Predator suppression by a toxic invader does not cascade to prey due to predation by alternate predators

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Abstract  Invasive species often have catastrophic direct effects on native species through increased competition and predation. Less well understood are indirect, cascading effects across trophic levels. To reveal trophic disruptions caused by invasive species, it is necessary to document interactions between species at different trophic levels and across guilds. Here, we take this approach to quantify the impact of the invasion of cane toads at a riparian site in the Kimberley, northwest Australia. These toads are toxic to many native vertebrate predators and following toad arrival we observed the expected severe population decline in monitor lizards. Contrary to expectations however, this did not facilitate species in the next trophic level down: the abundance of their reptilian prey, as well as nest success of a songbird whose nests were predominantly depredated by monitor lizards, remained unchanged. Instead, detailed observations suggest a change in the suite of nest predators, with monitor lizards being replaced by other—mainly avian—predators, possibly reflecting their release from competitors that are more efficient nest predators. Hence, our findings highlight complex indirect effects of an invasive species across trophic levels and indicate that trophic cascades can go undetected when failing to include direct observations on predator–prey interactions.

Keywords  Cane toad · Nest predation · Trophic cascade · Predator–prey interaction · Facilitation · Purple-crowned fairy-wrens

Introduction

The invasion of environments by non-native species is ever increasing, posing a significant threat to ecosystems globally (Seebens et al. 2017). Invaders cause significant declines in native species richness and abundance through, for example, direct competition over shared resources, increased predation, and disease transmission (Castorani and Hovel 2015; Gallardo et al. 2016; Mollot et al. 2017; Snyder and Evans 2006). Because invasive species can alter the relative abundance of species across trophic levels, they can also have indirect ecological effects that are mediated through trophic webs (Gallardo et al. 2016; White et al. 2006). For example, invasives can shift the balance of interspecific interactions and release native species from competition, parasites and/or predation (i.e. facilitation) (Bruno et al. 2003; Doody et al. 2013, 2006; Rodriguez 2006; Snyder and Evans 2006; Thomsen et al. 2010). As a result, the introduction of alien

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species can cause major trophic disruptions, altering the structure and function of ecosystems and disrupting key processes such as pollination, seed dispersal, and nutrient-cycling (Feit et al. 2020; Gallardo et al. 2016; Mack et al. 2000; White et al. 2006). Yet, indirect effects are often overlooked in the study and management of invasives (Castorani and Hovel 2015; Gallardo et al. 2016; Mack et al. 2000; White et al. 2006), perhaps because they can be complex (see e.g. O’Dowd et al. 2003). Predator–prey relationships are predicted to be especially disrupted by alien species introductions (Castorani and Hovel 2015; Doody et al. 2015b; Estes et al. 2011; Rodriguez 2006). To enhance our understanding of how invasive species may alter predator–prey relationships and, ultimately, trophic food webs, we need to look in detail at interactions between species at different trophic levels rather than their abundances alone (e.g. Castorani and Hovel 2015).

The invasion of the cane toad, *Rhinella marina*, in Australia provides an excellent opportunity to study the diverse direct and indirect impacts that introduced species may have on native ecosystems (Jolly et al. 2015; Shine 2010). While toads can negatively impact native wildlife via predation and competition (Shine 2014), because toads are fatally toxic to many Australian predators, the most significant impacts are suffered by native predators that mistake them for non-toxic prey (reviewed in Shine 2010). Of the species affected, northern quolls (*Dasyurus hallucatus*) and large, predatory monitor lizards (varanids) have suffered some of the most severe population-level impacts (Doody et al. 2009, 2015b, 2021; Feit et al. 2018; Griffiths and McKay 2007). As monitors are top predators which consume eggs, nestling birds, smaller lizards and snakes (Doody et al. 2012, 2015a, 2015b), toad-caused declines in some monitor species appear to have disturbed existing relationships with the lower trophic levels, releasing prey from predators. Some studies have documented increases in the abundance and recruitment of prey species formerly consumed by monitors (i.e. facilitation) (Doody et al. 2013, 2009, 2006, 2015b; Feit et al. 2020, 2018). However, changes in predator–prey relationships may not become immediately clear based on abundance of predator and prey species alone. Therefore, to accurately reveal facilitation and other cascading trophic effects, we require detailed studies that incorporate direct observations on interactions between predators and prey before and after cane toad invasion (Doody et al. 2015b; Feit et al. 2020).

