, equipment, speed (c. 15 km h<sup>-1</sup>) and time (18:00–22:00 h). The ATV was driven 5–10 m from the water’s edge and the total distance within a site varied with the water level. The two banks were surveyed on consecutive days in random order. For each crocodile observed we recorded total length (estimated to the nearest 0.3 m) and location (bank, shallow water on edge,

weed mat, deepwater). In April and August 2010, we counted the number of cane toads observed within 2 m of each crocodile. Air and water temperatures were recorded at the start and end of the survey, and averaged. Data on lake water level were obtained from the Kununurra Water Corporation.

During each survey month we spent the day after the spotlight survey looking for dead crocodiles from 07:00 to 16:00 h from ATVs and boats, and also from an airboat in

August 2010. Any dead crocodiles were measured, and their stomach contents examined to determine whether or not they had eaten cane toads. We used older data sets from spotlight surveys (G. Webb Pty Ltd, 1989; WMI Pty Ltd 2005, 2009) and helicopter surveys (WMI Pty Ltd, 1992–2010) to explore overall changes in crocodile population structure at Lake Argyle.

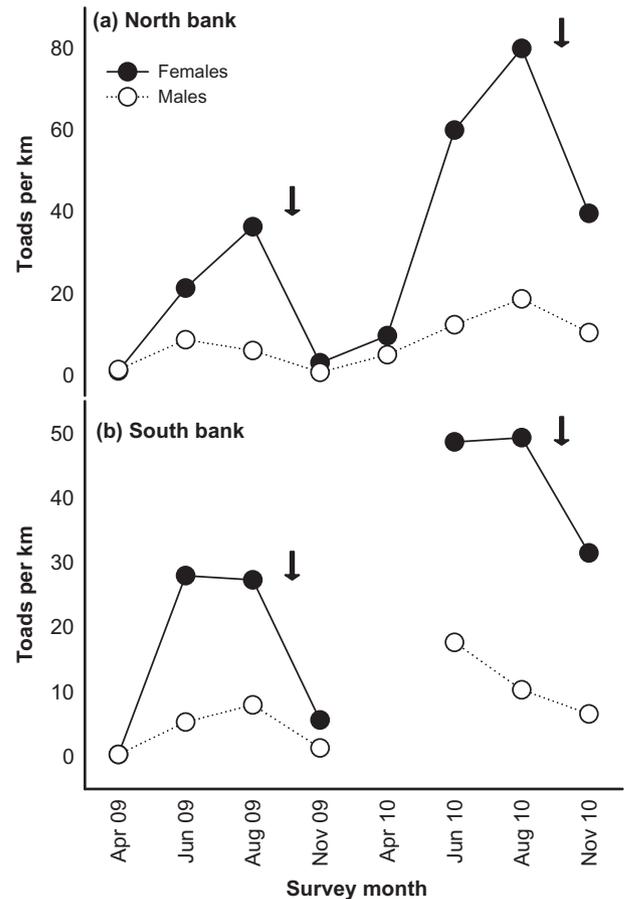
### Cane toad surveys

We conducted four surveys each during 2009 and 2010 to estimate cane toad numbers in the same study sites as mentioned earlier. The survey technique was the same as used for crocodiles. Each toad was categorized as a male, a female or a juvenile. The northern (78 km) and north-eastern (63 km) banks of Lake Argyle were also surveyed from a boat four times (in June and December in both 2009 and 2010) to map the spread of toads. At 200-m intervals, three observers in the boat scanned the banks and the water's edge for toads. Smaller creeks and puddles were checked on foot. Air temperature was recorded at the beginning of each survey. We included other occurrence data in our maps based on our encounters with toads during other work (until May 2011), and reliable reports from local residents and the community group Kimberley Toad Busters (KTB). During September 2009 and 2010, the community group Stop the Toad Foundation (STTF) conducted 'toad musters' in the area including at our sites, whereby volunteers manually collected and removed toads. We used these collections to study the population structure of toads.

