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## Environmental effects are stronger than human effects on mammalian predator-prey relationships in arid Australian ecosystems



Benjamin L. Allen<sup>a,\*</sup>, Alana Fawcett<sup>b</sup>, Alison Anker<sup>c</sup>, Richard M. Engeman<sup>d</sup>, Allan Lisle<sup>e</sup>, Luke K.-P. Leung<sup>e</sup>

<sup>a</sup> University of Southern Queensland, Institute for Agriculture and the Environment, Toowoomba, Queensland 4350, Australia

<sup>b</sup> University of the Sunshine Coast, Faculty of Science, Health, Education and Engineering, Sippy Downs, Queensland 4556, Australia

<sup>c</sup> Robert Wicks Pest Animal Research Centre, Biosecurity Queensland, Department of Agriculture and Fisheries, Toowoomba, Queensland 4350, Australia

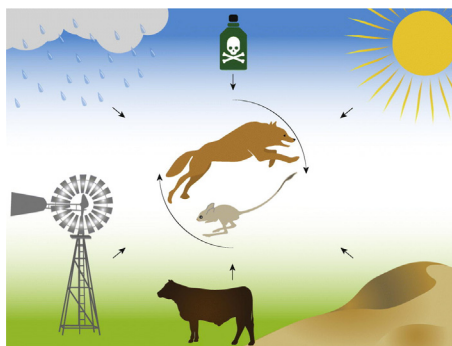
<sup>d</sup> National Wildlife Research Centre, US Department of Agriculture, Fort Collins, CO 8051-2154, USA

<sup>e</sup> University of Queensland, School of Agriculture and Food Sciences, Gatton, Queensland 4343, Australia

### HIGHLIGHTS

- Hopping-mice distribution was driven by geological factors, or habitat availability.
- Hopping-mice abundance was driven by climate, rainfall or food availability.
- Hopping-mice abundance and distribution fluctuates independent of predator control.
- Predator control is unlikely to increase hopping-mice distribution or abundance.
- Small mammals may benefit most from increased habitat and food availability

### GRAPHICAL ABSTRACT



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### ABSTRACT

Climate (drought, rainfall), geology (habitat availability), land use change (provision of artificial waterpoints, introduction of livestock), invasive species (competition, predation), and direct human intervention (lethal control of top-predators) have each been identified as processes driving the sustainability of threatened fauna populations. We used a systematic combination of empirical observational studies and experimental manipulations to comprehensively evaluate the effects of these process on a model endangered rodent, dusky hopping-mice (*Notomys fuscus*). We established a large manipulative experiment in arid Australia, and collected information from relative abundance indices, camera traps, GPS-collared dingoes (*Canis familiaris*) and dingo scats, along with a range of related environmental data (e.g. rainfall, habitat type, distance to artificial water etc.). We show that hopping-mice populations were most strongly influenced by geological and climatic effects of resource availability and rainfall, and not land use, invasive species, or human effects of livestock grazing, waterpoint provision, or the lethal control of dingoes. Hopping-mice distribution declined along a geological gradient of more to less available hopping-mice habitat (sand dunes), and their abundance was driven by rainfall. Hopping-mice populations fluctuated independent of livestock presence, artificial waterpoint availability or repeated lethal dingo control. Hopping-mice populations appear to be limited first by habitat availability, then by food availability, then by predation. Contemporary top-predator control practices (for protection of livestock) have little influence on hopping-mice behaviour or population dynamics. Given our inability to constrain the effects of predation across broad scales, management actions focusing on increasing available food and habitat (e.g. alteration of fire

\* Corresponding author.

E-mail addresses: [benjamin.allen@usq.edu.au](mailto:benjamin.allen@usq.edu.au) (B.L. Allen), [alanafawcett@live.com.au](mailto:alanafawcett@live.com.au) (A. Fawcett), [Richard.M.Engeman@aphis.usda.gov](mailto:Richard.M.Engeman@aphis.usda.gov) (R.M. Engeman), [alisle@uq.edu.au](mailto:alisle@uq.edu.au) (A. Lisle), [luke.leung@uq.edu.au](mailto:luke.leung@uq.edu.au) (L.K.-P. Leung).

and herbivory) may have a greater chance of improving the conservation status of hopping-mice and other small mammals in arid areas. Our study also reaffirms the importance of using systematic and experimental approaches to detect true drivers of population distribution and dynamics where multiple potential drivers operate simultaneously.

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## 1. Introduction

Food web structure and stability in terrestrial systems are influenced by a myriad of biotic, abiotic, and anthropogenic factors (Kershaw, 1969; Krebs, 2008). Commonly discussed factors include climate change, land use change, deforestation and invasive species (e.g. Petchey et al., 1999; Kinnaird et al., 2003; Tylianakis et al., 2008; Sinclair et al., 2013). While the effects of bottom-up factors (e.g. geology or habitat, climate or rainfall) on subsequent population growth within flora and fauna communities may be readily understandable (Robin et al., 2009; White, 2013), a growing body of research points to the effects that top-predators can have in shaping food web structure and stabilising the influence of other factors (Estes et al., 2013; Ripple et al., 2014). Through their suppressive effects on mesopredators and prey, top-predators might provide indirect benefits to some prey and vegetation at lower trophic levels, thereby maintaining ecosystem health and resilience. The strength of such trophic cascades is dependent on the complexity of the system and the number of trophic levels represented (Finke and Denno, 2004; Holt and Huxel, 2007), with top-predators typically exhibiting stronger effects in simpler systems with fewer trophic levels. These findings have led some to suggest that the maintenance, restoration or encouragement of top-predators is essential for the recovery of threatened fauna populations, communities and ecosystems (Ritchie et al., 2012; Ripple et al., 2014). However, there is also a large and growing body of evidence that these expectations are often not realised in situ given highly context-dependent factors and the complexities of even 'simple' systems (Sergio et al., 2008; Allen et al., 2014a; Haswell et al., 2017), especially those modified by humans (Linnell, 2011; Fleming et al., 2012; Wikenros et al., 2015). Understanding the relative influence of top-down and bottom-up factors on ecosystems remains a key priority for managers of predators and threatened fauna.

