BENEFITS OF RABBIT BIOCONTROL IN AUSTRALIA: AN UPDATE

COLLABORATION INNOVATION IMPACT

CENTRE FOR INVASIVE SPECIES SOLUTIONS

In memory of Greg Mutze 1957-2022

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Native orchid regeneration after RHDV reduced rabbit grazing, Coorong National Park (SA), Sept. 2016 (photo by David Peacock). Rabbit image by Laurence Sanders.

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EXECUTIVE SUMMARY

Australians have been battling the impacts of the European rabbit (Oryctolagus cuniculus) since the mid-19th century .

This report provides the evidence base for ongoing investment in biocontrol research, development and engagement (RD&E), and the release of new agents to further suppress rabbit abundance when appropriate. It should be read in conjunction with the Centre's updated Rabbit Biocontrol Pipeline Strategy (CISS 2021).

This report also documents key parts of the substantial body of research that analyse the economic, environmental and social impacts of rabbits on Australia, the effectiveness of biocontrol, and qualitative and quantitative benefits that derive from biocontrol.

Historical context

Following its successful introduction on mainland Australia between 1857 and 1860, the European rabbit became the fastest colonising terrestrial mammal anywhere in the world due to a lack of natural predators and its successful adaption to a variety of environments. The rapid expansion of rabbits across Australia was enhanced by their prolific breeding potential. Rabbits can begin reproducing at four months of age and, in favourable conditions, may produce five or more litters per year that results in between 50 to 60 offspring per year per female rabbit. Under favourable conditions, the reproductive activity of a single pair of rabbits can result in a population of 184 rabbits in 18 months. Within 70 years of their release, rabbits had spread to cover almost 70 per cent of Australia's landmass, to an area estimated at 5.3 million square kilometres.

Rabbits quickly became Australia's worst terrestrial vertebrate pest with plagues causing major damage to agriculture, the developing economy, rural communities and the environment. The National Museum of Australia has identified the success of their introduction to the continent as one of the "defining moments in Australian history".

Initial control efforts centred around trapping, rabbit warren ripping, fumigation and bounty systems. Later, as noted by the Museum, "Fences became an integral component of what settlers in the late 19th century began to see as a war against the rabbits." It is estimated that there were 320 000 kilometres of rabbit proof-fence across Australia at the height of the fencing boom. Colonial governments also moved to make it compulsory for landholders to destroy all rabbits on their farms and stations and made it illegal to aid their spread. Despite these early rabbit control efforts, Australians were fighting a losing battle.

In 1943, in response to growing public pressure to find alternative rabbit control solutions, CSIRO conducted initial tests using the rabbit specific myxoma virus (MV). These tests initially appeared to fail but following good rain in late 1950 the virus was rapidly spread by mosquitos. It had a dramatic effect on the rabbit population, then numbering around 600 million, reducing rabbit numbers by as much as 99 per cent especially in arid areas. Infections were further assisted by the release of two flea vectors in 1969 and 1993.

The major success of the myxoma virus as a biocontrol put Australia on the path to becoming world leaders in the management of pest rabbits. However, as has been the experience of later biocontrol agents, resistance to MV in the rabbit population led to a gradual recovery in their numbers.

The continued development of biocontrol knowledge for controlling rabbits through RD&E has become essential in the ongoing fight against wild rabbits. It has enabled the 1995 release of the rabbit haemorrhagic disease virus, RHDV1, and a new strain, RHDV1-K5, in 2017. The release of RHDV1 initially reduced the rabbit population by up to 98 per cent, particularly in arid areas.

Serendipitously, a new viral agent, RHDV2, appeared in Australia from unknown sources in 2014. In less than two years RHDV2 had spread through the Australian rabbit population. This had a significant initial impact and reduced rabbit abundance by 60 per cent on average. However, its emergence also restricted the ability of RHDV1-K5 to spread within rabbit populations. While this led to the impacts of the managed release of RHDV1-K5 being suppressed, combined they effectively impacted the rabbit population. At present RHDV1 and RHDV2 are coexisting in the environment however it is uncertain if this will be the case into the future. RHDV2 may become the dominant field strain.

The impact of rabbits and the benefits of rabbit biocontrol

Prior to the release of the myxoma virus, the financial impact of rabbits on agriculture was some $2 billion a year. Rabbit biocontrol based on the myxoma virus and RHDV1 Czech 351 strain reduced this impact to about 15% of the pre-release cost. This is equivalent to $81.8 billion in agricultural productivity in the sixty years to 2011 (expressed in 2020-dollar terms; Reserve Bank of Australia, 2022). The RHD viruses introduced (or naturalised) since 2014 — that is, RHDV2, RHDVa and RHDV1 K5 — are expected to generate benefits of a further $4 billion over the next 30 years. This is on top of the ongoing benefits derived from myxoma virus and the RHDV1 Czech 351 strain.

