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REVIEW ARTICLE

Recovering Australia's arid-zone ecosystems: learning from continental-scale rabbit control experiments

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Introduced rabbits are a continuing threat to native Australian flora and fauna. Three interventions using biological control agents, myxomatosis, European rabbit fleas, and rabbit hemorrhagic disease, have reduced rabbit abundance and kept numbers low over the last 70 years. We considered the benefits of biological control for native fauna to put the role of rabbits in influencing vegetation cover, food supply, and predation into better perspective. Numerous examples exist demonstrating increases in native vegetation and the expansion and recovery of native animal populations at landscape scales following intense rabbit suppression. Ongoing research on methods for supplementing the impact of biological control agents and managing introduced predators are needed to restore Australia's arid-zone ecosystems. However, many biologists and rangeland managers first need to reevaluate the misconception that removing rabbits also introduces other serious and insurmountable problems such as prey-switching by introduced cats and foxes.

Key words: **myxomatosis, native fauna, predators, prey-switching, rabbit fleas, rabbit hemorrhagic disease, restoration, vegetation**

Implications for Practice

- Restoration of native mammal populations in inland Australia now focuses heavily on reducing predation by introduced cats and foxes, but rabbit control should be considered too.
- Control of rabbits facilitates wider reestablishment of arid-zone ecosystems, not just mammal populations.
- Benefits from rabbits for some native fauna or perceived risks involved with controlling rabbits are heavily outweighed by threats to hundreds of other native plant and animal species.
- Restoration of Australia's arid-zone ecosystems would be hastened if rabbit control were recognized as being equal to predator control and a better balanced, integrated approach was taken.
- Biologists should stop concerning themselves over relatively unimportant issues to rabbit management such as prey-switching and concentrate on the hard issue of removing rabbits from Australia's arid-zone.

Introduction

Australia's conservation record on terrestrial mammals is poor. Of 273 endemic terrestrial mammal species, 28 have become extinct since European settlement began in 1788. An additional 56 species are threatened and 52 species near threatened according to International Union for Conservation of Nature Red List criteria (Woinarski et al. 2015).

Those losses and listings are attributed to many different causes (Kearney et al. 2019). However, in inland Australia, pioneer pastoralists in the nineteenth century misjudged the land's productivity and climatic variability. Extreme overgrazing by livestock during drought, and changed land management compared with Aboriginal practices, took a severe toll (Cooke 2017; Fletcher et al. 2021). Moreover, cats (*Felis catus*) were taken to new pastoral runs where they became feral, and rabbits (*Oryctolagus cuniculus*) and subsequently red foxes (*Vulpes vulpes*) were introduced (Fenner 2010; Abbott et al. 2014). These new

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competitors and predators proved highly detrimental, especially for medium-sized native fauna (Johnson & Isaac 2009).

Nonetheless, scientific interest in Australia's unique mammals was high. Specimens were widely collected for both Australian and international museums. Publications such as Gould's *The Mammals of Australia* summarized the state of knowledge at that time and provided information on the former distributions of mammals as a baseline for today's conservation endeavors (Gould & Richter 1863).

Over time, public sentiment favoring Australia's natural flora and fauna increased and today both federal and state governments are involved in restoring damaged ecosystems. The key legislation is the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act, Commonwealth of Australia 2015) and Australian states and territories have matching legislation. Universities contribute to research and nongovernment organizations are increasingly involved in managing land for conservation.

Fenced reserves, called wildlife havens, have been created in many places; their carefully designed fences exclude livestock, cats, and foxes, and often rabbits (Moseby & O'Donnell 2003; Finlayson et al. 2008; Read et al. 2011; Legge et al. 2018). However, although some havens exceed 60 km^2, and have required enormous, sustained effort for establishment and maintenance, they constitute only a miniscule part of Australia's 3,697,109-km^2 arid zone (48% of the continent). Furthermore, they are not normal ecosystems, and in the absence of predators, reintroduced animals can overgraze natural pasture plants (Linley et al. 2017). Animals in havens may also develop traits unsuited to life outside (Jolly et al. 2018; Moseby et al. 2018; Jolly & Philips 2020). Attempts to create more balanced ecosystems within havens include reintroducing native predators such as woma python (*Aspidites ramsayi*) and western quoll (*Dasyurus geoffroii*) (Johnston et al. 2010; West et al. 2020).

