



Impacts of invasive cane toads on an Endangered marsupial predator and its prey

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ABSTRACT: Recent research has revealed that impacts of some invasive species are chronic. Invasive cane toads Rhinella marina have apparently caused rapid and severe population-level declines of the Endangered northern quoll Dasyurus hallucatus across tropical Australia; however, more targeted, quantitative impact data are needed to disentangle this from other threats such as fire regimes, disease, feral cats and dingos. Moreover, repeatable counts before, during, after and long after toad invasion are needed in order to determine if short-term impacts are chronic vs. transitory. We used game cameras to monitor 2 quoll populations and their prey over a 5 yr period spanning the invasion of the toxic cane toads in 2 gorges in northwestern Australia. We predicted severe declines in quolls with the toad invasion, and predatory release of 2 prey species of quolls, a rodent and a smaller marsupial. Quolls declined quickly upon arrival of toads, becoming undetectable in one gorge and barely detectable in the other. Identification of individuals via unique spot patterns confirmed that the declines in detection rates were due to changes in relative abundance rather than decreases in activity. Despite quoll declines we found no evidence of mesopredator release; small mammals generally declined as toads arrived. Our research confirmed rapid population-level declines of quolls, and possibly smaller mammals, associated with arrival of invasive cane toads. Importantly, our surveys provide a baseline for future surveys to determine whether these short-term impacts are chronic or transitory, and whether recovery requires assistance from managers.

KEY WORDS: Chronic effects \cdot Recovery \cdot Lethal toxic ingestion \cdot Mesopredator release \cdot Quoll \cdot Toad \cdot Rhinella marina \cdot Dasyurus hallucatus

1. INTRODUCTION

Animal diversity is globally imperilled due to the 5 main anthropogenic threats of habitat loss, introduction of invasive species, overharvest, pollution and climate change. Of these threats, species invasions may be the second leading cause of species loss (Bellard et al. 2016). Unfortunately, the effects of invasive species on native species and communities are difficult to predict due to complex interactions between traits of invaders, native species and the context of in-

vaded communities (Olyarnik et al. 2009). Nevertheless, our rapidly increasing knowledge of the impacts of invasive species has informed conservation and management (Strubbe et al. 2011), and will prove invaluable because the number of species invasions shows no signs of levelling off (Fournier et al. 2019).

Although the study of invasive species and their impacts has exploded in recent decades, we are in urgent need of understanding longer-term effects of species invasions on biological communities. Are short- and medium-term impacts chronic, thus re-

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quiring management to reverse or reduce impacts? Chronic effects, although not always considered as such, are widespread (Strayer et al. 2006, Strayer 2012, Menke et al. 2018). Alternatively, short- or medium-term effects might be transitory. Exposing transitory effects would be particularly useful in reducing costs of management, for example, by freeing up resources urgently needed for management of other invasive species or conservation problems.

The ideal design for determining the ultimate extent of the impacts of invasive species on biological communities requires monitoring the absolute or relative abundance of impacted populations before, during, after and long after the invasion. Unfortunately, this is not often possible due to the typical lack of pre-invasion data and because monitoring longer-term impacts requires sustained funding and effort. A key recurring problem is that by the time an invader establishes and spreads, it is too late to measure pre-invasion (relative) abundance of impacted species (reviewed by Lockwood et al. 2013).

One invasion for which there has been ample time to measure pre-invasion abundance is that of cane toads *Rhinella marina* across tropical Australia. Since their introduction into the northeast of the country in 1935, toads have been steadily spreading westward, a journey that will end within the next ~5–10 yr when they will reach the west coast (Doody et al. 2018), providing nearly 100 yr of opportunity for scientists to measure their impacts (Shine 2010). Although quantitative studies on the impacts of cane toads in Australia did not begin until around 2000, there are now ample studies revealing that the toxic toads cause population-level impacts on native wildlife that attempt to consume them, and in some cases, species declines are chronic (Doody et al. 2017).

