

Population-level declines in Australian predators caused by an invasive species

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Abstract

The cane toad *Bufo marinus* has been migrating westward across northern Australia since its introduction as a biological control agent in 1935. It has been implicated in the widespread decline of many native frog-eating predators. To investigate the impacts of this invasive species on native predatory reptiles, annual surveys were conducted from 2001 to 2007 to document variation in the relative abundances of three varanid lizards (*Varanus mertensi*, *Varanus mitchelli* and *Varanus panoptes*) and one crocodile *Crocodylus johnstoni* species known to consume toads. In addition, the indirect effects of this variation on one agamid lizard *Amphibolurus gilberti*, a known prey item of *V. panoptes*, were also examined. Surveys were performed at two sites in northern Australia before and after the arrival of *B. marinus*. Significant declines in the relative abundances of all three species of varanid lizard were observed following toad arrival. Declines in the abundance of *V. panoptes*, *V. mitchelli* and *V. mertensi* at the two sites ranged 83–96, 71–97 and 87–93%, respectively. In contrast, *A. gilberti* increased by 23–26%; whereas there were no significant population-level declines in *C. johnstoni* despite observations of individual effects (i.e. several dead crocodiles with *B. marinus* in their stomachs). These findings suggest population-level changes in Australian lizards caused by an invasive species.

Introduction

'Invasive species' largely refers to non-native species that are introduced intentionally, or arrive accidentally, to novel locations, spread and then cause ecological or economic harm (Sakai *et al.*, 2001; Chornesky & Randall, 2003). Their ecological impacts range from the reduction of single species to system-level impacts that alter ecological processes (Vitousek, 1990; Chornesky & Randall, 2003). Invasive species are known to reduce native species populations through predation, competition, parasitism or disease (Sakai *et al.*, 2001; Chornesky & Randall, 2003). Alternatively, native predators may consume invasives, thereby reducing invader populations while increasing their own biomass (Roemer *et al.*, 2001; Noonburg & Byers, 2005). An increase in predator biomass may result in a decrease in native prey (Roemer *et al.*, 2001; Rand & Louda, 2004). Predation on non-native species is considered to be an important component of biotic resistance to species invasion (Levine, Adler & Yelenik, 2004; Noonburg & Byers, 2005). Studies that investigate the consequences of introduced species on native predator populations may provide an insight into community dynamics and serve as tools for invasive species management (Noonburg & Byers, 2005).

The cane toad *Bufo marinus* is native to Central and South America, but has been introduced to more than 50 countries throughout the world including Australia (East-eal, 1981; Lever, 2001). It was released into north Queensland as a biological control agent of the cane beetle *Dermolepida albohirtum* in 1935 (Freeland & Martin, 1985). Since its release, *B. marinus* has spread slowly south-east and rapidly westward across northern Australia (van Beurden & Grigg, 1980; Phillips *et al.*, 2007). Like most members of the family Bufonidae, *B. marinus* has parotoid glands on the back of the head that secrete a poison when the toad is attacked (Flier *et al.*, 1980; Tyler, 1987). Because *B. marinus* does not occur naturally in Australia, the native fauna generally lack resistance to its toxin (Smith & Phillips, 2006); however, a recent study has revealed rapid evolutionary responses in some species (Phillips & Shine, 2006).

Although some native predators can successfully prey on *B. marinus* (e.g. *Milvus migrans*, Mitchell, Jones & Hero, 1985), there are numerous reports of death associated with ingestion of this species (Catling *et al.*, 1999; Woinarski, Milne & Wanganeen, 2001; Phillips & Fitzgerald, 2004; Letnic & Ward, 2005). Moreover, declines in native mammal populations associated with toad consumption have