Although both domestic livestock and rabbits caused much initial damage to soil and vegetation in inland Australia, wild rabbits were completely unmanaged and today are internationally recognized as "ecosystem engineers" capable of holding vegetation in an early successional stage by preventing the regeneration of grasses, shrubs, and other vegetation (Somers et al. 2005; Gálvez et al. 2008). This realization is critically important because vegetation condition, and change in primary producer communities, directly affects herbivore feed availability, invertebrate abundance, shelter, and predation (Jacob 2008; Stobo-Wilson et al. 2020).

Unfortunately, rabbits are commonly ignored or underestimated by many Australian biologists and rangeland land managers (Mutze 2016). Furthermore, biologists all too often point to examples where the elimination of rabbits might be detrimental for native species yet do not weigh up the significance of their observations against the greater need to take action to reduce uncontrolled rabbit grazing.

As an example, Read et al. (2008) list native animals observed to use rabbit warrens for shelter, and this is often taken as a reason for not destroying rabbit warrens to reduce rabbit abundance. Furthermore, without a clear assessment of whether rabbit warrens have become essential for the survival of those sheltering native species, uncertainty remains, leading to inaction. In practice, however, many of these matters are relatively easy to resolve. For example, Read et al. (2008) recorded echidnas (*Tachyglossus aculeatus*) entering and leaving rabbit burrows, but echidnas occur Australia-wide, including areas where there are no rabbits. They are well adapted to arid conditions and can avoid extreme heat by entering caves, hollow logs, or burrowing directly into the soil (Brice et al. 2002); they do not need rabbit warrens to maintain persistent populations.

Thus, for species like the echidna, the observations of Read et al. (2008) should be regarded as precautionary. Actions taken to manage rabbits should not be based solely on the limited benefits rabbit burrows might provide for a few native animal species but on the far greater problem that rabbits drastically affect hundreds of other native animal and plant species. The deleterious impacts of rabbits clearly outweigh any benefits when it is considered that rabbits threaten 322 plant and animal taxa listed under Australia's environment protection and biodiversity conservation (EPBC) Act (Kearney et al. 2019).

Rabbit impacts include direct herbivory, reducing tree and shrub regeneration; competition for food resources; land degradation through soil erosion; weed infestation; and supporting large populations of introduced predators (Kearney et al. 2019). These matters are often interrelated, especially during droughts when rabbits overexploit limited food supplies and starve, and the cats and foxes they previously supported rely increasingly on native fauna. For native Australian mammals in the critical weight range (35 g–5.5 kg) most readily taken by cats and foxes this has been disastrous (Johnson & Isaac 2009; Radford et al. 2018). Yet, there are also conflicting worries that, with the present low abundance of native mammals, a collapse of rabbit numbers could leave native predators, such as Wedge-tailed Eagles (*Aquila audax*) or large monitor lizards (*Varanus* spp.), without food (Cooke 1999).

A stronger approach to managing rabbits in Australian landscapes is clearly warranted, but to do this, much of the current confusion about rabbits needs to be resolved. Eliminating rabbits entirely is unlikely, but further progress is essential to ensure that native mammals have high-quality plant food to maximize reproduction and increased vegetation cover to reduce predation (Loggins et al. 2019). Action will be needed on an exceptionally large scale.

Fortunately, there have previously been three large interventions which are instructive. All have involved biological control agents, namely myxomatosis, European rabbit fleas, and rabbit hemorrhagic disease (RHD), deliberately introduced to reduce the abundance of wild rabbits (Fenner & Fantini 1999). Here we examine the conservation outcomes, anticipating that the conclusions drawn should assist in demonstrating how further rabbit control should help in restoring those much-reduced mammal populations which have so far survived.

With these ideas in mind, our consideration of ecosystem responses to wide-scale rabbit population reduction aimed to document the benefits of biological control for native fauna as well as putting the role of rabbits in influencing vegetation cover, food supply, and predation into better perspective. This enabled us to improve and strengthen recommendations on rabbit management to meet conservation goals.

