A biological invasion impacts ecosystem services: cane toads change the rate of scavenging and the suite of scavengers

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Abstract. By affecting the abundance of key native species, invasive taxa may disrupt ecosystem services. In Australia, large monitor lizards (Varanus spp.) play critical roles as scavengers and apex predators. Our broadscale surveys (across two transects, 1300 and 2500 km) show that in tropical areas where the arrival of fatally toxic cane toads (Rhinella marina) has massively reduced the abundance of monitors (Varanus panoptes), rates of removal of deployed baits are more than halved, and the assemblages of scavengers are dominated by birds or mammals rather than reptiles. In contrast, populations of another monitor species in eastern Australia (Varanus varius) were little affected by toad arrival, as were scavenging rates and assemblages. The mechanisms responsible for those shifts, and their consequences on ecosystem services, warrant further research.

Key words: Bufo marinus; facultative scavenger; invasive; trophic cascade; trophic networks; Varanidae.

INTRODUCTION

Direct impacts of invasive species via predation, competition, and lethal toxic ingestion have attracted intense scientific scrutiny (Phillips et al. 2003, Miller and Gorchov 2004, Medina et al. 2011). However, less attention has been paid to indirect pathways that are often more difficult to study but potentially just as severe (White et al. 2006). For example, the parasites and pathogens carried by invading organisms can have devastating effects on native biota (Dunn et al. 2012). More generally, species within natural systems are connected via many functional links (e.g., food webs), such that invader-induced changes to the abundance of a single native taxon may have multiple flow-on effects to many others (David et al. 2017). Such secondary cascades may be especially important if the affected species is abundant, and plays an important ecological role (Morris and Letnic 2017). For example, changes in the abundance of an ecosystem engineer like the beaver can profoundly change habitat attributes and thus the species composition of a riparian site (Wright et al. 2002, Anderson and Rosemond 2007). To understand the broadscale impacts of an invasion, then, we have to move beyond the direct impacts of the invader on individual species.

Ecosystem services such as scavenging are important for energy flow through trophic webs, for disease risk, and for predation pressure (via shifting abundances of taxa that are facultative predators and scavengers: Cunningham et al. 2018). Thus, a biological invasion that reduced the abundance of important scavengers within a natural system might have ramifying effects on many other taxa. For example, the increased availability of decaying carcasses might benefit other scavengers (Allen et al. 2015), induce a dietary shift toward scavenging in facultative predator–scavengers (Blanco 2014),...
increase the abundance of omnivores (Pain et al. 2003), increase rates of disease transmission (Ogada et al. 2012), and/or modify rates of nutrient turnover (Morris and Letnic 2017).

One well-studied system in which an invader affects scavengers involves the spread of cane toads (Rhinella marina) through Australia. These anurans possess potent chemical defenses, which are lethal if ingested by many endemic Australian predators (Phillips et al. 2003, Shine 2010). In particular, the arrival of toads in an area is consistently followed by a precipitous decline of populations of large monitor lizards (family Varanidae; Doody et al. 2009, Shine 2010, Brown et al. 2013). Because these giant lizards play critical ecological roles as apex predators in many Australian ecosystems (Shine 1986, Weavers 1989), the virtual extirpation of varanids by toads has cascading effects on abundances of other species via reduced predation and mesopredator release (Doody et al. 2006, 2012). Impacts of toad invasion on scavengers have attracted less research, although the carcasses of road-killed toads provide an abundant food resource for avian scavengers (e.g., raptors; Beckmann and Shine 2011), rodents (Cabrera-Guzmán et al. 2012, 2015), and invertebrates (e.g., ants; Ward-Fear et al. 2010). As well as providing abundant carcasses, toads might also affect scavenger activity by killing varanids that are major contributors to carrion removal. In keeping with that speculation, Jolly et al. (2015) reported a short-term decline in rates of bait removal following toad-induced mortality of large varanid lizards in recently invaded sites in eastern Australia.

In the present study, we used similar methods to those employed by Jolly et al. (2015)—baited camera traps—to explore the longer-term trajectory of changes in rates of carrion removal and in the identity of scavengers following toad invasion. We examined the impacts of toad invasion on scavenger ecology in a transect across tropical Australia and along the eastern seaboard. Our sampling thus involved transects covering the 80-yr toad invasion and comprising a total of >3800 linear km, as opposed to <140 km and 25 yr post-invasion in the earlier study (Jolly et al. 2015).

