COMMENTARY

THE IMPACT OF INVASIVE TOADS (BUFONIDAE) ON MONITOR LIZARDS (VARANIDAE): AN OVERVIEW AND PROSPECTUS

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ABSTRACT

*Toads of the amphibian family Bufonidae possess toxins that can be lethal to monitor lizards (family Varanidae) when ingested. In Australia, populations of several species of monitors (*Varanus *spp.) have been heavily impacted via direct poisoning by invasive cane toads (*Rhinella marina*). It has been suggested that the invasion of Asian black-spined toads (*Duttaphrynus melanostictus*) through the Indonesian archipelago could have equally devastating effects on other monitors, especially the iconic Komodo dragon,* Varanus komodoensis. *We review published information to evaluate the risk posed by invasive toads to varanids worldwide, and identify critical gaps in knowledge (e.g., specific varanid lineages not yet tested for the genetic signature of toxin resistance; mechanisms that buffer toad impacts even on physiologically susceptible predators; toxicity of* D. melanostictus*). We conclude that population-level impacts of invasive toads are unlikely to be significant for most yet-to-be-affected species of monitors, including* V. komodoensis. *Nonetheless, the likely spread of* D. melanostictus *through southern Australia may affect monitors (e.g., heath monitor* V. rosenbergi*) that are not currently imperiled by cane toads and, more generally, wildlife managers need to evaluate potential impacts of these toxic invaders on vulnerable native predators.*

Introduction

INVASIVE species are a leading cause of extinction of native taxa over recent decades (Clavero and García-Berthou 2005; Gallardo et al. 2019) via pathways such as predation, competition, and transfer of pathogens and parasites (e.g., Kraus 2003; Shine 2014). Among amphibian invaders, some species of toads of the family Bufonidae have an unusual mode of impact: the toads' distinctive chemical defenses are highly toxic (sometimes fatal) to native predators that are not adapted to deal with those toxins (e.g., Ujvari et al. 2013). The most intensively studied invasion of toxic toads involves the cane toad (*Rhinella marina*), native to South America but translocated to many countries as a control for insect pests (e.g., Shine 2014, 2018). Another species, the Asian black-spined toad *Duttaphrynus melanostictus*, is invading not only through islands of eastern Asia (Kennedi et al. 2020), but also in Madagascar (Licata et al. 2019, 2020), raising concerns about impacts on the endemic fauna of those island systems (Figure 1). In the current paper we examine the likelihood that further spread of these two toad species will imperil large predatory lizards of the family Varanidae (often called "monitors" or "goannas").

Direct poisoning of toad-naïve predators is not the only mechanism by which invasive toads impact native communities, but it appears to be the most important. For example, there is no compelling evidence that invasive cane toads consume enough prey to imperil invertebrates or to substantially reduce food availability for competitors (Pearson et al. 2009; Greenlees et al. 2013; Döring et al. 2017). Additionally, the threat of predation by toads may induce behavioral shifts in native anurans (e.g., inactivity when toads are present; Greenlees et al. 2013; Mayer et al. 2015) but has not affected overall abundances of native frogs in Australia (see review by Shine 2014). Although the toads bring with them native-range parasites or pathogens, few native species are vulnerable to infection by these novel organisms (e.g., lungworms; Pizzatto et al. 2012; Rivory et al. 2020). However, the impacts on ecosystems caused by removing predators are twofold: the species of concern is directly impacted, and through their demise, indirect impacts ripple through the ecosystem in trophic cascades (Doody et al. 2013). Large varanid lizards are conspicuous predators that can play important ecological roles (de Miranda 2017). Thus, our review focuses on cases where invasive toads may threaten toad-naïve monitor species via lethal toxic ingestion. We do not consider invasions of toads to areas where there are already native toads present, such that monitors have coevolved to deal with

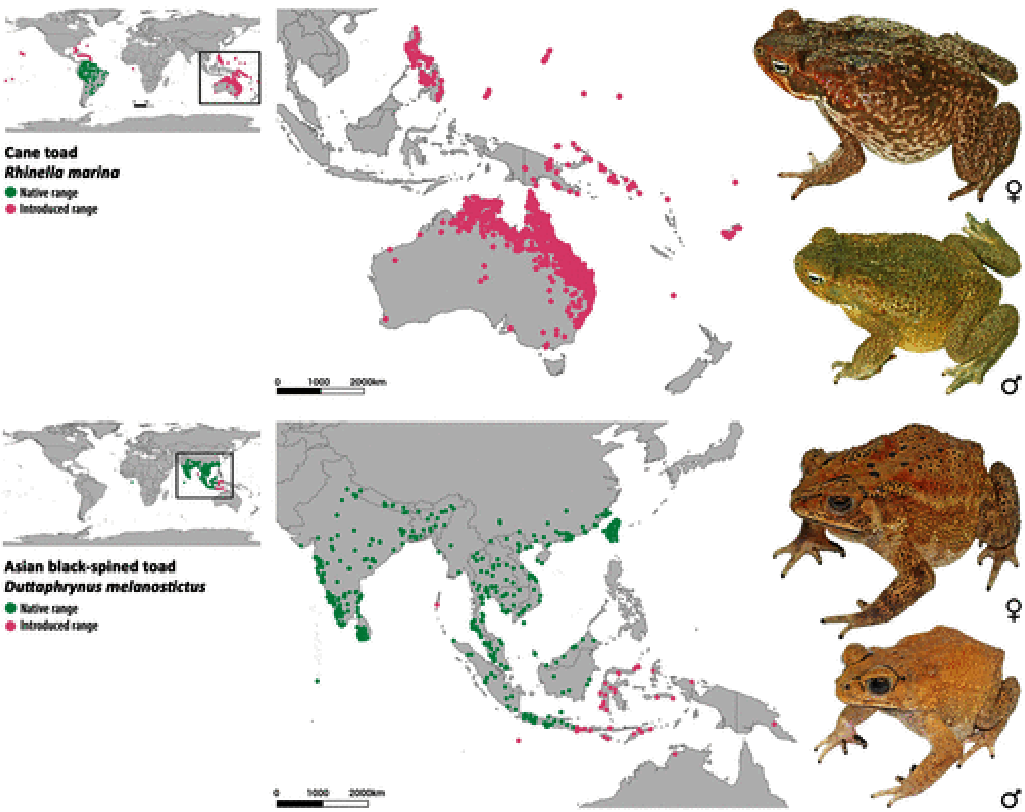

Figure 1. Two Species of Toxic Toads that Are Invading Areas Outside of Their Native Range