Perhaps the most severely toad-impacted native Australian species is the northern quoll Dasyurus hallucatus, a medium-sized carnivorous marsupial that succumbs to toad toxins during ingestion (O'Donnell et al. 2010), leading to severe populationlevel declines and even local or regional extinctions (Woinarski et al. 2008, 2011). In the Northern Territory, at least 4 populations were either decimated or were no longer detectable after toad arrival (Oakwood 2004, Watson & Woinarski 2003, 2004, Oakwood & Foster 2008). These declines and extirpations led to (1) the listing of D. hallucatus as Endangered at the federal (Environment Protection and Biodiversity Conservation [EPBC] Act 1999) and international levels (Oakwood et al. 2016), and to the listing of *R*. marina as a key threatening process to biodiversity under Australia's EPBC Act (Woinarski et al. 2008).

Despite the demonstrated impact of cane toads on quoll populations, quolls had already declined prior to toad arrival, possibly due to changed fire regimes, feral cats, disease or some combination of these factors (Woinarski et al. 2008). Thus, monitoring quoll populations just before, during and just after toad invasion are needed to disentangle toad impacts from other threats; moreover, such monitoring provides a basis for determining any recovery or future further declines. In the meantime, cane toads have continued to spread westward and into the Kimberley Region, one of the last wilderness frontiers in Australia.

We tested the hypothesis that cane toads directly cause quoll declines by monitoring 2 quoll populations for 5 yr in a remote area of the Kimberley Region in tropical northwest Australia. We used remote cameras to determine detection rates, a proxy for relative abundance, of 2 populations of northern quolls for 2 yr prior to, 1 yr during and 2 yr after the toad invasion. We predicted that quolls would decline quickly and severely upon toad arrival. Cameras also monitored 2 prey species of quolls, a rodent (rock rat Zyzomys argurus) and a carnivorous marsupial (Ningbing false antechinus Pseudantechinus ningbingi; hereafter NFA); we hypothesized that populations of these prey species would increase following quoll declines due to mesopredator release (D. hallucatus include small mammals in their diet). In contrast, we predicted no significant change in abundance of the scaly-tailed possum Wyulda squamicaudata associated with the toad invasion, because its size likely excludes it as common prey of quolls. Assuming that declines occurred in quoll populations, our study provides a baseline for monitoring any recovery of quolls in the future, and thus for determining whether toadinduced declines are chronic or transitory.

2. MATERIALS AND METHODS

2.1. Study area and survey methods

The 2 study populations were at Emma Gorge and El Questro Gorge, separated by ~17 km, and both located in the Cockburn Ranges within El Questro Wilderness Park, Western Australia (15° 53′ 42.12″ S, 128° 7′ 56.84″ E). The Cockburn Ranges rise to ~400 m above the adjacent floodplain and open savanna. The climate is wet-dry tropics, with little rainfall during the dry season (April–October) compared to ~800 mm of rain during the wet season (November–May) (Australian Bureau of Meteorology, www.bom.gov.au).

Preliminary camera data from 2009 and observations from El Questro tour guides indicated that quolls were common in the gorges. Both gorges feature perennial creeks, shading rainforest elements and cliffs 50–100 m above their respective perennial creeks. Emma Gorge is 1.6 km long, relatively wide with open scree slopes and terminates at a ca. 80 m high waterfall (see also Doody et al. 2015a). El Questro Gorge is 3.5 km long, relatively narrow, and mostly shaded by palms and other overstorey vegetation.

We monitored the relative abundance of quolls, rock rats, NFAs, scaly-tailed possums and cane toads in both gorges using game cameras for 5 yr (2010–11 through 2014–15). Rock rats are medium-sized omnivorous rodents that are common across much of tropical northern Australia (Van Dyck & Strahan 2008). NFAs are small carnivorous marsupials endemic to the Kimberley Region and surrounding area (Van Dyck & Strahan 2008). Scaly-tailed possums are medium-sized, mainly herbivorous Kimberley endemics that live in rock crevices and caves in gorge country (Van Dyck & Strahan 2008). Due to their smaller sizes, rock rats and NFAs are preyed upon by quolls (Radford 2012, Dunlop et al. 2017), whereas the larger (adult) scaly-tailed possums are likely not.