Here, we study direct interactions between (near) top predators and prey and their respective abundances, for two years prior to and three years following cane toad invasion. We focus on a trophic web in the riparian zone in the Kimberley, Western Australia, which is associated with high productivity and species richness as well as significant conservation value (Capon et al. 2013; Woinarski et al. 2000). We document the effect of the arrival of cane toads on local populations of native predatory reptiles (monitor lizards and snakes), predicting a decrease in abundance of these predators (as in Doody et al. 2009, 2015b, 2021; Feit et al. 2018; Griffiths and McKay 2007). We test whether this has in turn impacted species at lower trophic levels, including smaller reptiles normally eaten by these predators (e.g. small dragons, smaller snakes), predicting an increase in their abundance (as in Doody et al. 2013, 2009, 2006, 2015b; Feit et al. 2020, 2018). To investigate direct and indirect effects of predator and competitor release in detail, we focus on the endangered purple-crowned fairy-wren, *Malurus coronatus coronatus*, an avian indicator species of riparian habitat health (Skroblin and Legge 2012). This is a typical species predicted to be facilitated by the arrival of toads (Doody et al. 2015b) as purple-crowned fairy-wren nests are often depredated by monitor lizards (Teunissen et al. 2020). To test whether purple-crowned fairy-wrens experienced the predicted boost in recruitment due to reduced nest predation, we quantify their nest success. Additionally, we track the identity of nest predators pre- and post-invasion to test the prediction that changes in nest success result from changes in reptilian predator abundance and predation rate.

**Methods**

Research took place from 2016 to 2020 along 5 km of Annie Creek at Australian Wildlife Conservancy’s Mornington Wildlife Sanctuary in northwest Australia (S17°31’ E126°6’). Here, a colour-banded population of purple-crowned fairy-wrens has been studied since 2005. The advancement of cane toads along the invasion front was closely monitored prior to cane toad arrival, with the first toads arriving at our study site late during the 2016/2017 wet season, followed
by their establishment during the subsequent dry season. Hence, 2016 and 2017 were pre-toad years, and 2018–2020 post-toad years.

**Predator and prey surveys**

We conducted visual encounter surveys in the riparian zone between 7–25 April annually (2016–2020) to quantify abundance of monitor lizards and their reptilian prey, and any other known reptilian and avian predators of passerine nests. Each fairy-wren territory was surveyed separately by slowly (at ~2 km/h) walking from one end of the territory to the other and pausing in the centre of the territory for 10 min, while recording all predators and reptilian prey seen along the way (total mean duration ± SE = 14.5 ± 0.1 min). Since fairy-wren territories are aligned linearly and contiguously along the creek (Kingma et al. 2010; Rowley and Russell 1993), the entire 5 km length of creek was surveyed this way. Two surveys were conducted for each side of the creek—one in the morning (6:20–11:45 am) and one in the afternoon (1:25–5:45 pm), i.e. four surveys in total per territory—each year (N = 42–50 territories, i.e. 168–200 surveys per year). Temperature data corresponding to surveys were obtained from Fitzroy Crossing Aero station (Bureau of Meteorology weather station 003,093, ~ 93 km from our field site), and is highly correlated with temperature at our field site (Roast et al. 2019). The mid-point between minimum and maximum daily temperature was used for surveys conducted in the morning, and maximum daily temperature for afternoon surveys. Observers conducting the survey varied between years (8 observers in total), but one observer (N.T.) conducted surveys every year, allowing us to control for potential observer effects.

