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Ecosystem engineering by deep-nesting monitor lizards

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As the current biodiversity crisis approaches levels comparable to the rates of the five historical mass extinctions, increasing attention has focused on how to stop or slow species loss and preserve ecosystem function. The impact of the loss of an individual species on communities and ecosystems is heterogeneous, however. Removing some species has negligible effects while the removal of others can be catastrophic. Metaphorically, the scenario can be likened to Jenga, a popular block-balancing game in which players build a tower of wooden pieces, analogous to a dynamic ecosystem (DeRuiter et al. 2005). Players remove pieces (individual species extinctions), which can have no effect or cause partial or total collapse (of communities or ecosystems). Species that are invariably important to their communities and ecosystems include keystone species, umbrella species, and ecosystem engineers (Caro 2010). Ecosystem engineers are species whose traits have significant impacts on the physical structures of their habitats and the organisms that live in those habitats (Jones et al. 1994). Reptiles rarely feature as ecosystem engineers (e.g., review by Coggan et al. 2018), but monitor lizards excavate foraging burrows that trap leaf litter, viable seeds, and fruits (Whitford 1998), and these burrows have higher levels of labile carbon and mineralizable nitrogen than surface soils (James and Eldridge 2007, James et al. 2009). Herein we reveal that two species of large monitor lizards can serve a significant role as ecosystem engineers via their unique nesting behavior and remarkable communal nesting warrens.

The yellow-spotted monitor lizard, *Varanus panoptes* (Fig. 1, inset), is a large lizard, up to 1.4 m in length, that occupies riparian areas and floodplains in tropical Australia, a landscape where reptiles often dominate the top of the food web. Despite its size, its biology is little known, partly because its home in northern Australia is roughly the size of Europe but with less than three million people. Large males are bold and approachable, but the smaller females and female-sized males are secretive. Over the last decade or so, however, our research team has pried open a treasure trove of natural history information about this enigmatic species. First, when the arrival of the toxic, invasive cane toads (*Rhinella marina*) decimated populations of the yellow-spotted monitor, the lizard's previous extensive trophic reach within the food web became apparent (Doody et al. 2009, 2013, 2015*b*, 2017). In 2012, our research team discovered yellow-spotted monitor eggs in nests at depths up to 4 m—easily the deepest vertebrate nests on earth (Fig. 1)! This and further excavations revealed that the burrows were helical, like a work of art, much like fossil burrows of prehistoric beavers and stem reptiles that thrived tens to hundreds of millions of years ago (Fig. 1B; Doody et al., 2015*a*, 2018*a*, *b*). Subsequent excavations uncovered four more findings. First, the hatchlings do not use the mother's burrow to escape the nest: they excavate their own burrows straight up through 2–4 m of resistant soils (Fig. 1B; Doody et al. 2018*a*). Second, the warrens generally reflected communal and traditional nesting (Fig. 1B). Some warrens contained > 100 clutches of eggs and eggshells within a 4 × 4 m area (i.e., 16 m^2) (Doody et al. 2018*a*)! Third, Gould's monitor lizard, *V. gouldii*, the smaller, sister species to the yellow-spotted monitor, exhibited the same deep, communal nesting, with helices and separate hatchling escape burrows (Fig. 1B; Doody et al. 2018*b*). The Gould's monitor lizard is more widespread and is a major mesopredator in both tropical savannahs and desert ecosystems, falling prey to yellow-spotted monitor and a few other top predators. But the fourth and final finding would bring us back full circle, to the community and ecosystems to which the yellow-spotted monitor and Gould's monitor lizards belong.

