**Road transect surveys do not reveal any consistent
effects of a toxic invasive species on tropical reptiles**

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Abstract Effects of perturbations to wildlife often are measured by changes in rates of encounter with animals during standardized surveys, such as along roads. Previous work has predicted that the invasion of toxic cane toads (*Rhinella marina*) through the Australian tropics will cause massive mortality of anuran-eating snakes, and influence abundances of other native species. We surveyed three adjacent road transects for nocturnal snakes and lizards, beginning shortly before toads arrived at this site near Darwin, in the Northern Territory. In the wet-seasons of four successive years, we conducted surveys on 591 nights; on 302 of these nights, all three transects were surveyed. We recorded 8,880 live cane toads and 3,365 live reptiles. Toad numbers increased over time on all three transects but encounters with 13 species of native reptiles varied inconsistently. Eight of the 13 species of native reptile showed no significant change in encounter rates following the arrival of toads. Of the five species that did change in encounter rates, only one taxon (the bluetongue skink, *Tiliqua scincoides intermedia*) declined across all three transects. Encounter rates of the other four species often increased on at least one transect but decreased on at least one other. Thus, either the impact of cane toads on counts of reptiles differed between nearby sites, or (more likely) other factors had more influence on reptile numbers. A consistent decrease in reptile numbers on the busiest road over the study period suggests that local snake populations were affected more by road-kill than by invasive toads. Without spatial replication, this decrease could have been interpreted as an impact of toad invasion.

Keywords Abundance • Alien species • *Bufo marinus* • Ecological impact • Predator-prey • Surveys

Introduction

Biodiversity is under threat from a wide range of factors, ranging from local-scale effects (such as habitat degradation) through to landscape-scale processes (such as climate change). Faced with limited resources, managers must allocate their efforts towards mitigating the factors with the greatest potential impact. To do so, they need to measure the magnitude of impact. Measuring changes in abundance of native species as a result of a specific threatening process may be relatively easy in some cases, notably with large sedentary organisms (like trees) exposed to local threatening processes (e.g. habitat modifications to specific sites within an extensive and otherwise-unmodified matrix). However, other situations are more challenging. In this paper, we deal with a common difficulty: measuring the impact on relatively rare, highly vagile organisms of a threatening process that occurs across an entire region.

Standardised surveys are widely used to quantify abundances of mobile animals, under the assumption that encounter rates reflect abundances (Caughley 1977; Woinarski et al. 2001, 2004). Unfortunately, many other variables also affect animal observability, typically generating high variances around encounter-rate data. If no “control” areas (i.e. places not exposed to the putative threatening process) are available, we must rely on spatial consistency to test hypotheses about the causes of changes in encounter rates concordant with the advent of the putatively threatening process (Woinarski et al. 2004; Ujvari et al. 2011).

Native to South and Central America, and extending into the southernmost North America, cane toads (*Rhinella marina*, or *Bufo marinus* in previous nomenclatural schemes: Pramuk 2006) were brought to Australia in 1935, and have since spread over more than a

million square kilometres of that continent (Lever 2001). Lacking an evolutionary history of exposure to bufonid anurans, some Australian predators are highly sensitive to the toads' distinctive defensive toxins, and die if they attempt to consume a toad (Lever 2001; Shine 2010). Phillips et al. (2003) suggested that many Australian snake species within the toads' range would be severely affected by the invader. Field surveys have revealed dramatic (>70%) declines in population densities of some snakes, varanid and scincid lizards, freshwater crocodiles, and marsupial quolls within a few months of cane toad invasion (Griffiths and McKay 2007; Letnic et al. 2008; Doody et al. 2009; O'Donnell et al. 2010; Phillips et al. 2010; Price-Rees et al. 2010). Most such studies have focused on relatively small areas, for logistical reasons, without any "control" (non-invaded) areas for comparison (but see Woinarski et al. 2001, 2004). As a result, it is difficult to unambiguously attribute declines in predator abundance to toad invasion.

