

## Ecological Implications of Reptile Mesopredator Release in Arid South Australia

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**ABSTRACT.**—Few examples of mesopredator release, whereby subordinate predators increase in abundance in response to a reduction in dominant predators, have been demonstrated from reptile communities despite the important ecological role of large varanids and snakes. We tested the hypothesis that trophic cascades attributable to mesopredator release of varanids could explain the apparently perverse decline of some small reptiles following removal of exotic mammalian predators in a landscape-scale reserve in arid South Australia. We used counts of Sand Goanna (*Varanus gouldii*) tracks and diggings as a surrogate activity index in paddock-scale treatments with different assemblages of feral predators and reintroduced mammals. *Varanus gouldii* activity was five times higher in regions where cats and foxes were removed than where they were present. We hypothesize that the suppression of mammalian predators can have complex effects that extend to reptile communities and should inform conservation management decisions in environments with large reptile predators.

A reduction in the density or influence of higher-order predators typically leads to an increase in predators at lower trophic levels, or “mesopredators.” Although large prey species typically benefit from reduction in large predators, smaller prey may be more efficiently preyed upon by mesopredators and may decline. Ecological repercussions of such mesopredator release typically cascade to lower trophic levels (Palomares et al., 1995; Courchamp et al., 1999). For example an increase in smaller carnivore activity following a reduction in Coyote (*Canis latrans*) activity in North America resulted in significant declines of a number of bird species (Crooks and Soulé, 1999). Similar relationships have been demonstrated in other terrestrial mammal systems (Elmhagen et al., 2010) and marine ecosystems (Myers et al., 2007; Casini et al., 2008; Baum and Worm, 2009) but until recently have been largely overlooked where reptiles are the mesopredators (Sutherland et al., 2011).

Australian varanid lizards, or goannas, are considered to be the ecological equivalents of mammalian mesocarnivores, such as the Kit Fox (*Vulpes macrotis*) and *C. latrans* in North America (Pianka, 1986, 1989), although in some environments large varanid species are considered apex predators (Pianka, 1994). Sand Goannas (*Varanus gouldii*) are widespread in Australian arid regions and consume a wide range of reptile, mammal, and invertebrate prey (Pianka, 1982, 1986, 1994; Shine, 1986; Losos and Greene, 1988). Prey are encountered typically on the surface through active foraging or dug from diurnal retreats.

In arid Australian environments, exotic cats (*Felis catus*), Red Foxes (*Vulpes vulpes*), and naturalized Dingoes (*Canis lupus dingo*) prey extensively on goannas and to a lesser extent on snakes (Catling, 1988; Read and Bowen, 2001; Paltridge, 2002; Olsson et al., 2005). Although these mammalian predators also prey on reptiles and other important prey items of goannas and snakes, their mode and timing of hunting, and hence predation efficiency, likely differs from reptile predators (Sutherland et al., 2011). Therefore, changes in densities of exotic predators have the potential to precipitate trophic cascades through Australian reptile communities by affecting densities of large predatory reptiles.

Two 10-year predator exclosure experiments provide apparently conflicting signals on the response of Australian reptiles to

removal of exotic mammalian predators. European Rabbits (*Oryctolagus cuniculus*) sustain elevated levels of large predators in arid Australia (Read and Bowen, 2001) and, hence, were also removed from these exclosures to enable control of foxes and cats. Small lizard captures increased by 40% in a fox, cat, and rabbit exclosure in New South Wales compared to unfenced control sites (Olsson et al., 2005). In contrast, despite a sustained irruption of small mammals, numbers of common small lizards have, on average, declined in the rabbit-, cat-, and fox-free Arid Recovery Reserve in central South Australia (Moseby et al., 2009; Read and Cunningham, 2010). Diplodactyline geckoes, especially *Diplodactylus conspicilatus* and *Diplodactylus tessellatus* were particularly suppressed within the reserve, whereas capture rates of *Nephrurus levis* peaked in the reserve compared to four other grazing and predation treatments outside of the reserve (Read and Cunningham, 2010). *Diplodactylus conspicilatus* shelters in spider burrows (Read, 1999a) that are readily accessible to *V. gouldii* (pers. obs), whereas *N. levis* digs and backfills its own holes, concealing them from diurnal predators such as Sand Goannas.

