Invasive toads shift predator–prey densities in animal communities by removing top predators

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Abstract. Although invasive species can have substantial impacts on animal communities, cases of invasive species facilitating native species by removing their predators have rarely been demonstrated across vertebrate trophic linkages. The predictable spread of the invasive cane toad (*Rhinella marina*), however, offered a unique opportunity to quantify cascading effects. In northern Australia, three species of predatory monitor lizards suffered severe population declines due to toad-induced lethal toxic ingestion (yellow-spotted monitor [*Varanus panoptes*], Mertens' water monitor [*V. mertensi*], Mitchell's water monitor [*V. mitchelli*]). We, thus, predicted subsequent increases in the abundance and recruitment of prey species due to the reduction of those predators. Toad-induced population-level declines in the water monitor species approached 50% over a five-year period spanning the toad invasion, apparently causing fledging success of the Crimson Finch (*Neochmia phaeton*) to increase from 55% to 81%. The consensus of our original and published long-term data is that invasive cane toads are causing predators to lose a foothold on top-down regulation of their prey, triggering shifts in the relative densities of predator and prey in the Australian tropical savannah ecosystem.

Key words: cane toad; common tree snake; Crimson Finch; Crocodylus johnstoni; Gilbert's dragon lizard; monitor lizard; Neochmia phaeton; Rhinella marina; top predator; trophic cascade; Varanus spp.

Introduction

Trophic downgrading, or the disappearance of top consumers, including apex predators, may be one of the most pervasive anthropogenic influences on nature, and has been linked to a plethora of processes worldwide, including biodiversity loss, the spread of invasive species, wildfire frequency, disease transmission, and alterations in water, atmosphere, and soil (Estes et al. 2011). The loss of top predators can influence biodiversity by shifting the relative abundance of species across trophic levels (Eisenberg 2010). Theory predicts that the largest impacts of the loss of predators will be on the next trophic level down, manifest as "facilitation," or the increase in density or biomass of one species through its interaction with another (Thomsen et al. 2010). Facilitation is a recent addition to ecological theory, despite its ubiquity and importance for ecological and evolutionary processes (Bruno et al. 2003, Kikvidze and Callaway 2009). At the biodiversity level, facilitation is now thought to play a major role in shaping communities and ecosystems (Terborgh and Estes 2010, Thomsen et al. 2010). As such, there is an urgent need for research to forecast the effects of trophic downgrading on future ecosystems (Estes et al. 2011).

Invasive species are a major threat to native species via individual direct effects such as predation, competition, and poisoning (reviewed in Simberloff and Rejmanek [2011]). If these individual effects are particularly strong, they may translate into population-level impacts, or even extirpations and extinctions (Blackburn et al. 2004, Doody et al. 2009). If the affected species are predators, we would predict further shifts in communities and ecosystems via facilitation. Indeed, a major type of facilitation is predatory release, or outbreaks, in species caused by declines in top predators (Soulé et al. 1988). Although there are numerous examples of predatory release, there are few demonstrated cases of releases triggered by an invasive species across trophic levels of vertebrates (reviews in Rodriguez [2006], White et al. [2006], Letnic et al. [2009]). Yet, invasive species that are dispersing in a predictable manner offer a unique opportunity to test predictions involving trophic cascades and trophic downgrading.

The (terrestrial) large mammal fauna of Australia is depauperate relative to other continents, leaving mon-

itor lizards to occupy a role of top or near-top predators (Johnson et al. 2007, Sutherland et al. 2010). However, Australian monitor lizards are evolutionarily naïve to the cane toad (*Rhinella marina*), a toxic invasive species that poisons many predators that attempt to ingest it (reviewed in Shine [2010]). The steady westward march of cane toads across tropical Australia offers an ideal opportunity to use before-and-after studies to determine the ecological impact of toads on native species, and research has revealed severe population-level declines in monitor lizards coincident with toad invasion (Griffiths and McKay 2007, Doody et al. 2009, 2014, Ujvari and Madsen 2009). Moreover, emerging from this research was evidence for increases in the monitors' prey following their demise (Doody et al. 2006, 2009, 2013, Brown et al. 2011).

Here, we address the prediction that cane toads are shifting the relative densities of predator and prey in animal communities in the riparian ecosystem of tropical Australia, via direct impacts on monitor lizards and indirect impacts on their prey. We quantified the relative abundance of predators and their prey for five years spanning the arrival of the invasive cane toad, including four species of predators (the monitor lizards *Varanus mertensi*, *V. mitchelli*, and *V. panoptes*, and the freshwater crocodile *Crocodylus johnstoni*), and three prey species of those predators (the Crimson Finch *Neochmia phaeton*, the Gilbert's dragon lizard *Lophognathus gilberti*, and the common tree snake *Dendrelaphis punctulata*). We review published data for other species to update the overall ecological impact of cane toads on the vertebrate food web. To inform managers, we predict future impacts of cane toads on animal communities as they invade the last remaining toad-free area of tropical Australia.

MATERIALS AND METHODS

Toad surveys

To determine the timing of toad arrival, we conducted five annual 13 km long surveys of the M1 Channel Road, which runs parallel to the M1 Channel and stems from the Ord River, near Kununurra, Western Australia (15°41′22.41″ S, 128°44′31.08″ E to 15°47′3062″ S, 128°43′04.05″ E; Fig. 1, see Plate 1). Surveys were conducted by two observers and one driver on rainless nights at 19:30–21:00 h in late May and early June, 2009–2013, from a car travelling at 15 km/h. Surveys involved visual searches for toads with the aid of spotlights.