been reported (Braithwaite & Griffiths, 1994; Oakwood, 2004). Laboratory experiments have shown that several native frog-eating reptiles including some snake, freshwater turtle and lizard species exhibit very low tolerances to toad toxin, whereas crocodylians display the least susceptibility (Phillips, Brown & Shine, 2004; Smith & Phillips, 2006). Furthermore, the effect of the toxin may be dependent on the body size of the consumer. For example, small death adders *Acanthophis praelongus* are less resistant to the toxin than larger individuals (Webb, Shine & Christian, 2005). Still, published studies that have demonstrated population-level declines for any of these species are rare. Griffiths & McKay (2007) reported that Merten's water monitor *Varanus mertensi* declined substantially after the arrival of *B. marinus* at Manton Dam Recreation Area (Northern Territory), and Burnett (1997) anecdotally suggested that varanid lizards declined following the arrival of *B. marinus* in Kakadu National Park. Presumably, the logistical impediments of surveying and measuring rare and mobile species have impeded the study of the impacts of *B. marinus* on predator populations (Burnett, 1997; Phillips, Brown & Shine, 2003).

Herein, we report the results of a multi-year study designed to assess the population-level impacts of *B. marinus* on four lizard and one crocodile species at two sites in northern Australia. We hypothesized that predatory lizard populations (*Varanus panoptes*, *V. mertensi* and *Varanus mitchelli*) would decline significantly and as a result a prey species (*Amphibolurus gilberti*) would increase, and that freshwater crocodile *Crocodylus johnstoni* populations would be the least impacted due to their lower susceptibility to toad toxin. We also tested the hypothesis that *B. marinus* would have a size-mediated effect on crocodiles.

Methods

Study sites and design

For the period of 2001–2007, we surveyed for five reptile species along two 35 km sections (*c.* 30 km apart) of the Daly River, Northern Territory, Australia, before and after the arrival of *B. marinus* (Fig. 1). The upper section, or Upper Daly, began *c.* 15 km downstream of Oolloo Crossing (14°00'18"S, 131°14'25"E) and terminated at the Douglas River junction (13°47'17"S, 131°17'49"E). The Lower Daly section started at Daly River Township (13°46'29"S, 130°43'16"E) and terminated upstream near the Rock Candy Range (13°56'51"S, 130°51'27"E). Five surveys were conducted at both sites each year, except that surveys did not begin at the Lower Daly site until 2003 due to logistical constraints. These sites were chosen because (1) the abundance and visibility of the study species made it possible to conduct reliable surveys and (2) they facilitated the use of the Before–After Control Impact experimental design (Stuart-oaten, Murdoch & Parker, 1986) implemented to detect and measure environmental stressors.

Study species

The yellow-spotted monitor *V. panoptes*, Mitchell's monitor *V. mitchelli* and Merten's water monitor *V. mertensi* belong to the diverse assemblage of medium- to large-sized carnivorous lizards, which occupy Africa, southern Asia and several Pacific Islands in addition to Australia. These species are generalist predators that consume frogs, small mammals, birds and their eggs, small reptiles and their eggs and several invertebrate species (Cogger, 2000). Moreover, they are known to ingest small- to medium-sized *B. marinus* (Catling *et al.*, 1999; Doody *et al.*, 2006; Griffiths & McKay, 2007). These species occupy the same habitats as *B. marinus*, although *V. panoptes* is primarily terrestrial, whereas *V. mitchelli* is exceedingly arboreal and *V. mertensi* is highly aquatic (Cogger, 2000). All three lizards can be observed foraging and basking on fallen logs, pandanus trees and riverbanks. The foraging behavior of varanids involves digging for invertebrates, eggs and inactive, nocturnal prey including frogs and toads (King & Green, 1998).

Gilbert's dragon *A. gilberti* is a small agamid lizard that is widespread throughout northern Australia (Cogger, 2000). It is a diurnal hunter that relies on both visual and auditory cues to capture its invertebrate prey (Thompson & Thompson, 2001). It is mainly arboreal (Cogger, 2000), but can be observed foraging and scurrying on riverbanks throughout the day (*pers. obs.*). *Amphibolurus gilberti* is a known prey item of *V. panoptes* (R. Lloyd, *pers. comm.*).