Rabbit biocontrol has had major benefits for native plant and animal species, and in arid inland Australia has been attributed as the single most important and cost-effective conservation action for small, threatened mammals and a range of ecosystems in recent decades. An associated benefit enabling their recovery has been a reduction in abundance of foxes and feral cats which is directly attributed to the removal of their primary prey, the rabbit.

While the benefits from rabbit control have been enormous, rabbits persist in the Australian landscape and continue to have a severe impact. Many Australian native plants are especially sensitive to rabbit browsing. Recruitment for some slow growing species such as Mulga are negatively impacted by rabbits with densities as low as one rabbit/km^2 (0.01 rabbit/ha). The impact rabbits have on both native plants and animals is the reason they impact 322 nationally threatened species – the most for any vertebrate pest. They also continue to cause $217 million a year in lost agricultural productivity.

In summary, controlling rabbits at a landscape scale with biocontrol methods results in less erosion and weed growth and fewer feral predators of native animals. Importantly, the use of biocontrol is critical to reducing the abundance of rabbits at large scales to less than 0.5 rabbits per hectare allowing the survival and growth of palatable native plant seedlings. This leads to more native animals, plant species and vegetative growth. It also increases carbon sequestration, makes food production more sustainable, and improves ecosystem and landscape health — factors essential to the welfare and prosperity of all Australians.

While a silver bullet for the eradication of wild rabbits remains elusive, biological control over the vast range of rabbit distribution in Australia has been highly successful. However, biocontrol remains an ongoing process: rabbit populations continue to have the ability to build resistance to introduced pathogens and for their abundance to increase.

The need for ongoing biocontrol RD&E has been recognised by governments, research agencies and industry organisations and has led to two Centre five-year R&D plans under a long-term Rabbit Biocontrol Pipeline Strategy:

- Phase two of the Strategy was implemented by the Invasive Animals Cooperative Research Centre (2012–2017)
- Phase three of the Strategy is currently being implemented by the Centre for Invasive Species Solutions (2017–2022).
- Phase four of the Strategy is currently being prepared by the Centre for Invasive Species Solutions (2022–2027).

Phase four offers the potential of new biocontrols that include genetic biocontrol technologies and the monitoring of rabbit abundance impacts through new satellite imaging methodologies and the use of artificial intelligence.

Glossary of abbreviations

CSIRO Commonwealth Scientific and Industrial Research organisation.

IA CRC Invasive Animals Cooperative Research Centre that has transitioned into the Centre for Invasive Species Solutions.

MV Myxoma Virus, the first successful rabbit biocontrol intentionally released in Australia in 1950.

RCV-A1 An endemic benign Rabbit Calicivirus detected in 2009 and which provides partial protection to lethal RHDV1 infection.

RHDV(s) Rabbit Haemorrhagic Disease Virus — used in this report as a generic descriptor for all Rabbit Haemorrhagic Disease viruses.

RHDV1 The initial Czech-351 strain of Rabbit Haemorrhagic Disease Virus released in Australia in 1995

RHDV1-K5 The naturally occurring Korean strain of Rabbit Haemorrhagic Disease Virus released in Australia in 2017

RHDV2 The variant of RHDV detected in Australia in 2014 that was not intentionally imported or released.

INTRODUCTION

This report reviews the distribution, abundance and impacts — environmental, economic and social — of European rabbits (Oryctolagus cuniculus) since the mid-19th century to the present day. It examines the history and effectiveness of the biocontrol agents that were released in Australia — MV, RHDV1, RHDV1-K5 and two flea vectors — or serendipitously appeared (RHDV2). It outlines the demonstrated environmental, economic and social benefits of rabbit biocontrols in Australia, and makes the demonstrable case for ongoing national investment in rabbit biocontrol research, development and engagement (RD&E).

This report should be read in conjunction with the Centre's report on the third phase of the Rabbit Biocontrol Pipeline Strategy (CISS 2021).

Overview of rabbit distribution, abundance and impacts

Wild rabbits were successfully introduced onto the Australian mainland in the mid to late 19th century at multiple locations, with primary releases in South Australia and Victoria between 1857 and 1860 (Peacock and Abbott 2013). An analysis of rabbit ancestry genetics suggests there were a number of successful rabbit introductions to Australia (see Figure 1; Iannella et al. 2019).

Within 70 years rabbits had spread from release locations to inhabit 70 per cent of Australia's landmass (5.3 million km²). They are widespread throughout most locations where they are found (NLWRA and IA CRC 2008). Figure 2 shows the rate of spread of wild rabbits since their primary introductions in 1857-60 to their known distribution as reported in 2012. Figure 3 shows the reported abundance of rabbits across Australia including rabbit sightings as recorded in RabbitScan from 2009 to 2013.