To obtain data on short-term movements and microhabitat use of toads (during wet and dry seasons), we attached spool-and-line tracking devices (Wilson, 1994; designed following the methods of Tozetti & Toledo (2005) but with cotton gauze waistbands instead of elastic bands) to 80 toads (SVL > 65 mm) in April and August 2010. The mass of the device (8 g) was less than the recommended maximum of 10% of body mass (Richards, Sinsch & Alford, 1994). The elastic nature of the cotton gauze allowed the whole package to slip from the toad if it became entangled. Toads with spools attached were released at their capture sites (along the lakeshore) at 18:00 h and we followed the trail of thread the following day (from 08:00 to 11:00 h). Distances moved by the toads were measured, and dispersal rates were calculated by dividing the distance travelled by the time between observations.

### Statistical analysis

Data were analysed using the statistical software JMP 5.01 (SAS Institute, Cary, NC, USA). We used one-way analysis of variance (ANOVAs) to analyse changes of toad densities over time and across sites. Two-way *t*-tests and linear regressions were conducted to evaluate the effects of toad sex and size on movements during each season. Encounter rates between crocodiles and cane toads were calculated as the number of crocodiles within 2 m of a toad divided by the number of crocodiles sighted at each site. Prior to analysis,



**Figure 2** Changes in numbers of invasive cane toads along the two banks of Matilda Creek at Carl Bay of Lake Argyle. Cane toad removal campaigns were conducted by a community group ('Stop the Toad Foundation') in September 2009 and 2010 (shown by arrows). We did not survey the south bank in April 2010.

data on crocodile numbers during surveys were ln-transformed, after adding a small arbitrary value (0.05), to maintain variance homogeneity. The ln-transformed data were compared using *t*-tests or ANOVA tests followed by Fisher's protected least significant difference (PLSD) *post hoc* tests to determine the location of any differences in crocodile densities before versus after the arrival of toads, and the changes in crocodile population structure (relative numbers of different size classes) with time since toad arrival.

## Results

### Cane toad abundance

Cane toads were first observed in our Lake Argyle study site in March 2009. The number of adult toads increased significantly with time ( $F_{6,75} = 5.58$ ,  $P < 0.0001$ ; Fig. 2) at a similar rate in the two banks (survey\*bank:  $F_{6,75} = 0.35$ ,  $P = 0.9$ ). Most of the adult toads were females (80.5%) and breeding was first observed at Carl Bay in June 2009. Over 20 days in

September 2009, community groups removed 1143 toads (73.1% of them adult females; mean snout-vent length  $127.1 \pm 17.7$  mm; mean mass  $243.8 \pm 101.8$  g) from the Matilda Creek/Carl Bay site (STTF, 2009) while 4153 (61.3% adult females) were removed from the same site in 2010 (STTF, 2010). A further 6036 animals were removed from other shores of Lake Argyle in 2010 (STTF, 2010). Toad numbers were reduced significantly by these 'toad musters' in September 2009 and 2010 (August vs. November:  $F_{1,70} = 15.18$ ,  $P = 0.0002$ ), but increased in the four subsequent surveys prior to the next muster ( $F_{3,59} = 5.88$ ,  $P = 0.0014$ ).

### Cane toad spread

Along the banks of Lake Argyle, toads spread an average of 6.9 km per month towards the west and 3.6 km per month towards the south during the first year of invasion. Our estimate for the south bank may be too low, because of lower sampling effort. Most toads were found in the shallow, muddy banks of tributaries flowing into the lake and in vegetated bays rather than along the rocky shoreline of the lake. By May 2011, toads had spread all around the lake and were recorded in 21 of the 27 islands (90–1140 m from the nearest mainland) that we surveyed. Both adult female and male toads (SVL range 96–172 mm) were observed swimming in open water both by day and by night.