Variation in the Effectiveness of Biological Control Agents

Although each of the three biological control interventions greatly increased rabbit mortality, each agent had different characteristics and therefore produced different conservation outcomes. The myxoma virus was mainly transmitted by mosquitoes when first released and although reducing rabbit abundance by over 95% in wetter areas with numerous mosquitoes, it had less impact in drier inland Australia. The development of resistance to myxomatosis in rabbits further limited the period when it was highly effective (Fenner & Fantini 1999). The introduction of European rabbit fleas enhanced the benefits from myxomatosis by spreading it in winter, greatly increasing mortality among young rabbits and reducing damage to growing spring pasture vegetation (Cooke 2021). However, the fleas failed to persist where annual rainfall was less than 200 mm and made no difference to myxomatosis epidemiology in Australia's driest regions (Cooke 1984). By contrast, RHD was highly effective in arid regions but less so in higher rainfall areas where a related non-pathogenic rabbit calicivirus (RCV-A1) circulates and can temporarily cross-protect rabbits against lethal RHD (Strive et al. 2008; Strive et al. 2010; Liu et al. 2014).

Figure 1, modified from Cooke (2018), indicates how each intervention reduced rabbit abundance and gives an example, following the spread of RHD, where responses within populations of native rodents were recorded.

Ecological Responses to Wide-Scale Rabbit Control Interventions

Myxomatosis

After myxomatosis greatly reduced Australia's massive rabbit problem, the wool, sheep meat, and beef industries resumed growth after 70 years of rabbit-induced stagnation as extra pasture vegetation became available (Waithman 1979). However, few contemporary conservation benefits were reported. Among researchers assessing myxomatosis impact, only Lines (1952) mentioned vigorous growth of native grasses, and little was formally documented because research focused on livestock production rather than conservation.

There was no sudden surge in arid-zone vegetation regeneration in the livestock-free T.G.B. Osborn Vegetation Reserve at Koonamore (Hall et al. 1964), possibly because mosquito vectors for myxomatosis were scarce. Crisp and Lange (1976) concluded that rabbits were still heavily suppressing regeneration of Birkitt's acacia (*Acacia birkittii*) at Koonamore, although Woodell (1990) produced a less pessimistic prognosis and concluded that "reduction of rabbit populations by myxomatosis, and rare high rainfall events were responsible for the recommencement of successful regeneration in some populations." Nonetheless, widespread and recurrent regeneration of most tree and shrub species was observed at Koonamore only when rabbits were finally eradicated by poisoning and burrow fumigation (Sinclair 2005). So, clearly myxomatosis alone had not reduced rabbit numbers enough to enable frequent widespread vegetation regeneration, years of very high rainfall being exceptions.

Even in a coastal area where mosquito vectors were abundant, Cooke (1988) found that sheoaks (*Allocasuarina verticillata*) had only regenerated briefly over 6 or 7 years, before rabbits became resistant enough to myxomatosis to regain densities where they could destroy every sheoak seedling.

Aitken (1971) considered that southern hairy-nosed wombats (*Lasiorhinus latifrons*) had declined after rabbits spread across Australia's inland but noted some recovery had followed the introduction of myxomatosis in 1950. Subsequently, Swinbourne et al. (2017) have independently supported this view.

