



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



James D. Rees*, Richard T. Kingsford, Mike Letnic

Centre for Ecosystem Science, University of New South Wales, NSW, 2052, Australia

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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).

* Corresponding author.

E-mail addresses: james.rees@live.com.au (J.D. Rees), richard.kingsford@unsw.edu.au (R.T. Kingsford), m.letnic@unsw.edu.au (M. Letnic).

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

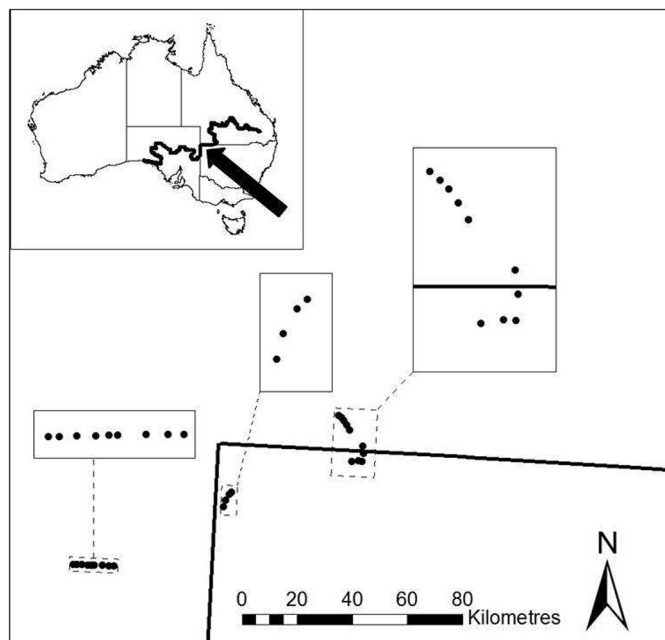


Fig. 1. Map of the study area. At each point (indicated by a black dot) we surveyed and sampled native pastures on an adjacent dune top, dune base and swale. In the study area (mapped in detail and indicated by the black arrow in the inset), the Dingo Barrier Fence (bold line on map and inset) arbitrarily 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 exclosures 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 (exclosure and control) started from a level baseline with zero ground layer vegetation. Exclosures and control plots were positioned in pairs, with corresponding exclosures and control plots spaced 50 m apart and each pair of plots spaced approximately 1 km apart. Each exclosure was surrounded by a tensioned, 2 m tall, galvanised wire mesh (100x100mm apertures) fence to exclude large herbivores (Fig. 2a). At

a)



b)



Fig. 2. (a) An enclosure and (b) its corresponding control plot, in July 2016, two years and 11 months after they were constructed. Green patches visible outside the enclosure are fleshy groundsel *Senecio gregorii*, a daisy unpalatable to large grazers (Cunningham et al., 2011). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

each control plot, we installed steel posts, as used for enclosures, but not wire mesh, so that large herbivores could still access the plot (Fig. 2b).

In June and July 2016, we surveyed grasses and rushes within four 1m² quadrats in each control and enclosure plot. In each quadrat we counted plants and seed heads and clipped, bagged and dried grasses and rushes using the same methods described above (Section 2.3). We calculated the mean densities of grasses and rushes, densities of their seed heads and dry pasture biomass for each enclosure and control plot for analysis (i.e. one replicate = mean score for one plot; $n = 8$).

2.5. Statistical analyses

We used Welch two sample t-tests to compare the dry pasture biomass, plant density and seed head density (i) between sites within like-habitat types (dune top, dune base or swale) in areas with dingoes and areas where dingoes were functionally extinct, and (ii) between

enclosures and control plots. We compared kangaroo densities between areas with dingoes and areas where dingoes were functionally extinct using a paired t-test, with samples paired by visit (month-year). All t-tests were performed in R (version 3.2.1).