Predator and prey surveys

To determine direct effects of toads on the relative abundance of native predators, we used visual encounter surveys from a boat, standardized by time of year, time of day, and observers. Predator species counted were Mitchell's water monitor (*Varanus mitchelli*), Mertens' water monitor (*V. mertensi*), the yellow-spotted monitor (*V. panoptes*), and the freshwater crocodile (*Crocodylus johnstoni*), all of which experienced severe population-

level declines in previous studies (Letnic et al. 2008, Doody et al. 2009, 2014). Prey species of these predators counted during these surveys were the Gilbert's dragon (*Lophognathus gilberti*) and the common tree snake (*Dendrelaphis punctulata*). Five surveys were conducted annually during May–June 2009–2013 along the Ord River, Western Australia (15°48′30.01″ S, 128°44′15.12″ E to 128°59′06.29″ S, 128°42′14.74″ E; Fig. 1). Surveys were conducted under sunny conditions, and each survey involved counts along 46 km of river during 08:30–15:30 hours (Fig. 1). Surveys involved visual searching for target species on the shoreline, on trees and logs, vegetation (terrestrial, emergent, and floating), and man-made structures (piers and docks). The boat was kept between 7–10 m from the shoreline during surveys. There were three observers, including the driver, and one scribe, who did not observe. Air and water temperature were taken five times during each survey at 08:30, 10:15, 12:30, 14:15, and 15:30 hours.

Crimson Finch fledging success

To determine if toads facilitated Crimson Finches (*Neochmia phaeton*) by boosting fledging success, we used a snapshot nest appearance method to estimate fledging success across 2011–2013 along 13 km of the Ord River (Fig. 1). We collected nests late in the nesting period (2011, $N = 42$ nests; 2012, $N = 35$ nests; 2013, $N = 48$ nests) and scored each nest as preyed upon or fledged, based on nest appearance and condition, presence of feces or egg shells, and signs of damage, such as holes, tearing, or distorted entrances.

We validated the snapshot method in 2011 by comparing the estimate for each nest to its known fate; the known fate was determined in an intensive study of reproductive success of a larger sample of nests in 2011 that included the 42 nests in the above estimate (Soanes 2011). During the intensive study, visual searches for active finch nests among shoreline vegetation were conducted by boat along the same 13 km of the Ord River used in the snapshot method (Fig. 1). When possible, adult birds were opportunistically followed for several minutes to attempt to discover their nest site, but the majority of nests were located directly, due to their conspicuousness (in emergent *Pandanus* trees just above water). Once located, the stage of each nest was determined (building, laying, incubation, or chick rearing) and its contents, such as the number of eggs or chicks and chick developmental stage, were assessed. Notes on parent and chick behavior during monitoring were also recorded. All active nests were checked by boat, on average, every three days until fledging or nest failure occurred. To prevent attracting predators, all sites were flagged ~5 m from the nest.

Identification of finch nest predators

The observation of a Mitchell's water monitor preying upon Crimson Finch eggs at the site implicated the lizard as a potential chief predator (Doody et al. 2010).
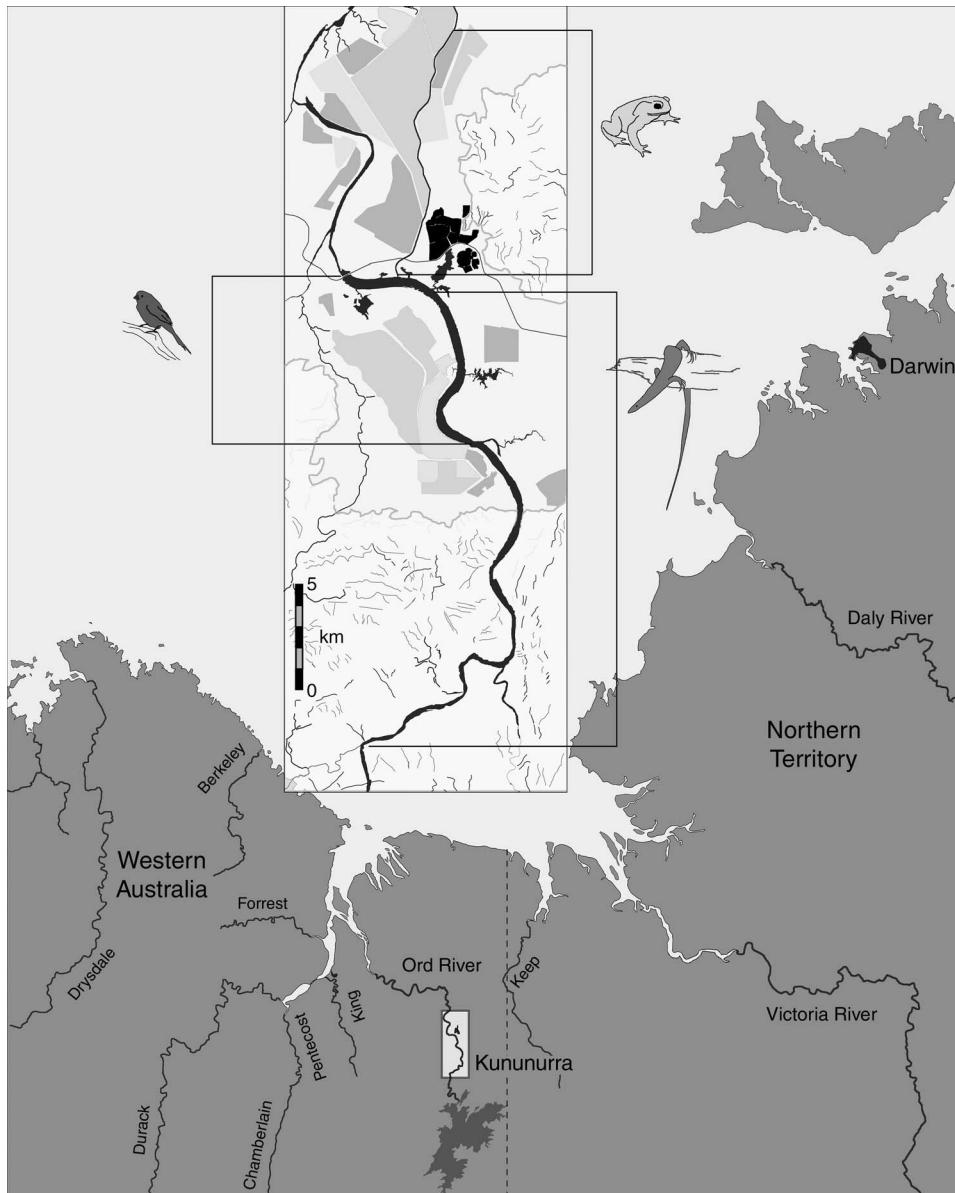
FIG. 1. Map of northwestern Australia showing the study areas for the surveys of the invasive cane toad (*Rhinella marina*), predatory monitor lizards (*Varanus mitchelli* and *V. mertensi*), and the Crimson Finch (*Neochmia phaeton*). The black lines demarcate the limits of the river or channel study stretches. Although the toad survey area does not overlap with the other areas, their migration from the west resulted in similar arrival times in both areas. The scale bar covers 5 km.