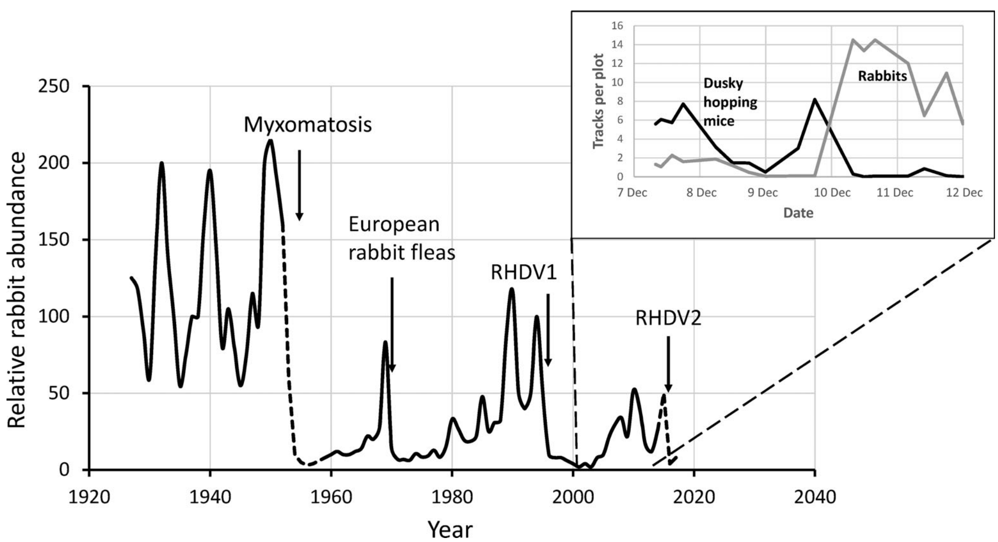

Figure 1. Illustration of the method used to assess the importance of managing rabbits to achieve beneficial conservation outcomes. When the abundance of rabbits was reduced following the introduction of biological control agents, and especially RHD, native mammals such as the dusky hopping mouse increased in abundance even though there was no direct control of cats and foxes. Figure modified from Cooke (2018).

From past documents it can also be argued that red kangaroos (*Macropus rufus*) increased after myxomatosis spread. Newspapers in the 1870s reported numerous kangaroos in semiarid north-eastern South Australia as rabbits spread in the 1880s (e.g. Anonymous 1884), yet in 1891 the colonial government restricted the hunting of red kangaroos because of their scarcity by imposing an annual 6-month close season (South Australian Parliament 1891). However, after myxomatosis spread, landholders in the region were suddenly "involved in a shooting war with kangaroos" (Anonymous 1954) leading to the establishment of a large commercial kangaroo harvesting industry (Thomsen & Davies 2007; Boom et al. 2012).

Field experiments have since confirmed that red kangaroos increased when rabbit abundance was heavily reduced by destroying their warrens (Mutze et al. 2008). Cooke and Mutze (2018) concluded that rabbits needed to be reduced below 0.5 rabbits/ha before red kangaroo abundance increased, consistent with findings that rabbits must be kept low to restore rangeland vegetation (Eldridge 2002; Mutze et al. 2016*a*).

European Rabbit Fleas

Although European rabbit fleas failed to establish in very arid areas, they reduced rabbit abundance by over 90% in the drier eastern Mount Lofty Ranges of South Australia, and native grasses became more prolific along the eastern scarp of the ranges (Cooke 1998). Southern hairy-nosed wombats expanded into the ranges in several places in a repetition of events after myxomatosis first spread (Aitken 1971). The distribution of swamp wallabies (*Wallabia bicolor*) also expanded in western Victoria and the south-east of South Australia as European rabbit fleas spread (Cooke 2020). Nonetheless, replicated experiments in the same region showed that extra efforts to reduce rabbit abundance were needed before significant increases in western gray kangaroo (*Macropus fuliginosus*) and common wombat (*Vombatus ursinus*) populations were seen (Bird et al. 2012).

Rabbit Hemorrhagic Disease

After RHD spread through inland Australia, there was widespread regeneration of native vegetation, including native pine (*Callitris glaucophylla*), needle bush (*Hakea leucoptera*), umbrella wattle (*Acacia ligulata*), witchetty bush (*A. kempeana*), and twin-leaved emu bush (*Eremophila oppositifolia*) (Cooke 2014; Mutze et al. 2016*b*; Cooke & Soriguer 2017). Burrell et al. (2017) analyzed satellite data to confirm that over large parts of the Simpson and Strzelecki Deserts there had been a sharp increase in the accumulation of natural vegetation cover.

In the Ikara–Flinders Ranges National Park, red kangaroos became two to three times more abundant in areas where they had previously been limited by rabbits (Mutze et al. 2008). More importantly, Pedler et al. (2016) attributed major expansions in the distribution of three species of native desert rodents, dusky hopping mice (*Notomys fuscus*), spinifex hopping mice (*N. alexis*), the plains rat (*Pseudomys australis*), and a small marsupial carnivore, the crest-tailed mulgara (*Dasycercus cristicauda*), to the release of RHD. The rodents recolonized former habitat over thousands of square kilometers, and the mulgaras increased because natural prey, including native mice, became more abundant, associated with improved vegetation to support these species, and likely reduced predation from higher order predators (Pedler et al. 2016; Contos & Letnic 2019).