To our surprise, as we excavated warrens across a ~ 1,200-km stretch of northern Australia, we discovered small animal communities occupying the burrow

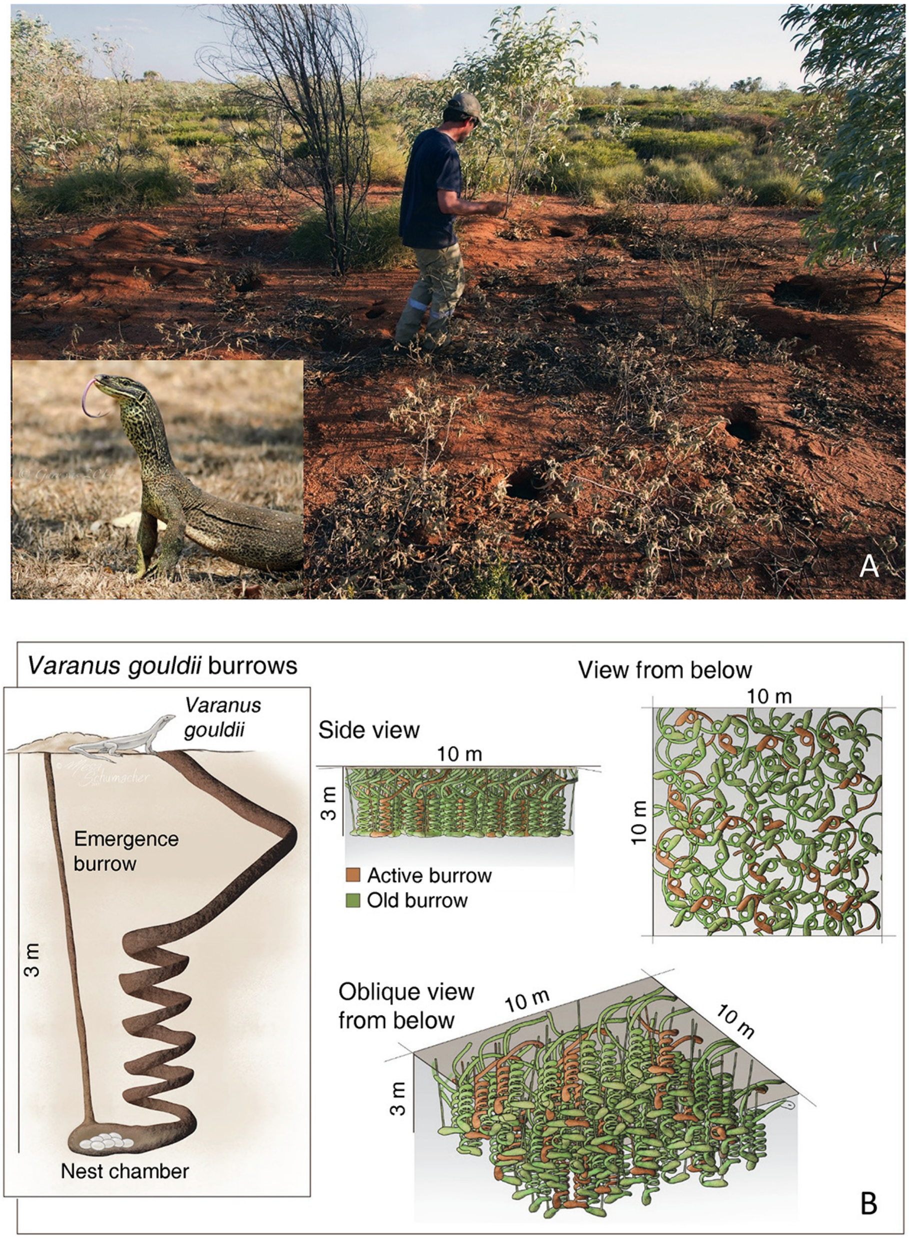

Fig. 1. (A) Gould's monitor lizard (*Varanus gouldii*) communal nesting warren before excavation (photograph by Brendan Schembri); (B) three-dimensional reconstruction of an excavated *V. gouldii* communal nesting warren, showing a helical burrow created by a mother and the labyrinth of new and older multiple burrows that created habitat for small animals (Illustration by Mesa Schumaacher). Inset shows *V. panoptes*, the other ecosystem engineer (photograph by Gary Vas).