The freshwater crocodile *C. johnstoni* is a medium-sized species that is endemic to Australia. It inhabits freshwater wetlands and occasionally tidal zones of river systems in the northern portion of the continent. *Crocodylus johnstoni* consumes fish, frogs, turtles, birds, small mammals and invertebrates (Cogger, 2000). In addition, *B. marinus* has been extracted from its stomach contents (Letnic & Ward, 2005). Although primarily nocturnal, this species can be observed basking throughout the day, especially during the winter dry season (Seebacher, 1997, 1999).

Bufo marinus is mainly nocturnal and occupies a variety of habitats (Lever, 2001). It consumes virtually any prey item that it is able to swallow, although invertebrates are ingested most frequently (Freeland, Delvinqueir & Bonnin, 1986). Its feeding habits have been implicated in the decline of small reptile fauna by having an indirect effect on their food supply (Catling *et al.*, 1999). Year-round breeding can occur in *B. marinus*, and spawning usually takes place in still pools and along muddy, sloping riverbanks (Hagman & Shine, 2006). A female can lay more than 50 000 eggs in a single spawning event (Seabrook, 1993). Eggs and tadpoles are poisonous; thus, predation is limited on these life stages; consequently, this species is able to increase rapidly in numbers (Bradshaw *et al.*, 2007). *Bufo marinus* populations often occur at very high densities (Freeland, 1986).

Count surveys

To determine the relative abundance of lizards and crocodiles, three observers conducted river surveys from a

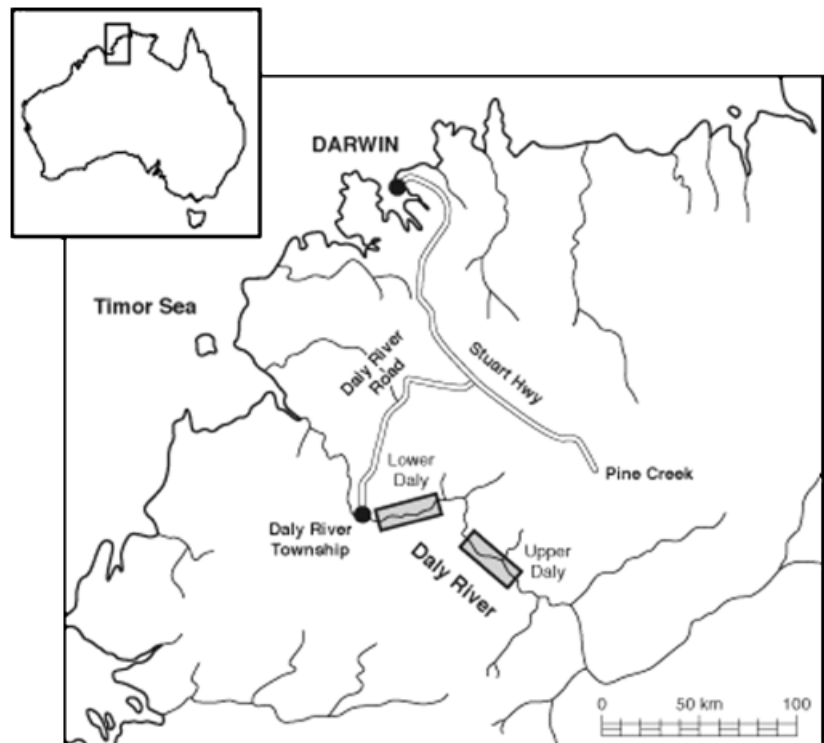


Figure 1 Map of the western top end region of the Northern Territory, Australia, showing the two study sites along the Daly River.