To obtain a broader view of toad impact, we monitored encounter rates with nocturnal snakes and lizards by conducting standardised surveys along three road transects within low-lying areas near the Adelaide River, 60 km east of the city of Darwin (12.45°S, 130.84 W), for a four-year period beginning just before the arrival of the cane toad invasion. We included all of the reptile species that we encountered in these surveys. Some of these taxa would be expected to decline as a direct result of cane toad arrival, based on detailed studies in this and nearby areas (e.g. Price-Rees et al. 2010) whereas others might benefit from toad arrival (perhaps because of reduced numbers of native predators, that are killed by the toxic toads: Brown et al. 2011). The possibility of such indirect effects (i.e. mediated through toad impacts on other, interacting species) renders *a priori* predictions difficult, prompting us to include all native species in our analyses.

Methods

Study area and road transect selection

In the Australian wet-dry tropics, temperatures are high year-round (mean monthly maximum temperature $>30^{\circ}\text{C}$ in every month) but rainfall is highly seasonal ($>75\%$ of the annual precipitation at our study site falls within the “wet-season” from January to March: Shine and Brown 2008). Faunal activity is tightly linked to this rainfall seasonality, with most species encountered more frequently as soon as rains begin in October, and continuing through the wet-season (Shine and Brown 2008). We thus confined our surveys to this period of maximal reptile activity (October to March) in four successive years (2005–06, 06-07, 07-08 and 08-09). Cane toads arrived at this site midway through the 2005–06 wet-season (see below).

We selected three road transects within a 7.5 km radius for detailed surveys (see Fig. 1 for a map showing these roads). On all three transects, we identified and counted live reptiles on both the forward and return journeys. The number of cane toads was recorded for the forward journeys only, to avoid counting the same individuals more than once (toads typically remain on the road, whereas snakes are seen only as they are crossing). We do not include data on dead (road-killed) animals, because of uncertainty about the duration of their presence on roads. The transects were:

- (1) A 2.8-km stretch of sealed road that runs 1.3 km through mixed woodland and then 1.5 km along the wall of Fogg Dam (= FD), with water on one side of the road and floodplain on the other (see Dubey et al. 2009). Traffic is light, with most vehicles being driven

slowly by tourists looking for wildlife. Our surveys were conducted on foot and from a slow-moving vehicle (<15 km/h).

(2) A 6.4-km stretch of sealed road (Anzac Parade, = AP) that links Fogg Dam to the nearest major road (Arnhem Highway). The road serves local agricultural enterprises (crocodile and barramundi farms, mango and citrus orchards, pastoral grasslands) as well as tourists travelling to Fogg Dam; usage is thus higher and most vehicles travel rapidly (>80 km/h). Our surveys were conducted from a vehicle moving at 40 km/h.

(3) An 11.3-km stretch of the Arnhem Highway (= AH) bordering Beatrice Hill Farm, including the Adelaide River bridge. This road runs through floodplain and floodplain margin habitat, skirting around an area of rocky hills isolated in the midst of the floodplain. It is the major arterial linking Darwin to Kakadu National Park, and experiences heavy traffic, with most vehicles travelling at the posted speed limit of 130 km/h. We surveyed this roadway from a vehicle moving at 40 km/h.

Road surveys

Surveys for reptiles and toads at all three sites were conducted at night (1930–2230 h Central Standard Time), because most snakes in this area are nocturnal (as are adult toads). Surveys were conducted between 1 October and 31 March between 2005 and 2009. Fogg Dam was surveyed on 591 nights over this period, Anzac Parade on 576 nights and the Arnhem Highway on 382 nights. All three sites were surveyed concurrently on a total of 302 nights. We did not include local weather conditions as covariates in our analyses, because of very low correlations between weather conditions and snake encounter rates in this system (Brown and Shine 2002). There was no linear change in temperature or rainfall over the course of the study

that could be confused with toad impacts: mean monthly values of rainfall, maximum temperature and minimum temperature, averaged over the survey period (October to March, 2005–2009) were not significantly correlated with time (i.e. number of months since toad arrival: all $F_{1,22} < 0.47$, all $p > 0.50$).