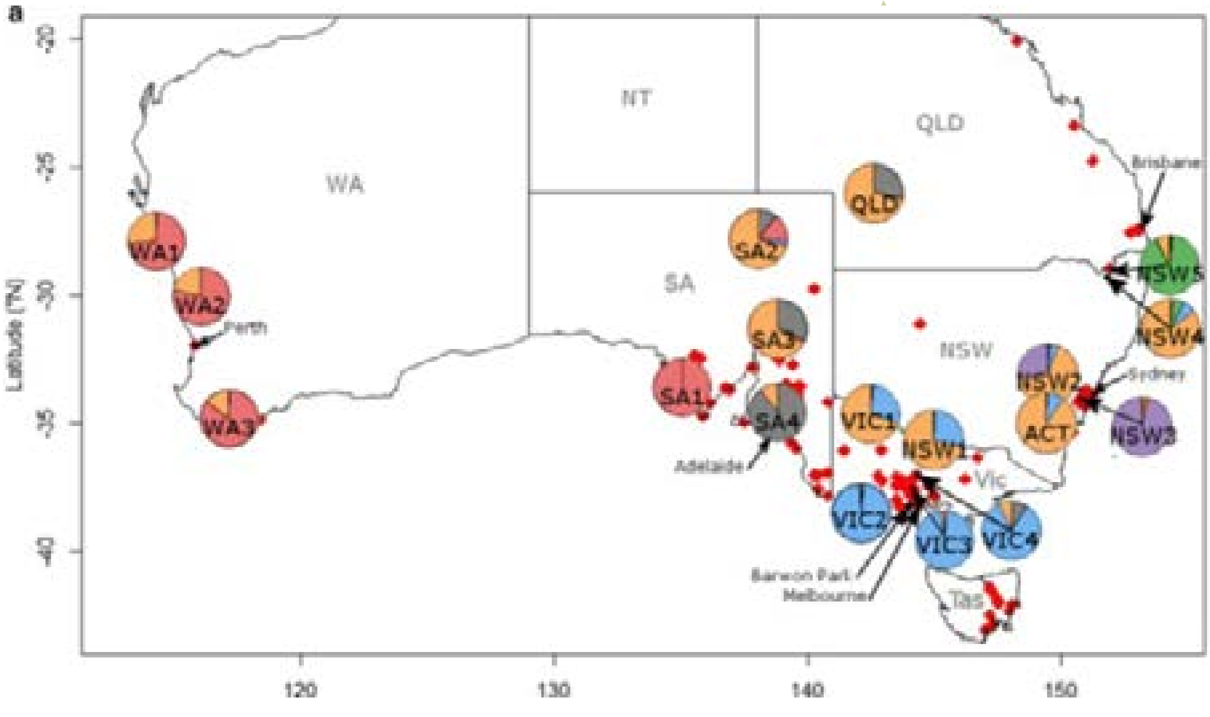


Figure 1: Rabbit ancestry genetics in Australia. Pie charts indicated proportion of ancestry at each site as estimated by fastSTRUCTURE with a K=6. Historical rabbit introduction records of successful or unknown outcome reported by Peacock and Abbott (2013) are represented as red diamonds, noting some may be hidden by pie charts. The Barwon Park release site in Victoria and state capital cities are specifically indicated. Red diamonds indicate historical introduction points (Ianella et al. 2019).