The complete removal of top-predators can have profound effects on ecosystem health and resilience (Estes et al., 2011), but whether or not their restoration can reverse these effects and restore ecosystems to previous benchmarks is less clear (e.g. Marshall et al., 2013). Moreover, whether or not the temporary suppression of common and widespread top-predators causes the same effects as complete predator removal is even less certain (Fleming et al., 2012; Allen et al., 2014a). Bottom-up factors, such as habitat availability, fire, rainfall or drought, are the primary drivers of fauna populations (White, 2013; Lawes et al., 2015). Top-down and bottom-up processes occur simultaneously, and also interact. For example, climate change may foster increased predation of prey fauna reliant on vegetation for food and refuge by increasing the frequency and severity of rainfall and subsequent vegetation shortages (Whetton et al., 1993; Letnic and Dickman, 2010). Such effects of climate change may be particularly important for irruptive or 'boom and bust' prey species, typical of desert biota, by extending the period that prey are exposed to high levels of predation (Newsome et al., 1989; Allen and Fleming, 2012). Extended periods of drought are known to exacerbate predation risks to irruptive fauna that typically persist in isolated and low-density populations (e.g. Dickman et al., 1999; Letnic and Dickman, 2006). However, there remains a dearth of studies demonstrating these expected functional relationships for many threatened fauna persisting in desert ecosystems, and identifying the strongest factors influencing prey populations has proved difficult (Holmes, 1995; Marshall et al., 2014; Peterson et al., 2014). All components of food webs interact to some extent (Allen et al., In press), but few interactions

are strong enough to shape them. Although general ecological patterns may already be apparent, the outcomes of global environmental change are highly unpredictable, and 'the greatest single challenge will be to determine how context alters the direction and magnitude of effects on biotic interactions' (Tylianakis et al., 2008).

In this study, we investigate the influence of multiple biotic and abiotic factors affecting predator-prey relationships in the arid Strzelecki Desert region of central Australia. The Strzelecki Desert is characterized by a depauperate mammal assemblage comprised of one top-predator (dingoes, *Canis familiaris*), two mesopredators (European red foxes, *Vulpes vulpes*, and feral cats, *Felis catus*) and two common mammalian prey species, European rabbits (*Oryctolagus cuniculus*) and dusky hopping-mice (*Notomys fuscus*; hereafter hopping-mice). Other predator and prey species are present (Van Dyck and Strahan, 2008), but persist in variable or low densities that likely have relatively minimal influence on these mammals (Allen et al., 2014a). Beef-cattle grazing is the primary land use in this region (Allen, 2015a). Dingoes, foxes, cats and rabbits were each introduced to Australia. Dingoes arrived approximately 5000 years ago, whereas foxes, cats and rabbits were introduced soon after European colonisation in the late 1700s (Johnson, 2006); each are widespread and common (West, 2008). All three predators are relatively small (<16 kg mean adult body weight), generalist carnivores with highly overlapping diets primarily consisting of medium and small-sized mammals (e.g. Pavey et al., 2008; Cupples et al., 2011; Glen et al., 2011; Allen and Leung, 2012). Hopping-mice are native and endemic to Australia. Their range has declined by over 90% since the arrival of Europeans and the subsequent ecological changes associated with the introduction of livestock and invasive species (e.g. foxes, cats and rabbits). The Strzelecki Desert is the last stronghold of hopping-mice (Lee, 1995; Moseby et al., 1999; Van Dyck and Strahan, 2008), which are an endangered, 'old world' or conilurine rodent (Muridae) with irruptive population cycles typical of many small mammals in arid areas.

Previous desktop, snap-shot and correlative studies (compiled and reviewed in Allen et al., 2013b) have developed the following hypotheses about the contemporary relationships between dingoes and hopping-mice in this study system:

1. Dingo abundance is positively correlated with hopping-mice abundance (presumably because dingoes provide indirect refuge to hopping-mice from mesopredators).
2. The presence of dingoes positively affects hopping-mice foraging behaviour (presumably because hopping-mice perceive foraging in the presence of dingoes to be less of a risk than foraging in their absence).
3. The lower abundance of hopping-mice in the east of the Strzelecki Desert is due to the relative absence of dingoes there (which are excluded by the dingo barrier fence).
4. Contemporary dingo control practices (i.e. repeated broad-scale poison-baiting, undertaken to protect cattle from dingo predation) reduces the abundance of dingoes, and increases the abundance of mesopredators, which reduces the abundance of hopping-mice.
5. Dingoes do not eat hopping-mice in quantities sufficient to threaten the persistence of hopping-mice populations.

Alternative hypotheses for these observations have seldom been assessed, however, and limited experimental work has been undertaken to identify causal relationships driving the observed correlations between dingoes and hopping-mice (Allen, 2011a; Allen et al., 2013b;

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