### Cane toad movements

We spool-tracked 68 female toads and 12 male toads. They moved an average of  $51.3 \pm 38.1$  m along the shoreline per night, and this distance was similar during the two seasons ( $F_{1,78} = 0.02$ ,  $P = 0.88$ ) and between the two sexes ( $t_{1,78} = 0.09$ ,  $P = 0.76$ ), regardless of the size of the toad ( $F_{1,78} = 0.56$ ,  $P = 0.45$ ). Spooled toads moved up to 57 m from shore and into floating vegetation mats, where they were observed foraging or inactive. Dispersal rates were higher during the dry season ( $t_{1,78} = 15.82$ ,  $P < 0.001$ ), reflecting the need to move further from the water's edge to reach a moist retreat site at this time of year (minimum distance of 182.05 m, vs. 134.25 m during the wet season). These mean values underestimate maximum levels, because 24 animals ran out of line in their spools during the dry season (20 females, 4 males), as did four (2 females, 2 males) during the wet season. Diurnal retreats were under grass or herbaceous vegetation (63.5%), under logs (25%), in burrows (3.8%) or under boulders (7.7%). Many toads followed cattle tracks along the grassy banks to reach their retreat sites.

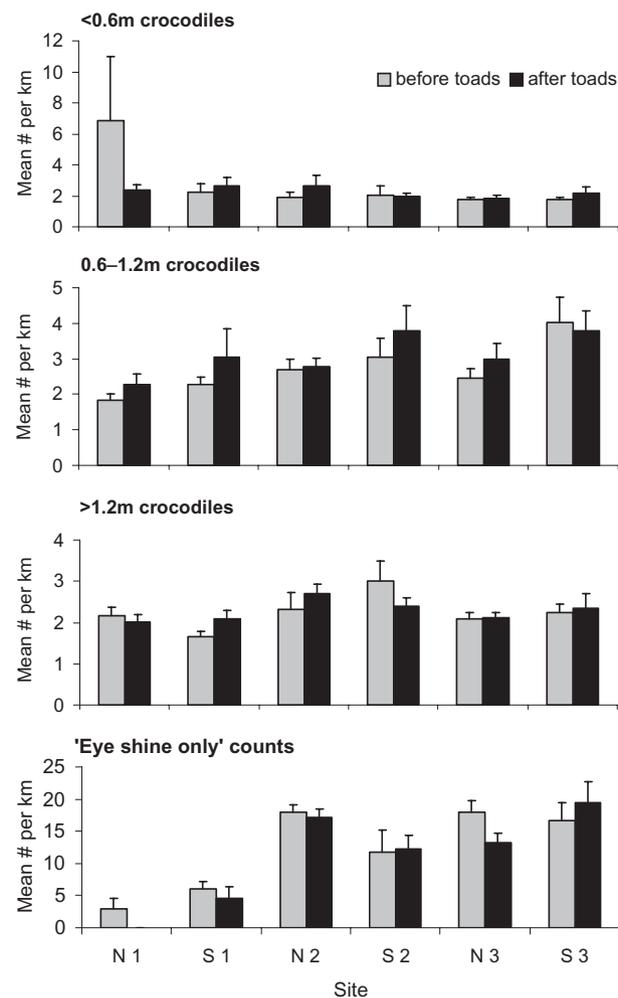
### Encounters between toads and crocodiles

Of 223 crocodiles observed in April 2010, 15% were seen within 2 m of a toad at Matilda Creek; this value fell to 3.5% (out of 230) during the dry season in August 2010. On 36 occasions we observed crocodiles (total lengths of 30–180 cm) holding cane toads in their mouths at the

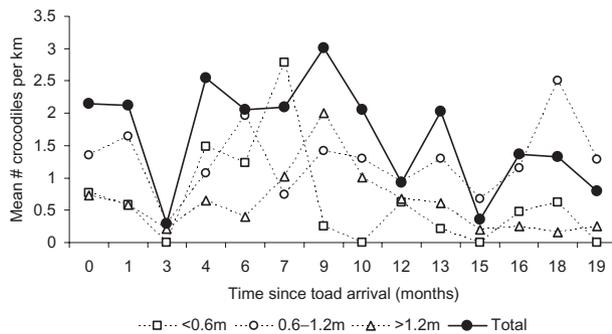
water's edge. On 23 of these occasions the crocodile ingested the toad; in the other cases the crocodile released the toad ( $n = 7$ ), or fled to deeper water while holding the toad ( $n = 6$ ).

