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How introduced rabbits *Oryctolagus cuniculus* limit the abundance of red kangaroos *Macropus rufus* and other native grazers in Australia

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ABSTRACT

The successive releases of myxoma virus, rabbit fleas and rabbit haemorrhagic disease virus in Australia greatly reduced the abundance of introduced rabbits, but also reduced enquiry into any continuing role of rabbits in modifying native pasture vegetation or competing with native grazing mammals. We argue here, however, that despite these biological controls, rabbits still compete with red kangaroos for limited pasture resources such as native grasses. This is based on: (a) long-term trends in kangaroo numbers, (b) increases in kangaroos following removal of rabbits, (c) similarities between the quality of foods selected by rabbits and those needed by young kangaroos, (d) the low availability of native grasses as a food source in degraded arid-zone pastures, (e) correlations between abundance of grasses and abundance of rabbits (negative) and kangaroos (positive) and (f) inadequate alternative explanations. Rabbits remain ubiquitous and even at densities of <1 rabbit ha^{-1} can change pasture composition and quality. Consequently, our results have major implications for managing and conserving native pastures and native grazing mammals.

1. Introduction

Wild rabbits *Oryctolagus cuniculus* introduced from Britain spread across southern Australian rangelands in the late 1800s (Stodart and Parer, 1988). Severe economic losses and ecological damage resulted, often reported in terms of native vegetation loss which affected sheep and cattle production (South Australia, 1898). Rabbits destroyed native shrubs and pastures, contributing to soil erosion (Ratcliffe, 1938). Overgrazing by livestock and rabbits eliminated summer-growing native grasses, and opened the way for invasion by introduced pasture species, especially those from Mediterranean Europe adapted to resist grazing e.g. short life cycle, spines or chemical defences (van der Meijden et al., 1988). This produced a new ecosystem unlikely to return to the former native climax ecosystem where native grasses were predominant (Williams, 1970).

That dynamic changed with the introduction of biological control agents, including myxoma virus (MYXV) in 1950, European rabbit fleas *Spilopsyllus cuniculi* as MYXV vectors in the 1970s and rabbit haemorrhagic disease virus (RHDV) in 1995. These agents greatly reduced rabbit abundance (Fenner and Fantini, 1999) and the understanding that rabbits could cause extreme damage soon faded. Since the spread of myxomatosis, rabbits have been widely ignored as a problem in Australia's pastoral lands despite the population partially recovering. In many areas, rabbits remain common enough to consume more vegetation than domestic livestock (Cooke, 2012, 2014; Mutze, 2016). Economic damage caused by remaining rabbits approaches AUS $200 million annually (Gong et al., 2009) requiring continuing expenditure on chemical and mechanical rabbit control measures.

Rabbits also continue to affect native marsupial herbivores. Cooke (1998) argued that the southward contraction of the distribution of common wombats *Vombatus ursinus* in South Australia was associated with the arrival of rabbits in the 1880s rather than the arrival of livestock 35 years earlier. Uncontrolled rabbits over-grazed summer-growing native grasses, leaving wombats unable to raise pouch-young on the summer-dry residues of introduced annual grasses. Trials in the Coorong National Park further supported that idea. From 1991 to 1993, rabbit numbers were heavily reduced on two experimental plots by poisoning and selective warren destruction (wombats also live in complex burrow systems). Both wombats and western grey kangaroos *Macropus fuliginosus* increased about three-fold but remained uncommon on two plots where rabbits were not removed (Cooke, 1998). In 1997, only 18 months after the release of RHDV, the experiment was repeated, this time using three plots where rabbits were removed with three matching experimental controls, each between 50 and 120 ha in area (Bird et al., 2011). Very similar results were again obtained; even MYXV and RHDV working together apparently failed to fully alleviate rabbit impacts on native herbivores.

In a similar experiment in the semi-arid Ikara Flinders Ranges National Park and adjoining Gum Creek sheep station, interactions

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between rabbits, sheep, red kangaroos, *Macropus rufus*, and euros, *Macropus robustus*, were measured on eight plots of 3 km^{-2} from half of which rabbits were removed (Mutze et al., 2008). Over three years (1992–1994 inclusive), spotlight counts showed that kangaroos increased three-fold where rabbits were removed but remained at lower densities on experimental control plots. Furthermore, in 1995, when RHDV reduced rabbits to about 5% of former population levels, kangaroos no longer congregated on those experimental plots where rabbits had been removed. They dispersed across the whole area, then began to increase again, on both treated and untreated areas (Mutze et al., 1998; Mutze et al., 2008).

While these experiments showed that removing rabbits enabled native herbivores to increase, the idea that native grasses played an important role was indicated but not fully investigated. Grasses are heavily preferred by common wombats in the Coorong National Park (Mallet and Cooke, 1986) and native grasses regenerated when rabbits were excluded from experimental plots (Cooke, 1998). Plant succession recorded over eight years saw introduced unpalatable weeds such as *Anagallis arvensis* quickly disappear, while introduced Mediterranean grasses such as *Vulpia myuros* flourished for two or three years until native spear-grass *Austrostipa* (*Stipa)* spp became the most abundant pasture species after five years (Fig. 1; Cooke, 1998).