The cane toad (*Rhinella marina*; upper right) is native to South America (upper left) but translocated to many countries in the Australasian region (upper middle) as a control for insect pests. The Asian black-spined toad (*Duttaphrynus melanostictus*; bottom right), is native to parts of Asia and expanding in range through islands of eastern Asia (bottom middle). Distribution records from the Global Biodiversity Information Facility (GBIF) and Australia Living Atlas (ALA) and accessed on 6 October 2020; then refined based on Khan (2000), Lever (2003), and Bessa-Silva et al. (2020). Live toads not shown to scale. Photographs by Ruchira Somaweera. See the online edition for a color version of this figure.

these toxic amphibians (e.g., the guttural toad *Sclerophrys gutturalis* is spreading beyond its native range in southern Africa; Measey et al. 2012, 2017; *D. melanostictus* spreading in Southeast Asian islands such as Bali that already contain native toads; Somaweera 2020).

Both *Rhinella* and *Duttaphrynus* possess potent chemical defenses that can be fatal to predators within areas into which toads are currently extending (e.g., Shine 2010). This is the primary mechanism of ecological impact of cane toads in Australia, where the toad has had devastating impacts on endemic predators (Shine 2010). Fatal poisoning due to ingestion of cane toads has also been reported for snakes in Japan (Kidera and Ota 2008) and the West Indies (Wilson et al. 2011). Broad similarity in toxins among *Rhinella* and *Duttaphrynus* means that we expect similar impacts of these two kinds of invasive toads (regardless of specific toad species) on frog-eating predators that have not coevolved with toads (Shine 2010). Toad toxins comprise a cocktail of chemical compounds (Hayes et al. 2009) and physiological resistance to even a single type of toad toxin varies dramatically among different species of frog-eating predators because small genetic changes can massively decrease vulnerability to those toxins. Such changes are consistently associated with the inclusion of toads as dietary items (Ujvari et al. 2013, 2015; but see Mohammadi et al. 2016 for exceptions to that generalization).

Although many species of native predators can be killed by eating cane toads in Australia, population-level impacts are restricted to relatively few species (Shine 2010) because others either can tolerate the toad's toxin, do not eat toads, or rapidly learn not to (O'Donnell et al. 2010; Cabrera-Guzmán et al. 2015). The victims of the toad invasion include a marsupial carnivore, the northern quoll *Dasyurus hallucatus* (O'Donnell et al. 2010), a large scincid lizard, the northern blue-tongued skink *Tiliqua scincoides intermedia* (Price-Rees et al. 2010), some species of elapid snakes (Phillips and Shine 2004), and some populations of the freshwater crocodile *Crocodylus johnstoni* (Letnic et al. 2008; Somaweera et al. 2013). However, the most important impacts of cane toads in Australia involve catastrophic mortality of large monitor lizards of the family Varanidae. These large reptiles play critical ecological roles in Australian ecosystems (Pianka 2017), so the decline of varanid populations due to toad-poisoning has significant flow-on effects for the abundance of other taxa (former prey and competitors; Brown et al. 2013; Doody et al. 2013), for ecosystem services such as scavenging (Jolly et al. 2015), and for indigenous culture (Bird et al. 2013).

Concern has been expressed about the impact of cane toads on several taxa of Australian varanid lizards, notably the yellow-spotted monitor *Varanus panoptes* (Brown et al. 2013; Doody et al. 2013), sand goanna *V. gouldii* (Burnett 1997), lace monitor *V. varius* (Jolly et al. 2016), Mertens' water monitor *V. mertensi* (Griffiths and McKay 2007), and Mitchell's water monitor *V. mitchelli* (Doody et al. 2013, 2014). The most extensive data on impacts of toads involve *V. panoptes*, a large species that has experienced declines of more than 90% within a few months of the arrival of cane toads at several sites across tropical Australia (Ujvari and Madsen 2009; Brown et al. 2013; Doody et al. 2013). The causal link to ingestion of toads is clear for this species because training varanids to avoid consuming toads buffers the impact of toad invasion (Ward-Fear et al. 2016). Anecdotal reports of population recovery for this species in areas long-colonized by toads (Doody et al. 2020) are only partly supported by recent quantitative surveys (recovery occurs, but is uncommon; Pettit 2020). Data are more limited for the aquatic *V. mertensi*, with reports of substantial decline (Griffiths and McKay 2007), but long-term persistence in toad-colonized areas (R. Shine, pers. obs., 2019). The only other species for which data are available over large geographic areas is *V. varius*, a large inhabitant of east-coast woodland habitats. Many individuals are killed by lethal toxic ingestion when toads arrive, but populations recover rapidly and there is little to no long-term impact on abundance (Jolly et al. 2016; Pettit 2020).