Data analyses

Our analysis focuses on two issues: (1) the degree of spatial consistency in encounter rates during a given night (i.e. were counts of a species along one transect predictable from counts along the other transects on the same night?); and (2) whether encounter rates with native reptiles have shifted significantly since the time of cane toad arrival. These are separate issues, but are related; for example, high spatial consistency in encounter rates would make it easier to detect an overall impact of toads.

We quantified spatial consistency in encounter rates by calculating Spearman correlation coefficients between counts of a species at different sites on the same nights. There were 34 possible pairwise correlations estimable for the 302 nights on which all three sites were surveyed. We omitted cases where a species was never recorded at one of these sites on any of these surveys, thereby deleting datasets involving *Morelia spilota variegata* and *Boiga irregularis* on the Arnhem Highway (because neither of these species was recorded along this transect on any of these 302 survey sessions) and *Pseudonaja nuchalis* and *Furina ornata* on Anzac Parade (never recorded at this site on any of these 302 nights).

We assessed toad impacts by looking at changes in nightly counts of each species over 42 months subsequent to toad arrival. Cane toads arrived on the Adelaide River floodplain in February 2005 and our surveys commenced seven months later (October 2005), at the

beginning of the next wet-season. The surveys were conducted during 6-month periods (October to March) over four years (2005–06 to 2008–09; a total duration of 42 months, 24 of which were surveyed). We used the number of months since initiation of the surveys (i.e. 1–6, 13–18, 25–30, and 37–42) as the independent “time” variable. If the presence of toads reduce encounter rates with snakes, we predict a negative relationship between encounter rates and this “time” variable.

Our count data for all species contained a high proportion of zeroes (i.e. there were many nights when a given species was not encountered on a survey transect). Therefore we used zero-inflated count regression analyses to assess changes in encounter rates over time and among sites using the ‘pscl’ package in R (Zuur et al. 2009; Jackman 2011). We assessed fits of zero-inflated models based on both Poisson and negative binomial distributions and chose the best fitting model for each species.

Traffic volume

To elucidate spatial differences in count changes (see Results), we sought data on patterns of traffic flow along our survey roadways. We were able to obtain data on total monthly traffic volume during portions of the survey period for two of our three survey transects. Data for AH were provided by the Northern Territory Department of Lands and Planning, and data for FD were provided by the Parks and Wildlife Commission of the Northern Territory. Traffic data for the Fogg Dam road were missing for 2006, and for the Arnhem Highway there were no data available for January to March 2009. No traffic flow data were available for our third site, AP.

Results

Overall patterns in encounter rates with toads and reptiles

We recorded 8,880 live cane toads and 3,365 live reptiles during our surveys (Table 1). Most reptiles encountered were snakes, including pythons (water python *Liasis fuscus* 65% of live reptiles seen; Children's python *Antaresia childreni* 1%; carpet python *Morelia spilota variegata* <1%), colubrids (keelback *Tropidonophis mairii* 12%; slatey-grey snake *Stegonotus cucullatus* 10%) and elapids (death adder *Acanthophis praelongus* 4%; all others <1% = small-eyed snake *Cryptophis pallidiceps*, moon snake *Furina ornata*, king brown *Pseudechis australis*, western brown *Pseudonaja nuchalis*). Only two lizard species were recorded: a small snake-like pygopodid (Burton's legless lizard *Lialis burtonis*, 3%) and a large heavy-bodied scincid (bluetongue lizard *Tiliqua scincoides intermedia*, 1%).

Encounter rates were much higher for some species than for others; the five most common species (water pythons, keelbacks, slatey-grey snakes, death adders, Burton's legless lizard) accounted for 94% of all records. Most species were seen more frequently on one of the transects than others, despite their close proximity (Table 1). For example, death adders were encountered about 30 times more often on the Arnhem Highway than along Anzac Parade, although our survey methods were identical at the two sites (which were separated by <10 km: see Fig. 1). Contingency-table analysis showed that within each of the four years of the study, the relative numbers of species varied significantly among sites (all $df > 20$, all $\chi^2 > 127.7$, all $p < 0.0001$).