flat-bottomed boat travelling at $c. 10 \text{ km h}^{-1}$. Surveys were performed during the dry season between 20 May and 10 June from 2001 to 2007. Surveys began at 08:30 hours and finished at 17:30 hours. Observers scanned microhabitats (e.g. riverbanks and partially submerged branches) along one side of the river for 35 km, followed by a return search along the opposite side of the river for the same 35 km section. The boat was maintained at a distance between 7 and 10 m from the shoreline throughout the surveys, which were performed on sunny days with little to no cloud cover. The species and time of the day were recorded when a study animal was observed. Air and water temperatures were also recorded at 08:30, 10:30, 15:30 and 17:30 hours during each survey to provide daily means. If a dead animal was encountered, its condition was recorded and its stomach contents were examined to determine whether *B. marinus* had been ingested. To investigate the size-mediated effect of *B. marinus* on *C. johnstoni*, the body size of crocodiles was visually estimated to the nearest 0.3 m by the same observer in all years. We hypothesized that small crocodiles would have a higher susceptibility to the toxin and therefore would be observed less frequently than larger individuals following the arrival of *B. marinus*. Changes in relative abundance, expressed as a percentage, were calculated for each species at each site by comparing the grand mean of individual counts in years before toad arrival to years after toad arrival with one qualification. In species/years showing a lag in declines, the grand mean of post-toad counts began when the counts stopped declining (no significant differences from year to year). Simply using

post-toad counts in these species/years would underestimate the extent of the declines in counts.

Roads are commonly utilized by *B. marinus* (Seabrook & Dettman, 1996; Brown *et al.*, 2006). To estimate the arrival time of *B. marinus* and to determine its long-term presence at each site, surveys for this species were conducted along road transects (Griffiths & McKay, 2007). During each year of the study, three surveys were conducted by car on Oolloo Road at the Upper Daly Site and Daly River Road at the Lower Daly site. Surveys to count the number of *B. marinus* present began at 19:30 hours and consisted of driving at 40 km h^{-1} with high-beam headlights switched on for 8 km. Surveys, which were performed by two observers and one scribe, were conducted in the evenings following sunny days. Air temperature was recorded at the beginning of each survey.

Statistical analyses

To test for differences in the relative abundances of lizards and crocodiles among years, a repeated measures analysis of variance (ANOVA), followed by Bonferroni's corrections for multiple comparisons, was used. Air and water temperatures were included as covariates because these variables are known to influence basking rates in reptiles (Seebacher, 1999). Before these analyses, Pearson's test for serial correlation of count data within years was performed because the data were collected on consecutive days. An ANOVA with year as a fixed effect and day as a random effect was used to

test for size-mediated effects of *B. marinus* on *C. johnstoni*. Statistical significance was accepted when $P \leq 0.05$.

Results

Arrival time of *B. marinus* and its long-term presence

Bufo marinus arrived at the Upper Daly site during the 2003–2004 wet season (November–April) and at the Lower Daly site during the 2004–2005 wet season. Its presence was recorded thereafter at both sites throughout the study period. The mean toad counts were 17.4 ± 7.5 (1 SE) for the Upper Daly site and 3.6 ± 0.7 at the Lower Daly site. There were no dead lizards or crocodiles observed before the arrival of toads; however, the first dead individuals were located at the Upper Daly site in 2004 and the Lower Daly site in 2005. More specifically, four dead *V. panoptes* and five *C. johnstoni* were recorded at the Upper Daly site, and one dead *V. mitchelli* and two *C. johnstoni* were recorded at the Lower Daly site. All seven crocodiles had *B. marinus* in their stomachs, while only one *V. panoptes* had evidently consumed a toad.

Variation in the abundances of lizard and crocodile populations

There were no significant serial correlations for count data within years for any of the study species at either site, with the exception of a weakly significant positive correlation between counts for *C. johnstoni* at the Upper Daly site in 2004 (Pearson's test: $r = 0.955$, $P = 0.045$). The number of *V. panoptes* observed was significantly different among years at both the Upper Daly site (ANOVA: $F_{6,10} = 49.47$, $P < 0.001$) and the Lower Daly site ($F_{4,4} = 36.74$, $P = 0.002$) (Fig. 2). At the Upper Daly site, the number of *V. panoptes* was significantly higher in years before the arrival of *B. marinus* than in years after their arrival (2001–2003 vs. 2004–2007, all $P \leq 0.025$). Likewise, the number of *V. panoptes* at the Lower Daly site was significantly higher in 2003 before the arrival of *B. marinus* than in every year after their arrival (2003 vs. 2005–2007, all $P \leq 0.027$); however, the counts in 2004 were only significantly higher than in 2007 ($P < 0.009$). The declines in the relative abundance of *V. panoptes* were 83% at the Upper Daly site and 96% at the Lower Daly site. Air temperature positively influenced *V. panoptes* counts at both the Upper Daly site ($F_{1,3} = 6.53$, $P = 0.020$) and the Lower Daly site ($F_{1,3} = 17.59$, $P = 0.024$).