Given that most species of native wildlife have not been directly affected by cane toads in Australia (Shine 2010), why have so many varanid lizards been vulnerable? The answer may lie in a constellation of traits that include physiology (Australian varanids lack resistance to bufadienolides; Ujvari et al. 2013, 2014, 2015), behavior (varanids are generalist predators, sometimes taking large prey such as adult toads; Shine 1986; Losos and Greene 1988), morphology (varanids have keen vomeronasal senses for prey detection and can find toads even at low abundances), and ecology (varanids are found in a broad range of habitats, including riparian areas that toads use for hydration and breeding). These traits are widespread not only in varanids from Australia, but also congeneric species from other parts of the world (e.g., Pianka and King 2004). Thus, arguably the vulnerability of varanid species to toad invasion may extend to those outside of Australia. Indeed, Ujvari et al. (2014) and Reilly et al. (2017) have suggested that the eastward spread of *D. melanostictus* through the Indonesian archipelago may imperil the largest and most iconic monitor species, the Komodo dragon (*V. komodoensis*). Also, an invasion of *D. melanostictus* into Australia (a likely event; Tingley et al. 2018) might imperil Australian varanids that have not been affected by cane toads (depending on factors such as the toxin content of Asian black-spined toads relative to that of cane toads, which has yet to be measured).

To clarify the threat posed by toad invasion to varanid lizards worldwide, we review published information on the phylogenetic relationships and geographic distributions of varanids, the physiological susceptibility of varanids to bufonid toxins, and the likely distributions of invasive toads into the near future. Our aim is to assess the potential ongoing and future risk that invasion of toxic toads may pose to varanids worldwide.

Assessing Vulnerability of the Lineages of Varanid Lizards

Closely related species often exhibit similar levels of vulnerability to a specific threatening process because of similarities in traits (such as physiology, behavior, morphology, and ecology) that determine that vulnerability (e.g., Reed and Shine 2002; González-del-Pliego et al. 2019). Thus, a phylogenetic perspective offers a logical and useful way to predict the likely susceptibility of varanids to toads. The alpha taxonomy of monitors is contentious, with some authorities elevating many island-specific forms to full species status (see Koch et al. 2013), whereas other authorities treat these as varieties within more widespread taxa. Based on the most recent analysis (Brennan et al. 2021), we separate the living species of monitor lizards into the following clades, which are discussed below.

african lineages

All species within the closely related subgenera *Psammosaurus* and *Polydaedalus*, basal to the rest of the Varanidae phylogenetically, are from Africa (Brennan et al. 2021; see Figure 2). Some are from arid habitats, but others (such as the Nile monitor *V. niloticus*) are highly water-associated (Dalhuijsen et al. 2014). Toads occur broadly over the area occupied by species within this lineage, and have been recorded as prey for at least two species within *Polydaedalus* (savannah monitor *V. exanthematicus*, *V. niloticus*; Losos and Greene 1988). Genetic changes that confer resistance to bufonids also have been reported in three species within this subgenus (white-throated monitor *V. albigularis*, *V. exanthematicus*, *V. niloticus*), consistent with a long period of sympatry between toads and varanids (Ujvari et al. 2013, 2015). Species of *Psammosaurus* have yet to be evaluated genetically for this trait, but they likely are physiologically resistant to toad toxins also. Losos and Greene (1988) report a toad as natural prey of *V. griseus*. In summary, African varanids are likely resilient to toad invasion because of a physiological capacity to tolerate toad toxins, although *Psammosaurus* species remain untested.

solomon islands lineage

The monotypic subgenus *Solomonsaurus* is restricted to the Solomon and Bougainville islands and contains the Solomon Island spiny monitor *V. spinulosus* (Böhme and Zielgler 2007). Dwyer (2008) suggested that introduced cane toads at San Jorge Island might negatively affect the local population of *V. spinulosus*. However, the species' basal position within varanid phylogeny, close to the African taxa (Brennan et al. 2021), suggests that *V. spinulosus* may be resistant to toad toxins. Given that the distribution of this species renders it potentially vulnerable to invasion by toads, however, genetic testing of this species would be useful.

asian lineages

Lizards of the varanid subgenera *Philippinosaurus*, *Hapturosaurus*, *Euprepiosaurus*, *Empagusia*, and *Soterosaurus* are distributed widely through Asia, including on many islands (e.g., Koch et al. 2013; see Table 1 for species list). Vulnerability to toad invasion likely differs among members of this lineage, as discussed below.

Genetic testing suggests that species within the subgenera *Empagusia* and *Soterosaurus* (Bengal monitor *V. bengalensis*, Dumeril's monitor *V. dumerilii*, roughneck monitor *V. rudicollis*, and Asian water monitor *V. salvator*) are physiologically resistant to toad toxins. Consumption of toads has been reported for *V. salvator* (Losos and Greene 1988), *V. bengalensis* (Karunarathna et al. 2017), and yellow monitor *V. flavescens* (Auffenberg et al. 1989).

FIGURE 2. SPECIES OF VARANID LIZARDS KNOWN OR PRESUMED TO TOLERATE TOAD TOXINS

Long-term sympatry has resulted in monitors in the African lineage such as the Nile monitor (*V. niloticus*: A) of subgenus *Polydaedalus* being able to consume toads without ill effects. The sole member of the subgenus

Indeed, *V. salvator* was the first varanid species to be reported to consume cane toads without ill effect (Alcala 1957; Gaulke 1992).

In contrast, species within the subgenus *Euprepiosaurus* (= *V. indicus* group, often separated into several species-level taxa) may be vulnerable to toads. Indeed, Dryden (1965) claims that cane toads were intentionally brought to the island of Guam to control numbers of mangrove monitors *V. indicus*, and that this translocation achieved its aim. However, McCoid et al. (1994) attribute the decline of monitor populations on Guam to a broader range of factors, including fatal ingestion of cane toads but also encompassing impacts of urban development, hunting, and predation by other introduced carnivores, including snakes, feral dogs, and pigs. In their review of conservation threats to Asian varanids, Koch et al. (2013) suggest that at least one insular race of *V. indicus* (which they recognize as specifically distinct, under the name *V. obor*) may be at threat if cane toads invade the island of Sanana (in the Moluccas), the only known locality for this form. Other forms within the *V. indicus* lineage occur on other small islands, and presumably are at similar risk (frogs have been reported as dietary items in the quince monitor *V. melinus*; Pianka and King 2004). However, running speeds of *V. indicus* from Australia were more than tenfold less affected by a given dose of bufotoxin than were those of sympatric *V. panoptes* (Smith and Phillips 2006), suggesting that the toxin resistance of *V. indicus* is intermediate between that of African and Australian lineages. Physiological resistance to bufotoxins may be conferred by a variety of mechanisms; for example, crayfish are unaffected by bufotoxins despite lacking the genetic signature of bufotoxin resistance (Wilson and Williams 2014). Also, some predators circumvent toad toxins by selectively consuming nontoxic body parts (e.g., Shine 2010; Beckmann and Shine 2011; Clarke et al. 2020; Parrott et al. 2020; and see Bringsøe et al. 2020 for an example of snakes selectively consuming internal organs of *D. melanostictus*).