Mesopredator release may be responsible for the divergent outcomes in these two predator exclosures. *Varanus gouldii*, likely to be more efficient predators of small terrestrial lizards than are either cats or foxes, were excluded from the New South Wales exclosure (Olsson et al., 2005) but not removed from the Arid Recovery Reserve.

Our objective was to test the hypothesis posed by Moseby et al. (2009) and Read and Cunningham (2010) that the decline in reptile abundance in the Arid Recovery Reserve could be attributable to increased activity or behavioral changes in key reptile mesopredators as a result of the elimination of Dingo, fox, and cat predation. This study enables the potential mesopredator role of varanids posed by Sutherland et al. (2011) to be tested and should assist in determining the natural dynamics of reptile communities before the widespread ecological changes wrought by the introduction of rabbits, cats, and foxes into arid Australia. The Arid Recovery Reserve presents a particularly valuable site for investigating these dynamics because of historical sampling before the elimination of exotic predators and the absence of the confounding influence of fire succession, which is an important driver of other arid reptile assemblages (Pianka, 1986; Pianka and Goodyear, 2012).

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## MATERIALS AND METHODS

*Site Description.*—The Arid Recovery Reserve near Roxby Downs in northern South Australia (30°29'S, 136°53'E), includes an 86-km<sup>2</sup> fenced section from which all rabbits, cats, and foxes were removed between 1997 and 1999 (Moseby et al., 2011). The climate is arid (mean annual rainfall 166 mm), and the landscape is dominated by parallel orange sand dunes superimposed upon a chenopod shrub plain. Two of the three experimental treatments were located within this predator-free section of the reserve. The “reintroduced mammals” treatment included the Main Exlosure (14 km<sup>2</sup>) and First Expansion (8 km<sup>2</sup>) of the reserve, where four native mammals had been successfully reintroduced following removal of feral species (Fig. 1). The “control” treatment was the Second Expansion (8 km<sup>2</sup>) of the reserve where foxes, cats, and rabbits had been removed, but no native mammals had been reintroduced. A third treatment, “exotics,” was located in areas east and west of the reserve from which cats, foxes, and rabbits had not been removed (Fig. 1).

The Arid Recovery Reserve was historically lightly grazed by sheep, then cattle, until being fenced incrementally from 1996–2000. Low intensity cattle grazing continued outside the reserve during this study (Read and Cunningham, 2010). The density of perennial grasses (Moseby et al., 2009) and recruitment of palatable shrubs and trees (Munro et al., 2009) have increased inside the reserve relative to surrounding pastoral regions. Red Kangaroos (*Macropus rufus*) were present within the reserve but were controlled by limited accessibility to water and intermittent harvesting to maintain low densities (Moseby et al., 2009). Although the Arid Recovery Reserve extends outside the Dingo Fence, where Dingoes play an important role in structuring predator and large herbivore assemblages, all exotic sites used in this study were inside the Dingo Fence where Dingoes were controlled and comparatively rare.

*Sampling Techniques.*—Adult *V. gouldii* are surveyed inefficiently in the small pitfall traps used for general terrestrial fauna surveys at the Arid Recovery Reserve (Moseby et al., 2009) because they can walk over or climb out of traps. However, *V. gouldii* leave distinctive spoor, including walking tracks, foraging digs, and burrows that can be counted to compare activity levels in different treatments.