systems. The labyrinth of fresh and older burrows (Fig. 1B) hosted snakes, geckos, skinks, monitors, frogs, toads, scorpions, centipedes, beetles, ants, and a marsupial, sometimes one at a time, other times in great numbers. One warren even contained 418 individual frogs. Overall we found 747 individuals of 28 species of vertebrates in just 16 warrens ($N = 558$; Appendix S1: Table S1) and 14 individual foraging burrows ($N = 189$). Warren sizes were not precisely measured, but ranged from ~ 2–120 m^2 in two-dimensional space. Species richness and abundance of burrow associates appeared to be higher in the larger warrens that are nested in traditionally (year after year), because they contained more open burrows with various burrow entrances and caved-in openings to the surface. The timing of our excavations revealed clues as to why a given species was using the warrens. For example, the frogs we found were in aestivation/brumation because they are not active during the dry season winter, while the small reptiles were likely using the warrens as temporary refuges for thermoregulation, protection from predators, or foraging. Finally, the soil in the warrens, loosened by the yellow-spotted monitor and Gould's monitor lizards, attracted other nesting lizards; spiny-tailed monitor lizards (*V. acanthurus*) and spiny-tailed geckos (*Strophurus ciliarius*) both nested communally in the warrens, and a Gould's monitor nested in a yellow-spotted monitor warren. The warm, moist conditions (constant ~ 30°C, ~3% moisture by weight; Doody et al. 2015a) and the soil loosened by the yellow-spotted monitor and Gould's monitor were apparently ideal for eggs of other species.

Collectively, our data suggest a role for large, communally and deep-nesting monitor lizards as allogenic ecosystem engineers: their nesting burrows facilitated small animal communities by providing habitat for refugia, feeding and nesting (autogenic engineers also alter the structure of the engineer, such as trees; see Jones et al., 1994). Moreover, the massive surface and subterranean perturbation involved in creating the warrens undoubtedly also plays a role in modifying the ecosystem. A recent review and meta-analysis revealed only tortoises and sea turtles as reptilian ecosystem engineers (Coggan et al. 2018), but a convincing argument has since been made for crocodilians (reviewed in Somaweera et al. 2020). Our natural history observations, coupled with studies of foraging burrows (see also Feit et al. [2020] for small lizards using Gould's monitor lizard foraging burrows), suggest that deep-nesting monitors should also be included in this nascent list of reptilian ecosystem engineers. Monitor lizards are unique in possessing both burrowing and nest building as co-engineering functions, and together these could have significant effects on ecosystem function.

There are important extensions of our natural history observations. Foremost, arriving invasive cane toads effectively remove yellow-spotted monitor (and anecdotally, Gould's monitor) from their ecosystems (Doody et al. 2017) and we have observed, but have not yet quantified, abandoned warrens without open burrows and their small animal communities. We have already demonstrated trophic cascades as a result of the loss of yellow-spotted monitor itself, but how important is the loss of ecosystem engineered habitat provided by the warrens? Fleming et al. (2014) suggested that losses of digging mammals have contributed to the deterioration of ecosystems in Australia. Coggan et al. (2018) suggested that experimental removal of the engineer would be the ultimate test of the importance of the engineer to the community or ecosystem; the imminent arrival of cane toads at one of our sites will decimate the yellow-spotted monitor, thereby providing just such a "natural" experiment. Second, are there any other large burrowing lizard species that have been overlooked as ecosystem engineers, such as iguanas or tegus? Finally, we predict that the other large Australian monitor lizard that endures a long dry season, the perentie (*V. giganteus*), will also nest at great depths in the Australian desert, implicating a third possible engineering species. Our research team is currently testing this hypothesis by investigating the spatial and nesting ecology of this iconic species in the red center of Australia.

The revelation of deep-nesting monitor lizards as ecosystems engineers can pave the way for future questions pursuing the cutting edge of knowledge in this area. For example, how do species invasions affect ecosystem engineers? Do trophic roles of engineers complement or exacerbate their engineering impacts; and how will climate warming affect refuges created by engineers (Coggan et al. 2018)? The deep-nesting monitor lizards of Australia present an ideal system for pursuing these questions.

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