Relatively low resistance to bufonid toxins in at least some *Euprepiosaurus* species suggests that low resistance may also apply to the wider clade to which this subgenus belongs, including *Philippinosaurus* and *Hapturosaurus*. The former subgenus comprises frugivorous species only (Koch et al. 2013) so is unlikely to suffer from ingesting toads. However, the sister group to *Euprepiosaurus* is *Hapturosaurus*, comprising small arboreal varanids of the *V. prasinus* group, and these are generalist carnivores. Thus, they probably consume amphibians (but perhaps mostly arboreal ones) if these are available. Sprackland (1982) suggested that frogs comprised the most common dietary items for the emerald tree monitor *V. prasinus*, but Losos and Greene (1988) disputed that claim based on their own analyses (which revealed mostly invertebrate prey plus a rodent). Toxin resistance of these taxa does not appear to have been evaluated, but the occurrence of these lizards on Australia, Papua New Guinea, and nearby islands increases their probable exposure to invasion by bufonids.

AUSTRALIAN SPECIES OF VARANIDS

Two subgenera of varanids occur within Australia. Most species of *Odatria* are small, and many are arboreal or saxicolous (Pianka and King 2004) and, hence, may not often encounter toads. In contrast, species of the subgenus *Varanus* are large and many are found in riparian habitats. The two subgenera are each other's closest relatives (i.e., Brennan et al. 2021) and all appear to lack genetic

Solomonsaurus within the Solomon Islands lineage, the Solomon Island spiny monitor (*V. spinulosus*: B), is close to the African taxa within varanid phylogeny and thus may be resistant to toad toxins also. Within the Asian lineage, toxin resistance has not been evaluated for many species within the subgenera *Euprepiosaurus* such as the emerald tree monitor (*V. prasinus*: C). However, Asian species within the subgenera *Empagusia* and *Soterosaurus* (e.g., Asian water monitor *V. salvator*: D; and Bengal monitor *V. bengalensis*: E) are physiologically resistant to toad toxins and are known to consume toads. Photographs by Ruchira Somaweera, except *V. spinulosus* by Michael McCoy. See the online edition for a color version of this figure.

TABLE 1

Varanid species of the world and traits predicting their vulnerability to invasive toads

Clade*	Subgenus	Species	Common name	Distribution	Genetic resistance to toad toxins? (Y/N)	Sympatric with toads in native range? (Y/N)	Has encountered invasive toads? (Y/N)	Will likely encounter toads in future? (Y/N)	Likely impact of encounters with toads
Africa	*Polydaedalus*	*albigularis*	White-throated monitor	Namibia, Botswana, Republic of South Africa, Swaziland, Zimbabwe, Mozambique, Zambia, Angola, Tanzania, south Ethiopia, south Somalia, Kenya, Uganda, south Democratic Republic of the Congo (Zaire)	Yes	Yes	No	Yes	None
Africa	*Polydaedalus*	*exanthematicus*	Savannah monitor	Mauritania, Senegal, The Gambia, Guinea-Bissau, Guinea (Conakry), Sierra Leone, Liberia, Mali, Ivory Coast, Burkina Faso, Ghana, Togo, Benin, Niger, Nigeria, Chad, Cameroon, Central African Republic, Sudan, Ethiopia, Eritrea, Kenya, Uganda, north Democratic Republic of the Congo (Zaire), Zimbabwe	Yes	Yes	No	Yes	None
Africa	*Polydaedalus*	*niloticus*	Nile monitor	Republic of South Africa, Swaziland, Namibia, Botswana, Tanzania, Mozambique, Zimbabwe, Zambia, Angola, Malawi, Tanzania, Gabon, Democratic Republic of the Congo, Kenya, Uganda, Cameroon, Central African Republic, Ethiopia, Eritrea, Somalia, Sudan, Chad, Egypt, Liberia, Ivory Coast, Ghana, Togo, Benin, Burkina Faso, Niger, Nigeria, Mali, Mauritania, Senegal, The Gambia, Guinea	Yes	Yes	No	Yes	None
Africa	*Polydaedalus*	*ornatus*	Ornate monitor	Guinea, Togo, Benin, Liberia, Sierra Leone, Guinea-Bissau, Democratic Republic of the Congo, Cameroon, Gabon, Ivory Coast, Central African Republic	Yes?	Yes	No	Yes	None
Africa	*Polydaedalus*	*stellatus*	West African Nile monitor	Sierra Leone, Ghana	Yes?	Yes	No	Yes	None
Africa	*Polydaedalus*	*yemenensis*	Yemen monitor	Yemen, north Saudi Arabia	Yes?	Yes	No	No	None
Africa	*Psammosaurus*	*caspius*	No common name	Iran, Afghanistan, Pakistan, Turkmenistan	Yes?	Yes	No	No	None