Spatial consistency in encounter rates

Encounter rates with cane toads increased through time (Fig. 2a) and showed significant spatial consistency: on nights when we found many cane toads on one transect, we also found many on the other transects ($N = 302$: numbers of toads on FD vs. AH, Spearman $r = 0.39$, $p < 0.0001$; FD vs. AP, $r = 0.51$, $p < 0.0001$; AP vs. AH, $r = 0.53$, $p < 0.0001$). In contrast, encounter rates with snakes showed low spatial consistency. Of 31 pairwise comparisons, only three showed significant correlations between encounter rates at one site versus another (*Liasis fuscus*: FD vs. AH, $r = 0.12$, $p = 0.034$; *Cryptophis pallidiceps*: FD vs. AP, $r = 0.28$, $p < 0.0001$; *Acanthophis praelongus*: AP vs. AH, $r = 0.14$, $p = 0.015$). All 28 other correlations were non-significant (all $p > 0.28$). If we adopt a more stringent criterion by applying Bonferroni corrections for multiple comparisons (so that critical $p = 0.0015$), only one of the correlations involving snakes was significant (*C. pallidiceps*, FD vs. AP). All three comparisons involving cane toads remained significant under this more stringent criterion.

Spatial consistency in apparent impacts of cane toads

Little consistency was apparent in patterns of change in reptile encounter rates subsequent to toad arrival. Zero-inflated count regression (with site and month since the survey's initiation as factors) revealed significant time*site interactions for four taxa: that is, the ways in which encounter rates changed through time differed among the three transects (Table 2). The spatial divergence took different forms in different species. Cane toad numbers increased at all three sites, but increased most rapidly at Fogg Dam. Death adder numbers decreased on the Arnhem

Highway, remained stable on Anzac Parade, and increased at Fogg Dam. Counts of Burton's legless lizards declined rapidly over time on the Arnhem Highway, declined more slowly on Anzac Parade and remained stable at Fogg Dam. Western brown snakes declined over time on the Arnhem Highway but remained stable (at low levels) on Fogg Dam. Keelback numbers increased at Fogg Dam but remained stable at the other two sites. Bluetongue skinks declined at all three sites, but most dramatically on the Arnhem Highway and on Anzac Parade.

One common pattern was for encounter rates to increase at Fogg Dam, but remain stable or decline at the other two transects, as seen in the snakes *Tropidonophis mairii* (Fig. 2b) and *Acanthophis praelongus* (Fig. 2d). Other taxa showed a general tendency to decline in encounter rate through time, but with higher rates of decline at some sites than others (e.g. *Pseudonaja nuchalis*, *Tiliqua scincoides intermedia*: Figs 2f, 3a). On the busiest highway (AH), encounter rates with virtually all taxa declined consistently over the course of the study (Figs 2,3,4).

For species without significant interactions between site and month, main effects are interpretable. For *Liasis fuscus*, encounter rates declined overall, but not significantly so; these snakes were encountered more frequently at Fogg Dam than at either of the other sites (Fig. 3b). The slatey-grey snake (*Stegonotus cucullatus*), brown tree snake (*Boiga irregularis*), and moon snake (*Furina ornata*) did not show any consistent change in counts through time, but were found more commonly at some sites than others (Figs 2c, 3d, 4c). These differences in count were not related to the different lengths of the transects, because in all cases the species were more commonly encountered on the shortest transect (Fogg Dam).

Traffic volumes

We performed an ANCOVA to assess changes in average monthly traffic flow on AH and FD (i.e. traffic = Month + Site + Month*Site). The interaction term in the model was not significant ($F_{1,35} = 1.37, p = 0.25$), but both main effects were significant. Traffic volume increased over time ($F_{1,35} = 6.39, p = 0.016$), and was about tenfold higher on the Arnhem Highway than along the wall of Fogg Dam (Least Square means 25,352 vs. 2,626 vehicles/month: $F_{1,35} = 474.1, p < 0.0001$). Mean monthly traffic flow increased from about 20,000 to 30,000 vehicles per month on the Arnhem Highway over the course of our study, and from about 2,000 to 3,000 vehicles per month along the wall of Fogg Dam.