The number of *V. mitchelli* observed was significantly different among years at both the Upper Daly site ($F_{6,11} = 43.39$, $P < 0.001$) and the Lower Daly site ($F_{4,7} = 77.52$, $P < 0.001$) (Fig. 2). At the Upper Daly site, the number of *V. mitchelli* observed in the years before the arrival of *B. marinus* was significantly greater than most years after toad arrival (2001–2003 vs. 2006–2007, all $P \leq 0.037$), except for 2004 and 2005 (2001–2003 vs. 2004–2005, $P > 0.050$). Similarly, the number of *V. mitchelli* observed at the Lower Daly

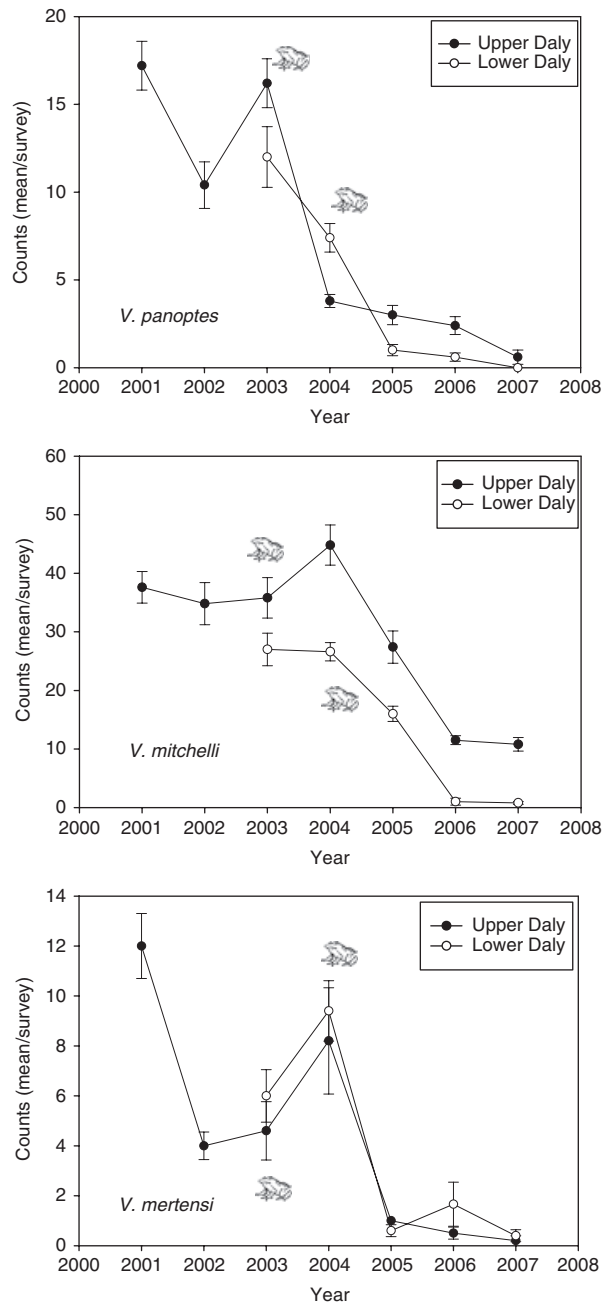


Figure 2 Relative abundance of predatory lizards at two sites (Upper Daly and Lower Daly) before and after the arrival of *Bufo marinus*. Counts are the means of five surveys per year. Error bars are ± 1 SE. Cartoon frogs indicate the arrival of toads at each site. Top graph = *Varanus panoptes*, middle = *Varanus mitchelli*, bottom = *Varanus mertensi*.

site was significantly higher in the years before the arrival of *B. marinus* (2003 vs. 2006–2007, all $P \leq 0.005$; 2004 vs. 2005–2007, all $P \leq 0.008$), except that 2003 was not significantly greater than 2005 ($P = 0.134$). The declines in the relative abundance of *V. mitchelli* were 71% at the Upper Daly site and 97% at the Lower Daly site. Air temperature

had no significant effect on *V. mitchelli* counts at either site (Upper Daly: $F_{1,7} = 0.13$, $P = 0.728$; Lower Daly: $F_{1,4} = 0.22$, $P = 0.659$).