Red kangaroos are primarily grass-eaters although they consume some forbs (Dawson and Ellis, 1994; Moss and Croft, 1999; Munn et al., 2013). Dawson and Ellis (1994) considered that red kangaroos ate mainly grasses, except in wet seasons when forb intake was high. In dry seasons shrubs were also eaten but in severe drought grass intake was almost 90%. Sheep ate similar foods but although grass was important in their diet, they ate more forbs in wet times and much more browse in dry conditions than the kangaroos. Rabbits had broad diets in good conditions but ate largely browse (bark, twigs and roots) in drought. Moss and Croft (1999) found that red kangaroo body condition correlated best with the abundance of green grass, especially the native grass *Enneapogon avenaceus* which was a high proportion of their diet.

Importantly, Mutze et al. (2016) found that even where palatable native grasses were most abundant, they covered only 3–5% of the surface area of quadrats used to measure pasture in the Ikara Flinders Ranges National Park. Furthermore, grasses disappeared completely where there were >1–2 rabbits ha^{-1}. Nonetheless, red kangaroos can readily move to areas where grasses are most abundant (Newsome, 1965) and congregate where palatable grass cover is highest, avoiding areas heavily grazed by rabbits during summer-autumn food shortage (Mutze et al., 2016).

Combined, this information led us to consider several hypotheses for understanding why red kangaroos increased following experimental removal of rabbits and again after rabbit haemorrhagic disease first

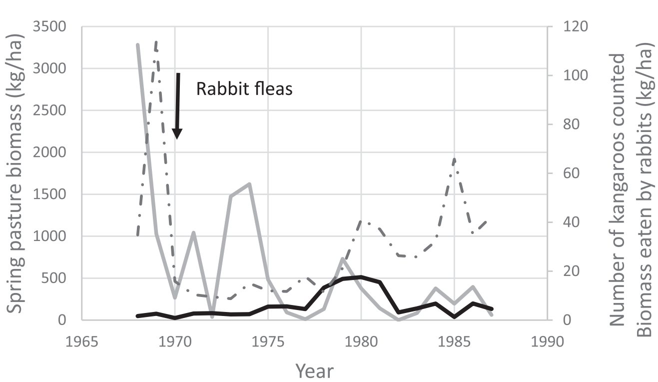

Fig. 1. Mean number of red kangaroos counted on Witchitie transects each year (black line) in relation to spring-time pasture biomass (grey) and the amount of pasture biomass rabbits consumed (broken line) proportional to spring-time rabbit abundance. Arrow shows where rabbit fleas, introduced in 1969, became widespread and numerous enough to spread myxomatosis.

spread. The simplest, which incorporates all information, is that red kangaroos depend on a relatively small component of today's degraded pastures and, despite biological control, rabbits remain abundant enough in many places to compete for, or even eliminate that essential pasture element.

To test this hypothesis in the field, we sought evidence indicating that kangaroo numbers declined whenever rabbits were abundant enough to eat most of the available grass or other limited pasture components kangaroos needed. That would depend not only on rabbit abundance but also pasture productivity. In drought years, with low pasture productivity, rabbits might eat most of the pasture kangaroos need even though their own abundance was low.

Here, we present a study based on a 20-year data set from Witchitie sheep station in South Australia. The original information was collected mainly to assess the introduction of European rabbit fleas as vectors of myxomatosis but also included estimates of pasture biomass and the abundance of rabbits, foxes and red kangaroos as recorded during regular spot-light transects. Fortuitously, flea-borne myxomatosis helped keep rabbit numbers consistently low for several years (Cooke, 1983) effectively providing an opportunity for unravelling the importance of other variables such as pasture abundance also likely to influence kangaroo numbers which continued to vary annually.

From these data, the annual rate of change of the red kangaroo population (λ) could be considered in relation to pasture biomass, and we could ask whether rabbits were numerous enough to eat out the grassy component or other nutritious plants. We used the data to derive a value for the proportion of pasture biomass rabbits might have eaten before λ became negative for kangaroos. As this value was small, it was consistent with the idea that rabbits and kangaroos compete for limited pasture components. We also confirmed from an un-replicated trial on the site that kangaroos increased in abundance after rabbits, but not sheep, were removed.

We also considered alternative explanations to determine whether these might provide better explanations. These alternatives mainly dealt with assumed kangaroo grazing in response to pasture biomass (Caughley, 1987; Bayliss and Choquenot, 2002), but also considered any potential role of foxes as predators affecting rabbit abundance (Newsome et al., 1989) or kangaroo abundance or behaviour (Banks et al., 2000).

2. Methods

2.1. Background

Witchitie sheep station is about 60 km from the Ikara Flinders Ranges National Park where Mutze et al. (2016) described the impact of rabbits on native pastures and red kangaroos. Ikara Flinders Ranges National Park was established on the former Oraparinna sheep station whereas Witchitie remains a working sheep station. Witchitie was also the first experimental site for assessing European rabbit fleas as vectors of myxomatosis in semi-arid South Australia (Cooke, 1983, 1984). After rabbit fleas became widely established in 1970, rabbit abundance was substantially reduced and remained low until 1978 before increasing steadily again. As rabbit numbers increased, damage to pastures became increasingly obvious and in early 1992 the station manager used a tractor and ripper to destroy the rabbit warrens on one half of the study site. This provided an opportunity to record changes in red kangaroo abundance following rabbit removal.

2.2. Site description

The Witchitie study site lies in a wide shallow valley, flanked by stony hills covered in spinifex *Triodia irritans* or scattered trees and shrubs including mulga *Acacia aneura*, needlebush *Hakea leucoptera* and *Dodonea* spp. The original shrub-steppe vegetation of the valley floor was severely overgrazed in the past and replaced with annual

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