Long-term monitoring reveals declines in an endemic predator following invasion by an exotic prey species

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ABSTRACT

Invasive predators can cause population declines in native prey species, but empirical evidence linking declines of native predators to invasive prey is relatively rare. Here we document declines in an Australian freshwater crocodile (*Crocodylus johnstoni*) population following invasion of a toxic prey species, the cane toad (*Rhinella marina*). Thirty-five years of standardized spotlight surveys of four segments of a large river in northern Australia revealed that the density of freshwater crocodiles decreased following toad invasion, and continued to decline thereafter. Overall, intermediate-sized freshwater crocodiles (0.6–1.2 m) were most severely impacted. Densities of saltwater crocodiles (*C. porosus*) increased over time and were generally less affected by toad arrival, although toad impacts were inconsistent across survey sections and size classes. Across the entire river, total freshwater crocodile densities declined by 69.5% between 1997 and 2013. Assessments of this species' status within other large river systems in northern Australia, where baseline data are available from before the toads arrived, should be prioritised. Our findings highlight the importance of long-term monitoring programs for quantifying the impacts of novel and unforeseen threats.

INTRODUCTION

Biological invasions are a major threat to global biodiversity (Lövei, 1997; Chornesky & Randall, 2003). Introduced predators, in particular, have caused declines and extirpations of many vertebrate species (Fritts & Rodda, 1998; Wiles *et al.*, 2003; Johnson, 2006). Similarly, competitive interactions between invasive and native species have caused extinctions or extirpations in various vertebrate groups (island birds, Sax, Gaines & Brown, 2002; freshwater trout, Allendorf & Lundquist, 2003; freshwater turtles, Cadi & Joly, 2004). However, empirical evidence linking invasive prey species to declines in native predator populations is relatively rare.

One notable exception involves the invasion of cane toads (*Rhinella marina*) throughout tropical Australia (Phillips *et al.*, 2007). Cane toads were introduced to eastern Queensland from 1935–1937 to control two beetle pests in sugarcane crops (Tyler, 1976; Easteal, 1981). Since their introduction, the toads have colonised more than 1.2 million km² of Australia (Urban *et al.*, 2007). The invasion has had deleterious effects on a range of native Australian fauna because the toads possess a cardiac glycoside to which much of the native fauna has no prior evolutionary history (Gowda, Cohen & Khan, 2003; Shine, 2010). Ingestion of the toxin causes mortality in many frog-eating predators (Burnett, 1997), including quolls, lizards, and snakes (Lever, 2001; Phillips, Brown & Shine, 2003; Pearson *et al.*, 2013). However, with few exceptions (Brown, Phillips & Shine, 2011), there remains a paucity of monitoring data before and after the arrival of toads with which to assess their longer-term impact on native fauna at the population level.

The short-term impact of cane toads on freshwater crocodiles (*Crocodylus johnstoni*) has been the subject of several studies in Australia, but results remain equivocal, with reported impacts varying from very significant (Letnic, Webb & Shine, 2008; Britton, Britton & McMahon, 2013) to negligible (Catling *et al.*, 1999; Doody *et al.*, 2009; Somaweera & Shine, 2012). Interestingly, where negative impacts have been reported, declines have been biased toward intermediate-size classes (Letnic *et al.*, 2008; Britton *et al.*, 2013). Nonetheless, previous studies have mostly involved single surveys before and after the arrival of toads, and have only considered impacts two to three years post-invasion. The longer-term effects of cane toads on freshwater crocodile population size and structure remain unknown. Because effects of invasive species can be temporary or amplified over time (Strayer *et al.*, 2006; Strayer, Cid & Malcom, 2011; Willis & Birks, 2006), understanding the impacts of cane toads requires consideration of both short-term and long-term perspectives. Laboratory trials suggest that the other Australian crocodile species, the saltwater crocodile (*C. porosus*), is less vulnerable to the toad's toxin than is the freshwater crocodile (Smith & Phillips, 2006), which is generally supported by a lack of reports of dead saltwater crocodiles following toad invasion. Here, we use standardized monitoring data gathered over 35 years (Webb, Manolis & Ottley, 1994; Fukuda *et al.*, 2013), from a large river in the Northern Territory of Australia with tidal and non-tidal segments, to document changes in density and population structure of freshwater and saltwater crocodiles, before and after the invasion of cane toads.