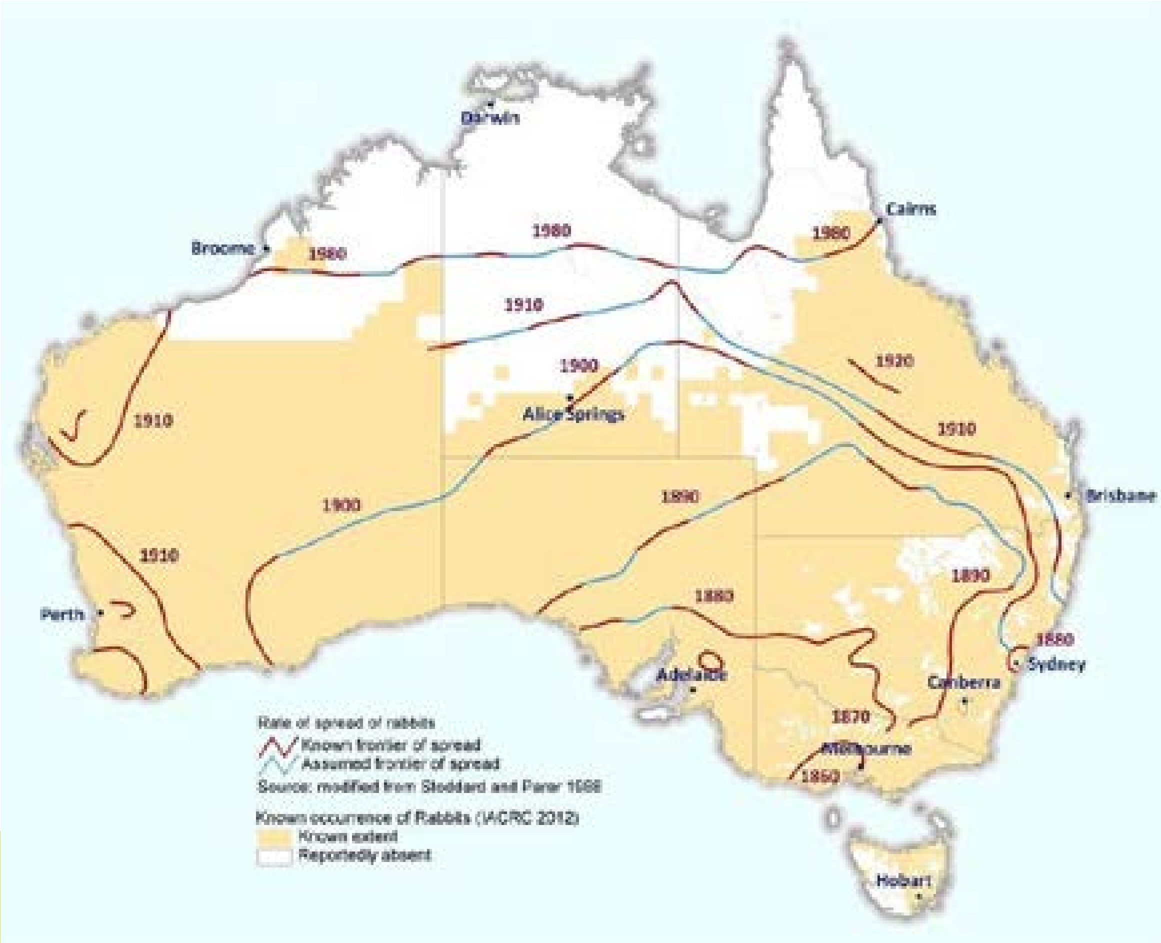


Figure 2: Rate of spread of wild rabbits since their primary introductions in 1857–60 and their known occurrence as reported in 2012. (IA CRC. Stodart amd Parer. 1988).