Discussion

Our data set on wildlife encounter rates is larger (>4,000 sightings) than most previous analyses of cane toad impact, and incorporates spatial replication (three transects). We could not include “control” areas; because the toad invasion front travelled at >50 km per annum as it came through our study area (Phillips et al. 2006, 2007), there were no non-invaded areas close to the invaded sites. Thus, all we can do is look for consistency in trends of reptile counts through time since toad arrival. Contrary to *a priori* predictions of major ecological impact (Phillips et al. 2003), our data do not reveal any overall decline in encounter rates since toad arrival.

The most surprising feature of our survey data is its spatial heterogeneity, despite the proximity of the transects (within a 7.5 km radius). Some species were far more commonly encountered along some transects than others, presumably reflecting divergences in habitat

suitability. Of greater interest, however, is the spatial divergence in count patterns through time. Commonly, rates of encounter with a species were low on one transect on the same night that they were high on a nearby transect; and on a longer-term basis it was common for numbers of a given species to increase through time along one transect, while decreasing at a nearby site. In isolation, it would be easy to attribute such a long-term decline to the impact of cane toad invasion. We would expect toad impact to affect all populations similarly, however, because counts of toads increased at similar rates in all sites. Most of the cases of increasing snake populations occurred at the site (Fogg Dam) where toad numbers also increased most strongly. Thus, spatial divergence in whether encounter rates increased or decreased is likely to reflect factors other than cane toad impact.

Two main issues thus arise from our results. First, why do we see such strong spatial divergence in rates of encounter, and in the direction of change in those rates through time? Second, why was the impact of cane toads apparently minor compared to other sources of variation? Below, we deal with each of these questions in turn. First, our data do not identify any causal mechanisms responsible for shifts in counts through time, but general patterns in the data suggest plausible candidates. Most notably, rates of encounter with all species of native reptiles decreased through time along transects on a busy highway. During our surveys of this transect, we often counted as many dead (road-killed) reptiles as live reptiles of the same species (overall average = 41% of snakes on the road were dead when found, SE = 7%, based on annual means for each species, combined into a single estimate). Local populations may be unable to sustain such high mortality rates. There is a clear cautionary tale in this pattern, because surveys that were restricted only to transects along this well-travelled road would have detected a consistent decrease in wildlife numbers coincident with toad arrival, and likely have attributed such a decrease to the arrival of cane toads. We fell into this trap

ourselves, attributing death adder declines along the Arnhem Highway to the impact of cane toads (Phillips et al. 2010). Another result from our surveys was the low correlation between encounter rates of the same species on different transects on the same night. Although sample sizes are small for many species, the general lack of spatial consistency in counts militates against the hypothesis that broad-scale weather conditions (such as temperature, rainfall, moon phase, wind, etc.) determine reptile activity levels. Correlational tests on a smaller data set reached the same conclusion (Brown and Shine 2002).

Second, why did we see so little effect of cane toad invasion on reptile counts? For some of the species we studied, a direct negative impact of cane toad invasion was strongly predicted by prior research. For example, death adders readily attack toads and are highly sensitive to toad toxins, and radiotelemetric monitoring in an area midway between our Arnhem Highway and Anzac Parade transects documented >20% mortality of death adders due to toad ingestion (Hagman et al. 2009). Increasing numbers of death adders at some transects (Fig. 2d) thus are perplexing (see also Shine 2010; Brown et al. 2011). Some of the other reptile species that we encountered are not likely to be vulnerable to lethal toxic ingestion of toads, either because the reptiles do not eat anurans (e.g. water pythons: Madsen et al. 2006) or can tolerate bufotoxins (e.g. keelbacks, slatey-grey snakes: Phillips et al. 2003; Llewelyn et al. 2009). Nonetheless, we might have expected the arrival of a large abundant anuran insectivore to have affected other reptile species by indirect pathways, including competition for food and shelter-sites, parasite transfer, and modifications of prey and predator abundances (Doody et al. 2006; Griffiths and McKay 2007; Ujvari and Madsen 2009; Shine 2010). Given the relatively long generation times (>1 year) of most of our study species, it is difficult to imagine that any immediate impacts of cane toad invasion would have been reversed by local adaptation within the four-year timeframe of our surveys. Either toads did

not affect reptile numbers, or this effect happened in different ways in different areas, or its influence was minor relative to other proximate sources of variation in our counts of reptile numbers along roads. A longterm data set on snake counts at one of our three transect sites, incorporating surveys conducted before as well as after toad invasion, also suggests that cane toad impacts were minor (Brown et al. 2011).