*Varanus gouldii* tracks were counted along 1-m wide transects in each treatment during February 2009. Dunes in each treatment were divided into numbered 500-m transects using aerial photography. Transects were spaced at least 500 m apart based upon previous measurements of *V. gouldii* home range in the reserve being 5.9 ha ( $\pm 1.0$ ,  $N = 9$ ) (Bolton and Moseby, 2004) and 500 m from the treatment boundaries to ensure independence and exclude possible edge effects (Turner, 1996; Laurance, 2000). A random number table was used to allocate 12 replicates for each treatment from 47 possible transects over all three treatments. Each transect was prepared by dragging a 1-m metal bar behind a quad bike at low speed (10 km/h) through the dunes. Transect length was measured using the quad bike odometer with start and end point of each transect recorded on a hand held GPS (accurate to  $\pm 4$  m). Drags were completed between 0630 and 0830 h and checked 24 h later. *Varanus gouldii* were sometimes active by 0800 h; therefore, to assess daily activity indices, it was imperative that transects were checked before activity commenced on the day following the monitoring period. Six transects were counted once in each of the three treatments, with two drags completed in each treatment each day. The order of transect dragging was randomized, and all

transects were completed within a 6-day period. *Varanus gouldii* and large elapid snake tracks, clearly distinguishable from any other tracks in the region, were counted along each transect from the quad bike traveling at less than 10 km/h. We counted tracks separately if they completely departed from and re-entered the 1-m wide transect, the same procedure used to derive robust activity indices of reintroduced mammal populations at the Arid Recovery Reserve (Moseby et al., 2011).

*Varanus gouldii* activity on dune bases was also compared by counting their foraging digs at eight replicate sites in each of the three treatments. Sites were selected a priori in each treatment using computer generated points not less than 500 m apart, on geographically rectified aerial photographs. Foraging digs at each site were counted in a 1,256-m<sup>2</sup> area defined by a 20-m radius from points on both north and south facing lower dune flanks at each site because goanna digs are typically most prevalent on the base of the dunes (Bolton and Moseby, 2004; James and Eldridge, 2007). *Varanus gouldii* digs were evident by their triangular shape, which, unlike sympatric Burrowing Bettong (*Bettongia lesueur*), Greater Bilby (*Macrotis lagotis*), or rabbit digs, typically follow the prey burrow straight down, leaving a pile of sandy spoil on only one side of the dig (Moseby et al., 2010).

*Varanus gouldii* diet was assessed by dissecting stomach samples of road-killed specimens retrieved from within 50 km of the Arid Recovery Reserve to determine important prey types that may be affected by changes in goanna activity.

*Analysis Techniques.*—Differences in the number of goanna digs and track counts along replicated transects within the three treatments were analyzed statistically with the null hypothesis assuming equal track counts and digs between treatments. Data were tested for normality using the Wilks–Shapiro test, and data for tracks, but not digs, were found to be normally distributed ( $W \geq 0.85$ ,  $P < 0.05$ ). No successful transformations could be performed for *V. gouldii* digs; thus, data were tested using a one-way Kruskal–Wallis test. In contrast, *V. gouldii* track counts were tested using a one-way ANOVA where post hoc comparisons employed a pairwise comparison test for digs and Tukey’s HSD for track counts. Statistical significance was set at  $P \leq 0.05$ , and all statistics were computed using Statistix Version 8 (Software 2000). Insufficient numbers of large elapid tracks were recorded to warrant statistical or even inferential analyses.

## RESULTS

*Goanna Track Counts.*—*Varanus gouldii* tracks were recorded five times as frequently (mean = 8.17,  $F = 15.83$ ,  $df = 2,18$ ,  $P = 0.0001$ ) on transects inside compared to outside the Arid Recovery Reserve (mean = 1.5, Fig. 2). Pairwise comparisons indicated no significant difference in *V. gouldii* tracks recorded from reintroduced mammals and control treatments inside the reserve.

*Abundance of V. gouldii Foraging Digs.*—*Varanus gouldii* foraging digs per 1,256 m<sup>2</sup> were over four times as abundant (mean = 5.19) and significantly different ( $H = 6.7163$ ,  $P = 0.0348$ ) inside and outside (mean = 1.25) the Arid Recovery Reserve (Fig. 3). Pairwise comparison revealed no significant difference in the number of foraging digs between the inside reserve treatments of reintroduced mammals and control.