3. Results

3.1. Kangaroo abundances

Kangaroos were 99.96% more abundant in SNP, where dingoes are functionally extinct ($\bar{x} = 5.92 \pm 0.78$ kangaroos spotted km⁻¹), than in adjacent areas outside the DBF where dingoes remain common ($\bar{x} = 0.003 \pm 0.002$ kangaroos spotted km⁻¹; $t(13) = -7.59$, $p < 0.001$). Four kangaroo species were recorded: red kangaroo *Macropus rufus*, western grey kangaroo *M. fuliginosus*, eastern grey kangaroo *M. giganteus* and euro *M. robustus*. Between 91 and 100% of kangaroos spotlighted during each survey were red kangaroos, but we

Table 1

Means of dry pasture biomass, density of grasses and rushes, density of their seed heads and statistics for Welch two-sample t-tests comparing these variables between areas with dingoes (dingo) and areas where dingoes were functionally extinct (no dingo). Significant p-values ($p < 0.05$) are shown in bold.

Variable	Habitat	\bar{x} (Dingo)	\bar{x} (No dingo)	t	d.f.	p
Dry pasture biomass (grams)/m ²	Dune crest	37.92	3.31	3.24	14.29	0.006
	Dune base	15.72	1.97	4.95	15.37	< 0.001
	Swale	28.77	0.5	3.83	14.05	0.002
Grass and rush plants/m ²	Dune crest	14.73	6.78	1.49	19.97	0.15
	Dune base	32.8	86.67	-2.1	9.41	0.06
	Swale	65.07	46.56	0.75	18.44	0.46
Grass and rush seed heads/m ²	Dune crest	83.73	12.56	4.37	15.29	< 0.001
	Dune base	119.93	12.78	5.99	15.68	< 0.001
	Swale	220.8	6	4.56	14.05	< 0.001

consider the four kangaroo species collectively here because all consume grasses and are preyed on by dingoes (Ellis et al., 1977; Letnic et al., 2012).

3.2. Grasses, grass biomass and grass seed production

Dry pasture biomass and density of grass seed heads within grass patches were significantly greater in areas with dingoes than in areas where dingoes were functionally extinct, on dune tops, dune bases and in swales (Table 1, Fig. 3). Grass assemblage composition also differed between areas with dingoes and areas where dingoes were functionally extinct (*manyglm*: deviance₍₇₀₎ = 521.5, $p = 0.001$; see Appendix S1 for species' densities and reproductive outputs), with density (plants m⁻²) of five minute grass *Tripogon loliformis* greater in areas where dingoes were functionally extinct (dingo: $\bar{x} = 15.64 \pm 3.72$; dingo functionally extinct: $\bar{x} = 31.56 \pm 7.85$; $\beta = 0.70$, $p = 0.02$) and densities of broad-leaf wanderie grass *Eriachne aristidae* (dingo:

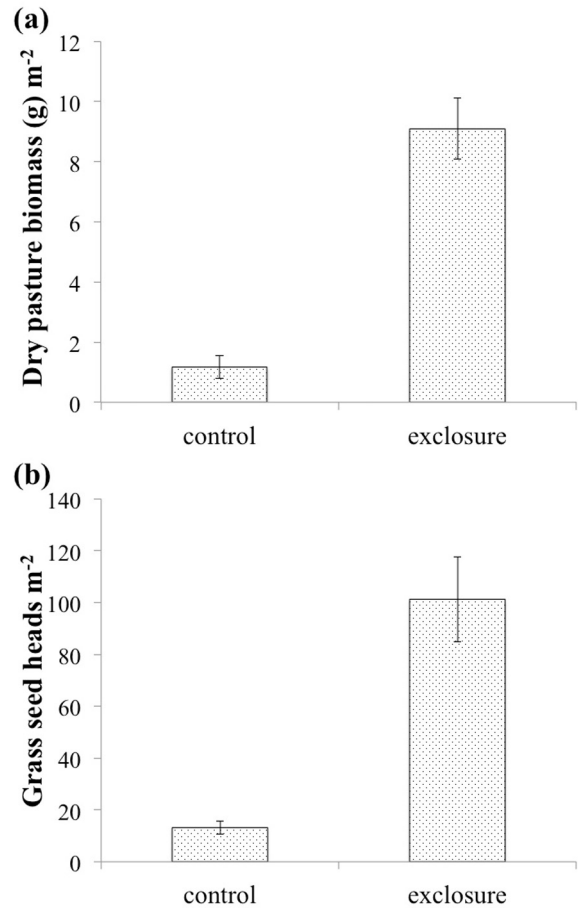


Fig. 4. a) Dry pasture biomass and b) density of grass seed heads in large herbivore exclosures and control plots in SNP, an area where no livestock grazing has occurred in over 40 years, but dingoes are functionally extinct and kangaroos are abundant.