### Changes in crocodile numbers at Carl Bay

Our highest count in the six sites at Carl Bay was 435 crocodiles (in November 2009) while the lowest was 223 in April 2010. The total numbers of crocodiles counted differed among the six sites ( $F_{5,339} = 2.60$ ,  $P = 0.03$ ; highest at the north 2 at 4.16 per km and lowest at the north 1 at 2.56 per km) but not with time since toad arrival ( $F_{1,339} = 0.59$ ,  $P = 0.44$ ; Fig. 3; interaction site\*time since toads  $F_{5,339} = 0.38$ ,  $P = 0.86$ ; Fig. 4). Changes in crocodile densities were similar among size classes of crocodiles (crocodile size



**Figure 3** Changes in the density of crocodiles in six sites at Carl Bay of Lake Argyle before and after the arrival of cane toads. Sites in the north bank are labelled with 'N' and those in the south bank with 'S'. Within a given size class of crocodiles, densities differed significantly among sites, but not before versus after the arrival of cane toads at a given site. Error bars show standard errors.



**Figure 4** Fluctuations in the density of crocodiles at Carl Bay of Lake Argyle with time since toad arrival. Because the six sites were colonized in sequence (N1 and S1 first, N3 and S3 last), each survey obtained data on crocodile numbers at sites with a range of times since toad arrival. All three size classes of crocodiles showed significant fluctuations in numbers, but with no overall trend of decline. The total count also includes the 'eye shine only' counts.

class\*time since toads  $F_{3,343} = 2.34$ ,  $P = 0.07$ ). The densities of crocodiles were similar at the north versus south banks among seasons (season\*bank  $F_{2,345} = 0.23$ ,  $P = 0.79$ ) and at different sites (season\*site  $F_{10,333} = 1.23$ ,  $P = 0.26$ ). Water level did not affect the counts differently at different sites (water level\*site  $F_{2,345} = 1.77$ ,  $P = 0.17$ ) and nor did water temperature (water T\*site  $F_{2,345} = 2.68$ ,  $P = 0.07$ ). However, the relative numbers of crocodiles that we saw at different sites was influenced by air temperature (air T\*site  $F_{2,345} = 3.11$ ,  $P = 0.045$ ).

## Changes in crocodile numbers in Lake Argyle as a whole

### Helicopter surveys (1992–2010)

Densities of non-hatchling crocodiles in the lake during helicopter surveys in 16 sections (1992–2004 and 2006–2010; all surveys in June) differed significantly among sites ( $F_{15,258} = 7.79$ ,  $P < 0.0001$ ) as well as among years ( $F_{17,256} = 2.77$ ,  $P = 0.0003$ ; highest in 2010 at 7.79 per km and lowest in 1998 at 2.48 per km: *post hoc* Fisher's PLSD test,  $P < 0.05$ ). When only the 12 sections with a complete set of survey data were considered (i.e. those surveyed every year), there was no significant change in crocodile density in sites with versus without toads (before/after\*toad/no toad  $F_{3,20} = 0.86$ ,  $P = 0.43$ ; Fig. 5).

### Lake-wide spotlight surveys (1989, 2005 and 2009)

When the 'eye shine only' category is excluded from analysis, total crocodile densities differed significantly among 18 survey sections of the lake ( $F_{17,324} = 3.89$ ,  $P < 0.0001$ ) and among the three survey times ( $F_{2,324} = 5.99$ ,  $P = 0.003$ ), but these changes within sections were similar among the three surveys (section\*survey  $F_{34,324} = 0.64$ ,  $P = .94$ ). Two sections

had toads by August 2009, and there was no significant change in the crocodile densities in these sites compared with those without toads (before/after\*toad/no toad  $F_{3,20} = 0.86$ ,  $P = 0.48$ ; Fig. 6).