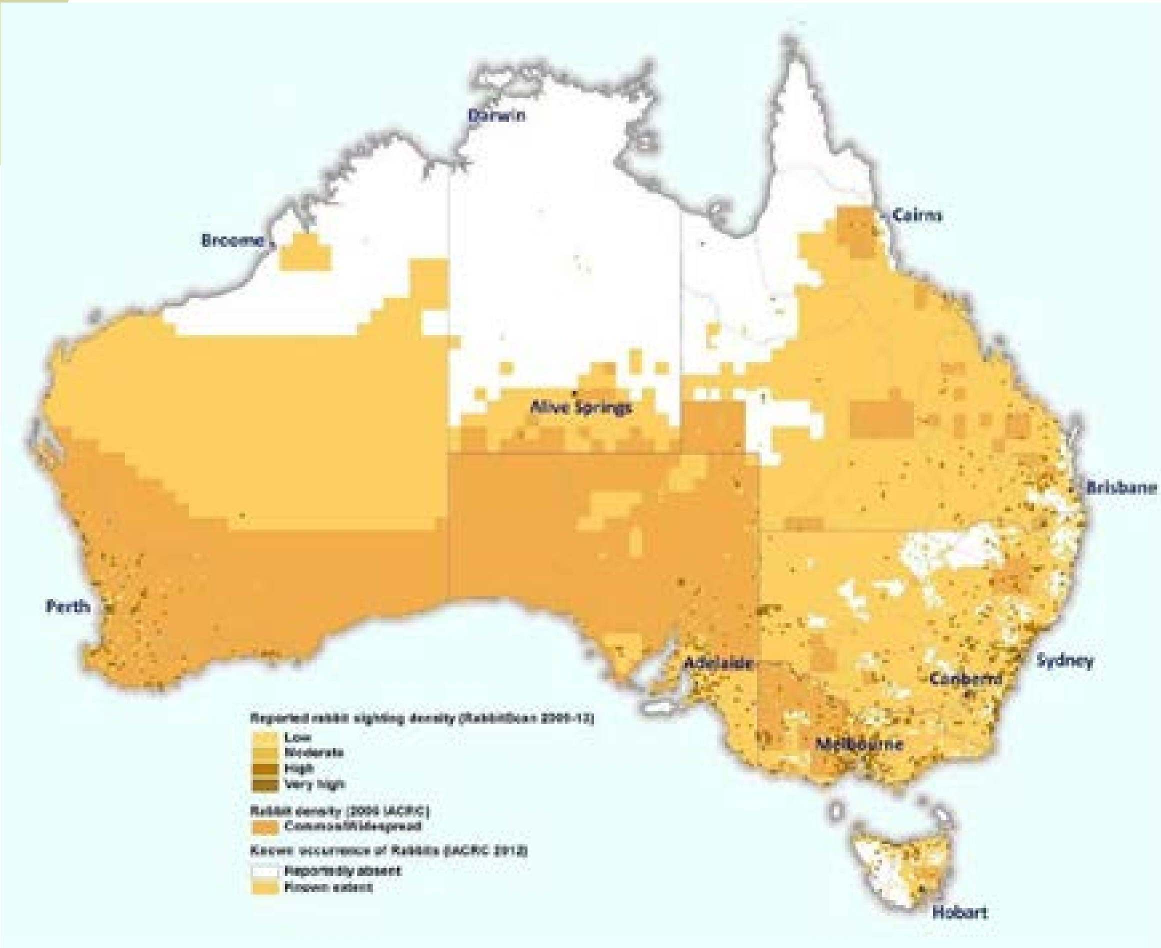


Figure 3: Reported abundance of rabbits across Australia (IA CRC, NLWRA/IA CRC 2008, RabbitScan 2009–13).

Whether rabbits have reached the limits of their absolute range is not certain. The 'Background document to the Threat abatement plan for competition and land degradation by rabbits' (DAWE, 2016a) cites the view of NLWRA and IA CRC (2008) that rabbits have largely reached their ecological limit in terms of range. Since rabbit populations respond to weather conditions, they are likely to extend their range into areas they currently do not occupy when these are favourable but when weather conditions deteriorate, their range may contract back to previous limits. As such, the average range of rabbits may have been reached, although climate change predictions for hotter temperatures could reduce their average range over coming decades. For example, Pavey and Bastin (2014) predict that rabbits could become absent from large areas of the centre and west of the NSW Rangelands by 2050.

The rapid expansion of rabbits across Australia was enhanced by their prolific breeding potential. Rabbits can begin reproducing at four months of age and, in favourable conditions, may produce five or more litters per year (NSW DPI 2007). A short gestation period coupled with females generally mating within hours of giving birth can result in between 50 to 60 offspring per year per female rabbit. Under favourable conditions, the reproductive activity of a single pair of rabbits can result in a population of 184 rabbits in 18 months (Agriculture Victoria 2021).

Environmental impacts

When rabbits feed they remove vegetation to ground level, browsing, chewing bark and ringbarking, and digging for roots. This can result in significant soil destabilisation and erosion, leading to the desertification of heavily impacted areas. Their excavation of extensive warrens adds to this damage, particularly in ecological sensitive areas. This is further exacerbated by their prolific breeding — in good seasons their populations can increase seven to tenfold. Overall, rabbits have an impact on 322 nationally threatened species (Kearney et. al. 2018) and nine ecological communities listed under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (DAWE 2016b) (Figure 4).