MATERIALS AND METHODS

Study species

Two crocodilian species occur in northern Australia, where they are generally considered apex predators, feeding on insects, crustaceans, fish, frogs, turtles, mammals, and waterfowl (Webb & Manolis, 1989, 2010). The endemic Australian freshwater crocodile, *C. johnstoni*, is usually restricted to freshwater habitats. The saltwater crocodile, *C. porosus*, occurs throughout the Indo-Pacific region and inhabits freshwater, brackish water, and saline water (Webb & Manolis, 1989). Both *C. johnstoni* and *C. porosus* are known to prey on *R. marina* (Covacevich & Archer, 1975; Letnic & Ward, 2005).

Freshwater and saltwater crocodiles in Australia were extensively hunted for their skins until they were protected in 1964 and 1971, respectively. The population of saltwater crocodiles in the Northern Territory is now thought to be similar to the population size before extensive commercial hunting began (Fukuda *et al.*, 2011). The post-hunting increase in the abundance of freshwater crocodiles is assumed to be similar to the recovery recorded for saltwater crocodiles (Webb *et al.*, 1994).

Study Area

Crocodile surveys were conducted on the Daly River in the Northern Territory, Australia (Fig. 1). Climate in the study area is tropical monsoonal with a distinct dry season (May–October) and wet season (November–April). The Daly River is tidal and seasonally saline for approximately 100 km upstream from the mouth, where the banks are generally lined with mangroves. The upstream reaches of the Daly River extend for 200 km and are freshwater, non-tidal, and contain a mix of sandy and rocky banks dominated by riparian trees (e.g., *Pandanus* and *Melaleuca* species).

Cane toads invaded from the east and were established in the upper reaches of the Daly river drainage at Katherine and in Nitmiluk National Park by 1999-2000 (I. Morris, J. Burke, personal communication), although some earlier sightings were reported (FrogWatch, 2013). Standardized nocturnal road surveys revealed that the toads then spread downstream along the Katherine River and were established in the Daly River at Oolloo by 2003 and Nauiyu by 2005 (Doody *et al.*, 2009; G. Wightman, personal communication). Adult cane toads can apparently survive in 40% seawater (Liggins & Grigg, 1985), allowing them to inhabit the lower reaches of the Daly River.

Monitoring data

Crocodile surveys were carried out once a year from 1978-2013 in four sections (A–D in Fig. 1). Section A (87.6 km) is the most downstream, tidally-influenced section, with a salt wedge moving progressively upstream during the dry season. Section B extends upstream from a concrete road crossing that stops tidal influences and the upstream penetration of saline water. Sections B (51.4 km), C (57.8 km) and D (16.5 km) are freshwater, with sandy and rocky banks. Survey frequency differed between survey sections, with section A having the most frequent surveys (23/35 years), followed by sections B and C (18 surveys each) and section D (17 surveys) (Table A1 in Supplementary Material).

Crocodile monitoring in each section followed standardized spotlight survey protocols (Messel *et al.*, 1981; Fukuda *et al.*, 2013). Surveys were conducted during the dry season, at night, mostly during the cooler period of the year (July to September), and at low tide in tidal areas, when mudbanks were exposed below the mangroves during the surveys. Under these conditions, spotlight river surveys are precise and repeatable for detecting long-term

population trends of crocodilians (Webb, Bayliss & Manolis, 1987; Fujisaki *et al.*, 2011; Fukuda *et al.*, 2011). Crocodiles were located by experienced observers with a spotlight (100W or 200 000 candlepower) from a boat travelling at 15-20 km/hr along the river. Each crocodile sighted was approached as closely as possible to determine species (based on their distinctive head morphology) and to estimate total length in contiguous 0.3 m size classes: the smallest animals were grouped as a <0.6 m class. Saltwater crocodiles <0.6 m are usually hatchlings from the preceding (current calendar year) nesting season, while freshwater crocodiles in this size class include individuals <3 years of age.

During these surveys, animals which could not be approached closely enough to confirm species and/or size were noted as “eyes only”. The proportion of “eyes only” animals varies with observer confidence in making species and size determinations (Webb *et al.*, 1987), crocodile density, water depth (affecting the ability to approach), wariness, and other factors. On average, 55.4% (SE = 1.7, N = 77 surveys from 1978–2013) of crocodiles sighted were “eyes only”. These observations were excluded from the analysis here, which required both species and size to be known, which added randomly to the variance around our relative abundance estimates, but not to the trends in those estimates over time.