We asked the following questions:

1. How do rates of scavenging (number of scavengers arriving at a bait station and rate of removal of baits) change with the arrival of a toxic invader?
2. Is a decrease in abundance of varanid lizards compensated for by an increase in scavenging rates by other taxa?
3. How does the rate of scavenging, and the species composition of the scavenging guild, change through time after the arrival of a toxic invader?

MATERIALS AND METHODS

Study species

Cane toads (R. marina, formerly Bufo marinus) are large anurans native to South America that were released in Australia in 1935 in a failed attempt to control pests of sugarcane crops (Zug and Zug 1979; Fig. 1a). The toads have since spread across much of the continent (Urban et al. 2007).

Widely distributed throughout the east coast of Australia, lace monitors (Varanus varius) are among the largest lizards in the world, with adult males exceeding 2 m in length and weighing up to 14 kg (Weavers 1988; Fig. 1b). Lace monitors may be impacted by toads in the short term (Jolly et al. 2016), but populations are resilient over longer timescales (L. Pettit et al., unpublished manuscript). Lace monitors have a broad diet and commonly consume carrion (Weavers 1989, Guarino 2001, Pascoe et al. 2012).

Yellow-spotted monitors (Varanus panoptes) are large (to 7 kg) apex predators that once were abundant across the wet/dry tropics of northern Australia (Fig. 1c). However, yellow-spotted monitors have experienced massive population declines (>90%) in areas colonized by invasive cane toads (Doody et al. 2009, Brown et al. 2013, Ward-Fear et al. 2016). Importantly, this species remains rare even in populations that have coexisted with toads for over 80 yr (L. Pettit et al., unpublished manuscript). Yellow-spotted monitors are dietary generalists and frequently consume vertebrate prey as carrion (Shine 1986, Cross et al. 2019, Ward-Fear et al. 2020).

Study area

We conducted surveys at 21 sites along a 1300-km transect running broadly north–south down the east coast of Australia (within the range of
lace monitors) in 2017–2018 and 24 sites along a 2500-km transect running east–west across the wet/dry tropics of northern Australia (within the range of yellow-spotted monitors) in 2019 (Fig. 2). In our transect along the east coast, five sites in northern NSW and SE Queensland were free of toads. The 16 toad-present sites (occupied by toads for 1–80 yr) were interspersed among toad-free sites, extending north to Townsville in northeastern Queensland. In our transect within the wet/dry tropics, six sites were located in toad-free areas between Fitzroy Crossing and Broome. The remaining 18 sites (where toads have been present for between 4 and 84 yr) extended eastwards from the Kimberley region (also in Western Australia) to Townsville. Sites were grouped into four invasion stages (uninvaded, recently invaded, mid-term invaded, and long-term invaded), categorized by the number of generations of varanid lizards that had been sympatric with toads. Generation time was based on the shortest known age to sexual maturity in each species (see L. Pettit et al., unpublished manuscript for details). Briefly, our sites were classified as uninvaded (toad-free), recently invaded (1–12 goanna generations), mid-term invaded (13–29 goanna generations), and long-term invaded (30–80 goanna generations). Monitors were abundant at all sites prior to toad invasion, based on contemporary or historical records (Griffiths et al. 2004, Brown et al. 2013, Jolly et al. 2016, Ward-Fear et al. 2016, Lei and Booth 2017). Within logistical constraints, we randomized the order and time that sites were surveyed to minimize any confounding effects of time of day or season.

Quantifying toad impacts on scavenging

We deployed eight bait stations monitored with remote-sensing cameras (ScoutGuard

![Fig. 1. Images of a (a) cane toad (*Rhinella marina*), (b) lace monitor (*Varanus varius*), (c) yellow-spotted monitor (*Varanus panoptes*), and (d) cane toads scavenging at a wallaby (*Notamacropus agilis*) carcass (image courtesy of M. Crossland).](image)
SG560K, Shenzhen, China) at each site. At our east coast sites, cameras were placed in two 100 × 100 m grids, separated by 2 km, for one sampling session per site (2 d, totaling 16 trap days per site). Baits consisted of one chicken neck in a PVC container attached to a star picket (thus not removable by a scavenger), and a consumable egg placed at the base of half the bait stations at 13 sites (the variation in consumable bait deployment across sites was due to a concurrently run behavioral experiment).