## Dead crocodiles

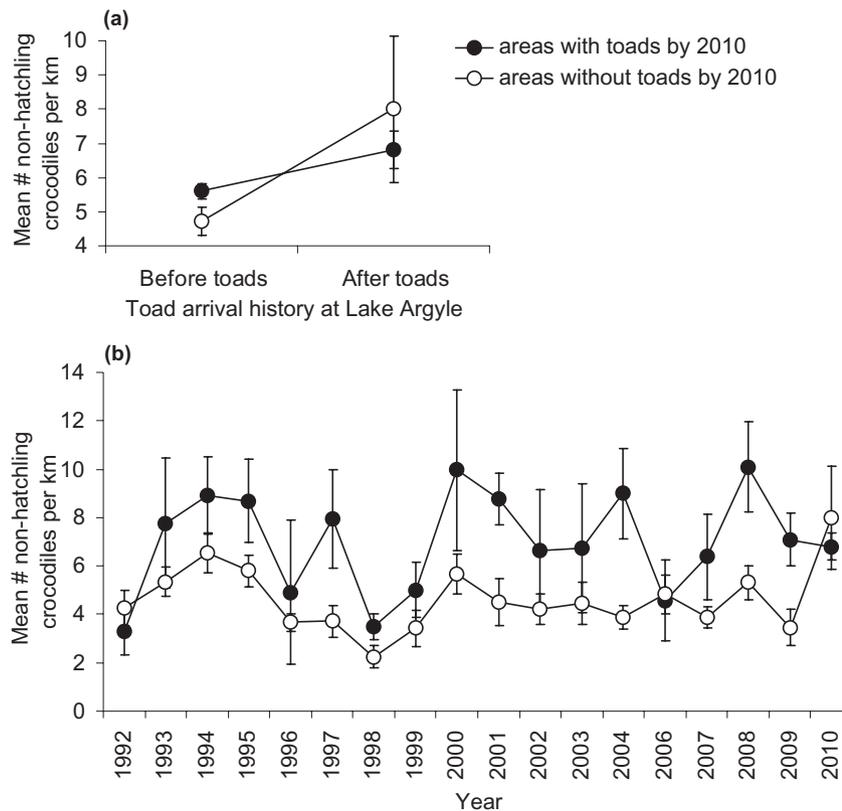
Dead crocodiles were frequently observed before the toad invasion, mostly because of drowning in commercial catfish nets (e.g. WMI Pty Ltd, 2003). Since March 2009, we found 18 dead crocodiles at Carl Bay during our surveys. All fresh carcasses ( $n = 11$ ) were males and the average total length of the dead animals was 157.4 cm (vs. 60–120 cm for toad-killed crocodiles at Victoria River: Letnic *et al.*, 2008). None of the fresh carcasses had cane toads in their stomach contents, but neither did they show signs of entanglement in fishing nests (dead crocodiles obtained from fish nets often had deep cuts on the snout and around the neck) nor signs of fighting with other crocodiles (bite marks, missing body parts, rake marks).

## Discussion

Our survey and monitoring data allow us to (1) document the cane toad invasion in detail; (2) evaluate the rates at which invasive toads are likely to be encountered by crocodiles in this system; (3) assess the impact of toad invasion on crocodile populations; and (4) identify implications for future management of cane toads and their impact on native fauna. In the following paragraphs, we address these issues in turn.

In this arid landscape, the year-round availability of water and food allowed cane toads to colonize Lake Argyle rapidly. Within 24 months of their arrival, cane toads were spread along > 300 km of lakeshore, and had reached all of the larger (> 2500 m<sup>2</sup>) islands within the lake. The steady spatial expansion of toad sightings (Fig. 1), and the high dispersal rates of spool-tracked toads suggest that direct displacements were the primary mechanism for range expansion, as has been shown for the Northern Territory invasion front also (Phillips *et al.*, 2007, 2010a). However, occasional toads found well ahead of the toad front line (e.g. KTB, 2010; DEC pers. comm.) may be due to (presumably inadvertent) translocations of 'stowaways' in vehicles and boats (White & Shine, 2009) or to overwater dispersal on floating grass mats (see later).