$\bar{x} = 2.8 \pm 0.95$; dingo functionally extinct: $\bar{x} = 0.63 \pm 0.28$; $\beta = -1.49$, $p = 0.04$), neverfail *Eragrostis setifolia* (dingo: $\bar{x} = 1.49 \pm 0.68$; dingo functionally extinct: $\bar{x} = 0 \pm 0$; $\beta = -15.21$, $p = 0.02$) and bristle-brush grass *Paractaenum refractum* (dingo: $\bar{x} = 4.27 \pm 1.63$; dingo functionally extinct: $\bar{x} = 0.52 \pm 0.38$; $\beta = -2.11$, $p = 0.02$), greater in areas with dingoes.

3.3. Grazing manipulation

After three years, ground-layer vegetation was regenerating within kangaroo exclosures but the ground was mostly bare in adjacent, unfenced control plots (Fig. 2). Dry pasture biomass m⁻² was 87% greater inside exclosures ($\bar{x} = 9.09 \pm 1.02$) than inside control plots ($\bar{x} = 1.17 \pm 0.38$; $t(3.81) = -7.29$, $p = 0.002$; Fig. 4a) and density of grass seed heads was 87% greater in exclosures ($\bar{x} = 101.19 \pm 16.38$ m⁻²) than in control plots ($\bar{x} = 13.19 \pm 2.51$ m⁻²; $t(3.14) = -5.31$, $p = 0.01$; Fig. 4b). Density of grass plants did not differ significantly between exclosures ($\bar{x} = 112 \pm 35.84$ m⁻²) and control plots ($\bar{x} = 93.13 \pm 26.58$ m⁻²; $t(5.53) = -0.42$, $p = 0.69$) and grass species composition did not differ between exclosures and control plots (*manyglm*: deviance₍₃₀₎ = 132.6, $p = 0.23$; see Appendix S2 for species' densities and reproductive outputs).

4. Discussion

Our results indicate that the near-absence of dingoes is the root cause of kangaroo overabundance and severe overgrazing in SNP and

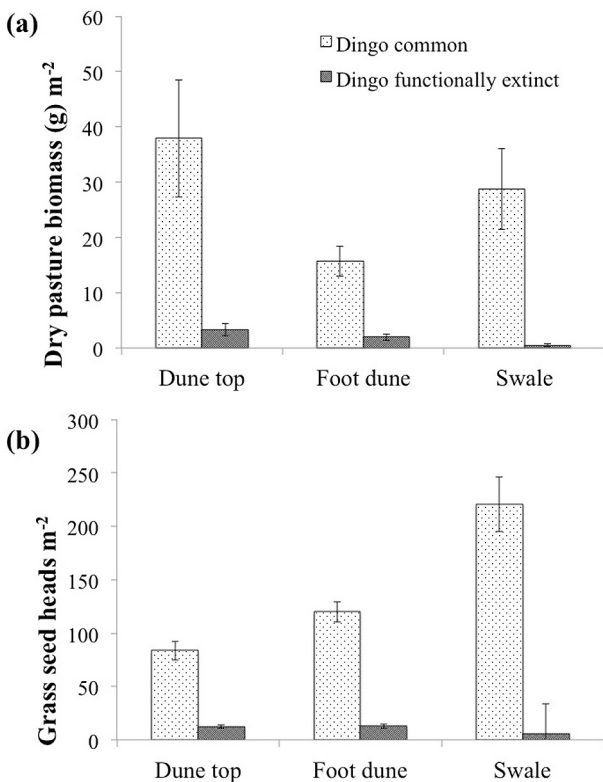


Fig. 3. a) Dry pasture biomass and b) densities of grass seed heads in grass patches in the Strzelecki Desert, in areas with dingoes and in areas where dingoes were functionally extinct, in June and July 2016.