Outcomes from Biocontrol Interventions

As indicated earlier, there is strong evidence that native vegetation partially recovered and native mammals increased and spread following each biocontrol intervention. These advances were not always long-lasting, and others took many years to become apparent. For example, because of highly variable rainfall, it took about 10 years to recognize that the dusky hopping mouse population was expanding and over 20 years before Pedler et al. (2016) were confident enough of their data for other animal species to conclude that the spread of small mammals was a consequence of biocontrol.

Native mammals that have benefitted from the biological control of rabbits, apart from mulgaras, are generally too large (kangaroos, wallabies, and wombats) or too small (rodents and smaller dasyurids) to fall within the critical weight range of animals that have apparently been heavily suppressed or exterminated by cats and foxes. Consequently, if native mammals outside the critical weight range benefitted from removal of rabbits, then similar benefits should also apply to species heavily preyed upon by cats and foxes. Thus, rather than relying on predator control alone to reintroduce native fauna, there is robust evidence to suggest that more effective rabbit control would contribute substantially to ecosystem restoration.

This review indicates that there are two general issues to be studied in more detail. The first concerns rabbits influencing vegetation quality and structure that potentially limits the reproductive output of native fauna, forces them to range further in search of food, and deprives them of vegetation cover where they can escape from predators. The second involves the role of rabbits in supporting large populations of introduced predators and the consequences for native fauna when rabbit populations collapse during drought and predators seek alternative prey. Again, experiences with the wide-scale application of biological control provide insights into both matters and help put these issues into better context from a management perspective.

Native Herbivorous Mammals Are Disadvantaged by Rabbit Grazing

Rabbits consume a high proportion of the vegetation produced in Australia's arid zone, especially during dry years, exacerbating the severity of drought. As shown, the introduction of biological controls partly resolved this problem, nonetheless, even at today's lower densities, rabbits continue to severely damage native vegetation. Mutze et al. (2016*b*) quantified the relationship between rabbit density and regeneration of native vegetation and showed that regeneration of palatable shrubs and native grasses can only be assured when rabbits are reduced below a density of 0.5 adult rabbits/ha, equivalent to about one rabbit warren to 10 ha. At these rabbit densities native plants begin to outcompete and replace unpalatable introduced weeds that tolerate rabbit browsing (Mutze et al. 2016*a*). Rabbits not only change native vegetation communities through their selective grazing and digging but also spread undigested weed seeds in their feces (Twigg et al. 2009). Overgrazing, whether by rabbits or overabundant native species, reduces the complexity of understory vegetation, grass cover, species richness of grasses, forbs, and shrubs, and depletes soil carbon and phosphorous, leading to increased soil density and consequently reduced soil porosity and increased soil compaction (Mills et al. 2020).

By eating the seedlings of shrubs and trees, rabbits hold native vegetation communities in early successional stages. This delays ecosystem recovery. Munro et al. (2009) showed that even where cattle had been removed, but low post-RHD populations of rabbits remained, the rates of recruitment of mulga (*Acacia aneura*), silver cassia (*Senna artemisioides*), and sandhill wattle (*Acacia ligulata*) were below those observed in fenced havens where greater bilbies, burrowing bettongs (*Bettongia lesueur*), and stick-nest rats (*Leporillus conditor*) had been reintroduced. This confirmed observations that rabbits alone could prevent the reestablishment of vegetation communities (Hall et al. 1964; Sinclair 2005), while native animals in moderate numbers remained conducive to regeneration. Nonetheless, when native bettongs became very abundant, they also began consuming seedlings of *A. aneura* and *A. ligulata* (Linley et al. 2017).

Linley et al. (2017) showed that, during drought-induced food shortages, burrowing bettongs relied on ruby saltbush (*Enchylaena tomentosa*) and to a lesser extent, creeping saltbush (*Rhagodia spinescens*). However, they did not eat corrugated sida (*Sida corrugata*) despite its persistence during drought. The significance of these observations becomes apparent on considering premyxomatosis observations that climax vegetation in semiarid New South Wales included a ground layer of both ruby- and creeping saltbush but grazing by sheep and rabbits resulted in ground cover dominated by corrugated sida (Moore 1953*a*, 1953*b*).

