



In the absence of an apex predator, irruptive herbivores suppress grass seed production: Implications for small granivores



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ABSTRACT

Many examples exist of species disappearing shortly after the extinction of a previously co-occurring apex predator, however processes connecting these events are often obscure. In Australian deserts, dingo *Canis dingo* eradication is associated with declines in abundances of small granivorous birds, even though dingoes and these flying birds rarely directly interact. We hypothesised that dingoes facilitate small granivores by reducing populations of large, grazing kangaroos *Macropus* spp., thereby increasing grass seed production and availability. To test this prediction, we monitored kangaroo abundances and surveyed grass seed production and biomass of native pastures in matched, desert habitats with dingoes and where dingoes were functionally extinct. Dingo absence was associated with 99.9% greater abundances of kangaroos, 88% - 98% lower pasture biomasses and 85% - 97% lower densities of grass seed heads. To test that these vegetation effects were related to kangaroo grazing, we constructed large herbivore exclosures in areas where dingoes were functionally extinct and there were no grazing livestock. After three years of kangaroo exclusion, pasture biomass and grass seed production were each 87% greater than in adjacent, grazed control plots. Regeneration of vegetation within the kangaroo exclosures demonstrated that kangaroo grazing was responsible for the differences in native pastures we had observed associated with the functional extinction of dingoes. Our results indicate that reduction of grass seed availability by kangaroo grazing is a likely explanation for the relative rarity of small granivorous birds in areas where dingoes are functionally extinct. In areas where apex predators have been eradicated, reintroducing and conserving apex predators or intensively controlling mammalian herbivores would be necessary to mitigate destructive herbivory.

1. Introduction

Predator extinctions create imbalances between populations of lower-order consumers and producers, compromising ecosystem integrity (Paine, 1969; Terborgh et al., 2001). When released from top-down regulation, prey populations increase, initiating trophic cascades that sequentially impact successive lower trophic levels (Beschta and Ripple, 2009; Ripple and Beschta, 2012). Coevolved predators and prey usually coexist in equilibrium in intact ecosystems, because preys have evolved sufficiently rapid rates of reproduction to compensate for losses to familiar predators (Sinclair and Pech, 1996). But when predators become scarce or extinct, this high, normally compensatory reproduction and high survival increase prey populations unsustainably (Salo et al., 2010). Such predation-free prey populations are bottom-up regulated, i.e. limited primarily by availability of food, and impact lower trophic levels and consumers because they increase until food resources diminish (Caughley, 1970; Kaeuffer et al., 2010).

Large predators prey on large herbivores, directly regulating large

herbivore populations and indirectly moderating herbivory (Ripple et al., 2014). Irrupting populations of large herbivores often consume edible plants faster than these plants can grow and reproduce, depleting these plants' populations (Ripple et al., 2001; Terborgh et al., 2001). When food plants become scarce, intraspecific and interspecific competition for food plants intensifies, eventually resulting in starvation and death or emigration of herbivores and their competitors (Caughley et al., 1985). In such contests, large herbivores can outcompete many smaller plant-dependent species (Berger et al., 2001), because large herbivores often have larger home ranges and a greater ability to survive fasts than their smaller competitors (Demment and Van Soest, 1985; Lindstedt et al., 1986). By mitigating large herbivores' effects on their food plants and competitors, large predators maintain biodiversity and propagate ecosystem processes (Ripple et al., 2014).

In Australian ecosystems, dingoes *Canis dingo* are the largest terrestrial predators and they prey upon and regulate populations of kangaroos *Macropus* spp. (Letnic et al., 2012), large grazers that consume the leaves, stems and inflorescences of grasses (Ellis et al., 1977).

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In areas where dingo populations are functionally extinct, i.e. reduced to densities at which their influence in ecosystems is negligible, kangaroo populations increase and kangaroo grazing reduces grass cover (Letnic et al., 2012). Kangaroo grazing-effects on ground-layer vegetation are most obvious in arid regions, where productivity is limited by low soil nutrients and low rainfall (Letnic et al., 2012), but also occur in mesic habitats (Howland et al., 2014; Howland et al., 2016). In arid ecosystems, bottom-up regulated populations of kangaroos could impact other species that depend on grasses for food and habitat.

In recent decades, granivorous bird populations have declined markedly in Australia's vast, undeveloped rangelands (Franklin, 1999). Stocking rates and time since introduction of livestock are inversely correlated with granivore abundances, suggesting competition with grazing livestock is a key factor explaining granivore declines (Franklin et al., 2005). However, small granivorous birds have also declined in some large conservation reserves, where livestock are excluded, but where functional extinction of dingoes allows kangaroos to occur in high abundances (Rees, unpublished data). Grazers could affect granivores by consuming seed-producing plants, thereby reducing seed availability (O'Connor and Pickett, 1992). Conceivably, bottom-up regulated kangaroo populations may be outcompeting birds that feed specifically on grass seed in reserves and other areas.

We hypothesised that functional extinction of a top predator (dingo) would increase large herbivore (kangaroo) populations, with associated increases in grazing reducing the biomass, abundances and seed production of edible grasses and a grass-like rush. We tested our predictions by surveying dingoes, kangaroos and grasses in areas with dingoes and areas where dingoes were functionally extinct in the Strzelecki Desert in inland southern Australia.