Ten Moultrie I-35® cameras were deployed annually at Emma Gorge; at El Questro Gorge, 10 cameras were employed in 2010–11 and 5 cameras for the remaining 4 yr. Cameras were set to take 1 picture min⁻¹ when triggered by motion during the day or by heat (infrared) at night. Cameras were placed 200–300 m apart in the same exact positions each year (cameras were strapped to trees or rocks). Most cameras were deployed along the gorge walls to maximize detection rates (no baits were used). Cameras were typically deployed in late June and retrieved the following May; battery life resulted in cameras operating for 3–11 mo.

2.2. Data analyses

To account for the fact that game cameras ran for different numbers of nights due to varying battery life, the total number of photographs of each target species (cane toads, quolls, rock rats, NFAs, scalytailed possums) from each of the game cameras was tallied, divided by the number of nights each camera ran and multiplied by 100 to give a relative abundance of animals per 100 trap-night units. A generalised linear mixed model (GLMM) with Poisson distribution and log link function was constructed in SAS (version 9.4) using the 'glimmix' procedure, with

fixed effects for toad presence, site (i.e. gorge) and their interaction. A random effect of survey year was added to account for year-to-year variability not explained by either toad presence or site. For quolls, where a zero count across all cameras was recorded in some years after the arrival of toads, a single record was added to the data set for one camera in that year in order for the models to converge. This approach is conservative, as it would theoretically lead to a slight underestimate of the significance and magnitude of decline for that species after the arrival of toads. Where there was a significant effect of site or an interaction between site and toad invasion, differences in least squares means were examined for the 2 sites independently to facilitate commenting on the patterns of change. Means for invasion stage are fitted model means incorporating random effect of year, except in the case of quolls post-toad invasion at Emma Gorge, where a false record was added (see above); in this case, the reported mean remained as zero. In cases where animal abundance associated with the toad invasion decreased or increased significantly, the % magnitude of the change was calculated by dividing the mean relative survey count post-toad invasion by the mean relative count pretoad invasion, and multiplying by 100.

To determine if changes in quoll detection rate determined by cameras reflected changes in quoll abundance vs. changes in quoll activity by a consistent number of individuals, we explored the relationship between quoll detection and the minimum known number of quoll individuals at a given site in a given year, determined from photographs. Individuals were identified by their unique spotting pattern. We ran a linear regression in JMP (version 14) testing the relationship of annual quoll detections, site and the interaction between the 2 factors against the minimum number of individuals recorded each year for each site.

3. RESULTS

3.1. Timing of toad invasion

Cameras revealed that toads were absent in Emma Gorge in 2010–11 and 2011–12, invaded in low numbers in 2012–13 (N=9 detections), and were very abundant in 2013–14 (N=870) and 2014–15 (N=730). Cane toads were not trapped in a pitfall line at Emma Gorge during 2012 (May–July), but 9 individual toads were detected on Emma Gorge cameras later that year (12 July, 30 August, 31 August, 2 Octo-

ber, 5 October, 6 October, 18 November, 10 December, 10 March [2013]). In June and July 2012, we also discovered a few dead toads in the Emma Gorge plunge pool that had apparently fallen over the Emma waterfall. Finally, we discovered 3 toads while on a hike above the waterfall in the Cockburn escarpment in July 2012. By 2013 cane toads were abundant throughout the gorge including along both sides of the toad fence.

Cameras revealed that toads were absent in El Questro Gorge in 2010–11 and 2011–12, appeared in very low numbers in 2012–13 (N = 3) and 2013–14 (N = 3), and were abundant in 2014–15 (N = 126). The 3 toads on camera at El Questro Gorge in 2012–13 were detected on 20 January (N = 2) and 16 April 2013. El Questro Gorge is approximately 17 km southwest of Emma Gorge.