Predator and prey species recorded were yellow-spotted monitors (*Varanus panoptes*), Mitchell’s water monitors (*V. mitchelli*), Mertens’ water monitor (*V. mertensi*), spotted tree monitors (*V. scalaris*), black-headed monitors (*V. tristis*), common tree snakes (*Dendrelaphis punctulatus*), olive pythons (*Lialis olivaceus*), greater black whipsnakes (*Demansia papuensis*), king brown snakes (*Pseudochis australis*), dragons (predominantly Horner’s dragons, *Lophognathus horneri*), collared sparrowhawks (*Accipiter cirrocephalus*), brown goshawks (*Accipiter fasciatus*), pheasant coucals (*Centropus phasianinus*), blue-winged kookaburras (*Dacelo leachii*), and brush cuckoos (*Cacomantis variolosus*). Since cryptic reptile species might go undetected or remain unidentified more frequently during visual encounter surveys, we also recorded any reptiles that were only heard or seen at a glimpse and therefore could not be identified as either monitor lizard or dragon. The abundance of such detections did not change following cane toad arrival ($B ± SE = −0.00 ± 0.17, z = −0.02, P = 0.98$), indicating that any observed change in abundance of monitor lizards or dragons cannot be attributed to a difference in observers’ detection or identification ability between years.

Of the species detected during surveys, pythons, small-sized monitor lizards (all species listed above except yellow-spotted monitors), and all avian species listed above are potential predators of fairy-wren nests (Teunissen et al. 2020; see also Results and supplementary information 2 for a full list of all recorded predators). However, since surveys were conducted during the day, nocturnal reptilian nest predators (notably brown tree snakes, *Boiga irregularis*; see Results) were not detected. Of species detected, all monitor lizards and some larger snake species are expected to reduce in number following introduction of cane toads (Doody et al. 2009, 2015b; Feit et al. 2020, 2018; Griffiths and McKay 2007; Phillips et al. 2003). Dragons and smaller snakes (e.g. common tree snakes) are in turn prey of these larger predators (Brown et al. 2011; Doody et al. 2013, 2015b; Feit et al. 2020; Shine 1986) (see also Fig. 3).

**Purple-crowned fairy-wren nest predation**

Purple-crowned fairy-wrens are riparian habitat specialists endemic to northern Australia, and an important biological indicator for riparian habitat health (Rowley and Russell 1993; Skroblin and Legge 2012). They face similar threats as other riparian species, with the western subspecies listed as endangered as a result of habitat degradation by cattle and intense fire (Skroblin and Legge 2010, 2012). They face high rates of nest predation (57% of nests over a 5-year period at our study site; Hidalgo Aranzamendi 2017), mostly by reptiles such as monitor lizards and snakes (Teunissen et al. 2020). Groups form territories that are defended year-round (Kingma et al. 2010; Rowley and Russell 1993). Most breeding takes place during the wet season (Dec–Apr). Incubation lasts for approximately 14 days, and the nestling period lasts
for around 13 days (Kingma et al. 2010; Teunissen et al. 2020).

To monitor nest predation pre- and post-toad arrival, we followed nest activity of ~50 fairy-wren groups per year throughout the wet season (Dec–Apr) in 2016, 2017, 2018 and 2020 (for simplicity, December is included in the following year, e.g. Dec 2016 is included in “Year” 2017). All 462 nests found were monitored for egg laying, hatching, and fledging through regular nest checks at approximately three-day intervals. For all failed nests, their cause of failure was recorded (e.g. flooded, starved, depredated). To identify nest predators, we placed camouflaged motion-triggered trail cameras (Bushnell Trophy Cam Aggressor Low Glow) at 202 nests with eggs or nestlings. Cameras were attached to surrounding vegetation 1–3 m from the nest, set to record a 10 s video each time they were triggered, and left until the nest failed or fledged.