Africa	*Psammosaurus*	*griseus*	Desert monitor	Turkey, Morocco, Algeria, Tunisia, Libya, Egypt, Israel, Syria, Jordan, Lebanon, Iraq, Saudi Arabia, United Arab Emirates, Qatar, Oman, Turkmenistan, Kazakhstan, Uzbekistan, Tajikistan, Kyrgyzstan, Western Sahara, Mauritania, Mali, Niger, Chad, Sudan, Afghanistan, Iran, Pakistan, northwest India	Yes?	Yes	No	No	None
Asia	*Empagusia*	*bengalensis*	Bengal monitor	Iran, Afghanistan, Pakistan, India, Sri Lanka, Bangladesh, Nepal, Bhutan, China, Myanmar	Yes	Yes	No	Yes	None
Asia	*Empagusia*	*dumerilii*	Dumeril's monitor	Peninsular Thailand, Myanmar, west Malaysia, Indonesia, Sarawak, Singapore	Yes	Yes	No	Yes	None
Asia	*Empagusia*	*flavescens*	Yellow monitor	Pakistan, India, Nepal, Bhutan, Bangladesh	Yes?	Yes	No	Yes	None
Asia	*Euprepiosaurus*	*caerulivirens*	Turquoise monitor	Indonesia	No?	No	Yes	Yes	Minor
Asia	*Euprepiosaurus*	*cerambonensis*	Ceram mangrove monitor	Indonesia	No?	No	Yes	Yes	Minor
Asia	*Euprepiosaurus*	*doreanus*	Blue-tailed monitor	New Guinea, northern Australia	No?	No	Yes	Yes	Minor
Asia	*Euprepiosaurus*	*douarrha*	New Ireland monitor	New Guinea	No?	No	Yes	Yes	Moderate?
Asia	*Euprepiosaurus*	*finschi*	Finsch's monitor	New Guinea	No?	No	Yes	Yes	Moderate?
Asia	*Euprepiosaurus*	*indicus*	Mangrove monitor	Australia, New Guinea, Indonesia	No?	Yes	Yes	Yes	Moderate?
Asia	*Euprepiosaurus*	*jobiensis*	Peach-throated monitor	New Guinea, Indonesia	No?	No	Yes	Yes	Moderate?
Asia	*Euprepiosaurus*	*juxtindicus*	Rennell Island monitor	Solomon Islands	No?	No	Yes	Yes	Moderate?
Asia	*Euprepiosaurus*	*melinus*	Quince monitor	Indonesia	No?	Yes	Yes	Yes	Moderate?
Asia	*Euprepiosaurus*	*prasinus*	Emerald tree monitor	New Guinea, Australia	No?	No	Yes	Yes	Moderate?
Asia	*Euprepiosaurus*	*yuwonoi*	Black-backed mangrove monitor	Indonesia	No?	Yes	Yes	Yes	Moderate?
Asia	*Hapturosaurus*	*beccarii*	Black tree monitor	Indonesia	No?	Yes	Yes	Yes	Moderate?
Asia	*Hapturosaurus*	*keithhornei*	Canopy goanna	Australia	No?	No	Yes	Yes	Moderate?
Asia	*Hapturosaurus*	*kordensis*	Biak tree monitor	New Guinea	No?	No	Yes	Yes	Moderate?
Asia	*Hapturosaurus*	*macraei*	Blue-spotted tree monitor	New Guinea	No?	No	Yes	Yes	Moderate?
Asia	*Philippinosaurus*	*bitatawa*	Northern Sierra Madre forest monitor	Philippines	Frugivore	Yes	Yes	Yes	None
Asia	*Philippinosaurus*	*mabitang*	Panay monitor	Philippines	Frugivore	Yes	Yes	Yes	None
Asia	*Philippinosaurus*	*olivaceus*	Gray's monitor	Philippines	Frugivore	Yes	Yes	Yes	None

continued

TABLE 1
Continued

Clade*	Subgenus	Species	Common name	Distribution	Genetic resistance to toad toxins? (Y/N)	Sympatric with toads in native range? (Y/N)	Has encountered invasive toads? (Y/N)	Will likely encounter toads in future? (Y/N)	Likely impact of encounters with toads
Asia	*Soterosaurus*	*cumingi*	Yellow-headed water monitor	Philippines	Yes?	Yes	Yes	Yes	None
Asia	*Soterosaurus*	*marmoratus*	Marbled water monitor	Philippines	Yes?	Yes	Yes	Yes	None
Asia	*Soterosaurus*	*nuchalis*	Large-scaled monitor	Philippines	Yes?	Yes	Yes	Yes	None
Asia	*Soterosaurus*	*palawanensis*	Palawan water monitor	Philippines	Yes?	Yes	Yes	Yes	None
Asia	*Soterosaurus*	*rudicollis*	Roughneck monitor	Burma, Thailand, Malaysia, Indonesia	Yes	Yes	Yes	Yes	None
Asia	*Soterosaurus*	*salvator*	Asian water monitor	Sri Lanka, India, Bangladesh, Myanmar, Cambodia, Laos, Vietnam, south China, Thailand, Malaysia, Singapore, Indonesia	Yes	Yes	Yes	Yes	None
Asia	*Soterosaurus*	*samarensis*	Yellow-headed water monitor	Philippines	Yes?	Yes	Yes	Yes	None
Asia	*Soterosaurus*	*togianus*	Togian water monitor	Indonesia	Yes?	Yes	Yes	Yes	None
Australia	*Odatria*	*acanthurus*	Ridge-tailed monitor	Australia	No	No	Yes	Yes	Minor
Australia	*Odatria*	*auffenbergi*	Peacock monitor	Indonesia	No?	Yes	Yes	Yes	Minor
Australia	*Odatria*	*balagardi*	No common name	Australia	No?	No	Yes	Yes	Minor
Australia	*Odatria*	*baritji*	Black-spotted ridge-tailed monitor	Australia	No?	No	Yes	Yes	Minor
Australia	*Odatria*	*brevicauda*	Short-tailed monitor	Australia	No?	No	No	Yes	Minor
Australia	*Odatria*	*bushi*	Pilbara monitor	Australia	No?	No	No	Yes	Minor
Australia	*Odatria*	*caudolineatus*	Stripe-tailed goanna	Australia	No?	No	Yes	Yes	Minor
Australia	*Odatria*	*eremius*	Rusty desert monitor	Australia	No	No	No	Yes (partial overlap)	Minor
Australia	*Odatria*	*gilleni*	Pygmy mulga monitor	Australia	No?	No	No	Yes (partial overlap)	Minor
Australia	*Odatria*	*glauerti*	Kimberley rock monitor	Australia	No?	No	Yes	Yes	Minor
Australia	*Odatria*	*glebopalma*	Black-palmed rock monitor	Australia	No?	No	Yes	Yes	Minor