3.2. Relative abundance of quolls

A minimum of 35 individual quolls was detected 135 times at El Questro Gorge, while a minimum of 9 individuals was detected 33 times at Emma Gorge (Table 1). Quoll detection rate was a strong and significant predictor of quoll abundance (F = 108.03, p < 0.001, $R^2 = 0.98$; Fig. 1). This was true across both sites, with no interaction effect of site and quoll detection rate on the minimum number of individual quolls (Fig. 1).

There was a significant effect of site on quoll abundance, with more quolls detected at El Questro Gorge compared to Emma Gorge ($F_{1, 55} = 8.73$, p > 0.01; Fig. 1). There was a significant effect of toad presence on quoll abundance, with the arrival of cane toads leading to a decrease in overall quoll detection in years post-toad invasion ($F_{1, 55} = 5.06$, p = 0.029; Fig. 2). Quoll detection decreased from fitted

Table 1. Minimum number of northern quoll *Dasyurus hallucatus* individuals based on unique spot patterns, compared to the total number of detections from camera traps for each year. EQG = El Questro Gorge, EG = Emma Gorge

Year	Trap nights		Quoll detections		Inividual quolls	
	EQG	EG	EQG	EG	EQG	EG
2010-2011	834	1041	37	10	11	3
2011–2012	855 920	1294 1293	29 59	23	6 16	6 0
2013–2014	414	945	0	0	0	0
2014-2015	611	1505	1	0	1	0
Totals	3634	6078	126	33	35	9

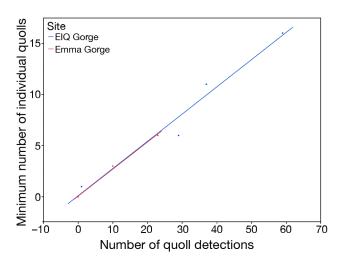


Fig. 1. Relationship between the minimum number of individual northern quolls and the number of quoll detections for each gorge: El Questro (ElQ) and Emma. Detection rates were from camera traps, while the minimum number of individuals was determined by comparing unique spot patterns in photographs

model means of 2.71 quolls per 100 trap nights preinvasion to 0.81 quolls per 100 trap nights post-invasion (70% relative decrease) at El Questro Gorge and from 1.39 quolls per 100 trap nights pre-invasion to zero detections post-invasion at Emma Gorge (100 % relative decrease). There was a significant interaction between site and toad presence ($F_{1.55} = 5.4$, p = 0.024), due to the difference in magnitude of decrease of quoll detection at the 2 sites, which is attributable to the first 'post-invasion' year at El Questro Gorge (2012–13) which did not experience a significant decrease in quoll detection (Fig. 2). This is most likely due to the fact that toads were not detected at that site until late January 2013, which is towards the very end of that wet season and the camera recording period for that year (and only 3 toads were detected in that time). This is in contrast to Emma Gorge, where toads were shown to have arrived very early in the 2012-13 season (first detected in July 2012).

3.3. Relative abundance of quoll prey

There was a significant effect of site on rock rat abundance, with more rock rats detected at El Questro Gorge compared to Emma Gorge ($F_{1,55}$ = 26.19, p > 0.001; Fig. 3). There was a significant effect of toad presence on rock rat abundance, with the arrival of cane toads leading to a decrease in overall rock rat detection in years post-toad invasion ($F_{1,55}$ = 6.86, p = 0.011; Fig. 3). Rock rat detection per 100 trap nights