To identify nest predators of the Crimson Finch, 15 Moultrie I-40 set infrared (IR) digital cameras (Moultrie Manufacturing, Moultrie, Georgia, USA) were used to monitor 22 arbitrarily chosen nests in the intensive study. Cameras were placed at nests in either the incubation or nestling stage, depending on the availability of surrounding vegetation to which cameras could be mounted. Cameras were attached to a suitable branch or stalk at least 1 m from the nest to minimize disturbance. The IR beam was then aimed directly at or across the nest entrance to maximize the likelihood of

predators triggering the camera. All cameras had a minimum delay period of one minute between trigger occasions. When the IR beam could not be aimed in a suitable position due to inadequate camera mounting sites, a small wireless sensor was employed. The sensor was encased in a plastic film canister (70 × 35 mm) and was taped to a *Pandanus* frond ~15–30 cm from the nest entrance. A remote chip inserted into the camera allowed still images of the nest to be recorded when the wireless sensor's IR beam was triggered. When using the wireless sensor, five photos were taken at every
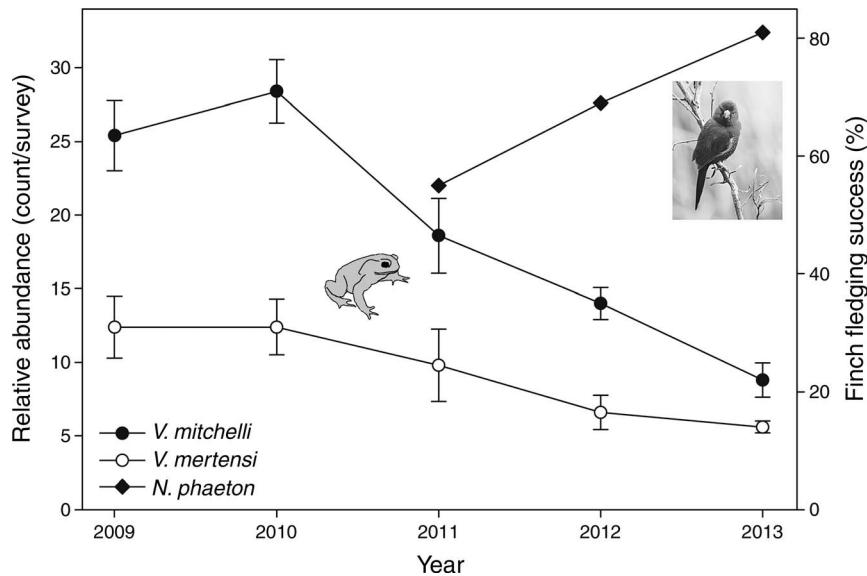
Fig. 2. Evidence for facilitation in the Crimson Finch (*Neochmia phaeton*). Fledging success of finches increased from 55% to 81% as a result of cane toad-induced declines in populations of two species of monitor lizards (*V. mitchelli* and *V. mertensi*). Data for predators are mean ± SE. Placement of the toad image denotes the timing of toad arrival. The finch image is courtesy of Tony Ashton.

trigger occasion, with a five second delay between images. Sensors were connected to a 12-volt battery placed in nearby vegetation. All cameras remained at the nest until it was preyed upon or fledged young, after which the camera was moved to a new nest. A total of 12 nests were monitored with cameras only, while 10 required the use of wireless sensors. Complete camera setup time varied between 10 and 40 minutes, depending on site condition and whether a wireless sensor was required.

Statistical procedures

To investigate differences in counts of the various species between years with and without toads, a generalized linear mixed model (GLMM) with Poisson distribution and log link function was performed for each data set in SAS using the glimmix procedure (SAS Institute, Cary, North Carolina, USA), with fixed effects for toad presence, air temperature, and water temperature. A random effect of survey year was added to account for year to year variability. Where effects of toads on counts were observed, a generalized linear model (GLM) with Poisson distribution and identity link function was performed in SAS using the genmod procedure (SAS Institute, Cary, North Carolina, USA) to investigate differences in mean counts between toad-present years to see whether there was continual decline in numbers, or if the decline leveled off. In these cases, year was changed from a random to a fixed effect, and Tukey's post hoc test was carried out on the least squares means to test for differences between individual years. All reported means for toad-present and toad-absent years are fitted model means, and are adjusted for

effects of air and water temperature on survey counts. Where significant effects of temperature on counts were found, the ratios for changes in counts per unit change in temperature were calculated.