Habitat quality assessments

Habitat quality may affect local predator abundance and thus nest predation risk. Therefore, we quantified habitat quality for each fairy-wren territory, enabling us to link habitat quality to individual nests and to predator abundance. We determined habitat quality for each territory by estimating Pandanus aquaticus cover, an established indicator of riparian habitat quality (e.g. Hidalgo Aranzamendi et al. 2016; Kingma et al. 2011). In 2015, 2017 and 2018, habitat quality surveys were conducted using methods described in detail in Hidalgo Aranzamendi et al. (2016). In 2020, a new method was used to estimate Pandanus aquaticus volume. The two methods are highly correlated, and estimates obtained using the new method were converted to the same scale as the older method (see Supplementary Information 1). Habitat quality surveys did not take place in 2016 and 2019, therefore data for these years were interpolated based on habitat quality in the preceding and the following year.

Statistical analyses

All analyses were performed in R 4.0.0 (R Core Development Team 2020). To assess whether predator and prey species have changed in abundance following the arrival of cane toads at our study site, we ran four generalised linear mixed models (GLMMs) using the ‘lme4’ (Bates et al. 2015) and ‘lmerTest’ (Kuznetsova et al. 2017) packages. These included as response variable the number of snakes, monitor lizards, dragons, and avian predators, respectively, encountered during a single predator and prey survey (i.e. on one side of the creek on one fairy-wren territory, conducted during the morning or afternoon). All snake species were combined because snakes were relatively rarely recorded (on 2% of 940 surveys). Similarly, all monitor lizard species recorded were combined (recorded on 7% of surveys). Avian predators (i.e. sparrowhawks, goshawks, pheasant coucals, kookaburras, and brush cuckoos) were also combined into a single category. Since a given predator or prey category was often not detected during a survey, we used GLMMs with negative binomial distribution. To test for a change in abundance following the arrival of cane toads, we included as fixed effects: toad status (absent 2016–2017, present 2018–2020), habitat quality (to control for potential habitat effects on abundance and/or detection probability of species), temperature at the time of observation, and the time at which the survey was conducted (to control for activity level of reptiles and birds; e.g. Manu and Cresswell 2013; Moore et al. 2020; Shine 1986; Spence-Bailey et al. 2010). Territory ID and Observer ID were included as random terms to account for replication across territories and potential observer effects.

To test whether the likelihood of predation of purple-crowned fairy-wren nests changed with the arrival of cane toads, we analysed daily nest survival rate using the logistic exposure method with a GLMM approach, which controls for variable exposure periods and stages at which nests are found (Shaffer 2004). Models were optimised using the ‘optimx’ package (Nash and Varadhan 2011). From the moment eggs were laid (N=314 nests: 32 in 2016, 109 in 2017, 103 in 2018, and 70 in 2020), each time a nest was checked we recorded the number of days since the previous nest check and whether the nest survived or failed during the preceding interval. To test for differences in nest survival pre- and post-toad arrival, we included survival (as binomial variable; survived = 1, failed = 0) as response variable and as fixed effects toad status at the field site (absent, present) and nest stage (eggs, nestlings, or brush cuckoo nestling), to control for potential differences in predation probability between nest stages. Cuckoo nestlings
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in particular may suffer higher predation rates compared to fairy-wren nestlings if for instance their begging calls are louder (Jelinek et al. 2016). The model also included habitat quality and month of the year (with December as month 1), and Nest ID as random effect. Nest failures due to causes other than predation (e.g. flooding; 11% of nests, or abandonment; 6% of nests) were censored as we were only interested in differences in nest survival as a result of changes in risk of predation.