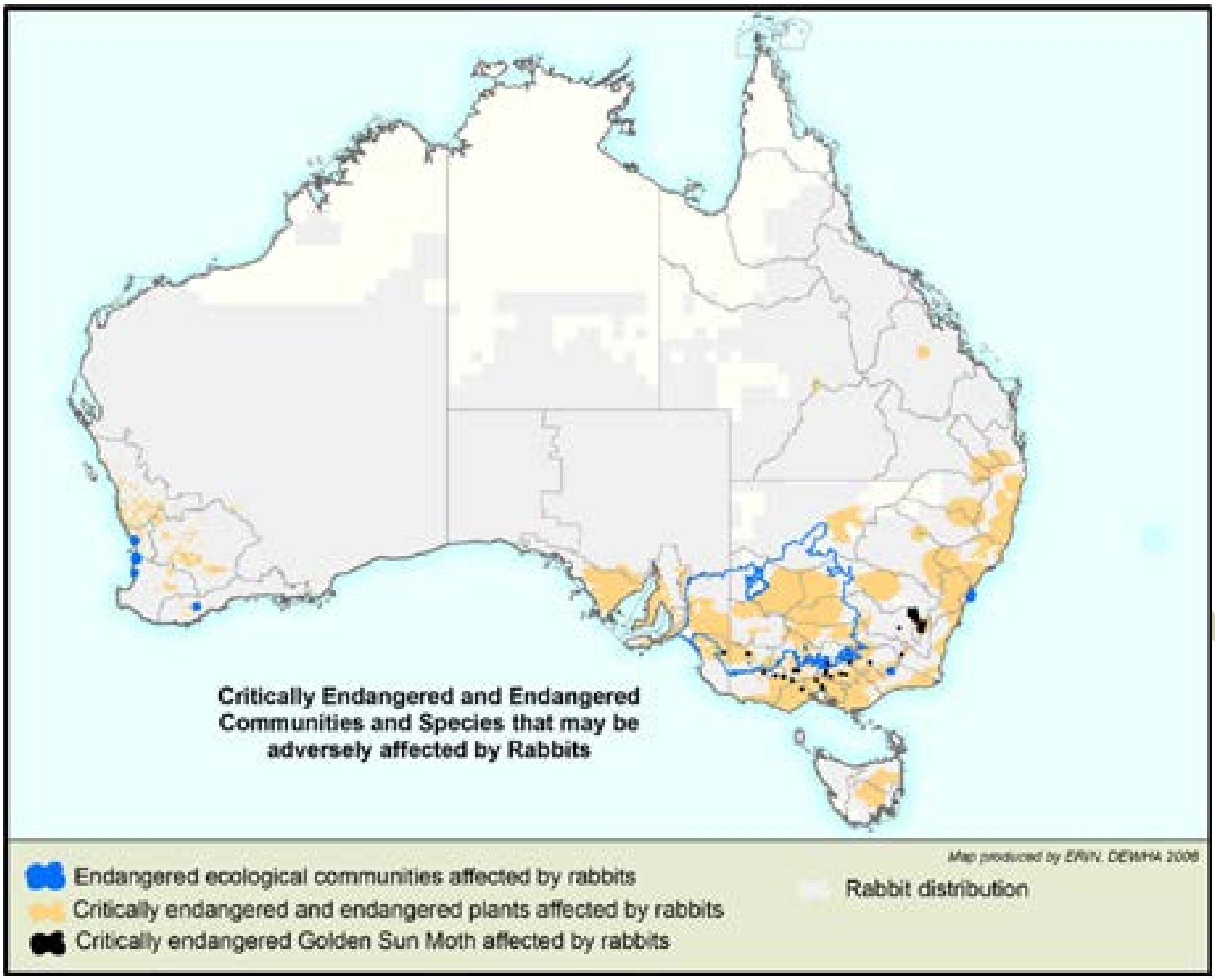


Figure 4: Locations of critically endangered and endangered communities and species that may be adversely affected by rabbits.

Research by the former Invasive Animals Cooperative Research Centre (IA CRC) and its partners has shown that Australian native vegetation is very sensitive to rabbit damage. A specific example is mulga (Acacia aneura), which occurs across vast areas of central Australia. Recruitment of mulga seedlings is negatively impacted by rabbit densities as low as one rabbit/km2 (0.01 rabbits/ha) (Mutze et al. 2008). This greatly impedes the natural regeneration of mulga in many areas where rabbits are present in central Australia. Rabbits have similar negative impacts on the recruitment of a variety of palatable trees and shrubs across much of their distribution in Australia (Cooke 2012, Forsyth et al. 2015, Mutze et al. 2016a). Highly palatable species are severely damaged from selective grazing pressure at low densities equal or greater than 0.5 rabbits per hectare, with moderately palatable plant species being severely damaged at two rabbits per hectare (Mutze et al 2016b).

Examples of local environmental impacts from browsing

Figure 5 shows a dryland tea tree (Melaleuca lancelota) that grew during a period of rabbit relief after the spread of MV, but with increasing rabbit numbers due to developing resistance to MV, the understory has been removed by grazing. The photograph also shows browsing of the tree to rabbit height.

Figure 5: Rabbit grazing of the understory and browsing of this dryland tea tree (Melaleuca lancelota) to rabbit height (Photo: Brian Cooke).

Figure 6 shows ring barking of large native pines (Callitris glaucophylla) by rabbits at Holowiliena, South Australia, during winter 1991 and pre-RHDV1 release.

Figure 6: Ring barking of large native pines by rabbits. (Photo: David and Carol Warwick)

Many other native species are susceptible to rabbit browsing. Figure 7 shows browsing occurs even at low rabbit densities and during periods when other feed is available which is detrimental to both the growing plant and the level of recruitment to those plant populations.