Where rabbits have prevented the regeneration of plant communities for over 130 years, many former pasture species are missing, and many shrub populations consist of old scattered individuals (Crisp & Lange 1976; Foran et al. 1985). It will take decades for these communities to become reestablished even if rabbits are controlled well enough for regeneration to begin. Arid-zone shrubs grow only slowly because of low rainfall. It can take 10–20 years before they reach a height where they are safe from destruction by rabbits (Sykora 1997). Even more time should be allowed before insects and plant parasites such as mistletoes recolonize those plants as part of the widest possible ecosystem restoration (Cooke 2014).

It is seldom asked whether lack of plant cover or adequate food supplies for reintroduced native animals influence ongoing predation losses to cats and foxes. However, despite initial success, the likely long-term prospects for reestablishing brush-tailed possums (*Trichosurus vulpecula*) in the Flinders Ranges in South Australia has been questioned because of the limiting effects of rabbits on regeneration of hollow-bearing trees and important food plants (Mutze et al. 2016*a*, 2016*b*; Moseby et al. 2020; Bannister et al. 2021). Similarly, food resources were barely adequate for brush-tailed bettongs (*Bettongia penicillata*) released into Yathong Nature Reserve in western New South Wales where past overgrazing and the continuing presence of rabbits reduced habitat quality (Leigh et al. 1989; Eldridge 2002; Priddel & Wheeler 2004). The bettongs regained weight lost after initial release, but recaptured females were never recorded with large pouch-young before they were killed by predators. These examples reemphasize the importance of reducing rabbit abundance to improve habitat quality and reduce predation. If native animals have good quality food and adequate cover, they should better withstand predation.

In Table 1 we summarize results of these varied approaches to ecosystem restoration to show some of the advantages and disadvantages of each.

Rabbits and Predators

Rabbits are the major prey species of introduced cats and red foxes in southern Australia (Read & Bowen 2001; Holden & Mutze 2002; Doherty et al. 2015). These predators can suppress low-density rabbit populations, but rabbits frequently increase rapidly enough to escape predator-dependent control (Newsome et al. 1989; Pech et al. 1992). In the past, overgrazing by rabbits, especially during droughts, was followed by a population collapse and although predators benefited while feeding on starving rabbits, after a short lag, they too became short of food and turned increasingly to carrion and native fauna. However, when seasons were favorable again, because of their high reproductive capacity, rabbits quickly rebounded and invariably escaped predator-dependent control to reach plague numbers and overexploit their food supply again. This perpetuated boom and bust cycles every 5–7 years (Cooke & Soriguer 2017).

When RHD first spread in 1995–1996 and the rabbit population fell heavily, cats and foxes ate a larger proportion of native animals as prey, but this was offset by a much larger proportional fall in predator abundance, with the net result being a reduction in predation (Bowen & Read 1998; Read & Bowen 2001; Holden & Mutze 2002). There was only one report indicating the possible loss of a small population of black-flanked rock wallabies (*Petrogale lateralis*) due to starving predators switching from rabbits to native prey. But even then, other explanations were possible (Moseby et al. 1998).

Pech and Hood (1998) used modeling to demonstrate that declines in predator populations following biological control were quite different from those which followed rabbit population crashes imposed by food shortages. With RHD keeping rabbit abundance low, rather than rabbits rapidly recovering and predators also increasing, fewer predators and fewer periods when hungry predators sought alternative prey were expected. Pech and Hood's (1998) anticipated outcomes have been borne out and, since RHD was introduced 25 years ago, there has been no rabbit plague in inland Australia like those previously reported (Cooke & Soriguer 2017).

Table 1. Summary of information and conclusions from this review. Fencing costs from Long and Robley (2004) were adjusted to approximate 2021 values using an inflation factor of 1.47.