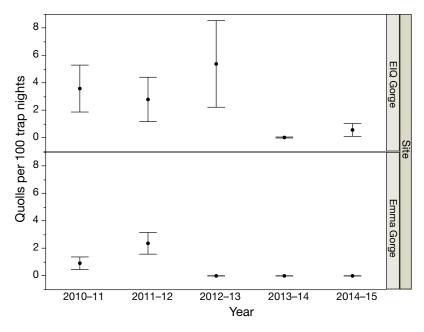


Fig. 2. Declines in detection rates of northern quolls *Dasyurus hallucatus*, before and after the arrival of invasive cane toads *Rhinella marina* at 2 sites in the eastern Kimberley. Toads arrived mid-2012 at Emma Gorge and early 2013 at El Questro Gorge. All data are mean detection rates \pm 1 SE

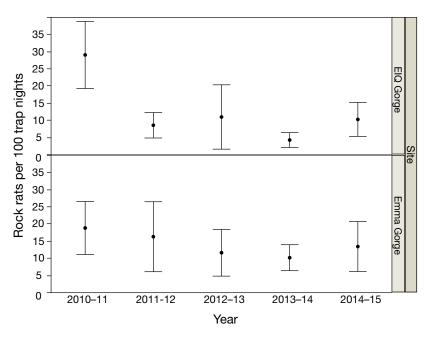


Fig. 3. Detection rate of common rock rats *Zyzomys argurus*, before and after invasive cane toad arrival at 2 sites in the eastern Kimberley Region. Details as in Fig. 2

decreased from fitted model means of 19.26 rats preto 8.46 rats post-toad invasion (56% relative decrease) at El Questro Gorge and from 10.58 rats preto 6.55 rats post-invasion at Emma Gorge (38% rela-

tive decrease). There was a significant interaction between site and toad presence ($F_{1, 55} = 6.07$, p = 0.017). One photograph showed a quoll with what appeared to be a rock rat in its mouth.

NFAs occurred in significant numbers only at Emma Gorge and were too few at El Questro Gorge to meaningfully model (only 6 were detected in all years prior to toad invasion at El Questro Gorge). At Emma Gorge, there was a significant effect of toad presence on NFA abundance, with the arrival of cane toads leading to a decrease in NFA detection in years post-toad invasion ($F_{1,32} = 4.42$, p = 0.04; Fig. 4). Detection rates per 100 trap nights decreased from fitted model means of 0.58 NFAs pre- to 0.11 NFAs post-invasion, an 81% relative decrease.

3.4. Other species

At Emma Gorge, detection rates of scaly-tailed possums were sufficient to determine any trends associated with cane toad arrival. Because this species is mainly herbivorous, however, and because there is no known trophic link between it and quolls, we anticipated no trend with the arrival of toads. Indeed, there was no significant effect of toad presence on scaly-tailed possum abundance ($F_{1, 32} = 0.01$, p = 0.95). Detection per 100 trap nights from the fitted model means was 0.53 possums prior to toad arrival and 0.56 possums post-toad arrival.

Cameras also detected other species that would be expected to be impacted by invasive cane toads, or to be included in the diet of quolls; however, these species were detected in numbers too low to confidently assign any trends to their detection rates relative to the toad invasion. These species included feral cats *Felis catus*, dingos *Canis lupus*, water rats *Hydro-*

 $mys\ chrysogaster$, echidnas $Tachyglossus\ aculeatus$, common tree snakes $Dendrelaphus\ punctulatus$, Mitchell's water monitors $Varanus\ mitchelli$, ridge-tailed monitors $V.\ acanthurus$, Kimberley rock monitors

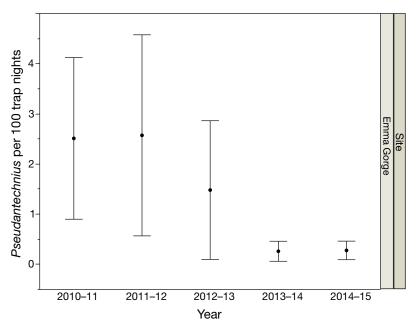


Fig. 4. Detection rate of Ningbing false antechinus *Pseudantechinus ning-bingi*, before and after invasive cane toad arrival at Emma Gorge in the east-ern Kimberley Region. Details as in Fig. 2

V. glauerti and black-palmed monitors *V. glebopal-ma*. Although detection rates of these species were too low to examine any declines, future comparative surveys could detect any increases due to toad-induced quoll declines (mesopredator release).