Lastly, we tested whether the likelihood of nest predation by each type of predator differed between pre- and post-toad years. For this, we used the 48 nests with trail cameras for which we could identify the predator responsible for nest failure. We ran four separate generalised linear models (GLMs) with binomial distribution that included as response variable whether it was depredated by a monitor lizard (0 = no, 1 = yes), a snake, an avian predator, or a centipede, respectively, and toad status as fixed effect.

Results

Predator and prey abundance

Following the arrival of cane toads, monitor lizards declined significantly in abundance by 71% (Table 1; Fig. 1b). Snake abundance was not significantly affected by toad arrival (Table 1). However, snakes were not commonly detected during surveys in general (6 times in 2016, and 3 times in each of the 2017–2019 surveys) and not at all in 2020 (Fig. 1a), therefore any change in abundance is more likely to go undetected. Although dragon abundance initially increased following toad arrival, numbers decreased in the following two years (Fig. 1c) and there was no clear difference in abundance of dragons between pre- and post-toad years (Table 1). Avian predator abundance did not change over time (Table 1; Fig. 1d).

Fairy-wren nest predation

Overall, 54% of purple-crowned fairy-wren nests with eggs or nestlings were depredated before toads arrived, compared to 48% after toad arrival. Daily survival rate of purple-crowned fairy-wren eggs and nestlings was similar before and after toads arrived at the site (mean daily survival rate ± SE before toad

| Parameter          | Snakes | Monitor lizards | Dragons |
|--------------------|--------|-----------------|---------|
| Intercept          | −0.96 ± 0.63 | −3.09 ± 1.31 | −1.36 ± 0.93 |
| Toad status        | 0.04 ± 0.34 | 0.96 ± 0.03 | 0.30 ± 0.01 |
| Habitat quality    | 0.13 ± 0.05 | 0.30 ± 0.06 | 0.15 ± 0.01 |
| Temperature        | 0.00 ± 0.05 | 0.21 ± 0.01 | 0.02 ± 0.01 |
| Time (hr)          | 0.34 ± 0.06 | 0.03 ± 0.01 | 0.04 ± 0.08 |
| Predation          | 0.11 ± 0.02 | 0.07 ± 0.04 | 0.02 ± 0.01 |

| Evidence for the expected strong decline in monitor lizards following the introduction of cane toads at a riparian site, but no changes in abundance of other reptiles or avian nest predators

| Parameter          | Snakes | Monitor lizards | Dragons |
|--------------------|--------|-----------------|---------|
| Intercept          | −0.96 ± 0.63 | −3.09 ± 1.31 | −1.36 ± 0.93 |
| Toad status        | 0.04 ± 0.34 | 0.96 ± 0.03 | 0.30 ± 0.01 |
| Habitat quality    | 0.13 ± 0.05 | 0.30 ± 0.06 | 0.15 ± 0.01 |
| Temperature        | 0.00 ± 0.05 | 0.21 ± 0.01 | 0.02 ± 0.01 |
| Time (hr)          | 0.34 ± 0.06 | 0.03 ± 0.01 | 0.04 ± 0.08 |

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| Time (hr)          | 0.34 ± 0.06 | 0.03 ± 0.01 | 0.04 ± 0.08 |
arrival \(= 91 \pm 1.0\%\), after toad arrival \(= 93 \pm 0.8\%\); GLMM: \(B \pm SE = 0.27 \pm 0.18, \ z = 1.52, \ P = 0.13\). Nest survival was unaffected by nest stage (nestling compared to egg stage: \(B \pm SE = 0.10 \pm 0.18, \ z = 0.55, \ P = 0.58\); cuckoo nestling compared to egg stage: \(B \pm SE = -0.16 \pm 0.35, \ z = -0.45, \ P = 0.65\) or time of breeding season (\(B \pm SE = -0.14 \pm 0.10, \ z = -1.39, \ P = 0.16\), but was positively related to habitat quality on the territory (\(B \pm SE = 0.04 \pm 0.02, \ z = 2.47, \ P = 0.01\)).