Larger freshwater crocodiles rarely venture far from the water at Lake Argyle, except when nesting (R. Somaweera, pers. obs.) and thus, many of the cane toads on the lakeshore were unlikely to encounter crocodiles. This is especially true during the dry season, when shallow banks keep crocodiles away from the shoreline in the eastern side of the lake and largely limit them to deeper waters or floating vegetation mats. This seasonal variation in water level was responsible for the lower proportion of crocodiles seen close to toads at this time of year, and might reduce any impact of toads during the dry season (when encounter rates were lower than in April). Nonetheless, our direct observations of



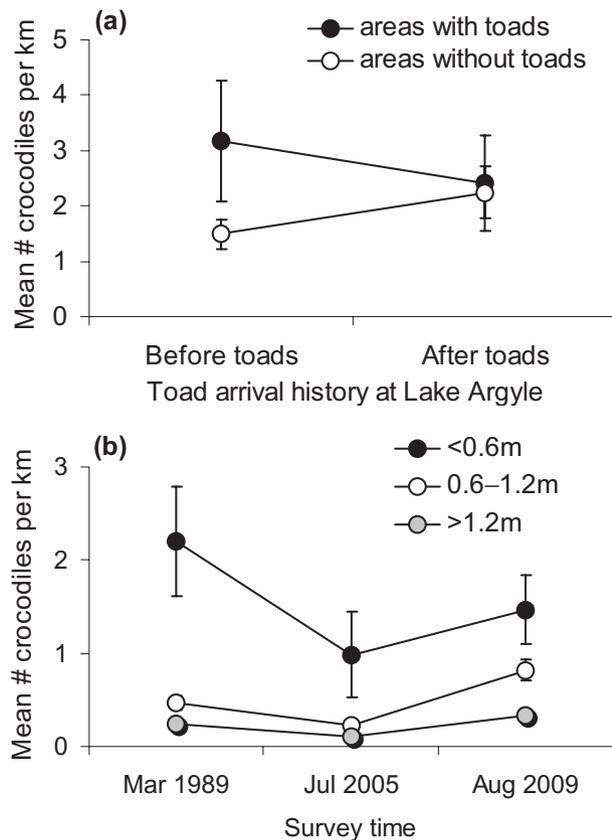
**Figure 5** Long-term changes in non-hatchling crocodile densities at Lake Argyle, based on diurnal helicopter surveys conducted by Wildlife Management International/Department of Environment and Conservation. Upper panel (a) shows the overall changes in crocodile densities in 12 survey sections of the lake. In August 2010 when the surveys were conducted, only some survey sections had cane toads (cane toads arrived at the study sites in early 2009). The lower panel (b) shows overall changes in crocodile densities each year in sites that had toads by 2010 compared with those that did not. Error bars show standard errors.

crocodiles with toads in their mouths, and the huge numbers of toads in the system (including, swimming in deep water) mean that encounters between toads and crocodiles would have occurred frequently enough to have a devastating impact on crocodile populations if (as suggested by previous work: e.g. Freeland, 1990; Smith & Phillips, 2006; Letnic *et al.*, 2008), ingestion of even a single large toad is likely to be fatal to an adult freshwater crocodile.

Contrary to this prediction, and especially to the hypothesis that freshwater crocodiles are likely to be at particular risk in more arid landscapes (Letnic *et al.*, 2008), our survey data suggest that cane toad invasion has had minimal (if any) impact on the population of *C. johnstoni* in Lake Argyle within the first 2 years after toad arrival. Our spotlight data show no population-level decline in crocodiles at Carl Bay during the 2 years since toad arrival. Similarly, helicopter surveys and lake-wide spotlight surveys showed no decline in the abundance of *C. johnstoni* in sites with cane toads. One caveat to this conclusion of 'no impact' is that population densities of crocodiles fluctuated considerably over the years preceding toad invasion (as is commonly the case: Webb, Manolis & Buckworth, 1983a,b; Hutton & Woolhouse, 1989; Fujisaki *et al.*, 2011), so that any impact

of toads might be obscured by a concurrent (climate driven?) upswing in crocodile numbers. Nonetheless, we would expect to have seen large numbers of dead crocodiles if lethal toxic ingestion of cane toads was a common event, and we found no evidence of this phenomenon (unlike the case in toad-impacted populations studied by White, 2003 and Letnic *et al.*, 2008).