	Projects Concentrating on Predators		*Projects Concentrating on Rabbits*		
Type of project	Wildlife refuges (havens)	Individual species reintroductions	Rabbit-free reserves	Mechanical and chemical eradication	Biological control
Examples	Arid Recovery (Linley et al. 2017); Scotia Sanctuary (Berry et al. 2019)	Bettongs (Priddel & Wheeler 2004); brush-tailed possums and quolls (Moseby et al. 2020; West et al. 2020)	Koonamore Vegetation Reserve (Sinclair 2005)	Ikara–Flinders Ranges National Park (Mutze et al. 2008); Bulloo Downs (Berman et al. 2011; Elsworth et al. 2019)	Myxomatosis, rabbit hemorrhagic disease (Fenner & Fantini 1999); European rabbit flea vectors (Cooke 2021)
Treatments	Fencing and removing predators and rabbits	Removal of predators: poisoning, shooting, trapping	Rabbit-proof fencing and removal of rabbits	Warren destruction using bulldozers, fumigation, explosives	Release of biological control agents to establish in the field
Landscape scale of studies	Local areas, up to 70 km^2 in some instances	Local areas, up to 100 km^2	Local areas, up to 5 km^2	Local areas, up to 100 km^2	Continental scale, up to 5 million km^2
Time scale of studies	Some havens have been maintained for over 25 years. Many small sub-projects completed in this period	Usually short-term experiments, 2–3 years, but extended if successful	Long-term projects. Koonamore study included 50 years before rabbit control, 45 years thereafter	Assessed 2–5 years after treatment to detect rabbit recolonization and vegetation/fauna improvements	Long-term: myxomatosis was first released in 1950, European rabbit fleas in 1969, and rabbit hemorrhagic disease virus (RHDV) in 1995; studies continue
Initial establishment costs	High cost of predator-proof fences, e.g. materials A $15,100/km (2021 prices)	Moderate-low; aerial baiting over very large areas can reduce costs	High-moderate, e.g. fence materials A $5,900/km (2021 prices)	Cost of warren ripping variable, often > $20/ha over large areas. Cheaper than fences	High initial investment, low long-term cost, e.g. A$12.6 million to bring RHD into Australia
Inspection/ maintenance costs	Very frequent inspection, high labor costs	Frequent, high-moderate	Frequent, moderate	Infrequent, low	Infrequent, low
Advantages	Absence of predators and competitors allows immediate, reintroduction of several native animal species	Removal of predators carried out as needed to reduce predation risk	Enables evaluation of plant ecosystem responses following rabbit removal	Useful experimental tool to demonstrate that rabbits supress native fauna and flora	Continental scale is major benefit: ecological responses seen in many different ecosystems
Disadvantages	Lack of predators leads to native herbivore increase and overgrazing. Native mammals lose predator-avoiding behaviors	Projects may fail because predators rather than basic resources are emphasized	Presence of predators limits possible fauna changes in rabbit-free vegetation reserves	Disruptive if not done carefully; some native species also shelter in rabbit warrens	Some ecosystem responses difficult to detect; may lag 20 years, but long-term studies compensate for this
Main review outcomes	Mid-sized or critical weight range (CWR) fauna can be reintroduced to inland Australia if introduced predators and competitors are excluded by fences	It may be possible to reintroduce some mid-sized fauna without fences if predators and competitors are controlled by other means	Rabbits have a huge impact on vegetation, affecting plant community succession and resources such as food and shelter needed by native fauna	Warren destruction can add to biological control further reducing damage. May also help to keep predators low where rabbits support high predator numbers	Rabbit biocontrol benefits natural ecosystems, providing greater plant diversity, food, and shelter. Species within the CWR have not responded to rabbit reduction, thus predator control remains important

Nonetheless, prey-switching by cats and foxes is still considered a major conservation issue by some authors (e.g. Doherty et al. 2015) despite evidence to the contrary from field studies associated with the introduction of RHD (e.g. Holden & Mutze 2002). Fortunately, however, the dependence of cats on rabbits has recently been experimentally demonstrated by removing rabbits by shooting. Within a month of removing 2,215 rabbits from the 37-km^2 experimental site, the survival rate of radio-collared cats ($n = 29$) dropped by 40% compared with that on the adjoining control area. The surviving cats ate more carrion, small reptiles and insects but there was no indication of increased predation on native rodents, confirming experimentally that rabbit suppression did not threaten native mammalian prey because prey-switching was offset by reduced cat survival (McGregor et al. 2020).