The relationship between finch fledging success and mean counts of the monitor lizards (in the years 2011–2013) was examined using logistic regression in JMP, version 9 (SAS Institute 2010). Where significant effects were found, odds ratios were used to calculate the size of the effect.

RESULTS

Toad surveys

Cane toads arrived at the Ord River sites during the wet season following the 2010 monitor surveys. Thus, 2009–2010 were pre-toad years, and 2011–2013 were post-toad years (Fig. 2).

Effects of toads on predators

Among the monitor lizards, significant declines occurred for both *V. mitchelli* and *V. mertensi*, as toads moved through the study area ($F_{1,18} = 12.03$, $P = 0.003$ and $F_{1,18} = 16.80$, $P < 0.001$, respectively; Fig. 2). Comparing the raw means of pre-toad and post-toad counts shows that *V. mitchelli* declined by 49%, while *V. mertensi* declined by 41%. Fitted model means for *V. mitchelli* decreased from 29.9 animals per survey in toad-absent years to 12.4 animals per survey in toad-present years, and from 16.0 to 5.9 animals per survey in *V. mertensi*. The decline continued in each of the three years post-toad invasion for *V. mitchelli* (likelihood ratio test [LRT] $\chi^2 = 17.94$, df = 2, $P < 0.001$) and between 2011 and 2013 for *V. mertensi* (LRT $< \chi^2 =$

TABLE 1. Generalized linear mixed model (GLMM) results for the effect of the presence of toads on relative abundance (counts) of four predator species, and two species of prey of those predators.

Species	Presence of toads		Air temperature		Water temperature	
	$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P
Varanus mitchelli	12.03	**0.003**	0.00	0.999	0.85	0.368
V. mertensi	16.80	**<0.001**	0.24	0.631	2.75	0.114
V. panoptes	4.02	0.058†	0.74	0.401	0.14	0.709
Crocodylus johnstoni	6.02	**0.025**	0.08	0.78	8.07	**0.011**
Dendrelaphis punctulata	0.02	0.90	12.95	**0.002**	0.55	0.469
Lophognathus gilberti	0.01	0.94	0.11	0.743	0.12	0.728

† Weakly significant.

6.36, df = 2, $P < 0.042$), although the counts had leveled off after 2012 ($P = 0.52$). While the decrease in *V. panoptes* counts was not significant ($F_{1,21} = 4.02$, $P = 0.058$), the decline from 0.75 to 0.05 animals per survey associated with toads is likely a real effect, especially considering that no animals were detected in either 2012 or 2013. However, pre-toad numbers of *V. panoptes* were low, probably due to the abundance of riparian rocky habitats. Air and water temperature did not explain changes in counts among years for the monitor species (Table 1).

Although freshwater crocodile numbers appeared to go up considerably with the arrival of toads, much of this variation was explained by water temperature ($F_{1,18} = 8.07$, $P = 0.011$; Fig. 3). Water temperature was inversely related to crocodile counts, with each increase by 2°C in water temperature reducing the mean crocodile count by a factor of 0.22. Despite this, and taking it into account, there was still an overall increase in numbers of freshwater crocodiles in the years following the toad invasion, with fitted model means of 32.5 animals per survey in toad-absent years, compared to 43.8 animals per survey in toad-present years ($F_{1,18} = 6.02$, $P = 0.025$). This represented a 26% increase in crocodile numbers by 2013. In the years following the arrival of toads (2011–2013), however, there was an overall decrease in crocodile counts (LRT $\chi^2 = 13.7$, df = 2, $P < 0.001$), which occurred predominately between 2012 and 2013 ($P = 0.009$), although this may be mostly related to the increase in mean water temperature in 2013, since crocodiles bask more at lower temperatures, causing our counts to increase (Fig. 3). There was no effect of air temperature on crocodile counts (Table 1).

Effects of toads on prey species

Common tree snake counts increased considerably the first two years following the arrival of toads (Fig. 4A).
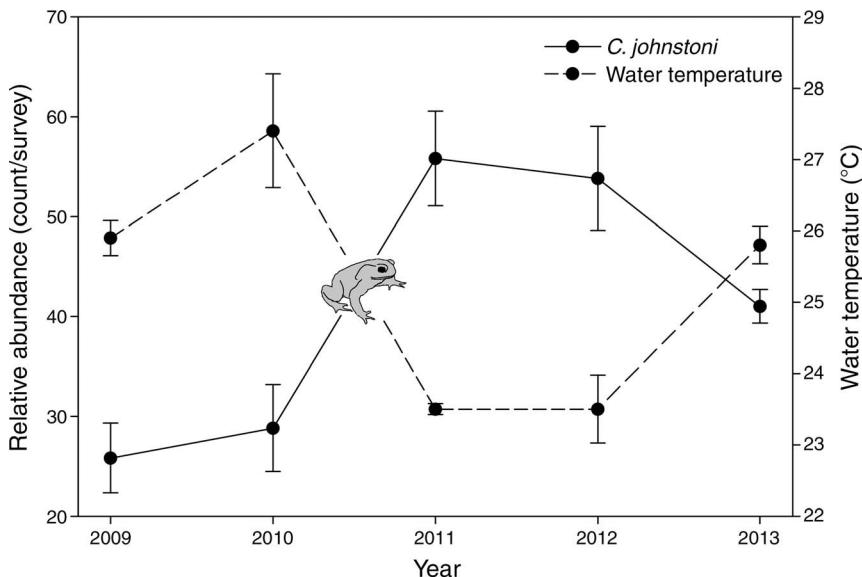