2. Methods

2.1. Study area

We surveyed kangaroos (*Macropus rufus*, *M. fuliginosus*, *M. giganteus* and *M. robustus*) and native pastures in the linear sandhills and clay swales of the arid (\bar{x} rainfall = 172.1 mm year⁻¹) Strzelecki Desert. We surveyed adjacent areas, inside (Sturt National Park (SNP)) and outside (Strzelecki Regional Reserve, Omicron Station, Lindon Station, Naryilco) the Dingo Barrier Fence (DBF), which arbitrarily follows the New South Wales-South Australia border (the 141st meridian east) and the New South Wales-Queensland border (the 29th parallel south). Dingoes are functionally extinct inside the DBF and common outside the DBF. SNP was established in 1972 and there has been no official livestock grazing in SNP, outside of gazetted stock routes, since that time. SNP contains earth tanks that sometimes held water, but were often dry during our study. Pastoral areas adjacent to SNP, outside the DBF, contained similar earth tanks to those within SNP, but also contained widely spaced troughs (approximately one per 100 km²), providing continuous water. If kangaroo abundances were dictated by water availability, we would expect to record greater numbers of kangaroos in the pastoral areas with permanent artificial water points outside the DBF than in SNP.

2.2. Survey of kangaroo abundances

Every three months between August 2012 and June 2016, we surveyed kangaroo densities in SNP, where dingoes were functionally extinct, and adjacent areas outside (north and west of) the DBF, where dingoes were common. We surveyed kangaroos by spotlighting at night (19:00–24:00), whilst driving vehicle tracks at a constant speed of 15 km/h. We could accurately estimate relative abundances of kangaroos using this method because we spotlighted in open, sparsely treed country where we could spot kangaroos at distances of up to approximately 800 m using a spotlight and binoculars. We estimated kangaroo densities by dividing total numbers of kangaroos observed by total

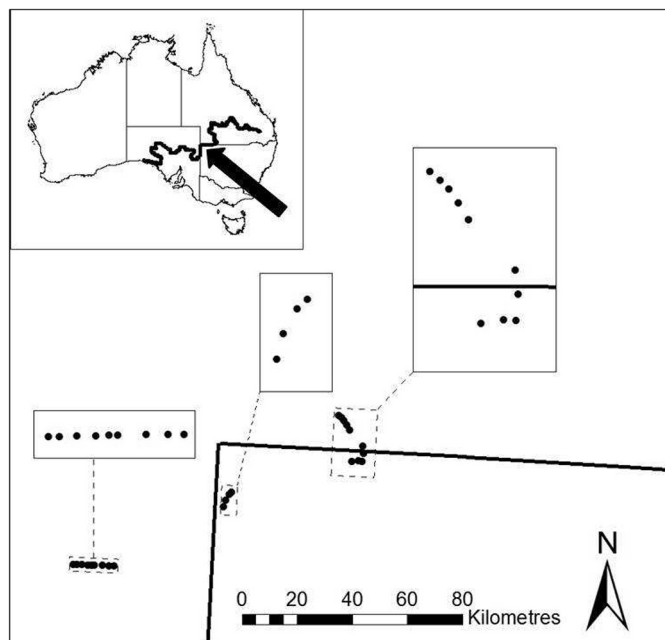


Fig. 1. Map of the study area. At each point (indicated by a black dot) we surveyed and sampled native pastures on an adjacent dune top, dune base and swale. In the study area (mapped in detail and indicated by the black arrow in the inset), the Dingo Barrier Fence (bold line on map and inset) arbitrarily follows state borders.

distance surveyed for areas with dingoes and areas where dingoes were functionally extinct, for each visit.

2.3. Survey of grasses and rushes, their biomass and seed production

In June and July 2016, we surveyed abundances, reproductive output (number of seed heads metre⁻²) and total biomass of grasses (Appendix S1) and one grass-like rush (*Fimbristylis dichotoma*) at 45 sites with dingoes and 27 sites where dingoes were functionally extinct (Fig. 1). We surveyed grasses and rushes within 1m² quadrats (1 quadrat/site), placed randomly within grass patches on dune tops ($n_{\text{dingo}} = 15$, $n_{\text{no dingo}} = 9$), dune bases ($n_{\text{dingo}} = 15$, $n_{\text{no dingo}} = 9$) and in swales ($n_{\text{dingo}} = 15$, $n_{\text{no dingo}} = 9$). We spaced quadrats at least one kilometre from the next nearest quadrat in similar habitat (i.e. dune top, dune base, swale) and never placed them in scalds, claypans or other bare areas. In each quadrat, we counted the total number of individuals of each species and the total number of seed heads for each species. We then clipped to ground-level all grasses and rushes, including their reproductive parts, and bagged them in paper bags labelled according to quadrat number and location. To obtain the dry pasture biomass for each quadrat, we first dried the bagged samples by widely scattering them across the floor of a dry, warm, well-ventilated room for three weeks, replacing bags for samples that became damp, until all the bags and their contents were thoroughly dried and then weighed them.

2.4. Grazing manipulation

In August 2013, we constructed four pairs of enclosures and control plots (10x10m) on recently burnt (< 6 months) dune bases in SNP, to investigate grazing effects on ground-layer vegetation. We chose recently burnt locations for plots so that all plots in both treatment groups (enclosure and control) started from a level baseline with zero ground layer vegetation. Enclosures and control plots were positioned in pairs, with corresponding enclosures and control plots spaced 50 m apart and each pair of plots spaced approximately 1 km apart. Each enclosure was surrounded by a tensioned, 2 m tall, galvanised wire mesh (100x100mm apertures) fence to exclude large herbivores (Fig. 2a). At

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