Statistical Analyses

To determine whether cane toad establishment influenced relative densities of saltwater and freshwater crocodiles (number of crocodiles per linear km), we conducted time-series intervention analyses (Huitema & Mckean, 2000). This approach is used to examine changes in a dependent variable before and after an intervention and is increasingly used in ecology [e.g., hurricane effects on snail abundance: (Prates *et al.*, 2011); algal blooms on cod

populations: (Chan *et al.*, 2003); canopy disturbance events: (Druckenbrod *et al.*, 2013); cane toad impacts: (Brown *et al.*, 2011)]. Specifically, we used segmented regression to examine changes in the level and slope of the relationship between relative crocodile density and time, before and after toads became common on the Daly River. For section A of the river, where we had the most complete crocodile survey data, we used 2005 as the date of cane toad arrival (based on consistent reporting of toads at Nauiyu). No crocodile surveys were conducted in sections B–D from 1998–2008, which covers the period of toad arrival. Specifying a precise date of toad arrival was therefore unnecessary for sections B–D.

Relative densities of freshwater and saltwater crocodiles in each survey section were modelled separately according to the following multiple regression equation:

$$Y_i = \alpha_0 + \beta_1 T_i + \beta_2 P_i + \beta_3 S_i + \varepsilon \quad (\text{eq. 1})$$

where Y_i is the untransformed relative density of crocodiles in year i ; α_0 is the pre-toad intercept, the relative density of crocodiles at time zero; β_n are regression coefficients describing the effects of independent variables T , P , and S ; and ε represents an error term. For year i , T represents the number of years since that survey section was first surveyed, P is the presence/absence of toads (coded as 0 before 2005, and 1 thereafter), and S is a variable that contains zeroes up to 2007 and the number of years since toads arrived thereafter (see Huitema & McKean, (2000) for further details).

Specifying the segmented regression in this way produces three intuitive regression coefficients, which can be interpreted as follows: β_1 is the pre-toad slope, which describes the average increase in relative density per year; β_2 is the post-toad level change, which measures the change in elevation of the time-series associated with the arrival of toads (i.e., the difference between the predicted values of Y_i before and after toad arrival), and β_3 is the post-

toad slope change, the difference between the post-toad and pre-toad slopes. Regression coefficients were estimated via maximum likelihood using generalized least squares in R 3.0.1 [*gls* routine in library *nlme*, (Barton, 2013; R Development Core Team, 2013)].

The errors in eq. 1, ε , are assumed to be independently and identically distributed with constant variance. To determine whether accounting for temporal autocorrelation and heterogeneous variances could improve model fit, we also built models that included first-order autocorrelation structures and constant variances within the two levels of variable T (toad presence). First-order autocorrelation structures model the residuals at time t as a function of the residuals at time $t-1$ (Zuur *et al.*, 2009). Different variances were estimated for each level of T because preliminary analyses suggested heterogenous spread in the residuals before vs. after toad arrival in some of the time-series, violating the homogeneity of variance assumption.

The appropriate level of model complexity for each time series was selected in two steps. First, four models with and without first-order autocorrelation and different variance structures were compared using Akaike's Information Criterion corrected for small sample sizes (AICc) (Zuur *et al.*, 2009), and the model structure with the lowest AICc was retained for subsequent analyses. These initial models contained all of the fixed effects in eq. 1. Second, we used AICc to rank five candidate models containing different combinations of fixed effects (ranging from an intercept-only model to a saturated model with all fixed effects). To account for model selection uncertainty, we calculated weighted averages of parameter estimates across the models comprising ~95% of the Akaike weights (Barton, 2013; R Development Core Team, 2013).

Effects of cane toads on freshwater crocodiles may be size-specific (Letnic *et al.*, 2008), and so we conducted the above analyses on all size classes of freshwater crocodiles combined, as well as on each size class separately. For saltwater crocodiles, we only fit models to data from sections A and B, as this species was rare in the upper freshwater reaches. Furthermore, size-specific models were only fit to data from section A for saltwater crocodiles, due to low numbers of observations in many size classes in the other sections. To examine whether the cane toad establishment influenced the size structure of freshwater crocodile populations, we repeated all of the aforementioned analyses using average total length as the response variable. These size structure analyses were only conducted on saltwater crocodile data from sections A and B.