4. DISCUSSION

We demonstrated significant population-level declines of northern quolls associated with the cane toad invasion at 2 sites, possibly resulting in extirpation at one of the sites (Fig. 2). Data on individual quolls confirmed that the changes in detection rates were due to decreases in abundance rather than individual activity (Fig. 1, Table 1). The declines were tightly coupled with the arrival of toads, and we could rule out most of the other possible threats to quoll populations, aside from disease. We did not find mesopredator release in 2 quoll prey species (rock rats and NFAs); rather, these species appeared to also decline with toad arrival (Figs. 3 & 4). Importantly, our study provides a baseline for determining the timing and extent of recovery of quolls, given that anecdotes suggest that recovery may have occurred in some areas without baselines.

Quoll detections decreased with the arrival of cane toads at both sites, but there were differences in timing and magnitude between sites. Quolls

began to decline in 2012–13 at Emma Gorge compared to 2013-14 at El Questro Gorge (Fig. 2); this difference can be explained by differences in the timing of arrival of the toads. According to camera data, toads began to arrive in mid-2012 at Emma Gorge compared to early 2013 at El Questro Gorge. Quoll detections declined to zero at Emma Gorge, while there were 3 detections at El Questro Gorge in 2014-15, after not being detected in 2013-14 (Fig. 2). The difference in the magnitude of the decline between sites may be at least partly due to higher pre-toad detection rates at El Questro Gorge compared to Emma Gorge, rather than a population difference in actual strength of impacts.

The tight coupling of quoll declines with the arrival of cane toads strongly suggests that the toad invasion was the cause of the decline. One camera

at El Questro Gorge illustrates the magnitude and speed of toad impacts on quolls. The camera photographed at least 16 individual quolls, distinguished by their spot patterns, 49 times from 27 June 2012 to 15 January 2013 (Fig. 5). The same camera photographed the first cane toad in the gorge on 20 January 2013 (Fig. 5), and quolls were not detected again by the camera, despite its continued deployment through 19 April 2013.

Cane toads are not the only threat to northern quoll populations; indeed, quolls were already in decline in the Top End of the Northern Territory prior to toad arrival (Braithwaite & Griffiths 1994). Cane toads may have exacerbated these declines, however (Woinarski et al. 2011), and populations were reported to have been decimated or to have disappeared around the time that toads arrived (Oakwood 2004, Watson & Woinarski 2003, 2004, Oakwood & Foster 2008). It is possible that other threats contributed to the quoll declines in our study. However, there were no fires coinciding with the declines, and we have no knowledge of disease or changes in predator numbers at that time. Although quolls are preyed upon by dingos and feral cats (Oakwood 2000, Cremona et al. 2017), both were apparently rare within the gorges based on very few photographs from our cameras, and both were there before and after toad arrival. Moreover, dingo populations may be reduced in the short-term, following toad arrival (Catling et al. 1999).





Fig. 5. 'Replacement' of northern quolls with cane toads in El Questro Gorge. (A) The last quoll photographed by one camera in 2013 (15 January). This camera photographed at least 16 individual quolls 49 times between 27 July 2012 and 15 January 2013. (B) First photograph of a cane toad (same camera) 5 d after the last quoll was photographed; quolls were never photographed again by that camera, despite the camera being deployed until 19 April 2013