Although it was anticipated that native avian predators such as Wedge-tailed Eagles (*Aquilla audax*), and rarer, Black-breasted Buzzards (*Hamirostra melanosternon*) might be short of food as RHD first spread (Falkenberg et al. 2000; Edwards et al. 2002), the abundance of eagles remained steady when RHD lowered the rabbit population by 85% in central Australia while the abundance of large varanid lizards apparently increased (Edwards et al. 2002). Steele and Baker-Gabb (2009) could not detect any effect of the introduction of RHD on the abundance of Wedge-tailed Eagles or any other raptors that normally take rabbits. Olsen et al. (2014) found that Wedge-tailed Eagles exploited the increased abundance of gray kangaroos (*Macropus giganteus*) as the rabbit population fell and there was no sudden decrease in eagle egg clutch size or fledgling survival associated with the spread of RHD. Again, contrary to expectations by some researchers, there was no strong evidence that reduction of rabbit prey seriously compromised native predators.

Discussion

The rapid decline of native fauna in Australia in the nineteenth century was caused by many changes associated with European colonization, including the introduction of wild rabbits. All too often, however, rabbits are disregarded as a conservation threat by rangeland ecologists and managers (Mutze 2016), although there are exceptions (e.g. Morton 1990). For protecting native fauna, fencing out introduced predators has taken precedence over the control of rabbits because predator removal produces immediate results. Nonetheless, the progressive implementation of three wide-scale biocontrol measures to reduce rabbit abundance resulted in slow but clear increases in arid-zone vegetation regeneration over the last 70 years and the recovery of several native mammal species. This has occurred without deliberate wide-scale predator control and shows that further progress and landscape-scale benefits could be attained by eliminating rabbits.

The native arid-zone mammals that have generally benefitted from the biological control of rabbits, apart from mulgaras, appear to be either too large (kangaroos, wallabies, and wombats) or too small (rodents and smaller dasyurids) to fall within the critical weight range of animals most heavily preyed upon by cats and foxes. Thus, our review does not suggest better rabbit control as an alternative to predator management. Rather, it suggests that additional rabbit control should complement and enhance predator control.

We conclude from our review that wide-scale removal of rabbits using biological control only temporarily increased predation risk for native mammals and did not heavily compromise native predators. The introduction of RHD broke the pattern of recurrent rabbit plagues that once prevailed in inland Australia. Since its introduction in 1995, there have been no major, widespread rabbit plagues, predator numbers have rarely been high with respect to the availability of rabbits and some small mammal populations have increased in abundance and distribution.

Recent attempts to reintroduce medium-sized species such as the tammar wallaby (*Macropus eugeneii*), western quoll (*Dasyurus geoffroii*), and brush-tailed possum (*Trichosurus vulpecula*) in unfenced areas are meeting with some success. All have focused on intensive predator control throughout large national parks (Sharp et al. 2010; Moseby et al. 2021). Nonetheless, because those introductions were commenced following the introduction of three biological control agents, lower rabbit numbers and habitat improvement likely contributed to successful project outcomes too (Mutze 2017; Ramsey et al. 2020).

We suggest that there is a risk in concentrating too heavily on control of predators without also considering better rabbit management because, if biological control agents alone cannot keep rabbit populations low enough to enable vegetation recovery, ecosystems could be increasingly degraded. There is the further complication that cats become more difficult to control if rabbits are readily available (Morris et al. 2004; Moseby & Hill 2011).

Clearly, progress is being made in restoring Australia's arid-zone ecosystems. However, extra work to better control rabbits should be included to provide the quality food and cover that would make native fauna in the critical weight range more resilient to predation by introduced cats and foxes. Short of finding new biological control agents, or improving the effectiveness of present ones, the most likely approaches for controlling rabbits will include well-known methods such as rabbit warren destruction using large bulldozers which can be cost-efficient and result in positive and long-lasting conservation benefits (Berman et al. 2011; Elsworth et al. 2019).

Planning for ecosystem restoration must also ensure that considerable human and financial resources are available for prolonged periods, certainly many decades, to keep rabbits below 0.5 rabbits/ha and to limit as far as possible the depredations of cats and foxes.

Rabbit management must remain a priority for conservation managers. Perceived obstacles, such as temporary prey switching, should not be used as an excuse to reduce rabbit control. Ecosystem restoration in inland Australia will only be successful where rabbits are substantially reduced or removed.

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