RESULTS

Relative freshwater crocodile densities on the Daly River declined following the colonisation of toads in all four river segments (Fig. 2). Relative density declined by 75.3% between 1997 and 2013 in Section A, but by 66.1% between 2004 and 2013 after the toads arrived. Relative densities declined by 68.6%, 67.5%, and 56.6% from 1997 to 2013 in sections B, C, and D, respectively. Across all four sections combined the relative density of freshwater crocodiles declined by 69.5% between 1997 and 2013.

Time-series intervention analyses revealed decreases in the level and slope of the relationship between freshwater crocodile densities and time coincident with the arrival of toads in all four survey sections (Table 1; Fig. 2). When each size class was analysed separately, intermediate-sized freshwater crocodiles were generally found to undergo the most dramatic declines (Fig. 3). Specifically, there was a strong decrease in the predicted relative densities

of 0.6–0.9 m and 0.9–1.2 m freshwater crocodiles across all four survey sections (post-toad level change: Fig. 4). There was also evidence that intermediate size classes started to decline following toad establishment (post-toad slope change: Fig. 4), although confidence intervals for slope-change estimates in some survey sections overlapped zero, and both smaller and larger size classes declined in section D relative to the other survey sections (Fig. 4). Across the entire river, freshwater crocodiles that were 0.6–0.9 m and 0.9–1.2 m declined by 90.9% and 89.6%, respectively, following toad arrival (1997–2013). These declines in intermediate size classes resulted in increases in the mean lengths of freshwater crocodiles sighted following toad arrival in all four sections (post-toad level change: Table 2; Fig. 5).

Across the entire river, relative saltwater crocodile densities increased by 74.2% between 1997 and 2013 (Fig. 2). In section A, relative densities increased by 25.1% between 2004 and 2013, whereas relative densities increased by 26.4%, 104.8%, and 300.0% in sections B, C, and D, respectively, between 1997 and 2013. Overall densities of saltwater crocodiles declined with distance upstream.

There was a positive relationship between saltwater crocodile densities and time in sections A and B, but the effect of toad arrival differed between survey sections. In section A, there was no evidence of a change in the level or slope of the relationship between total saltwater crocodile density and time coincident with the arrival of toads (Table 1). However, in section B, the relative density of saltwater crocodiles increased following toad arrival, but decreased thereafter (Table 1). Relative densities of 0.6–0.9 m and 1.5–1.8 m saltwater crocodiles decreased following toad invasion in section A (post-toad intercept change: Fig. 6), and there was a decrease in the slope of the relationship between density and time in the 0.9–1.2 m and 1.8–2.1 m size classes (post-toad slope change: Fig. 6). Although small sample sizes preclude

a formal statistical analysis, these patterns appeared to be generally inconsistent across the other three river sections (Figs. A1–A4 in Appendix). Trends in the mean length of saltwater crocodiles also varied across river sections (Fig. 5). In section A, sizes increased over time, but intercept and slope-change estimates were highly uncertain, with wide 95% confidence intervals (Table 2). In contrast, in section B, sizes declined following toad arrival.

During surveys in 2009, 2011, and 2013, we observed freshwater crocodiles feeding on cane toads, and occasionally found dead freshwater crocodiles with no obvious signs of trauma in the 0.9–1.5 m size range. No such observations were made on saltwater crocodiles.

DISCUSSION

Colonisation of the Daly River by cane toads coincided with declines in the densities of freshwater crocodiles. In all four survey sections, we detected declines in the elevation and slope of the density time-series concurrent with toad arrival. Declines in density were particularly pronounced in the 0.6–0.9 m and 0.9–1.2 m size classes. Across the entire river, these declines in intermediate size classes resulted in an increase in the average length of the surviving freshwater crocodiles, from 1.17 m in 1997 to 1.90 m in 2013. In contrast, there was less evidence that small (<0.6 m) crocodiles declined following toad arrival. The only exception was survey section D, where there were decreases in the level and slope of the density time-series. However, in all four survey sections, small crocodile declines appear to have begun before the arrival of toads. Freshwater crocodiles of different sizes feed on different prey items (Webb & Manolis, 2010) and Somaweera *et al.* (2011) found that free-ranging hatchlings were more likely to consume native frogs than cane toads, even though both prey items were common. Furthermore, cane toads that are small enough to be