Given that cane toads have had devastating population-level impacts on freshwater crocodiles in these other regions, why were they unaffected at Lake Argyle? Rates of encounter between crocodiles and cane toads may have been lower at Lake Argyle than in some other areas, because of extensive shallow-water areas around the edge of the lake, and abundant alternative prey; but nonetheless, Lake Argyle crocodiles definitely encountered toads, and sometimes tried to eat them. Given high densities both of toads and crocodiles, we would have expected to find many dead crocodiles even if only a small proportion of the total population was at risk. In practice, we found no unequivocal evidence of any mortality because of toad ingestion. Part of the answer to this paradox may lie in rapid learning of taste aversion; laboratory studies have shown that toad-naïve hatchling crocodiles from Lake Argyle quickly learn to avoid cane



**Figure 6** Long-term changes in crocodile densities at Lake Argyle based on nocturnal spotlight surveys conducted by Wildlife Management International/Department of Environment and Conservation. Upper panel (a) shows overall changes in crocodile densities in 18 survey sections of the lake. By August 2009 when the surveys were conducted, only some survey sections had cane toads. The lower panel (b) shows changes in densities of crocodiles at different size classes during the three surveys. Error bars show standard errors.

toads as prey, and free-ranging hatchlings consumed cane toads less often than frogs (Somaweera *et al.*, 2011a). The degree of risk posed by ingesting a cane toad depends upon the size of the toad (and, hence, its toxin content) relative to the size of the predator (and, hence, its ability to tolerate any given dose of toxin: Phillips & Shine, 2006). As crocodiles are gape-limited predators (Schmidt & Holbrook, 1984), hatchling crocodiles can consume only small toads, which rarely contain enough toxin to kill a hatchling. Adult crocodiles are at much greater risk of fatal poisoning, because they can ingest large toads (Smith & Phillips, 2006). In other studies, however, we have found no evidence of spatial heterogeneity in toxin resistance or prey preferences (Somaweera *et al.*, in prep.), so the cause of variation in toad impact among crocodile populations remains a challenge for future research.

Cane toads can influence native species through indirect as well as direct mechanisms (Shine, 2010). For example, in many areas, the invasion of cane toads has virtually

exterminated local populations of large varanid lizards (*Varanus panoptes* and *V. gouldii*), with the result that survival rates of species formerly consumed by varanids have increased markedly (e.g. Doody *et al.*, 2009 for turtle eggs). This process has influenced crocodile nesting success in the McKinlay River, where varanids are important egg predators (Webb & Manolis, 2010). However, the main predators on crocodile nests at northern Lake Argyle are dingoes (Somaweera, Webb & Shine, 2011b), which are not affected by cane toads (Shine, 2010). Hence, any impact of cane toad invasion on varanid lizards is unlikely to have flow-on effects to crocodile recruitment rates in these sites.

Our results have three direct implications for management. First, they clarify the effects of large-scale physical removal of cane toads by community groups, a practice that has been enthusiastically promulgated across the cane toad's entire Australian range (KTB, 2005; STTF, 2006; FrogWatch, 2011). The impact of intensive collecting activities on toad populations was variable among sites, but densities post-collection averaged about half of those pre-collection at most sites (Fig. 2). In each case, toad numbers recovered at a relatively steady rate over the ensuing months, and were higher a year later than they had been prior to the initial collecting effort (Fig. 2). These data show that 'toad-busting' activities can substantially depress toad abundances, and that the effect likely persists for several months. We do not know whether the rate of increase in toad populations at Lake Argyle would have been even higher without this physical removal of toads. Presumably, the reduced densities of toads (especially, immediately after the 'toad-busts') reduced encounter rates with native predators (including crocodiles), and may have reduced impact.