Yellow-spotted monitors in the wet/dry tropics were assayed over two sampling sessions (for 2 and 3 d, totaling 40 trap days per site). Cameras were placed along a 1-km transect and spaced at least 100 m apart. Baits consisted of 80 g of nonremovable sardines in oil placed in a PVC container attached to a star picket, a consumable chicken egg placed at the base of the picket, and a single sardine and cane toad leg placed 30 cm to either side of the picket under plastic lids with mesh windows, which could be manipulated to access the food item. As we were interested in recording not only the rate of scavenging, but also the assemblage of scavengers, all animals arriving at a bait were identified.

Analyses
All analyses were conducted in JMP (ver 14.2, SAS Institute, Cary, NC, USA). To investigate the changes over time since arrival of toads, we treated invasion stage (four levels, uninvaded,
recently invaded, mid-term invaded, and long-term invaded) as a categorical independent variable in all models. Levene’s test was used to test for equality of variances, and normality was checked visually. Data that were transformed to comply with parametric test assumptions are discussed below.

Identity of scavengers.—We examined camera footage from all bait stations to identify the species that arrived and that were seen to engage with the bait. Our statistical analyses are based on the 21 species seen to engage with the bait; the remaining 55 species are listed in Appendix S1 only.

Composition of the scavenging assemblage.—We assessed the total number of visits by scavengers to bait stations over the entire survey period to quantify how the overall number of scavenging events by lizards, birds, and mammals changed over the duration of toad invasion. As it was impossible to unequivocally distinguish individuals from the camera footage, we treated repeat visits of lizards as unique scavenging events if successive visits were separated by at least a 30-min interval of no arrivals. For mammals and birds (that spent less time at baits, but often in groups), we used the count of the highest number of individuals detected in a single video within 30 min of the first detection.

Rates of removal of baits.—To examine rates of bait offtake, we used one-way ANOVA or the equivalent Kruskal–Wallis nonparametric test with the Steel-Dwass all-pairs post hoc tests. The number of available baits at each bait station that were consumed was used as our continuous dependent variable. For the tropical transect, we ran two models, one with all bait types and another with toad legs excluded (because some scavengers develop an aversion to toads in toad invasion). To examine this, we grouped the scavengers into the same broad taxonomic categories (three levels: reptile, mammal, and bird), which we then used to derive the relative proportion of each scavenger group within a site. We used this relative proportion as the dependent variable in one-way ANOVAs. Again, transformations did not improve our dataset on east coast birds, so we analyzed that data with a nonparametric Kruskal–Wallis test, while all data for the tropical transect were 1 + x log-transformed to meet parametric test assumptions.

Rates of visits by scavengers of different vertebrate groups.—Splitting data by transect and scavenger group, we used one-way ANOVAs to test whether the mean number of visits by each type of scavenger changed over invasion stages. We treated the proportion of arrivals in the relevant scavenger group (reptile, bird, or mammal) at each site as our dependent variable. The east coast bird dataset was analyzed using a nonparametric Kruskal–Wallis test, while all data for the tropical transect were 1 + x log-transformed to meet parametric test assumptions.

Proportional composition of the scavenging assemblage.—We used data on the identity of scavengers to arrive at each bait station to quantify how the composition of taxa changed with the arrival of cane toads. To examine this, we grouped the scavengers into the same broad taxonomic categories (three levels: reptile, mammal, and bird), which we then used to derive the relative proportion of each scavenger group within a site. We used this relative proportion as the dependent variable in one-way ANOVAs. Again, transformations did not improve our dataset on east coast birds, so we analyzed that data with a nonparametric Kruskal–Wallis test. The tropical transect reptile data were square-root-transformed to meet parametric test assumptions.

**RESULTS**

Identity of scavengers

Twenty-one species were seen to engage with the bait (i.e., consume carrion; Table 1). These included four species of reptiles, three of birds, and 14 of mammals; relative numbers of species from each of these three vertebrate lineages did not differ significantly between east coast and tropical transects ($\chi^2 = 2.45$, 25 df, $P = 0.30$; see Table 1).