consumed by hatchling freshwater crocodiles typically possess very low levels of toxin due to strong allometry in toxin content (Shine, 2010). Despite this allometry, we also found that large freshwater crocodiles were less affected by toad establishment than were intermediate size classes. This finding accords with the results of Smith & Phillips (2006) which suggested that even a large cane toad may not possess a sufficient amount of toxin to kill a large freshwater crocodile. Taken together, these results indicate that the impact of cane toads on freshwater crocodiles is size-specific, and that intermediate size classes are at greater risk. Nevertheless, declines in intermediate size classes may ultimately impact densities of larger size classes if density-dependent factors cannot compensate for these declines (Webb *et al.*, 1983a; Webb, Manolis & Buckworth, 1983b). Freshwater crocodiles have very slow growth rates (e.g., males and females take roughly 31 and 26 years, to reach 1.8 m, respectively; Webb, Manolis & Buckworth, 1983a), and thus we were unable to detect strong temporally-lagged responses in larger size classes. Further surveys will be needed to ascertain exactly how the observed declines in smaller size classes will affect the abundance of larger individuals.

Our surveys paint a more uncertain picture of toad impacts on saltwater crocodiles. In section A, the total density of saltwater crocodiles continued to increase unabated following toad invasion. In section B, saltwater crocodile densities increased immediately following toad arrival but then began to decline. Furthermore, when each size class within section A was analysed separately, there were decreases in either the elevation or slope of the relative density time-series in the 0.6–0.9 m, 0.9–1.2 m, 1.5–1.8 m, and 1.8–2.1 m size classes, suggesting that 0.6–1.2 m individuals may be at greater risk in both crocodilian species. However, saltwater crocodile declines in these intermediate size classes appear to be less consistent across different river sections compared to the results for freshwater crocodiles.

Thus, overall, our results suggest that saltwater crocodiles were less affected by toad invasion than were freshwater crocodiles. This observation supports the results of laboratory trials, which demonstrated that saltwater crocodiles are less susceptible to the toad's toxin than are freshwater crocodiles, even in large doses (Smith & Phillips, 2006).

While our results show that significant declines in the density of freshwater crocodiles coincide with cane toad invasion, other factors may also have contributed to the decline. For example, we cannot reject the possibility that interspecific competition (predation and exclusion) with saltwater crocodiles, that are more tolerant to cane toad toxin, may have exacerbated the observed declines in freshwater crocodiles. However, several lines of evidence suggest that the arrival of cane toads rather than competition with saltwater crocodiles is a more plausible mechanism for the observed declines in freshwater crocodiles. First, freshwater crocodiles declined in the upstream sections of the Daly River, where saltwater crocodiles occur at extremely low densities (Fig. 2). Second, our findings accord with the results of laboratory trials, which suggested that saltwater crocodiles and larger freshwater crocodiles are less susceptible to cane toad toxin (Smith & Phillips, 2006). Third, the size classes that declined most dramatically in our analyses also suffered more serious declines following the arrival of cane toads on a different river system in the Northern Territory (Letnic *et al.*, 2008). Fourth, freshwater crocodiles (but not saltwater crocodiles) were observed feeding on cane toads during surveys and dead individuals with no obvious signs of trauma were in these intermediate size classes. It is also worth noting that crocodile habitats in the study area changed little over the study period (Fukuda, Whitehead & Boggs, 2007) and are unlikely to explain our results.

The magnitude of the declines reported here contrast with the results of Somaweera & Shine (2012) and Doody *et al.* (2009), which found no effects of toad arrival on freshwater crocodile populations. Somaweera & Shine (2012) studied freshwater crocodiles immediately following toad arrival in Lake Argyle, Western Australia, a large, permanent man-made water body. They used a different survey methodology (all-terrain vehicle) to that used here (boat), which could be implicated in the different findings. Doody *et al.* (2009) surveyed by boat, but did so in different sections of the Daly River to those we surveyed. That their surveys (2001–2007) found no differences in crocodile abundance before and after toad arrival is in complete contrast to our results. The longer timeframe of our study may help explain some differences, but the most plausible explanation is differences in survey method. Doody *et al.* (2009) conducted boat surveys for crocodiles during the day, whereas we surveyed with a spotlight at night (see Messel *et al.*, 1981; Fukuda *et al.*, 2013). Daylight surveys rely on seeing whole crocodiles (rather than eyeshines), and are highly biased towards large individuals (Webb *et al.*, 1987). The average total length of crocodiles sighted by Doody *et al.* (2009) was approximately 3 m, whereas the maximum average length we observed was 1.9 m in 2013, suggesting size estimation biases are also implicated in the different results obtained. During their survey period (2001–2007), which spanned the arrival of toads, the average length sighted in our surveys increased from 1.1 m in 2001 to 1.7 m in 2007: due to the disappearance of small and intermediate sized animals. Doody *et al.* (2009) reported no consistent change in the mean length of crocodiles sighted, which is to be expected if the surveys focus on only the largest animals. The very different conclusions that we have drawn concerning the impact of cane toads on freshwater crocodiles in the Daly River, highlights the importance of using survey methods that are appropriate for the management objective.