The number of *V. mertensi* observed was significantly different among years at both the Upper Daly site ($F_{5,5} = 44.27$, $P < 0.001$) and the Lower Daly site ($F_{4,11} = 24.61$, $P < 0.001$) (Fig. 2). At the Upper Daly site, the number of *V. mertensi* observed in 2001 was significantly greater than in some years after toad arrival (2001 vs. 2005–2007, all $P \leq 0.014$); however, counts in 2002 were only greater than in 2006 ($P < 0.027$) and there were no significant differences between counts in 2003 and any of the years following the arrival of *B. marinus*. The number of *V. mertensi* observed at the Lower Daly site was significantly higher in the years before the arrival of *B. marinus* (2003 vs. 2005 and 2007, all $P \leq 0.029$; 2004 vs. 2005 and 2007, all $P \leq 0.028$), except that the 2003 and 2004 counts were not significantly greater than 2006 ($P > 0.050$). The declines in the relative abundance of *V. mertensi* were 93% at the Upper Daly site and 87% at the Lower Daly site. Air temperature positively influenced counts at the Lower Daly site ($F_{1,3} = 28.06$, $P = 0.008$), but not the Upper Daly site ($F_{1,3} = 5.61$, $P = 0.099$).

The number of *A. gilberti* observed was significantly different among years at both the Upper Daly site ($F_{6,10} = 70.64$, $P < 0.001$) and the Lower Daly site ($F_{4,6} = 48.60$, $P < 0.001$) (Fig. 3). *Amphibolurus gilberti* counts increased after the arrival of toads. Counts at the Upper Daly site were generally higher in 2005–2007 than in 2001–2004, although differences were not always significant. For example, 2005 and 2007 counts, but not 2006 counts, were significantly higher than in 2001–2004 (all $P < 0.009$). A similar trend was evident at the Lower Daly site; the 2005–2007 counts were significantly higher than the 2001–2004 counts (all $P < 0.030$). The increase in relative abundance was 26% at the Upper Daly site and 23% at the Lower Daly site. Air temperature positively influenced

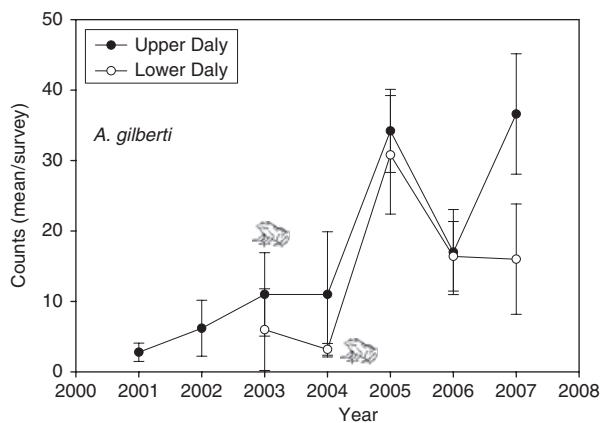


Figure 3 Relative abundance of *Amphibolurus gilberti* (a prey species of *Varanus panoptes*) at two sites before and after the arrival of *Bufo marinus*. Counts are the means of five surveys per year. Error bars are ± 1 SE. Cartoon frogs indicate the arrival of toads at each site.

counts at the Lower Daly site ($F_{1,15} = 19.00$, $P = 0.001$) and the Upper Daly site ($F_{1,4} = 11.84$, $P = 0.024$).