Rates of removal of baits

Rates of bait offtake did not change significantly over invasion time along east coast sites (ANOVA $F_{3.47} = 0.38$, $P = 0.77$; Fig. 3a). However, rates of bait offtake in the wet/dry tropics declined with the duration of toad occupation (models with toad legs included, Kruskal–Wallis $\chi^2 = 36.76$, $P < 0.0001$, Fig. 3b; excluded, Kruskal–Wallis $\chi^2 = 30.71$, $P < 0.0001$).

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Table 1. The identity of scavenger species detected by remote cameras at bait stations deployed at 21 sites along the east coast and 24 sites through the wet/dry tropics of Australia.

| Transect | Species | Common name | Invasion stage | Uninvaded 1 | Recently invaded 2 | Mid-term invaded 3 | Long-term invaded 4 |
|----------|---------|-------------|----------------|-------------|-------------------|-------------------|-------------------|
| **Reptilia** |         |             |                |            |                   |                   |                   |
| East coast | Varanus varius | Lace monitor |                | 20 (6) | 34 (8) | 5 (1) | 53 (9) |
| Aves | Varanus panoptes | Yellow-spotted monitor |                | 1 | 3 (1) | 2 |
| East coast | Corvus orru | Torresian crow |                | 5 (2) | | | 9 (1) |
| **Mammalia** |         |             |                |            |                   |                   |                   |
| East coast | Antechinus flavipes | Yellow-footed antechinus |                | 3 | (3) |
| | Antechinus stuartii | Brown antechinus |                | 4 (1) | 7 (2) | 1 (1) | |
| | Dasypus hallucatus | Northern quoll |                | 1 |
| | Felis catus | Cat |                | 1 |
| | Hydromys chrysogaster | Rakali |                | 1 (1) |
| | Isodon macrourus | Northern brown bandicoot |                | 2 (1) | 1 | 2 (2) | 6 (5) |
| | Perameles nasuta | Long-nosed bandicoot |                | 2 | 3 | 3 (3) | 2 (2) |
| | Rattus fuscipes | Bush rat |                | 35 (9) | 28 (6) | 13 (5) | 4 (3) |
| | Rattus rattus | Black rat |                | 31 (9) | 18 (4) | 28 (6) | 25 (9) |
| | Trichosurus caninus | Mountain brushtail possum |                | 5 (3) | 3 (2) | 1 (1) |
| | Trichosurus vulpecula | Brushtail possum |                | 1 (1) | 5 (3) | 1 (1) | 1 (1) |
| | Vulpes vulpes | Fox |                | 5 (2) |
| **Reptilia** |         |             |                |            |                   |                   |                   |
| Tropics | Varanus panoptes | Yellow-spotted monitor |                | 100 (33) | 6 (5) | 12 (2) | 11 (4) |
| | Varanus gouldii | Sand goanna |                | 1 (1) | |
| | Tiliqua scincoides | Eastern blue-tongued lizard |                | 7 (4) |
| **Aves** |         |             |                |            |                   |                   |                   |
| Tropics | Corvus orru | Torresian crow |                | 129 (20) | 234 (34) | 25 (3) | 31 (7) |
| | Haliastur sphenurus | Whistling kite |                | 3 |
| | Milvus migrans | Black kite |                | 1 | 15 (3) |
| **Mammalia** |         |             |                |            |                   |                   |                   |
| Tropics | Canis dingo | Dingo |                | 3 (1) | 14 (6) | 59 (10) | 3 (1) |
| | Felis catus | Cat |                | 17 (10) | 2 (2) | 10 (4) | 14 (4) |
| | Hydromys chrysogaster | Rakali |                | 46 (5) | 9 (2) |
| | Isodon macrourus | Northern brown bandicoot |                | 2 | 85 (16) | 49 (19) |
| | Rodentia | Various |                | 22 (5) |
| | Sus scrofa | Pig |                | 4 (2) | 18 (7) |
| | Trichosurus vulpecula | Brushtail possum |                | 9 (4) | 26 (13) | 19 (8) |

Notes: The numbers in each invasion stage category represent the number of visits to bait stations by that species, whereas numbers in brackets depict how many times that species was first to discover the carrion baits. Note that numbers for the two transects are not directly comparable because of differences in numbers of sites and in duration of monitoring; thus, comparisons are robust only within each transect.
Rates of bait removal by scavengers of different vertebrate groups