Australia	*Odatria*	*hamersleyensis*	Southern Pilbara rock goanna	Australia	No?	No	No	Yes	Minor
Australia	*Odatria*	*kingorum*	King's monitor	Australia	No?	No	Yes	Yes	Minor
Australia	*Odatria*	*mitchelli*	Mitchell's water monitor	Australia	No	No	Yes	Yes	Minor
Australia	*Odatria*	*pilbarensis*	Pilbara rock monitor	Australia	No?	No	No	Yes	Minor
Australia	*Odatria*	*primordius*	Northern ridge-tailed monitor	Australia	No?	No	Yes	Yes	Minor
Australia	*Odatria*	*scalaris*	Spotted tree monitor	Australia, New Guinea	No	No	Yes	Yes	Minor
Australia	*Odatria*	*semiremex*	Rusty monitor	Australia	No?	No	Yes	Yes	Minor
Australia	*Odatria*	*sparnus*	Dampier Peninsula monitor	Australia	No?	No	No	Yes	Minor
Australia	*Odatria*	*storri*	Storr's monitor	Australia	No	No	Yes	Yes	Minor
Australia	*Odatria*	*timorensis*	Timor monitor	New Guinea, Timor-Leste	No?	No	Yes	Yes	Minor
Australia	*Odatria*	*tristis*	Black-headed monitor	Australia	No	No	Yes	Yes	Minor
Australia	*Papusaurus*	*salvadorii*	Crocodile monitor	New Guinea	No?	No	Yes	Yes	Moderate?
Australia	*Varanus*	*giganteus*	Perentie	Australia	No	No	No	Yes (partial overlap)	Intense but localized?
Australia	*Varanus*	*gouldii*	Sand goanna	Australia	No	No	Yes	Yes	Intense but localized?
Australia	*Varanus*	*komodoensis*	Komodo dragon	Indonesia	No	No	No	Yes	Minor
Australia	*Varanus*	*mertensi*	Mertens' water monitor	Australia	No	No	Yes	Yes	Moderate
Australia	*Varanus*	*panoptes*	Yellow-spotted monitor	Australia, Indonesia, New Guinea	No	No	Yes	Yes	Intense
Australia	*Varanus*	*rosenbergi*	Heath monitor	Australia	No?	No	No	Yes (southern Australia)	Moderate
Australia	*Varanus*	*spenceri*	Spencer's goanna	Australia	No?	No	Yes	Yes (partial overlap)	Minor
Australia	*Varanus*	*varius*	Lace monitor	Australia	No	No	Yes	Yes (partial overlap)	Minor
Solomons	*Solomonsaurus*	*spinulosus*	Solomon Island spiny monitor	Solomon Islands	Yes?	No	Yes	Yes	None?

Authorities disagree on species-level recognition within some clades. Our table omits several taxa within *Euprepiosaurus* (*V. reisingeri*, *V. boehmei*, *V. telenestes*, *V. bogerti*, *V. beccarii*, *V. zugorum*) that are recognized by Ziegler et al. (2007) but not listed by Brennan et al. (2021)*.

FIGURE 3. AUSTRALIAN VARANID SPECIES THAT APPARENTLY CANNOT TOLERATE TOAD TOXINS
Within the Australian lineage of varanid lizards, smaller species in the subgenus *Odatria* such as the ridge-tailed monitor (*V. acanthurus*: A), the spotted tree monitor (*V. scalaris*: B), and Storr's monitor (*V. storri*: C)

resistance to bufonid toxins (Ujvari et al. 2013, 2015); thus, resistance appears to have been lost after the Asian ancestors of this lineage colonized Australia (Ujvari et al. 2013; see Figure 3).

For the subgenus *Odatria*, Ujvari et al. (2013) report no genes for toxin resistance in ridge-tailed monitor *V. acanthurus*, spotted tree monitor *V. scalaris*, Storr's monitor *V. storri*, or black-headed monitor *V. tristis*. Laboratory trials confirm low tolerance of bufotoxins in *V. scalaris* (Smith and Phillips 2006), and Pearson et al.'s (2014) study reported mortality in Kimberley rock monitor *V. glauerti*, black-palmed rock monitor *V. glebopalma, V. acanthurus, V. scalaris*, and *V. tristis* that were offered small live cane toads in captivity. However, none of four *V. storri* attacked toads that were offered. Further work is needed to see if *V. storri* is genuinely safe from toads. Dietary records for this rocky habitat species were primarily orthopterans, but included one lizard (Losos and Greene 1988). However, other *Odatria* species have been reported to consume anurans (e.g., rusty monitor *V. semiremex, V. glebopalma*; Pianka and King 2004). Relatively small body sizes (restricting maximum size of toads likely to be consumed) plus use of relatively arid habitats (reducing rates of encounter with toads and toadlets) suggest that most *Odatria* species are unlikely to be severely affected by toad invasion, although local populations might be at risk (see Table 1). Burnett's (1997) inference of a decline in the *V. scalaris* after toad invasion was based on anecdotal data, and stands in contrast to Watson and Woinarski's (2004) quantitative surveys that found no significant change in abundance of the Timor monitor *V. timorensis* (closely related to *V. scalaris*) due to cane toad invasion. Jackson (2005) reported that although specimens of *V. semiremex* were found dead after consuming cane toads, these lizards remained common in toad-invaded areas. The survey by Catling et al. (1999) similarly found no compelling evidence of a decline in *Odatria* species after toad arrival, and blue-tailed monitor *V. doreanus* remained common after toads invaded Cape York Peninsula (Natusch and Lyons 2017). Although these reports are encouraging overall, it is important to note that data are available for few species. Others may have declined.