most likely other conservation reserves inside the DBF. High densities of kangaroos in SNP compared to adjacent areas with dingoes manifest the powerful influence of dingo predation on kangaroo populations and are consistent with observations reported in previous studies of dingo-macropod interactions in this, and other, localities (Caughley et al., 1980; Pople et al., 2000; Letnic and Crowther, 2013). Water availability had no apparent influence on kangaroo abundance, with kangaroos consistently abundant in SNP (dingoes rare), where surface water was only available sporadically, but consistently scarce in pastoral areas outside the DBF (with dingoes), where water was permanently available at cattle troughs.

At the time of our study, SNPs irruptive kangaroo population had nearly exhausted their food supply and the park resembled chronically overstocked rangelands, despite receiving above average rainfall in preceding months (total rainfall: May 2016: 33.8 mm, June 2016: 33.2 mm; mean rainfall: May: 17.2 mm, June: 16.5 mm, Bureau of Meteorology) and having been destocked for over 40 years. By contrast, rangeland and conservation areas with dingo populations, adjacent to SNP, including areas used for conservative cattle grazing, were well populated with grasses and these were seeding prolifically, reflecting the low abundances of kangaroos in those areas. Our use of kangaroo exclosures confirmed that intensive kangaroo grazing was the cause of the reduced pasture biomass, losses of palatable grass species and reduced reproductive output of grasses we observed in SNP.

Our observation that dingo absence resulted in a near 100-fold increase in kangaroo abundance was consistent with previous studies linking rarity of dingoes to irruptions of kangaroos (Pople et al., 2000; Fillios et al., 2010; Letnic and Crowther, 2013) and more generally, rarity of top predators to irruptions of large herbivorous mammals (Messier, 1994; Ripple et al., 2001; Ripple and Beschta, 2012). Similar interactions to that we observed between dingoes, kangaroos and grasses also exist among the large carnivores, large herbivores and plants of other continents (Ripple et al., 2014), a well-documented example being the reduction of large ungulate populations and recovery of browsing-sensitive plants following the reintroduction of wolves to Yellowstone National Park in 1995 (Ripple et al., 2001; Beschta and Ripple, 2009; Ripple and Beschta, 2012). Our results and those of other studies provide evidence that large predators provide a valuable ecosystem service by controlling large herbivore populations.

Our results demonstrate that eradicating dingo populations could impact many species that depend on grasses for food and habitat. Previous studies of Australian arid ecosystems have revealed associations between populations of dingoes and small granivores (Rees, unpublished data; Letnic et al., 2009). We found evidence that the mechanism linking dingo functional extinction to declines of small granivore populations is the reduction of grass seed availability due to grazing by irrupting large herbivore populations. We observed between 97% and 85% fewer grass seed heads, on swales and dunes respectively, in areas where dingoes were functionally extinct than in areas with dingoes. In the former, grass seed heads were scarce, as grass plants were almost invariably grazed off at their bases by kangaroos. These reductions in grass seed availability could displace grass seed-feeding specialists, such as zebra finches *Taeniopygia guttata* and budgerigars *Melopsittacus undulatus*, which have rapid metabolisms and high food demands relative to body mass (Zann, 1996).

Currently, managers of National Parks in arid New South Wales conserve kangaroos and do not control overabundant kangaroo populations, but they intensively control dingo populations. Consequently, these predator-free kangaroo populations become destructive, irrupting and experiencing mass die-offs when they exhaust food resources. Rehabilitation of degraded arid ecosystems within SNP and other areas where dingoes are functionally extinct would require a complete change in direction to this management approach. In arid areas where dingoes are rare or absent, controlling kangaroo populations must be prioritised. Achieving effective control of kangaroos necessary to mitigate their grazing impacts would require either (i) reintroduction or

conservation of dingoes, or (ii) intensive and regular culling or harvesting of kangaroos, to simulate predation, and monitoring of kangaroo populations.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.06.037>.

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