FIG. 3. Counts of freshwater crocodiles (*Crocodylus johnstoni*) and water temperatures for five annual surveys during 2009–2013 (all data are shown as mean ± SE). Years 2009–2010 were pre-toad years, while 2011–2013 were post-toad years; placement of the toad image denotes the timing of toad arrival.
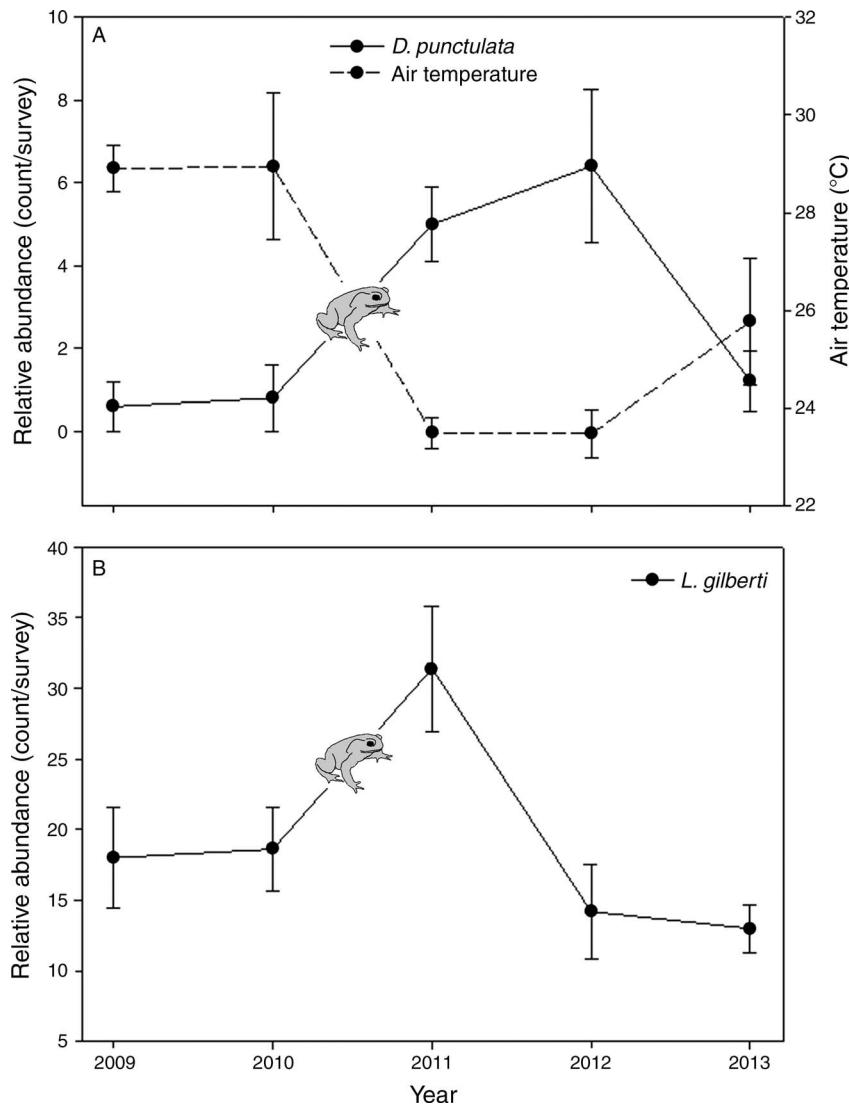
FIG. 4. Counts of (A) common tree snakes (*Dendrelaphis punctulata*) and (B) Gilbert's dragons (*Lophognathus gilberti*) and air temperatures for five annual surveys during 2009–2013 (all data are shown as mean ± SE). Years 2009–2010 were pre-toad years, while 2011–2013 were post-toad years; placement of the toad image denotes the timing of toad arrival.

However, almost all of this variation in numbers was attributable to air temperature ($F_{1,18} = 12.95$, $P = 0.002$; Fig. 4A). Snake counts were inversely related to air temperature; each increase of 2°C in water temperature reduced the mean tree snake count by a factor of 0.4. When the effect of air temperature was taken into account, there was no effect of the presence of toads on survey counts ($F_{1,18} = 0.02$, $P = 0.90$), with fitted model means of 1.3 animals per survey in toad-absent years and 1.4 animals per survey in toad-present years. There was no effect of water temperature on snake counts (Table 1).

There was no effect of the presence of toads, or air or water temperature on counts of Gilbert's dragons (toads, $F_{1,18} = 0.01$, $P = 0.94$; Fig. 4B; see Table 1 for temperature effects). Fitted model means showed that

an average of 18.5 animals per survey was detected in toad-absent years, and 18.0 animals per survey detected in toad-present years. A significant spike in numbers was observed in 2011 ($P < 0.001$).

Crimson Finch fledging success

In the intensive study (2011), fledging success of Crimson Finches, determined by monitoring the fate of eggs and nestlings, was 38% ($N = 162$ nests). High predation rates (53%) accounted for 90% of all nest failures (85 out of 94 nests). Nest predation was considerably higher during incubation (61%, $N = 52$ out of 85 nests) than in the nestling stage (39%, $N = 33$ out of 85 nests).