The danger that toads pose to native predators is highly size-dependent, because of a strong positive allometry of toxin content with toad body size (Phillips & Shine, 2006). Thus, 'toad-busts' might affect toad impact by modifying body-size distributions (perhaps by selectively removing larger toads, which are easier to find). However, toad-collecting activities will not affect body-size distributions of toads in the long term, because invasion-front cane toads are highly dispersive (Brown *et al.*, 2006; Phillips *et al.*, 2010a); the toads appearing at Lake Argyle in the second year post-invasion were thus immigrants from further east, rather than the progeny of the invasion-front animals. In summary, the activities of community groups substantially depressed toad abundances at Lake Argyle, potentially decreasing the impact of toads on native predators, but the effects reduced through time because of immigration.

A second management implication of our results involves the potential use of island populations as refugia for threatened fauna (e.g. Daugherty *et al.*, 1990; Abbott, 2000) including those that are threatened by cane toads (How *et al.*, 2009). As a tactic for conserving toad-vulnerable varanid lizards, Thompson and Withers (2005) suggested relocating these animals to islands in Lake Argyle, on the premise that the islands are far enough from the mainland

that they are unlikely to be invaded by toads. Unfortunately, toads are adept at colonizing even remote islands (Lever, 2001; Woinarski *et al.*, 2008), and our surveys indicate that they have already reached almost all the larger islands in the lake. This rapid dispersal has been achieved partly by adult cane toads actively swimming through deep water, but an equally important route may involve rafts of floating vegetation. Such rafts are common in Lake Argyle, are frequently colonized by adult toads (R. Somaweera, pers. obs.), and can move considerable distances under windy conditions. For example, two floating mats (each measuring about  $3 \times 5$  m) that we equipped with radio-trackers moved an average of 3.2 km in 8 days from east to west across the lake, driven by the prevailing wind (R. Somaweera, unpubl. data). Such movements may have significantly accelerated the spread of cane toads across the lake. Severe flooding at Lake Argyle in early 2011 may have further assisted the spread.

Finally, our results bear upon the concerns of population decline and proposals to actively manage crocodile populations to counter the threats thought to be posed by cane toads (KTB 2008, 2009). Two years after toads arrived at the lake, we still have no clear evidence of any impact, either negative (via lethal toxic ingestion) or positive (via reduced rates of egg predation). Over this period, toad-induced mortality of crocodiles was trivial compared with other sources of mortality such as nest predation by dingoes (up to 100% nest loss at some sites: Somaweera *et al.*, 2011b), bycatch in the catfish fishery (Fletcher & Santoro, 2010; Webb & Manolis, 2010) and annual deaths because of exhaustion in the fast-running overflow of Lake Argyle (Somaweera *et al.*, in prep.). The population of freshwater crocodiles in Lake Argyle increased at a mean rate of 3.8% per annum between 1996 and 2010 (Mawson, 2004; WMI Pty Ltd, 2010), suggesting that there is no immediate need to intervene in order to sustain this population's viability. However, given that freshwater crocodiles are long-lived animals (over 40 years: Webb & Manolis, 1998), the impact of toads on this population could change over time. In complex and variable systems such as this one, short-term surveys like ours may not provide robust predictions about future invader impacts (Brown *et al.*, 2011).

Given the large and growing number of species being introduced worldwide (Westphal *et al.*, 2008), and the many native taxa affected by these invasives (e.g. Sax & Gaines, 2008; Clavero *et al.*, 2009), studies such as our own can play a useful role in prioritizing conservation threats. Given the limited resources available for wildlife management, we need to distinguish populations that warrant active management from those that do not. Identifying which native species (or populations) are at risk, and the reasons for that risk, can facilitate rational approaches to managing impact (Simberloff, 2003; Townsend, 2003; Bradshaw *et al.*, 2007). The case of the Australian freshwater crocodile shows that impact levels from an invasive species can be strikingly different in different locations, and thus that attempts to summarize vulnerability on a species level may be inappropriate for some taxa.

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