In contrast to the studies mentioned above, Letnic *et al.* (2008) reported that freshwater crocodile populations in the Victoria River decreased by 45% two years after toad arrival, and that intermediate size classes were most severely impacted. Similarly, Britton *et al.* (2013) counted 23 freshwater crocodiles smaller than 1.4 m in isolated pools of the Bullo River, Northern Territory in 2008, but recorded only one crocodile in 2009 after toad arrival.

Our results demonstrate significant changes in the relative densities of freshwater crocodiles following the arrival of toads in section A of the Daly River in 2005, but densities of some size classes appear to have started declining before cane toads were consistently observed throughout this section of the river. This may be because many freshwater crocodiles in section A are migrants from the upstream sections where cane toads were already abundant in earlier years. Freshwater crocodiles require soft-sanded banks for nesting, typically on rock shelves near the water's edge (Webb, Manolis & Sack, 1983c; Webb & Manolis, 2010), and these breeding habitats are only available in sections B–D. However, we could not tell precisely when crocodiles started declining in sections B–D because of the absence of survey data between 1998 and 2008. It is also possible that the initial cane toad invasion front went undetected until the toad population reached appreciable densities.

These observations illustrate the difficulty of confidently attributing population declines to the arrival of an invasive species using correlative observational data. In most cases, it is unclear at what density an invader is likely to impact a population, and this density level will be species-specific. We used the date when toads became routinely seen by researchers (Doody *et al.*, 2009), local residents, and naturalists to examine population-level impacts, as toad sightings before this time were unverified and infrequent. However, Brown *et al.* (2013) documented rapid declines in a population of monitor lizards (*Varanus panoptes*) at another

site in the Northern Territory only months after the arrival of cane toads, when the toads were still at low density. The establishment of cane toads appears to involve two distinct phases. Initially, larger individuals colonize an area (Phillips & Shine, 2005), but exist at low density. This initial phase is then followed by increases in abundance due to smaller animals colonizing from already established areas and breeding from the initial arrivals. Although the expanding edge of the toad invasion front can move quite rapidly (Phillips *et al.*, 2007; Urban *et al.*, 2007), it can sometimes take years for toads to reach appreciable densities (Freeland, 1986; Seabrook & Dettmann, 1996; Shine, 2010; Brown *et al.*, 2013). While some species may exhibit a regional population-scale response to the toad front, for other species, declines may not be apparent until the toad population has become firmly established. This temporal lag in response may be particularly pronounced in species with slow life histories such as crocodiles, and means that even accurate records of the early arrival of cane toads may not correlate tightly with a decline in the local fauna.

The current status of the Australian freshwater crocodile on the IUCN Red List at global, national and state levels is “least concern”, but was last reviewed in 1996 (Webb & Manolis, 2010). However, across the entire Daly River, the density of freshwater crocodiles decreased by 69.5% between 1997 and 2013. As freshwater crocodiles are sexually mature at approximately 12 years of age (Webb & Manolis, 1989), this decline occurred in less than one and a half generations. Declines of this magnitude, which have not ceased or are not reversible, meet the IUCN decline criteria for Endangered at a regional level (IUCN, 2001, 2012; Maes *et al.*, 2012). Cane toads are likely to continue to impact freshwater crocodiles on the Daly River, as toads are difficult to eradicate (Lever, 2001). Critically, the declines we report here suggest that other populations of freshwater crocodiles across northern Australia may also be at risk from cane toads, and thus assessments in other river systems are

warranted. Such data would enable a global-level assessment of extinction risk for this endemic species, and may guide management decisions, such as annual egg harvest quotas. In this regard, it is worth noting that cane toads spread through areas of Queensland inhabited by freshwater crocodiles decades ago (Urban *et al.*, 2007). Although the impact that toads have had on these populations has not been thoroughly studied, the populations are currently not considered to be declining or endangered. This suggests that toad impacts may vary spatially (e.g., according to climate: Letnic *et al.*, 2008), or that crocodile numbers may eventually recover. Continued monitoring of the Daly River population will be needed to ascertain whether declines continue, and whether the population structure stabilises or remains in a state of flux. The management program in the Northern Territory allows for landowners to engage in limited commercial use of the wild population, although little harvesting has actually taken place for the last 15+ years. The results suggest that more caution needs to be exercised should landowners request harvests, particularly of some life stages.