Along the east coast, there was no significant change in the number of eggs scavenged by reptiles (ANOVA $F_{3,9} = 1.28$, $P = 0.31$; Fig. 4a), mammals (ANOVA $F_{3,9} = 1.64$, $P = 0.22$; Fig. 5c), or birds (Kruskal–Wallis $\chi^2 = 2.65$, $P = 0.45$; Fig. 5e). For the wet/dry tropics, the arrival of toads coincided with a reduced number of visits to bait stations by scavenging reptiles (ANOVA $F_{3,20} = 12.36$, $P < 0.0001$; Fig. 4b), an increased number of visits by mammalian scavengers (ANOVA $F_{3,20} = 12.05$, $P < 0.0001$; Fig. 5d), and no significant change in numbers of visits by scavenging birds (ANOVA $F_{3,20} = 2.88$, $P = 0.061$; Fig. 5f).

Proportional composition of the scavenging assemblage

Along the east coast transect, we found no significant difference across invasion stage categories in the proportions of scavenging events that were due to reptiles (ANOVA $F_{3,17} = 1.20$, $P = 0.34$; Fig. 6a), mammals (ANOVA $F_{3,17} = 1.32$, $P = 0.30$; Fig. 6c), or birds (Kruskal–Wallis $\chi^2 = 2.55$, $P = 0.47$; Fig. 6e). Along the tropical transect, reptiles (predominately yellow-spotted monitors) were the dominant scavenger prior to toads arriving (averaging 50% of all scavenging events), but their contribution to scavenging declined as soon as toads arrived (to 2.6%; $F_{3,20} = 13.35$, $P < 0.0001$; Fig. 6b) and did not recover over time. The proportion of mammalian scavengers was low in areas without toads and in recently invaded sites (14% and 11%, respectively), but mammals were the dominant scavengers in later invasion stages (averaging 83% and 79% of detections at carrion; $F_{3,20} = 37.02$, $P < 0.0001$; Fig. 6d). The proportion of avian scavengers increased in areas recently colonized by toads (from 35.8% to 86.2%), but declined in long-colonized sites (to 13.4% and 13.5%; $F_{3,20} = 13.96$, $P < 0.0001$; Fig. 6f).

Discussion

The invasion of toxic cane toads through tropical Australia has massively reduced the abundance of a formerly common species of large
monitor lizard, *V. panoptes* (Brown et al. 2013; L. Pettit et al., *unpublished manuscript*), triggering a strong shift both in the rate of scavenging (lower in areas colonized by toads than in toad-free sites) and in the species composition of the scavenger guild (dominated by reptiles in toad-free sites, by birds in sites recently invaded by toads, and by mammals in long-colonized sites). The increased proportional role of mammals as scavengers in long-colonized sites is not simply due to a reduction in reptilian scavengers; instead, absolute rates of scavenging by mammals are higher in such locations than in areas that lack toads or have had them only briefly. In strong contrast, the spread of toads southwards down the eastern seaboard of Australia has had little
detectable impact either on the population size of large monitor lizards in these sites (V. varius: L. Pettit et al., unpublished manuscript), or on the rate of scavenging or taxonomic composition of the scavenger assemblage.

Because our results are based on surveys conducted at a single point in time, we cannot confidently ascribe causation to the geographic patterns that we have documented. It remains possible that geographic variation in rates and identities of scavengers reflects underlying biotic or abiotic factors unrelated to cane toads. Thus, for example, more eastern sites on our tropical transect tend to have denser vegetation and hence may harbor higher densities of mammals (Williams et al. 2002). In such habitats, mammalian scavengers may have always been more important than reptilian or avian equivalents,
even before the arrival of cane toads. The strong pattern for rates of scavenging to continue to fall with time since toad invasion (Fig. 2b) seems unlikely to be due solely to the decrease in abundance of *V. panoptes*, because these giant lizards are rare in almost all toad-colonized sites rather than continuing to decline through time post-colonization (L. Pettit et al., *unpublished manuscript*).

Why should rates of scavenging continue to decline over a period when varanid numbers are low and stable? The pattern is driven primarily by a decreased rate of scavenging by reptiles after toads arrive and a decreased rate of scavenging by birds in long-colonized areas (Fig. 3). Again, low rates of scavenging by birds may represent a preexisting situation in eastern parts of...
tropical Australia, rather than having anything to do with cane toads.