Climate mapping by Tingley et al. (2018) predicts that if the Asian black-spined toad *D. melanostictus* establishes in Australia (as is likely, based on multiple records of arrival of specimens in freight), this toad likely will be able to spread over all areas currently invaded by cane toads, plus additional sites along the eastern seaboard as far south as Melbourne and westward across to a region around Perth (see Figure 3d in Tingley et al. 2018). Thus, varanid species in southern Australia, which are under no significant threat from the invasion of the more tropical cane toad, may be exposed to a future invasion of *D. melanostictus*. The tropical and arid-zone distributions of most *Odatria* species should minimize this risk, but southern populations of taxa such as *V. tristis* may be exposed (Table 1).

For the subgenus *Varanus*, Ujvari et al. (2013) report no genetic resistance to bufotoxins in rusty desert monitor *V. eremius*, perentie *V. giganteus, V. gouldii, V. mertensi, V. mitchelli, V. panoptes*, or *V. varius*. Consistent with those findings, field studies have reported cane toad-induced mortality in *V. gouldii, V. mertensi, V. mitchelli, V. panoptes*, and *V. varius* (Burnett 1997; Doody et al. 2007, 2013, 2014; Griffiths and McKay 2007; Britton et al. 2013; Brown et al. 2013; Jolly et al. 2016). However, the magnitude of impact has varied dramatically, ranging from near-extirpation of *V. panoptes* (Ward-Fear et al. 2016) to no detectable long-term effect on populations of *V. varius* (Pettit

do not exhibit the genetic changes associated with bufotoxin resistance. Larger species within the subgenus *Varanus* also lack genetic resistance to bufotoxins, but the magnitude of impact from invasive cane toads varies from no detectable long-term effects in the lace monitor (*V. varius*: D) to unknown (probably minimal) in perenties (*V. giganteus*: E) to significant population-level declines in Mertens' water monitor (*V. mertensi*: F) and yellow-spotted monitor (*V. panoptes*: G). Photographs by Ruchira Somaweera. See the online edition for a color version of this figure.

FIGURE 4. VARANID SPECIES WITH DIFFERING FUTURE VULNERABILITIES TO TOAD INVASION
The likely spread of the Asian black-spined toad (*D. melanostictus*) through southern Australia may affect the heath monitor (*V. rosenbergi*: A), which presumably lacks physiological resistance to toad toxins. The largest

2020). As noted above, varanids in southern Australia also may be imperiled by a future colonization by *D. melanostictus*. The taxon most likely to be at risk is the heath monitor *V. rosenbergi* (see Figure 4). It is a large species with a generalist diet (including frogs; Losos and Greene 1988), is closely related to the *gouldii-panoptes* clade that has been badly affected by cane toads (Brennan et al. 2021, and see above), and most of its range will be invaded by *D. melanostictus* under Tingley et al.'s (2018) predictions. Overlap with toads also may be significant for other taxa that are largely restricted to arid habitats, but whose ranges include some sites that are sufficiently mesic for toad incursions. Such taxa include the Spencer's goanna *V. spenceri*, and perhaps even the perentie, *V. giganteus*.

In summary, habitat preferences and small body size may reduce the vulnerability of most *Odatria* species to invasive toads, but at least some mortality is likely to be occurring due to cane toads, and more is likely if Asian black-spined toads also invade the continent. Toad invasion has dramatically affected populations of some species within the subgenus *Varanus*, while having only minor impacts on others. The likely future spread of Asian black-spined toads through southern Australia has the potential to negatively affect populations of species that occur in areas too far south to regularly encounter cane toads.

SPECIES FROM AUSTRALIAN LINEAGES THAT OCCUR OUTSIDE OF AUSTRALIA

As shown above, the resistance to bufonid toxins has been lost in the Australian varanid lineage. Therefore, any offshoot of that lineage that extends its range back into the Indo-Australian archipelago could be at risk from invading toads, both *D. melanostictus* and *R. marina*.

There are two main phylogenetic groups of lizards involved. The first group consists of small arboreal taxa within the subgenus *Odatria*. Koch et al. (2013) recognize three *Odatria* species (*V. timorensis*, *V. scalaris*, and *V. similis*) as occurring in the Indo-Australian archipelago, whereas all other taxa are restricted to mainland Australia. Based on genetic data from *V. scalaris* and related taxa (Ujvari et al. 2013), these lizards might be negatively impacted by invasion of either cane toads or Asian black-spined toads. However, populations of *V. timorensis* do not appear to have been affected by cane toad invasion (Watson and Woinarski 2004), and arboreal habits of these lizards should decrease rates of encounter with terrestrial toads.

The other clade consists of two species, closely related but allocated to different subgenera. The crocodile monitor *V. salvadorii*, endemic to Papua New Guinea, grows to very large body sizes, is the sole species within the subgenus *Papusaurus*, and is closely related to a group of large species including the *V. varius-V. komodoensis* clade (Brennan et al. 2021). There are no studies as yet on the genetics or ecology of *V. salvadorii* from which to evaluate vulnerability to toad invasion. The second taxon is the gigantic Komodo dragon *V. komodoensis*, within the subgenus *Varanus* and closely related to *V. varius* (Brennan et al. 2021). Komodo dragons evolved within Australia, then spread northward to Southeast Asia (Shine and Somaweera 2019).