Determining the fate of nests solely from their appearance and condition after incubation proved to
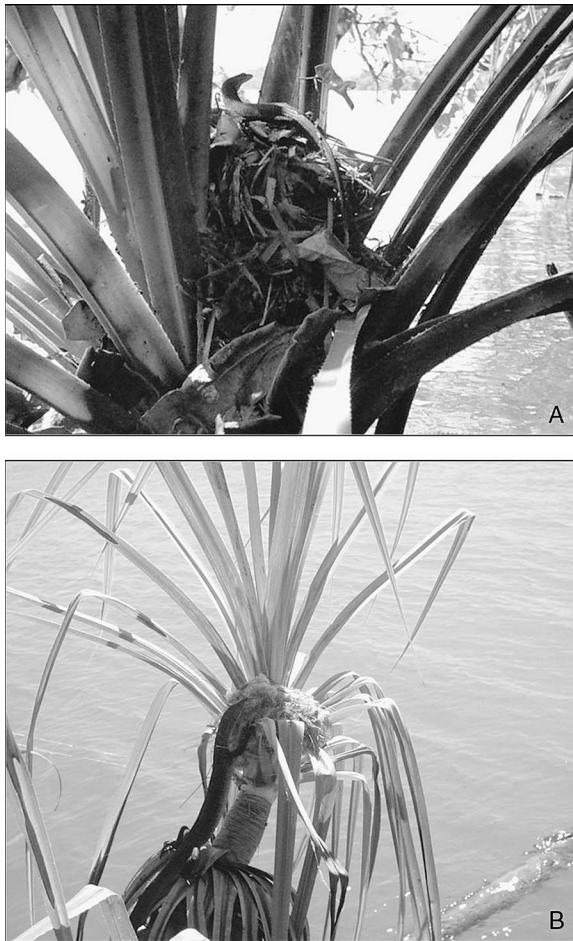
Fig. 5. Major predators of Crimson Finch eggs and hatchlings at the respective nests they raided, revealed by remote camera traps; (A) *V. mitchelli* and (B) *V. mertensi.*

be a reasonably accurate method of rapidly assessing nest fate; in 2011 the fate of 36 out of 42 nests (85.7%) was correctly assigned as preyed upon or fledged, based on appearance alone ($\chi^2 = 21.31$, df = 1, $P < 0.001$). Of the six incorrect allocations, four nests that successfully fledged young were classified as preyed upon and two that had been preyed upon were scored as fledged (for more details, see Soanes 2011).

The increase in finch fledging success during 2011–2013 was explained by the decline in *V. mitchelli* counts (LRT $\chi^2 = 7.43$, df = 1, $P = 0.006$) and the decline in *V. mertensi* counts (LRT $\chi^2 = 6.76$, df = 1, $P = 0.009$; Fig. 2). There was no significant interaction term. On average, a decrease in mean survey count of one *V. mertensi* led to a 31.6% increase in fledging success, and a decrease in mean survey count of one *V. mitchelli* led to a 13.6% increase in fledging success.

Identification of finch nest predators

The sole predator of finch eggs identified was the monitor lizard *V. mitchelli* ($N = 3$; Fig. 5A). Identified predators of finch nestlings were the monitor lizard *V. mertensi* ($N = 2$; Fig. 5B) and the water python, *Liasis fuscus* ($N = 2$). A Gilbert's dragon was suspected to have consumed young nestlings from one finch nest.

DISCUSSION

The present study revealed that toad-induced declines in predators can facilitate species that would not readily be predicted to be linked to cane toads. Although the Crimson Finch is a granivore, its eggs are preyed upon by predatory monitor lizards; severe declines in two monitor lizard species apparently resulted in a significant boost in fledging success over a three-year period. Although our baseline finch data began as toads arrived, declines in the predatory lizards had only just begun, and typically there is a one-year lag in those declines (Doody et al. 2009). Our results, along with recent published research, suggest that cane toads are shifting the relative densities of predator and prey species and thus reshaping animal communities in the riparian ecosystem of tropical Australia, via direct impacts on monitor lizards and indirect impacts on their prey (Doody et al. 2009, 2013, 2014, Webb and Manolis 2010).

Our toad–lizard–finch study was novel in demonstrating facilitation by a toxic invasive species via a predator–prey interaction affecting recruitment in a bird species. An intensive study of fledging success in the Crimson Finch population exposed *V. mitchelli* as the chief egg predator of finches, and *V. mertensi* as an important predator of finch nestlings; however, cane toads have apparently reduced the strength of this trophic link by causing population-level declines in those predators. Although it is difficult to unambiguously demonstrate a link between finch nest predation rate and monitor lizard declines, the reduction in the predatory lizards combined with high predation rates of finch nests by those predators (Fig. 2), requires such a link. Although water pythons were also identified as a predator of finch nestlings, pythons generally are not toad predators and do not suffer population declines when toads arrive (Brown et al. 2011).