In conservation terms, our results are encouraging in that (at least at a landscape scale), cane toad invasion has had less impact on this suite of nocturnal reptile species than has generally been predicted (including by us: Phillips et al. 2003). Most species do not seem imperilled by cane toad invasion. Declines in two species (king brown snakes and bluetongue lizards) may reflect the impacts of lethal toxic ingestion of cane toads, because these animals readily attempt to eat toads, and die when they do so (Price-Rees et al. 2010; Shine, 2010). For other potentially vulnerable taxa such as death adders, intraspecific variation in the propensity to attack cane toads may reduce overall levels of toad-induced mortality (Phillips and Shine 2007; Phillips et al. 2010). Factors other than cane toad invasion may threaten this snake assemblage, however. The consistent decline in reptile numbers on a heavily-travelled road, but not on less intensively-used roads, suggests that road-kill mortality may be a greater (albeit spatially focused) threat to these populations than is the more-widely-feared impact of invasive toads.

Lastly, our results are discouraging in terms of the difficulty of attributing causation to changes in reptile counts, at least in the wet-dry tropics. Perhaps reflecting strong temporal and small-scale spatial variation in habitat attributes, even nearby areas contained different assemblages of reptile species, and the numbers of animals encountered varied through time in different ways even between adjacent areas. The resultant spatial and temporal variation in encounter rates meant that our survey data were unable to detect consistent patterns in faunal

counts in these stochastic systems. Even when effects are strong and consistent across taxa (as for the decline in reptile counts on the major highway we studied), we cannot unambiguously attribute causation for the changing encounter rates through time. Alternative methods such as mark-recapture studies overcome the difficulty of inferring abundances from encounter rates, but are very labour-intensive, especially when conducted with the levels of spatial replication required for robust inference. If the underlying problem is that variance in faunal abundance indeed fluctuates strongly through time and space, either stochastically or in response to factors that vary over small spatial and temporal scales, then even mark-recapture data will fail to detect simple and consistent faunal responses to novel anthropogenic challenges. In such a system, the superficially simple problem of detecting an ecological impact of a putatively threatening process may pose formidable logistic obstacles.

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Table 1 Total number of nights surveyed (out of a possible 724 over the four-year study period) and total numbers of each species encountered at each site

		Anzac Parade	Fogg Dam	Arnhem Highway
Number of nights surveyed		576	591	382
Length (km)		6.4	2.8	11.3
Traffic volume (vehicles/month)		NA	2324	24891
Cane toad	<i>Rhinella marina</i>	2,362	3,854	2,664
Death adder	<i>Acanthophis praelongus</i>	10	27	149
Children's python	<i>Antaresia childreni</i>	6	8	15
Brown tree snake	<i>Boiga irregularis</i>	7	16	0
Small-eyed snake	<i>Cryptophis pallidiceps</i>	9	7	4
Moon snake	<i>Furina ornata</i>	3	3	8
Burton's legless lizard	<i>Lialis burtonis</i>	45	50	8
Water python	<i>Liasis fuscus</i>	59	1696	340
Carpet python	<i>Morelia spilota variegata</i>	3	4	0
King brown snake	<i>Pseudechis australis</i>	2	5	2
Western brown snake	<i>Pseudonaja nuchalis</i>	4	2	7
Slatey-grey snake	<i>Stegonotus cucullatus</i>	3	333	34
Keelback	<i>Tropidonophis mairii</i>	62	341	60
Bluetongue skink	<i>Tiliqua scincoides intermedia</i>	20	1	4