Genetic data suggest that *V. komodoensis* lacks physiological resistance to bufonid toxins, and hence might be at risk from the imminent arrival of Asian black-spined toads (Ujvari et al. 2014; Reilly et al. 2017; Kennedi et al. 2020). That inference is based on the catastrophic effects of cane toads on varanids in Australia (see above). However, the impact of Asian black-spined toads on Komodo dragons could be arguably reduced by several ecological, environmental, and management factors, including:

1. the size ratio between the predator and prey—the dragons are much larger than

monitor lizard, the Komodo dragon (*V. komodoensis*: B) of Indonesia, also lacks physiological resistance to toad toxins but the impact of *D. melanostictus* on this species could be reduced by ecological, environmental, and management factors. Photographs by Ruchira Somaweera. See the online edition for a color version of this figure.

any other varanid species and the Asian black-spined toads are smaller than cane toads. That size disparity lessens the effective dose of toxin per kg of predator;
2. juvenile Komodo dragons (the size class most likely to eat small prey such as toads) are largely arboreal (Imansyah et al. 2008), reducing rates of encounter;
3. with increasing body size, Komodo dragons switch from small (less than 10 kg) to large (more than 50 kg) prey, especially ungulates (Purwandana et al. 2016). Therefore, toads may not trigger feeding responses in adult Komodo dragons;
4. the arid conditions on the islands inhabited by the dragons would restrict distribution and breeding opportunities for amphibians (Auffenberg 1980), including toads (collectively, these islands possess less than 100 km^2 of suitable toad habitat);
5. likely resilience—the Australian species to which *V. komodoensis* is most closely related (*V. varius*; Brennan et al. 2021) has shown few impacts from the cane toad invasion (Pettit 2020); and
6. the restricted island distribution of Komodo dragons (with limited toad habitat) means that park staff are aware of the threat and, most importantly, are logistically capable of detecting and combating toad incursions (Somaweera et al. 2018).

Overall, then, life-history and ecological data plus existing management strategies for Komodo dragons suggests their populations are unlikely to be imperiled by the arrival of Asian black-spined toads. However, that risk level also depends upon the amount of toxin (and its chemical composition and, thus, potency) in Asian black-spined toads—a critical factor that has yet to quantified. If *D. melanostictus* possesses more, or more powerful, toxins than *R. marina*, the Asian species' impact may be greater than one might expect from its smaller size.

SYNTHESIS

Although invasive toads are spreading in several parts of the world, they pose no risk to native varanid lizards in places such as Europe and the Americas, outside the native range of varanids. Mainland Africa is also not a concern, because although it contains both toads and varanids, long-term sympatry has resulted in the African lizards being able to consume toads without ill effect. Although some species of toads thrive in arid habitats, the toads most likely to spread through the stronghold of varanids (Australia and islands to its north) are mesic-adapted taxa (cane toads and Asian black-spined toads). Thus, the many varanid species restricted to arid habitats in Australia are unlikely to be under population-level threat.

Of the two species of toads most likely to imperil varanids, one (the cane toad) has already spread through much of Australia and the other (the Asian black-spined toad) has already spread through much of the Indonesian archipelago. Hence, we might expect to already have a clear idea of the magnitude of impacts of invasive toads on varanids. In practice, the information is sparse, except for large-bodied members of the subgenus *Varanus* in tropical and eastern Australia. Clearly, some species have undergone dramatic declines (e.g., *V. panoptes*), others have been affected to an intermediate degree (e.g., *V. mertensi*), and the abundance of others has been virtually unaffected (*V. varius*). All of these species lack resistance to toad toxins, suggesting that ecological, behavioral, and environmental factors determine outcomes of the interaction between varanids and toads (Pinch et al. 2017). For example, *V. panoptes* persist in an arid habitat at the southern edge of their distribution (G. Ward-Fear, pers. obs., 2018), highlighting the nuances in assessing impacts wrought by invaders.

What species of varanid lizards should be of conservation priority because of the risk of impact from toads? Our analyses identify *V. rosenbergi* in southern Australia as potentially vulnerable if Asian black-spined toads manage to colonize those areas; it is thus important to stop that toad species from establishing and spreading in Australia (see Tingley et al. 2018 for a fuller discussion). Another species of concern may be *V. spenceri*, a large-bodied varanid capable of eating adult toads and with some overlap in range. Table 1 identifies other taxa requiring further study in this respect.

Our analysis also identifies several aspects where further information is required. For example, quantitative assessments of the impact of toad invasion on the abundance of varanids is lacking for most species of monitors, but should be feasible both within Australia (e.g., field surveys of numbers of *Odatria* in sites with and without cane toads) and Indonesia (e.g., numbers of *Euprepiosaurus* and *Hapturosaurus* in sites with and without Asian black-spined toads). The impact of cane toads has been studied in much more detail than has that of Asian black-spined toads, and many of the approaches applied to cane toads (e.g., analysis of toxin contents relative to toad body size, and of the amounts of toxin needed to kill a predator; Phillips and Shine 2006) could usefully be undertaken for Asian black-spined toads as well.

More broadly, the Varanidae have successfully diversified to fill an array of niches across a cosmopolitan distribution (Pianka and King 2004), although they remain genetically and morphologically conservative (80 species belonging to a single genus; Zhu et al. 2020). That framework lends itself to clarifying the relative influences of environmental and genetic factors on vulnerability to threatening processes. Incorporating phylogenetic relationships provides a relatively novel avenue for impact assessment when traditional methods focus predominantly on ecological overlap between the native and invader (Bartz and Kowarik 2019). An invader's mode of impact will determine how useful such an analysis of native species will be; nevertheless, this review highlights both the complexities of invasion ecology and the breadth of tools now available for conservation management.

Lastly, because wild varanids are difficult to work with (Pianka and King 2004), detailed information on ecology and behavior remains sparse for most species. Nonetheless, it is already clear that varanids can play critical ecological roles as predators, prey, and ecosystem engineers (Mukherjee and Sen Sarkar 2013; Bennett 2014; de Miranda 2017; Ward-Fear et al. 2020). Given the population densities reached by some species, varanids are likely to be more important ecological players than is usually envisaged (Sutherland et al. 2011; de Miranda 2017). Thus, any threat to the viability of their populations, as in the case of invasive toxic toads, warrants careful scrutiny and, if required, active management.

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