The high predation rates suffered by the nestlings and, especially, the eggs of Crimson Finches in the present study is apparently typical of this species; egg and nestling predation rates for the species were 60% and 40%, respectively, in a population ~330 km southwest of our study site (Milenkaya et al. 2011). The present study, however, was the first to identify the main predators, with *V. mitchelli* accounting for 100% of egg predation and *V. mertensi* for 40% of nestling predation in monitored nests. Although this sample size is modest, we can at least assume that these lizards are major predators of the eggs and nestlings, generating the prediction that their declines would cause an increase in finch fledging success. Indeed, our snapshot estimate of fledging success increased by 26% as both monitor species showed decreases in counts by 49% and 41%
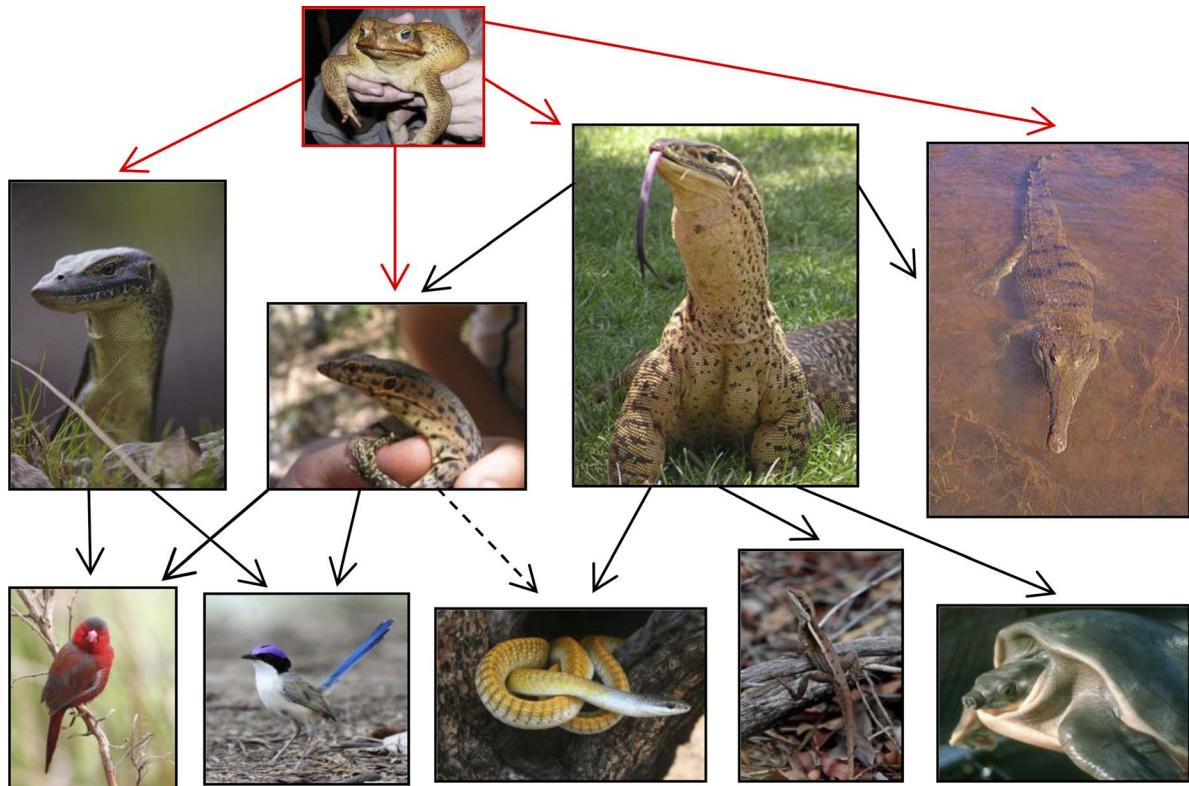
FIG. 6. Trophic links in the riparian vertebrate community of a savannah ecosystem in tropical Australia, as revealed by cane toads. Red arrows denote lethal toxic ingestion of toads by top predators (top row from left to right: *V. mertensi*, *V. mitchelli*, *V. panoptes*, *C. johnstoni*). Black arrows denote predation (bottom row from left to right): *N. phaeton* (eggs and nestlings), *M. coronatus* (eggs and nestlings), *D. punctulata*, *L. gilberti*, *C. insculpta* (eggs). The dashed arrow indicates possible predation. The finch image is courtesy of Tony Ashton. The cane toad image is courtesy of Graeme Sawyer.

(Fig. 2). Although finches can renest after a predation event, the costs to the individual of renesting (Williams 2005) can, presumably, reduce individual fitness and affect population growth. The relationship between Crimson Finch fledging success and these predatory lizards is likely to be general, as the finches essentially nest only in *Pandanus* bushes in riparian zones where both monitor species spend the majority of their time (Immelmann 1982, Verbeek et al. 1993, Christian 2004, Schultz and Doody 2004, Milenkaya et al. 2011). Thus, as toads continue to invade new areas of the Kimberley Region they will likely facilitate Crimson Finch populations by increasing fledging success.

The toad-induced declines did not cause increases in relative abundance of Gilbert's dragons or common tree snakes (Fig. 4), despite considerable increases in these species in a previous study in the Northern Territory (Doody et al. 2009, 2013). In that study, the chief predator implicated in the increases was *V. panoptes*, due to records of it preying upon those species (Doody et al. 2012*a*, *b*). However, the authors could not rule out the possibility that the increases were due to the other two toad-affected monitor lizards, *V. mitchelli* and *V. mertensi*. The lack of any increase in Gilbert's dragons

and common tree snakes in the present study supports the idea that the toad-affected predator responsible for increases in those species was indeed *V. panoptes*; although we quantified relative abundance of *V. panoptes* in the present study, and it declined with toad arrival, its pre-toad numbers were very low due to unsuitable (rocky) riparian habitat, probably precluding its ability to significantly regulate populations of the prey species. A caveat of the above is that many of the *L. gilberti* counted would typically bask on floating vegetation, but windy conditions during 2012–2013 caused wave action that battered that vegetation during the surveys. We are confident that the wave action reduced our counts, and, thus, caution against drawing strong conclusions for *L. gilberti* in the present study.

Freshwater crocodile counts increased by 26% in 2011 as toads arrived, even when accounting for the influence of water temperature on counts (Fig. 3). Although freshwater crocodiles can be facilitated by toad-induced declines in monitor lizards that consume their eggs (Webb and Manolis 2010), there was not enough time for this effect to be detected in the population (our counts did not include large numbers of very small crocodiles). Rather, the increase in crocodile counts in

PLATE 1.   View of the lower Ord River from Elephant Rock, near Kununurra, Western Australia. Photo credit: D. Rhind.