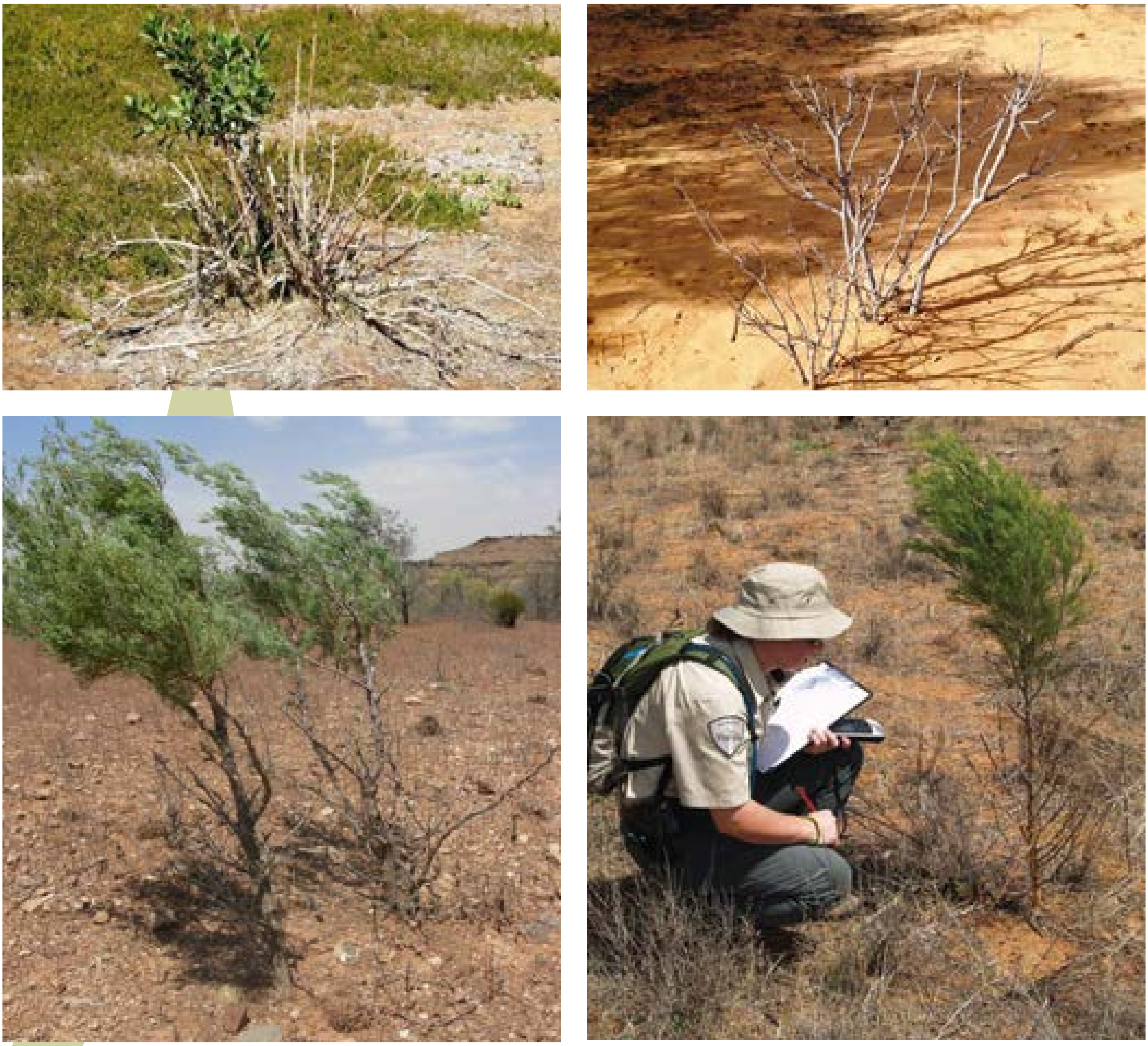


Figure 7: Native plants that are susceptible to rabbit browsing: Top left: Boobiala (Myporum insulare), Coorong SA. Top right: Sandhill wattle (Acacia ligulate), Hattah-Kulkyne National Park, VIC. Bottom left: White cypress pine (Callitris glaucophylla), Ikara-Flinders Ranges National Park, SA. Bottom right: Buloke (Allocasuarina luehmannii), Hattah-Kulkyne National Park, VIC. (Photos: Brian Cooke & David Peacock).

Impacts on native animals

While the direct impact of rabbits on vegetation has been clearly documented, their impact on native animals via competition is less clear. Both kangaroo (Macropus rufus, M. fuliginosus, and M. robustus) and wombat (Vombatus ursinus) populations increased following native vegetation regeneration after the release of RHDV and the sharp decline in rabbit abundance. This suggests that high rabbit populations may restrict these species (Mutze et al. 2008; Bird et al. 2012). A similar explanation has been proposed for the very restricted mainland distribution of the quokka (Setonix brachyurus) (Scholtz and DeSantis 2020).

The impact of rabbits on native pastures directly affects a variety of other species, including endangered or critically endangered species such as the plains-wanderer (Pedionomus torquatus) (Baker-Gabb 2002) and the golden sun moth (Synemon plana) (Clarke and O'Dwyer 2000). Competition and land degradation caused by rabbits is listed as a 'Key Threatening Process' under the Commonwealth Environmental Protection and Biodiversity Conservation Act 1999.

Economic impacts

Rabbits have had a major economic impact on Australian agriculture from the late 19th century to the present day. In earlier times, when agriculture was a major part of the nation's gross domestic product, the scale of this impact was felt on the national economy. Prior to the release of the myxoma virus, the financial impact of rabbits on agriculture was some $2 billion a year. (Cox et al. 20130).