451 **Table 2** Results from analyses of the effect of site (transect) and time (months since cane toad
 452 invasion) on encounter rates with cane toads and with a range of native reptile species during
 453 nocturnal surveys. Zero-inflated count regression models with either Poisson (P) or negative
 454 binomial (NB) distributions were used for analyses

Mean encounter rate for:	Regression type	Site 2 <i>P</i>	Month# 2 <i>P</i>	Site*Month# 2 <i>P</i>
Cane toad <i>Rhinella marina</i>	NB	463.65 <0.0001	222.90 <0.0001	19.13 <0.0001
Death adder <i>Acanthophis praelongus</i>	P	150.31 <0.0001	4.35 0.037	32.49 <0.0001
Children's python <i>Antaresia childreni</i>	P	1.99 0.37	0.57 0.45	0.85 0.65
Brown tree snake <i>Boiga irregularis</i>	P	6.82 0.01	3.35 0.067	1.85 0.17
Small-eyed snake <i>Cryptophis pallidiceps</i>	P	3.92 0.14	2.51 0.11	4.17 0.12
Moon snake <i>Furina ornata</i>	P	6.94 0.031	2.36 0.12	1.80 0.41
Burton's legless lizard <i>Lialis burtonis</i>	P	1.27 0.53	1.47 0.22	6.45 0.04
Water python <i>Liasis fuscus</i>	NB	545.1 <0.0001	1.20 0.27	5.69 0.058
Carpet python <i>Morelia spilota</i>	P	0.02 0.88	1.70 0.20	0.76 0.38
King brown snake <i>Pseudechis australis</i>	P	0.74 0.69	1.21 0.27	2.74 0.25
Western brown snake <i>Pseudonaja nuchalis</i>	P	20.15 <0.0001	0.008 0.93	12.42 0.002
Slatey-grey snake <i>Stegonotus cucullatus</i>	NB	69.43 <0.0001	0.42 0.52	3.48 0.18
Bluetongue skink <i>Tiliqua scincoides</i>	P	8.77 0.012	13.02 0.0003	2.03 0.36
Keelback <i>Tropidonophis mairii</i>	NB	16.35 0.0003	1.54 0.22	47.58 <0.0001

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457

Figure captions

Fig. 1 Map of study area and survey sites. Three roadways were surveyed: 2.8 km along Fogg Dam and adjacent woodland (FD), 6.4 km along Anzac Parade (AP) and 11.3 km along Arnhem Highway (AH). Stippled areas represent floodplain habitat and white areas represent mixed woodland/agricultural habitat

Fig. 2 Changes through four successive wet-seasons after cane toad invasion in the rates at which we encountered live cane toads and live reptiles on nocturnal road surveys along three transects at a study site in tropical Australia. The panels show changes in mean counts of live animals (as a function of number of months since toad arrival) in (a) cane toads *Rhinella marina*, (b) keelback snakes *Tropidonophis mairii*, (c) slatey-grey snakes *Stegonotus cucullatus*, (d) floodplain death adders *Acanthophis praelongus*, (e) small-eyed snakes *Cryptophis pallidiceps*, and (f) western brownsnakes *Pseudonaja nuchalis*

Fig. 3 Changes through four successive wet-seasons after cane toad invasion in the rates at which we encountered live reptiles on nocturnal road surveys along three transects at a study site in tropical Australia. The panels show changes in mean counts of live animals (as a function of number of months since toad arrival) in (a) bluetongue skinks *Tiliqua scincoides intermedia*, (b) water pythons *Liasis fuscus*, (c) king brown snakes *Pseudechis australis*, and (d) brown tree snakes *Boiga irregularis*

Fig. 4 Changes through four successive wet-seasons after cane toad invasion in the rates at which we encountered live reptiles on nocturnal road surveys along three transects at a study site in tropical Australia. The panels show changes in mean counts of live animals (as a function of number of months since toad arrival) in (a) Burton's legless lizards *Lialis burtonis*, (b) children's python *Antaresia childreni*, (c) moon snake *Furina ornata*, and (d) carpet python *Morelia spilota*

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