Toads can cause trophic cascades by essentially removing top predators; for example, marked toad-induced declines in the yellow-spotted monitor *Varanus panoptes* caused increases in several of their prey, including lizards, snakes, turtles and crocodiles (the latter two via egg predation) (Doody et al. 2006, 2009, 2013, 2015b, 2017; see also Feit et al. 2018, Radford et al. 2020 for cascades involving other monitor lizard species). Such cascades associated with toad-induced quoll declines were not evident in our study. Rather, rock rats decreased significantly in both gorges as cane toads invaded, although overall post-invasion numbers were generally within the range of pre-invasion numbers, whereas NFAs decreased markedly at the gorge in which we were able to detect sufficient

numbers for analysis (Figs. 3 & 4). Two cautions here: (1) our modest sample sizes may have not detected cascades that could be occurring; and (2) a lag in mesopredator release could have occurred, meaning that any increases in rock rats and NFAs could have occurred after our study. For example, a lag of 2-3 yr separated increases of common tree snakes following toad invasion (Doody et al. 2013). If decreases in detection rates of quoll prey in our study (rock rats and NFAs) reflect declines due to lethal toxic ingestion of cane toads, these populations may contain individuals that learn to avoid toads, as found in the laboratory for common planigales Planigale maculata (Webb et al. 2008). Some other small mammals declined after the arrival of toads, however, including the northern brushtailed phascogale Phascogale pirata, fawn antechinus Antechinus bellus, Kakadu dunnart Sminthopsis bindi, northern brown bandicoot Isoodon macrourus, common brushtail possum Trichosurus vulpecula, pale field rat Rattus tunneyi and black-footed tree-rat Mesembriomys gouldii (Woinarski et al. 2010). Declines in these animals and in the small mammals in our study may reflect the broader decline of small mammals in the Kimberley (Woinarski et al. 2011) rather than toad impacts. In support, rock rats ignored cane toads as food in laboratory experiments (Cabrera-Guzmán et al. 2015). Finally, the decreases in small mammals may reflect toad-induced increases (mesopredator release) in some other predator(s) such as pythons that feed on them (e.g. Radford et al. 2020). Further, more robust sampling at sites with baseline data in areas ahead of the toad invasion front are needed to determine the ultimate impact of cane toads on small mammals, which could reflect a complex mix of toad-induced declines, mesopredator releases and negligible effects.

Although baseline data are lacking, there is anecdotal evidence for the persistence (and perhaps recovery) of a few quoll populations in north Queensland where toads invaded many decades ago (Ujvari et al. 2013). Without baselines, we cannot readily distinguish between persistence and recovery. Our results offer baseline data for monitoring any recovery of northern quoll populations. First, we are confident, due to the timing of our study relative to the cane toad invasion, that the quoll declines we observed are attributable to toads. Second, our methods are easily repeatable; by sampling every 5-10 yr, for example, we can determine if quolls are recovering. By surveying the 2 gorges, we may also document variation in recovery across populations. Moreover, we can continue to monitor populations of quoll prey to determine if there is a strong population-level link between predatory quolls and their prey. Ultimately, our results should contribute

to disentangling the threat of cane toads from other threats to northern quolls. Given the difficulty in controlling cane toads (Shine & Doody 2011, Tingley et al. 2017), monitoring recovery of quolls would be invaluable for managers tasked with making decisions on where to invest resources.

More broadly, our study serves as a reminder that longer-term studies of the effects of invasive species are needed. Determining whether short-term impacts are transient or chronic can obviously change management tactics and the prudent use of resources. Relatedly, observations that recovery could potentially occur unassisted, via dispersal of individuals from resilient populations, provides a potential tool for conservation managers to help mitigate the impacts of invasive cane toads (Doody et al. 2020). Because the recovery of quolls from population crashes could take decades, the likely conservation challenge is managing the rapid loss of genetic diversity due to population bottlenecks (Frankham 2010, Doody et al. 2020). One strategy would be facilitated genetic rescue ahead of the toad front. Impacts could be theoretically reduced by moving individuals from resilient or recovered populations to populations ahead of the toad front (Madsen et al. 1999, Kelly & Phillips 2019), or simply by moving genes through the storage and transport of gametes and use of assisted reproductive technologies (Clulow & Clulow 2016, Tingley et al. 2017, Clulow et al. 2018, Doody et al. 2020).

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