The most compelling evidence for a direct impact of toads on scavenging rates comes from the comparison between the two transects: Rates of scavenging appear to have fallen precipitously in the tropics (where large varanids were almost eliminated by toads) but have been largely unaffected along the east coast (where the local monitor species was far more resilient). Given unequivocal evidence that toads cause dramatic population declines of *V. panoptes* (Doody et al. 2009, Brown et al. 2013, Ward-Fear et al. 2016), at least part of the shift in proportional importance of avian vs. mammalian vs. reptilian scavengers across the tropics is causally related to toad invasion. That is, proportions of each scavenger type changed as soon as toads arrived, because varanid lizards largely disappeared at that time (Fig. 5). Interestingly, the decline of varanids was not immediately followed by a compensatory increase in scavenging by other taxa. Although rates of mammalian scavenging in long-colonized sites increased, relative to those seen in toad-free areas, the overall pattern was that carrion was no longer removed at the rates that had existed prior to toad invasion (Fig. 2). Hence, although the toad-induced reduction in varanid populations in tropical Australia has caused compensatory increases in mesopredators and some taxa of former prey (Doody et al. 2012, 2015, Feit et al. 2020), the same does not appear to be true for scavenging—except, perhaps, as reflected by an increase in scavenging by mammals in long-colonized sites.

Our data may underestimate the magnitude of toad impact on scavenging, because the scavengers that were almost eliminated in tropical Australia (varanid lizards) are larger and more powerful than most of the alternative scavenger taxa (Table 1). Crows, cats, and bandicoots may be unable to open large thick-skinned carcasses such as those of road-killed macropods (Alvarez et al. 1976). If so, that category of carrion may remain unexploited in the absence of varanids or dingoes. Scavenging invertebrates, such as ants, might be the ultimate beneficiaries of such a shift. Likewise, our surveys do not capture more subtle changes in mesosavenger tactics, such as a trend to spend more time feeding on carrion when the top-order scavenger is absent (Cunningham et al. 2018).

The substantial reduction in overall rates of bait removal following cane toad invasion (Fig. 2) might have consequences for the toads themselves. Necrophagous invertebrates are an important driver of carrion decomposition, and increase in abundance if carcasses are left unsavaged by vertebrates (Munoz-Lozano et al. 2019). More broadly, cane toads key in on resource patches that offer abundant prey (González-Bernal et al. 2013, Feit et al. 2015). We observed many cane toads preying upon invertebrates attracted to our baits (Pettit et al. 2020) and upon invertebrates attracted to carcasses of domestic and native animals (G. Ward-Fear, personal observation; Fig. 1d), suggesting that toads may benefit from the ecosystem change they drive by fatally poisoning keystone reptilian scavengers, toads thereby increase their own prey availability.

The loss of scavenging function in our system mimics the situation in some other systems that have lost keystone scavengers. Although some studies have supported the mesosavenger release hypothesis (reviewed in O’Bryan et al. 2019), other research has reported an incomplete replacement of scavenger function following the reduction in keystone scavengers. Apex scavenger exclusion experiments have noted no functional replacement by mesosavengers, at least over the short term (Hill et al. 2018). In a broader spatial comparison, scavenger nestedness (and consumption efficiency) decreased with increased anthropogenic disturbance (Sebastián-González et al. 2020). Additionally, different types of scavengers may feed in different ways: Corvids, dogs, and foxes did not functionally replace raptors that were lost due to urban development (Huijbers et al. 2014).

Our results suggest that the invasion of cane toads across tropical Australia has severely disrupted an important ecosystem service, by almost eliminating the keystone scavenger. The disruption from that mortality extends beyond the vulnerable species itself and ramifies through the ecological links between the impacted taxa and other components of the ecosystem. In the case of cane toads killing varanid lizards, those effects appear to involve increases in mesosavenger and mesopredator abundance, and a general
reduction in rates of carrion removal. Thus, our study identifies yet another pathway by which toads negatively impact ecosystems in Australia (Shine 2010). Future research could usefully explore the mechanistic basis for geographic variation in rates and identities of scavengers, and look in more detail at how the behaviors and off-take rates of non-reptilian scavengers are modified by the loss of giant varanid lizards.

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