Finally, this investigation would not have been possible had not long-term, standardized monitoring programs been implemented and sustained for crocodiles within the Northern Territory, as a management safeguard. The ability to use the results to assess the impacts of cane toads on the abundance and population structure of crocodiles was thus serendipitous. Nevertheless, our findings highlight the importance of long-term monitoring programs, at least for key species.

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Figure 1. Distribution of cane toads (*R. marina*) in Australia, and the survey sections (A–D) where freshwater crocodiles (*C. johnstoni*) were monitored in the Daly River of the Northern Territory, Australia. Cane toad distribution data were taken from Tingley *et al.* (2014).

Figure 2. Trends in the relative densities of freshwater crocodiles (*C. johnstoni*) and saltwater crocodiles (*C. porosus*) at four sites (rows) in the Daly River, NT, Australia. The dotted line demarcates the point at which invasive cane toads became common in section A (first row). Note that the scale on the y-axis is consistent within sites, but differs between sites.

601 Figure 3. Trends in the relative densities of seven different size classes (columns) of freshwater crocodiles (*C. johnstoni*) at four sites (rows) in
602 the Daly River, NT, Australia. The dotted line demarcates the point at which invasive cane toads became common in section A (first row). Note
603 that the scale on the y-axis is consistent within sites, but differs between sites.
604

Figure 4. Model-averaged parameter estimates and 95% confidence intervals showing the effect of cane toad establishment on the relative densities of seven different size classes of freshwater crocodiles (*C. johnstoni*) at four sites (rows) in the Daly River, NT, Australia. Parameters in each panel illustrate level and slope estimates from regressions between relative freshwater crocodile densities and time, as well as changes in the levels and slopes of these regressions coincident with the arrival of cane toads. Absence of a parameter estimate for a given variable and size class indicates that the variable was not selected in the highest ranked models. The grey horizontal line in each plot demarcates 0.

Figure 5. Trends in the average total lengths of freshwater crocodiles (*C. johnstoni*) and saltwater crocodiles (*C. porosus*) in four sections (A-D) of the Daly River, NT, Australia. The

dotted line demarcates the point at which invasive cane toads became common in section A.

Average total lengths are not shown for *C. porosus* in sections C and D due to low low

sample sizes.

Figure 6. Model-averaged parameter estimates and 95% confidence intervals showing the effect of cane toad establishment on the relative densities of seven different size classes of saltwater crocodiles (*C. porosus*) in section A of the Daly River, NT, Australia (models were not fitted to the data from sections B-D due to low numbers of observations at these sites). Parameters in each panel illustrate level and slope estimates from regressions between relative saltwater crocodile densities and time, as well as changes in the levels and slopes of these regressions coincident with the arrival of cane toads. Absence of a parameter estimate for a given variable and size class indicates that the variable was not selected in the highest ranked models. The grey horizontal line in each plot demarcates 0.

Table 1. Model-averaged coefficients and 95% confidence intervals showing the effect of cane toad establishment on the relative densities of freshwater crocodiles (*C. johnstoni*) and saltwater crocodiles (*C. porosus*) in all size classes combined in the Daly River, NT, Australia (see Fig. 2 for raw data). Coefficients in each row represent level and slope estimates from regressions between relative crocodile densities and time, as well as changes in the levels and slopes of these regressions coincident with the arrival of cane toads. Bold 95% confidence intervals do not overlap 0. Absence of a coefficient estimate indicates that a variable was not selected in the highest ranked models according to AICc. Models were not fitted to the *C. porosus* data from sections C and D due to low numbers of observations at these sites.