*Varanus gouldii Stomach Contents.*—Beetles, centipedes, and grasshoppers were the most frequently consumed prey items from 53 road-killed *V. gouldii* collected near the Arid Recovery

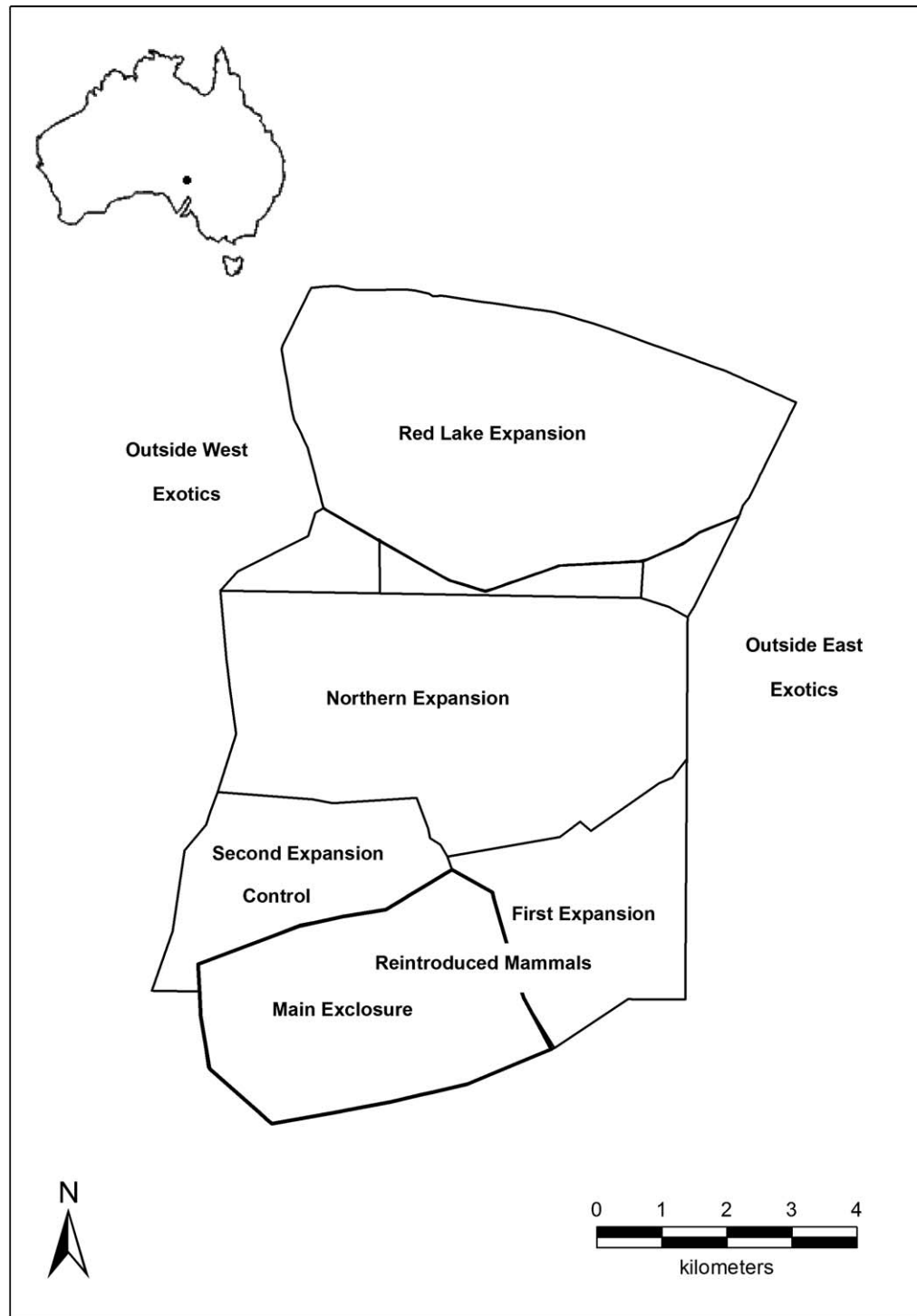


FIG. 1. Reintroduced mammals, control, and exotics treatments within and outside the 8,600-ha Arid Recovery Reserve in northern South Australia. Location of reserve indicated on map of Australia.