2011 may have been related to immigrating crocodiles associated with major flooding that year; in March 2011, the lower Ord River experienced significant flooding during one of the largest wet seasons on record for the east Kimberley Region (Palmer 2014). A similar increase was reported in the species in the adjoining irrigation channel the same year (Doody et al. 2014). Regardless, there was no evidence for population-level declines in crocodiles, despite our observations of 12 dead crocodiles, of which the four that were dissected had cane toads in their stomachs. This finding confirms the heterogeneity of responses in crocodile populations in response to the cane toad invasion (Letnic et al. 2008, Doody et al. 2009, 2014, Somaweera et al. 2013). Interestingly, three studies in one river catchment have found no population-level impacts of toads on freshwater crocodiles (Lake Argyle, Somaweera and Shine 2012; M1 Irrigation Channel, Doody et al. 2014; Ord River, present study). Because these three sites reflect very different habitats (lake, channel, and river), the heterogeneity in responses of crocodiles in general may not reflect habitat, but, rather, prey preference or some genetic-based resistance to toad toxins.

A spate of studies has recently revealed cascading effects as a result of cane-toad-induced trophic downgrading. Severe toad-induced population-level declines in *V. panoptes* virtually eliminated that species as a major egg predator of the pig-nosed turtle, *Carettochelys insculpta*. Turtle hatching success at the level of nest increased from ~20% in 1996–1998 to 100% in 2004 (Doody et al. 2006). Similarly, hatching success of the eggs of the freshwater crocodile increased by more than threefold upon the arrival of cane toads and the disappearance of *V. panoptes* (Webb and Manolis 2010). Thus, a toxic vertebrate facilitated a top predator by poisoning another top predator. The same toad-induced declines in *V. panoptes* affecting pig-nosed turtle recruitment also facilitated two more of its prey species; counts of adult Gilbert's dragons (*Lophognathus gilberti*) increased by three- to fourfold immediately following

sharp declines in *V. panoptes*, and counts of adult common tree snakes increased by approximately 36 times, 2–3 years after toad-induced population-level declines in the monitors *V. panoptes* and *V. mitchelli* (Doody et al. 2009, 2013). Finally, in a 12-year study using road transects, counts of three species of snakes increased considerably, coincident with a toad-induced population decline of *V. panoptes* (Ujvari and Madsen 2009, Brown et al. 2011).

The above studies provide compelling evidence for widespread facilitation via trophic downgrading as a result of an exotic species invasion. Collectively, direct impacts and indirect facilitation by cane toads are reshuffling densities of vertebrate predator and prey, and, in so doing, they are revealing the complexity of trophic relations in riparian animal communities of the savannah ecosystem in tropical Australia (Fig. 6). A caveat is that increases in some of the above species may have reflected behavioral release, rather than an increase in numbers, because predators not only kill prey but motivate changes in their prey's behavior (Ritchie and Johnson 2009). For example, with significantly fewer monitor lizards no longer patrolling the riverbanks, common tree snakes and Gilbert's dragons may forage more boldly in open areas, thus, increasing their counts due to increased conspicuousness (Doody et al. 2009). Regardless of the relative contribution of numerical vs. behavioral mechanisms, monitor lizards, which occupy a prominent role as top and near top predators in Australia, are losing their grip on top-down regulation in the tropical riparian savannah ecosystem.

How should this research inform management of cane toads? Cane toads are continuing their westward dispersal across northern Australia and are predicted to invade the last toad-free areas of tropical savannah (the Kimberley Region) within the next five years (S. Doody, *personal observation*). Thus, any before-and-after studies aimed at determining cascading effects of cane toads must be initiated within the next few years. We now have a reasonable idea of which predators

suffer major population-level impacts (Shine [2010], but see Somaweera et al. [2013] for a discussion of inter-population variation in responses of freshwater croco-diles). However, only now are we getting a picture of the cascading effects of those predator declines. Obviously, toads would be expected to continue to induce declines in *V. panoptes*, *V. mertensi*, and *V. mitchelli*, and the prey of those lizards would be expected to subsequently increase. Are there any additional animals that will be facilitated as toads complete their westward march? The western race of the Purple-Crowned Fairy Wren (*Malurus c. coronatus*) is federally threatened, occurring in isolated populations, including several in the Kim-berley Region. Like the Crimson Finch, it is a riparian species that is often an obligate *Pandanus* nester, bringing it into contact with the monitors *V. mitchelli*, *V. mertensi*, and sometimes *V. panoptes* (in less rocky systems). Also, like the finches, these wrens typically suffer ~50% nest predation from mainly unknown predators (van Doorn 2007; M. Hall and A. Peters, *unpublished data*); however, we confirmed nest (egg) predation by *V. mitchelli* (S. Doody, D. Rhind, and M. Hall, *unpublished data*). Thus, we predict a boost in recruitment in this threatened species, due to toad-induced declines in those monitor species. It is worth noting here that there are other prey species of the toad-affected monitor species for which we have no data on indirect impacts, including small and medium mammals, frogs, fish, crustaceans, and insects. We would expect at least some of these prey species to be facilitated by cane toads as they invade the Kimberley Region; only before-and-after studies across years will accurately reveal the magnitude and diversity of these effects. Another consideration is whether the facilitated prey are, in turn, causing significant decreases in their prey. Currently, there are no data demonstrating toad-induced cascading effects beyond three trophic levels (including toads as a trophic level). Regardless, when making decisions to control toads or mitigate toad impacts, managers should consider not only direct effects, but also facilitation, and perhaps any decreases in the prey of facilitated species.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Supplement is available online: http://dx.doi.org/10.1890/14-1332.1.sm