Species and survey section	Pre-toad level		Pre-toad slope		Post-toad level change		Post-toad slope change	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
<i>C. johnstoni</i> Section A	0.986	(-0.179, 2.15)	0.016	(-0.085, 0.117)	-1.696	(-2.746, -0.645)	-0.154	(-0.265, -0.042)
<i>C. johnstoni</i> Section B	4.89	(1.48, 8.29)	0.374	(-0.022, 0.769)	-10.675	(-17.293, -4.058)	-0.832	(-1.437, -0.227)
<i>C. johnstoni</i> Section C	2.75	(1.03, 4.47)	0.112	(-0.093, 0.317)	-3.351	(-6.609, -0.093)	-0.586	(-0.880, -0.291)

<i>C. johnstoni</i>	1.82	(-0.113, 3.75)	0.311	(0.105, 0.516)	-7.285	(-11.287, -3.282)	-0.585	(-0.870, -0.300)
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Section D

<i>C. porosus</i>	0.334	(-0.069, 0.736)	0.111	(0.090, 0.132)	-	-	-0.052	(-0.203, 0.100)
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Section A

<i>C. porosus</i>	-0.067	(-0.161, 0.028)	0.031	(0.021, 0.042)	0.598	(0.341, 0.855)	-0.217	(-0.280, -0.155)
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Section B

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Table 2. Model-averaged coefficients and 95% confidence intervals showing the effect of cane toad establishment on mean total length of freshwater crocodiles (*C. johnstoni*) and saltwater crocodiles (*C. porosus*) in the Daly River, NT, Australia (see Fig. 5 for raw data). Coefficients in each row represent level and slope estimates from regressions between mean total lengths and time, as well as changes in the levels and slopes of these regressions coincident with the arrival of cane toads. Bold 95% confidence intervals do not overlap 0. Absence of a parameter estimate for a given variable indicates that the variable was not selected in the highest ranked models. Models were not fitted to the *C. porosus* data from sections C and D due to low numbers of observations at these sites.

Species and survey section	Pre-toad level		Pre-toad slope		Post-toad level change		Post-toad slope change	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
<i>C. johnstoni</i> Section A	1.222	(1.049, 1.397)	-0.002	(-0.012, 0.008)	0.624	(0.363, 0.884)	0.015	(-0.055, 0.086)
<i>C. johnstoni</i> Section B	1.059	(0.898, 1.222)	-0.009	(-0.027, 0.009)	0.597	(0.172, 1.022)	-0.038	(-0.148, 0.071)
<i>C. johnstoni</i> Section C	0.906	(0.761, 1.050)	-0.006	(-0.022, 0.010)	0.509	(0.132, 0.886)	0.024	(-0.075, 0.123)

<i>C. johnstoni</i>	0.934	(0.791, 1.077)	-0.011	(-0.026, 0.004)	0.793	(0.440, 1.147)	0.049	(-0.036, 0.134)
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Section D

<i>C. porosus</i>	1.597	(1.338, 1.856)	0.023	(0.009, 0.038)	0.250	(-0.128, 0.628)	0.043	(-0.044, 0.131)
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Section A

<i>C. porosus</i>	2.223	(2.060, 2.387)	0.004	(-0.005, 0.014)	-	-	-0.029	(-0.051, -0.008)
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Section B

APPENDIX

Figure A1. Trends in the relative densities of different size classes of saltwater crocodiles (*C. porosus*) in section A of the Daly River, NT, Australia. The dotted line demarcates the point at which invasive cane toads became common in section A.

Figure A2. Trends in the relative densities of different size classes of saltwater crocodiles (*C. porosus*) in section B of the Daly River, NT, Australia.

Figure A3. Trends in the relative densities of different size classes of saltwater crocodiles (*C. porosus*) in section C of the Daly River, NT, Australia.

Figure A4. Trends in the relative densities of different size classes of saltwater crocodiles (*C. porosus*) in section D of the Daly River, NT, Australia.

669 Table A1. Frequency of spotlight surveys for freshwater and saltwater crocodiles in the Daly
670 River of the Northern Territory.

	Section			
	A (87.64 km)	B (51.36 km)	C (57.81 km)	D (16.54 km)
1978	✓			
1979				
1980				
1981				
1982				
1983		✓	✓	✓
1984	✓	✓	✓	
1985	✓	✓	✓	✓
1986	✓	✓	✓	✓
1987	✓	✓	✓	✓
1988	✓	✓	✓	✓
1989	✓	✓	✓	✓
1990	✓	✓	✓	✓
1991	✓	✓	✓	✓
1992	✓	✓	✓	✓
1993	✓	✓	✓	✓
1994	✓	✓	✓	✓
1995	✓	✓	✓	✓
1996	✓	✓	✓	✓
1997	✓	✓	✓	✓
1998	✓			

1999				
2000	✓			
2001	✓			
2002				
2003				
2004	✓			
2005				
2006				
2007	✓			
2008				
2009	✓	✓	✓	✓
2010				
2011	✓	✓	✓	✓
2012				
2013	✓	✓	✓	✓

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