Reserve. Agamids, rodents, skinks, and geckoes were each also recorded from at least 9% of the *V. gouldii* stomachs.

#### DISCUSSION

Significantly higher *V. gouldii* activity within versus outside the Arid Recovery Reserve is assumed to represent an increase in their abundance as a result of the removal of cats, foxes, and Dingoes that are the main terrestrial predators of this lizard. Varanids were the most important prey sustaining populations

of cat, fox, and Dingo in the spinifex grasslands of the Northern Territory (Paltridge, 2002) and also feature in the diets of these predators immediately adjacent to the Arid Recovery Reserve (Read and Bowen, 2001). Olsson et al. (2005) demonstrated that *V. gouldii* activity was over five times higher in areas where foxes were heavily controlled than in uncontrolled areas. Similarly, eradication of feral cats on Faure Island, Western Australia, precipitated a *V. gouldii* increase from undetectable to noticeably more frequent (Rowles, 2008).

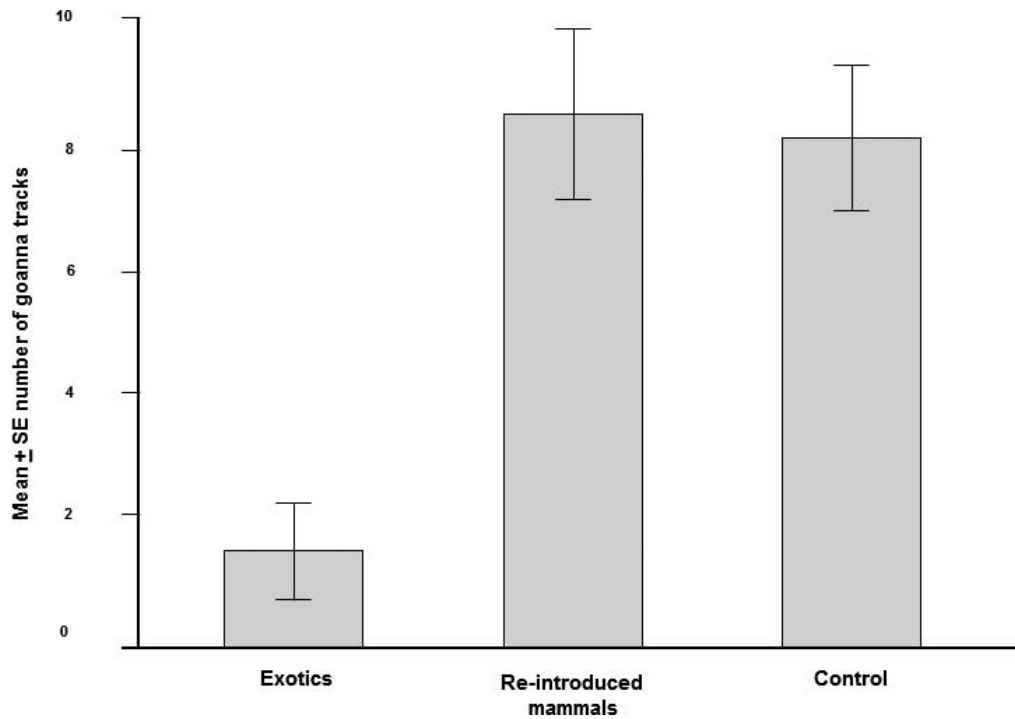


FIG. 2. Mean ( $\pm$  SE) *Varanus gouldii* tracks counted along 12 500-m transects in each of the treatments of exotics, reintroduced mammals, and control, at the Arid Recovery Reserve.