The number of *C. johnstoni* observed was significantly different among years at both the Upper Daly site ($F_{6,6} = 42.99$, $P < 0.001$) and the Lower Daly site ($F_{4,8} = 81.79$, $P < 0.001$) (Fig. 4). However, there were no significant differences in the number of crocodiles observed in the years before compared with the years after the arrival of *B. marinus* at either location (all $P > 0.05$). There was a significant effect of air temperature on *C. johnstoni* counts at both sites (Upper Daly: $F_{1,2} = 77.51$, $P = 0.007$; Lower Daly: $F_{1,2} = 53.93$, $P = 0.007$); however, water temperature influenced the counts at the Upper Daly site only ($F_{1,3} = 18.64$, $P = 0.014$). Still, the effect of water temperature on crocodile counts at the Lower Daly approached significance ($F_{1,3} = 7.47$, $P = 0.065$). The mean body size of crocodiles differed significantly among years at both the Upper and the Lower Daly sites (Upper Daly: $F_{1,6} = 6.07$, $P < 0.001$; Lower Daly: $F_{1,4} = 20.60$, $P < 0.001$) (Fig. 4). However, only one of the between-year comparisons (2001 vs. 2005) was significant ($P = 0.030$). Therefore, there was

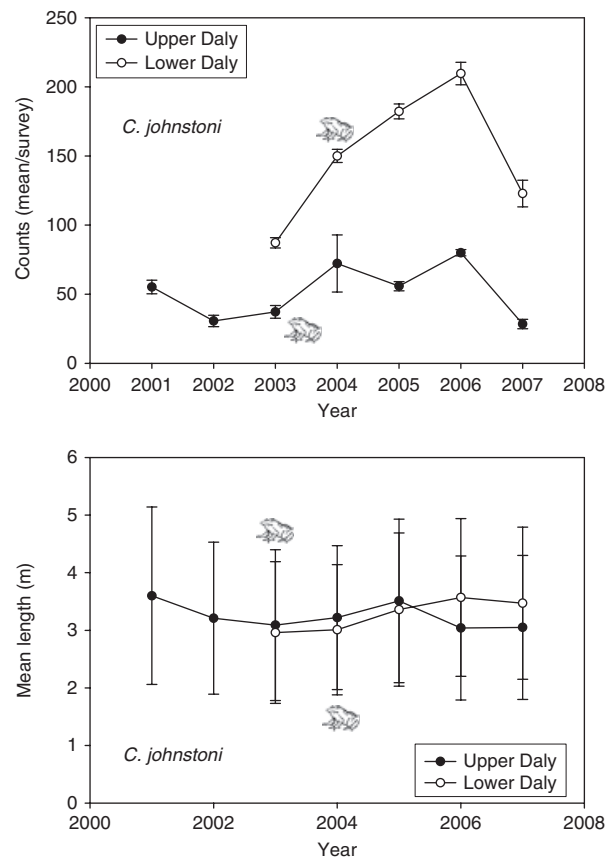


Figure 4 Impact of *Bufo marinus* on *Crocodylus johnstoni*. Top=relative abundance of *C. johnstoni* at two sites before and after the arrival of *B. marinus*. Counts are the means of five surveys per year. Bottom=body size before and after the arrival of toads. Error bars are ± 1 SE. Cartoon frogs indicate the arrival of toads at each site.

no consistent change in the mean body size following toad arrival.

Discussion

Population-level effects of *B. marinus* on predatory reptiles

Assuming no change in the detection probability of lizards among years, we observed population-level declines in Australian predatory lizards, followed by the arrival of an invasive species, *B. marinus*, at two sites along the Daly River. In contrast, there were no significant declines in populations of *C. johnstoni*. *Amphibolurus gilberti* populations increased substantially, presumably due to the losses in *V. panoptes*, a known predator of this species. These findings suggest that the invasion of *B. marinus* into this ecosystem caused a structural change in the lizard community. Changes in the abundance and community structure of predatory lizards may alter species–species interactions, in particular patterns of predation and competition and the energy dynamics of the ecosystem. Recovery from low numbers, and the possibility of local extinction, may depend on the control of *B. marinus* and/or the recolonization from individuals from the surrounding landscape.