Of 202 purple-crowned fairy-wren nests with cameras, 46% were depredated (14 of 25 nests in 2016, 31 of 66 nests in 2017, 16 of 63 nests in 2018, and 31 of 48 nests in 2020). Of these predation events, 48 (52%) were captured on video. Nests were depredated by monitor lizards (Mertens’ and Mitchell’s water monitors, spotted tree monitors), snakes (brown tree snakes, olive pythons, children’s pythons, Antaresia childreni), large centipedes (Scolopendrid centipedes), brown goshawks, pheasant coucals, blue-winged kookaburras, and brush cuckoos (see Supplementary Information 2 for full details on nest predator identities and frequencies). Nest predation by monitor lizards was less likely to occur post-compared to pre-toads (27% vs 64% of predation events, respectively; \(B \pm SE = -1.56 \pm 0.63, \ z = -2.49, \ P = 0.01\); Fig. 2). Instead, nest predation by avian predators increased 2.7-fold following toad arrival (38% vs 14% pre-toads; Fig. 2), although this effect was nonsignificant (\(B \pm SE = 1.37 \pm 0.74, \ z = 1.86, \ P = 0.07\)).
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P = 0.06). Likelihood of nest predation by snakes ($B \pm SE = 0.41 \pm 0.80$, $z = 0.52$, $P = 0.61$) and centipedes ($B \pm SE = 0.60 \pm 0.92$, $z = 0.65$, $P = 0.52$) did not change significantly following cane toad arrival at the site (Fig. 2).

**Discussion**

Detailed multi-trophic before-and-after studies can reveal the often complex direct and indirect impacts that new alien species can have on local ecosystem functioning (Doody et al. 2015b; O’Dowd et al. 2003). Our findings reveal that the arrival of invasive cane toads at a riparian site resulted in a drastic decline in monitor lizard abundance, as predicted, while the abundance of their reptilian prey was unaffected. Moreover, contrary to expectations, nest success of endangered purple-crowned fairy-wrens did not increase following cane toad arrival; instead, observations of predator–prey interactions suggest that the relative predation rates by different nest predators have changed (Fig. 3). Hence, these findings indicate that the impact of an alien species on different levels of the trophic food web may be difficult to predict, and any changes in predation risk by different predator guilds may only become apparent when investigating direct interactions between predators and their prey.

The severe decrease in abundance of monitor lizards we observed is comparable to that reported elsewhere in northern Australia following cane toad invasion (71% compared to previously reported declines ranging from 41 to 97% for *V. panoptes*, *V. mertensi*, and *V. mitchelli*; Doody et al. 2013; Doody et al. 2009; Doody et al. 2006; Doody et al. 2015b; Griffiths and McKay 2007). This reflects a direct effect of cane toads on these predators through lethal ingestion of toxic toads (reviewed in Shine 2010). Since monitor lizards are meso- or apex predators that play a key role in regulating animal communities, their decreased abundance is expected to have positive downstream effects on other trophic levels, via predator release (Doody et al. 2006, 2015b; Feit et al. 2020, 2018; Leo et al. 2019). However, contrary to expectations, we did not observe a clear increase in the abundance of common reptilian prey of monitor lizards. Although we were unable to test for a change in abundance of individual snake species, common tree snakes do not seem to have increased in abundance (as in Doody et al. 2015b but in contrast to Doody et al. 2013), although we should note that a change in abundance may have gone undetected in our study as we rarely detected snakes during surveys. The most common dragon at our study site is the Horner’s dragon, which is similar to Gilbert’s dragons in terms of morphology and position in the food web, and a common prey item of monitor lizards (Doody et al. 2012; Shine 1986). In fact, Horner’s and Gilbert’s dragons were considered the same species until 2018 (Melville et al. 2018), therefore we predicted an increase in dragon abundance as observed elsewhere (Doody et al. 2009). Instead, the initial increase in dragon abundance shortly after cane toad arrival, followed by a decrease the following two years (Fig. 1c), is similar to patterns reported by Doody et al. (2015b).