We cannot discount the possibility that decreased relative activity of *V. gouldii* outside the Arid Recovery Reserve was in part attributable to their greater wariness of foxes and cats. Prey species may alter their behavior because of the presence or scent

of predators (Sih, 1980; Colagross and Cockburn, 1993; Downes, 2002), and increased wariness in other reptiles has been demonstrated following increased harassment by predators (Rasilla, 2002; Stone et al., 1994; Blazquez, 1997). A reduction in

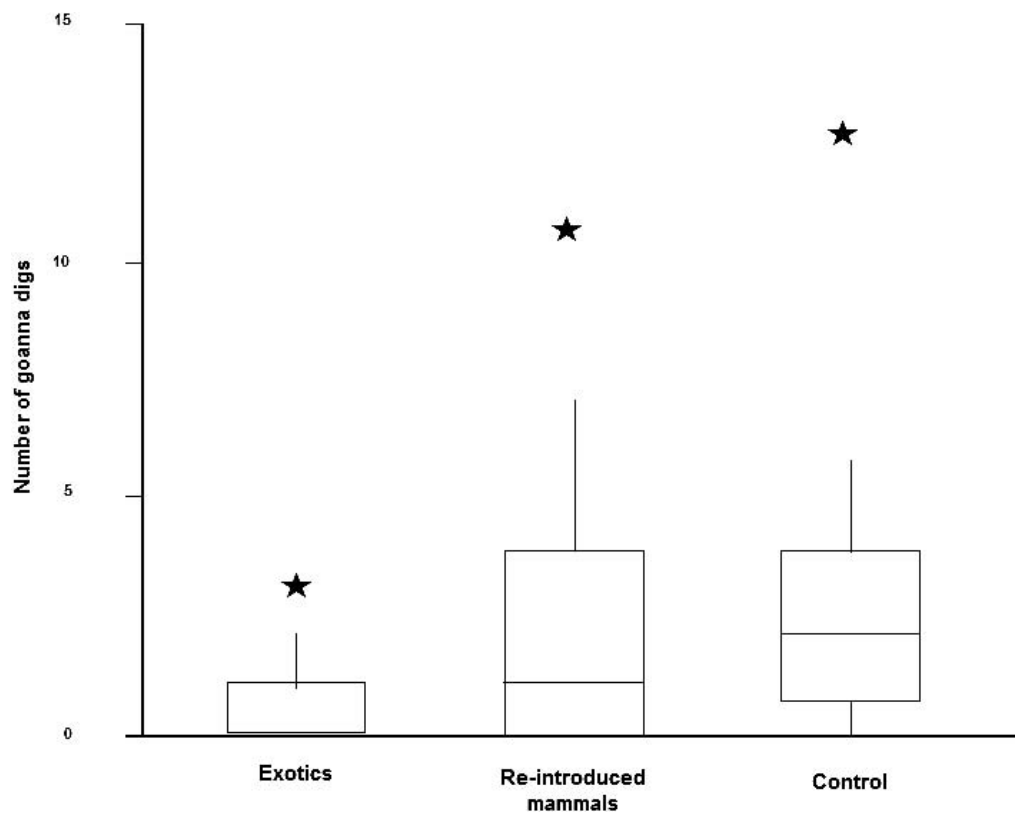


FIG. 3. Box-and-whisker plots showing the middle 50% of the count of *Varanus gouldii* digs in the box, bisected by the median line of *V. gouldii* digs counted in a 20-m radius ( $N = 8$ ) in the Arid Recovery treatments of exotics, reintroduced mammals, and control. Vertical whisker lines indicate the range of typical data values, and the stars denote possible outliers.

food resources within the reserve could also increase *V. gouldii* activity if they must forage longer or more widely. Although rabbit kittens that are typically born between June and September were unlikely to be a significant food source outside the reserve during the February sampling (Bowen and Read, 1998), higher reptile densities outside the Arid Recovery Reserve may have enhanced food availability compared to within the reserve. However, these alternative explanations are unlikely to account for the fivefold increase in *V. gouldii* activity recorded inside the reserve.

Interestingly, abundance of *V. gouldii* tracks or foraging digs did not differ significantly between paddocks of the Arid Recovery Reserve where threatened mammals have, or have not, been reintroduced. These reintroduced mammals could compete with goannas for resources, because *M. lagotis* and Western Barred Bandicoots (*Parameles bougainville*) consume a range of invertebrate prey, and *M. lagotis* have been observed hunting geckoes at the Arid Recovery Reserve (R. Pedler, pers. obs.). However, studies conducted within the reserve indicate that reptile abundance between these two treatments did not differ significantly at the time of our study (Moseby et al., 2009), suggesting that competition between *V. gouldii* and reintroduced mammals was less ecologically influential than exclusion of feral predators.