The onset of the declines in the predatory lizard populations differed temporally. *Varanus panoptes* populations declined immediately upon the arrival of *B. marinus*, while declines in the two smaller species, *V. mertensi* and *V. mitchelli*, were not observed until the following year. This 1-year lag in declines may be related to differences in body size among these species and the size of *B. marinus* upon arrival. *Varanus panoptes* may obtain a much larger body size than the other two species, which may facilitate the consumption of large toads at the invasion front. *Varanus mertensi* and *V. mitchelli* may be too small to consume the first arrivals, but large enough to eat juvenile toads after the first reproduction period of *B. marinus* the following wet season.

Prey diversity and abundance, season and habitat use influence the dietary habits of varanid lizards (Shine, 1986; King & Green, 1998; Blamires, 2004). Shine (1986) reported that dietary differences among *V. panoptes*, *V. mertensi* and *V. mitchelli* were mostly associated with variation in habitat use. In the present study, we observed similar decreases in abundance for each of these species despite habitat-use differences among them. Therefore, they were able to opportunistically exploit a locally abundant prey item that also occupied a variety of habitat types at our study locations.

There were no measurable declines in the abundance of *C. johnstoni* populations. This is consistent with laboratory studies that have demonstrated that crocodiles are more resistant to toad toxins than most varanid lizards (Smith & Phillips, 2006). If species-specific resistance is responsible for the difference in impacts observed in the present study, then biogeography may be the underlying reason for crocodiles being less impacted. The susceptibility of native fauna to the

impacts imposed by an invasive species may be related to their evolutionary experience with that invader (Cox, 1999; Ricciardi & Atkinson, 2004). Australian crocodiles have a recent Asian origin (Archer, Hand & Godthelp, 1991; Molnar, 1993); therefore, their evolutionary experience with toads may have led to a greater resistance to the toxin. Monitor lizards, on the other hand, have been isolated from toads for a much longer period of time (King & Green, 1993). Alternatively, the reduction in *V. panoptes* may have indirectly caused an increase in crocodile recruitment, as it may no longer be a significant predator of eggs. A decrease in egg predation rates by *V. panoptes* following the arrival of *B. marinus* has been demonstrated for the pig-nosed turtle *Carettochelys insculpta* (Doody *et al.*, 2006).

Indirect population-level effects of *B. marinus* on prey species

Losses in one of the top predators in the Daly River ecosystem *V. panoptes* are likely to have caused the observed increase in its prey species *A. gilberti*. *Varanus panoptes* is known to be a generalist predator that voraciously consumes a variety of reptile species and their eggs (Shine, 1986; Blamires, 2004). It has been shown that a loss in *V. panoptes* caused by the invasion of *B. marinus* has resulted in higher recruitment rates for the pig-nosed turtle *C. insculpta* (Doody *et al.*, 2006). The increase in *A. gilberti* abundance may have resulted from higher recruitment rates associated with a reduction in egg predation, or reduced predation pressure on adult and juvenile lizards. However, further investigation of the regulatory effects of *V. panoptes* on this species is required.

Conservation implications

Long-term ecological research provides a stable platform for generalizing research results and a more accurate assessment of disturbance in an ecosystem (Callahan, 1984). For instance, in the present study, variation in species counts often depended on year, and air and water temperatures. This variation could have been misinterpreted if documented only over the short term. Data collection over 7 years allowed for the assessment of the structural change in a lizard community caused by an invasive species, and the documentation of the time scale of this ecological phenomenon. The role played by *B. marinus* in changing the character of the community was detected through losses in three species and gains in another. The continuity of the pattern between two geographically and biologically similar study locations increases the predictive capability of the research results to other sites throughout the watershed where these species occur. The data presented here on the decline in the relative abundances of *V. mertensi* and *V. panoptes* have been applied toward their subsequent listing as 'Vulnerable' under the Territory Parks and Wildlife Conservation Act 2000. We recommend that *V. mitchelli* also be considered for listing. Future research should

investigate the rate of recovery of these species following the disturbance caused by *B. marinus*.

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