Surprisingly, nest success of purple-crowned fairy-wrens did not change notably following toad arrival, despite a substantial decrease in abundance of monitor lizards—the main predator of nests. This is also
in stark contrast to the increased fledging success observed in crimson finches (*Neochmia phaeton*), and predictions that invasive toads would result in similar positive effects on recruitment of purple-crowned fairy-wrens (Doody et al. 2015b). Interestingly, a reduction in nest predation by monitor lizards from 64% to only 27% of predation events indicates a change in the relative trophic influence of nest predators instead. Since overall nest predation rates did not change, and effects of individual predator classes...
were not significant, it seems plausible that rather than a single predator species or guild filling the partially empty niche left by monitor lizards, multiple alternative nest predators have slightly increased their frequency of nest predation (Fig. 2). Predation by avian predators increased the most, more than doubling (although this was not significant (p=0.06)). Avian predator abundance was unaffected by toad arrival, as expected (Beckmann and Shine 2009), therefore this is not because avian predators have simply increased in number. Instead, this finding suggests a change in predator array rather than fairy-wren prey experiencing predator release following a decrease in abundance of top or meso-predators. If the relative frequency of purple-crowned fairy-wren nest predation by different predators has indeed changed, this may be for several reasons. Firstly, centipedes constitute a prey item of monitor lizards (Doody et al. 2015a; Shine 1986), therefore predator release may result in increased abundance of, and thereby, nest predation by centipedes (Bruno et al. 2003; Rodriguez 2006; White et al. 2006). Unfortunately, we were not able to quantify centipede abundances during predator and prey surveys with the methods used here, and we also did not detect a significant increase in nest predation by centipedes (Fig. 2). Our observations strongly encourage future studies on the effect of cane toad invasion to also measure changes in abundance of invertebrate predators. Secondly, competition between predators may be strong. Monitor lizards, various snake species, and avian predators, are all known to frequently depredate passerine nests (e.g. Burton and Olsen 1997; Doody et al. 2015b; Soanes et al. 2015). The decreased abundance of monitor lizards may cause a higher relative density of active nests, which favours predation by less efficient predators because of reduced exploitative competition (Schmidt 1999). Hence, the loss of predators may result in facilitation of competitive species within the same trophic level, and the next trophic level down (Bruno et al. 2003; Kikvidze and Callaway 2009). It should be noted however that if this is the case here, such relaxed competition has not (yet) resulted in increased abundance of any of these predators. Studies tracking long-term abundances of predators and prey following alien species invasion may reveal the timeline over which relaxed competition may result in noticeable changes in predator abundance.

Our findings provide clear evidence for direct impacts of an invasive species on native top predators, resulting in reduced nest predation by that predator guild, but no change in abundance of predators and prey at lower trophic levels. Our results suggest that an invasive species may alter predator–prey dynamics in complex ways, through a combination of direct and indirect effects mediated through release of predation and competition. Moreover, our findings highlight that disturbances to trophic food webs can go unnoticed when considering changes in species abundances only. Instead, to enhance effective invasive species management and conservation, it is imperative to conduct detailed observations on key links within and between trophic levels.

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Author's contribution N.T. and A.P. conceived and designed the study; N.T. collected the data; N.T. analysed the data, with input from A.P.; N.T. wrote the manuscript, with contributions from A.P.

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Data availability The datasets generated and analysed during the current study are available on Figshare (https://doi.org/10.6084/m9.figshare.19453481).

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval All research was approved by the Monash University Animal Ethics Committee (BSCI/2015/11; 18794), Western Australian Department of Environment and Conservation (U29/2015-2018; U29/2019-2021; TFA 2020-0001), and the Australian Wildlife Conservancy (AWC).

Informed consent Both authors have contributed significantly to the work and agree with the content of the submission.

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