The significantly higher abundance of *V. gouldii* digs we recorded inside the Arid Recovery Reserve concurs with results from an independent study by James and Eldridge (2007). Most digs are attributed to foraging attempts because *V. gouldii* capture most of their prey in arid environments through digging (Shine, 1986; Pianka, 1994). Our data confirmed that reptiles, particularly geckos that are readily dug from their diurnal retreats (Pianka, 1994; Olsson et al., 2005), are important prey items sustaining goannas in arid environments (Mills et al., 1993; Menge et al., 1994; Pianka, 1994; Vandermeer and Maruca, 1998).

Large reptilian carnivores, including goannas, can be important predators and ecological competitors that drive interspecific interactions (Mirtschin, 1982; Rodda and Fritts, 1992; Pianka, 1994; Blamires, 2004). Sutherland et al. (2011) postulated that some varanids, including the *V. gouldii*, have the potential to initiate a mesopredator response following removal of exotic predators. Exclusion of goannas and exotic predators can precipitate significant increases in the density of small lizards, suggesting that predation can be a driver of lizard population dynamics (Olsson et al., 2005). We contend that increased activity of *V. gouldii* inside the Arid Recovery Reserve is the most likely explanation for the decline in abundance of small lizards recorded in two independent studies there since the removal of cats and foxes (Moseby et al., 2009; Read and Cunningham, 2010). Both of these studies employed multiple regional controls in pastoral and ungrazed areas that account for differences in vegetation cover, yet the influence of the predator exclusion was the most significant predictor of small lizard abundance. Trapping at multiple sites in matched habitats outside the reserve at the same time as the inside-reserve monitoring also enabled potential effects of dramatic seasonal variability in lizard abundances (Read et al., 2011) to be dismissed as a contributing factor. Although we did not test seasonal variability in *V. gouldii* activity in this study, the significant difference in activity within and outside the reserve in the same summer activity period suggests a treatment effect of mammalian predator exclusion over and above any seasonal variability. No significant increase in carnivorous dasyurid

marsupials has been detected within the reserve (Moseby et al., 2009), which largely eliminates other predators as the principal causal agent for the decline in small lizards. Restricted access to shelter sites following destruction of rabbit warrens within the reserve could also contribute to reduction in lizard abundance; however, the species that declined significantly (*D. conspicilatus*, *D. tessellates*, and large *Ctenotus*, Read and Cunningham, 2010) are not typical warren-commensal species (Read et al., 2008).

Our data support the hypothesis of Moseby et al. (2009), Read and Cunningham (2010), and Sutherland et al. (2011) that lower populations of geckoes inside the Arid Recovery Reserve may be the result of increased predation by *V. gouldii*, which have increased since feral predators were removed. Given that small lizards vulnerable to goanna predation are also major insectivores in arid Australian environments, a logical progression of this trophic cascade could include an increase in abundance of small invertebrates that are preyed upon by lizards. These invertebrates could be important detritivores, herbivores, or lower-level carnivores and also feature in the diets of reintroduced mammals, Trilling Frogs (*Neobatrachus centralis*, Read, 1999b), and other insectivores. On the contrary, larger invertebrates such as centipedes, large grasshoppers, and large beetles were common prey items of goannas in our study region, and populations of these taxa could be reduced by elevated goanna predation pressure. Therefore, through these trophic cascades, ecological effects of exotic predators may extend well beyond the vulnerable mammal and bird species that are typically considered to be the most susceptible fauna.

Land-use monitoring and impact assessment may be informed by the recognition of wider ecological implications of feral fox and cat predation. For example, potential declines in small nocturnal lizards should be considered where varanids are present and cats and foxes are controlled. Likewise increases in populations of small lizards may occur in varanid-occupied environments where feral predator populations are enhanced.

Recognition of different predation efficiencies between native and feral predators, and the potential for intricate and dynamic trophic cascades brought about by changes in abundance or activity of top predators, should inform conservation management decisions in environments with large reptile predators.

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