There have been many studies of the economic impact of rabbits on agriculture especially for wool, sheepmeat and beef production. The most contemporary comprehensive studies have been McLeod (2004), Gong et al. (2009) and McLeod et al. (2016). Other significant economic studies such as Cooke et al. (2013) and Hardaker and Chudleigh (2020) have focused on quantifying the economic benefits of biocontrol and are discussed later in this report.

The economic cost of rabbits is most pronounced in Australia's pastoral industries, however they remain significant pests in cropping, viticulture and horticulture. The main impacts on livestock industries are overgrazing of native grasslands, native pastures and improved pastures, a loss of plant biodiversity in pastures, and reduced livestock carrying capacity. The Department of Primary Industries and Fisheries Queensland (2008) have estimated that rabbits eat around fifteen per cent of their body weight per day — an amount five times greater than sheep and cattle which consume three per cent of their body weight per day.

The most comprehensive study on the economic impacts of vertebrate pests in Australia, including rabbits, is by Gong et al. (2009). This study quantified the direct economic impacts of invasive animals on agriculture (beef, wool, lamb and grains) in Australia, and the nationwide expenditure by governments and landholders on pest management, administration and research.

The economic impact from rabbits that Gong et al. identified was grazing competition. This saw a reduction in the carrying capacity of farmland. The grazing competition resulted in less livestock being carried, lower wool production per animal, reduced lambing percentage, lessoned wool quality, reduced sale weights and higher stock mortality.

Gong et al. calculated the overall impact of vertebrate pests as the sum of the effects on agriculture plus the expenditure on their management. Using the concept of the impact on economic surplus, Gong et al. estimated the total annual loss from rabbits was $206 million.

McLeod (2016) provided an update from the 2009 study of Australia-wide annual production loss costs and expenditure by governments and landholders on pest animal management including rabbits for 2013 –14. Assuming a fixed product price, McLeod estimated the annual production loss impact of rabbits for wool, sheepmeat and beef production at $217 million in 2013 –14 for an average rabbit impact scenario. McLeod also estimated production losses for low and high rabbit impact scenarios at $108 million and $251 million.

Care should be taken in generalising the results from studies such as Gong et al. (2009) and McLeod (2016) as an estimate of the ongoing annual cost for agriculture. The results are based on a large number of assumptions for which there are limited data — or the data changes from year to year — including product prices.

Social impacts

There has been little systematic research into the social impacts for any vertebrate pests in Australia with the exception of wild dogs (Fitzgerald and Wilkinson 2009, Thompson et al. 2013). However, there are some studies that look at the impacts of rabbits on people and communities. These particularly relate to the rabbit plagues of the late 19th and early 20th centuries.

Cooke (2017) examined the impact of rabbits on the economy and culture of the Diyari people of north-eastern South Australia. He argued that the catastrophic impacts of rabbits on their desert habitats and food resources was the primary factor leading the Diyari people being driven from their lands and becoming reliant on European support.

The impacts on pastoralists were also severe. There are accounts of pastoralists continuously battling rabbits and then having to abandon their pastoral leases because rabbits had eaten everything (Rolls 1969, Coman 1999, Cooke 2017). Similar accounts were given to the associated commissions and royal commissions during the 1890s (Anon 1890, 1893, 1898).

Quealy (2011) provides a collection of personal stories from those impacted by rabbits who were forced to leave their properties prior to the introduction of the myxoma virus. Many of these speak of the psychological distress at having to make a new life away from the farm.

The psychological distress and changing attitudes towards rabbits experienced by those battling these plagues were recorded by early CSIRO scientist, Francis Ratcliffe (Ratcliffe 1938). Such distress was sometimes exacerbated by conflict in communities arising between those prospering from high rabbit numbers such as commercial harvesters and pest controllers, and those suffering because of rabbit plagues (Coman 1999). This is perhaps best illustrated by the failed introduction of the mongoose to Australia as a tool to help control the plagues of the late 1880s, with the rabbiters that were making their living from killing rabbits being reported as a primary reason for the demise of the mongoose (Peacock & Abbott 2010).

More recently a study undertaken in the Hunter Valley region of NSW highlighted that residents were concerned by the impact of rabbits on mine rehabilitation sites, damage to grape vines and the risk of injury to horses due the presence of warrens (Fitzgerald and Wilkinson 2009).

The National Museum of Australia has acknowledged the social and other impacts of rabbits on Australia since their successful introduction to the continent as a “defining moment in Australian history” (National Museum of Australia 2021).

The Museum discusses the different methods of rabbit control that were applied and how: “Fences became an integral component of what settlers in the late 19th century began to see as a war against the rabbits.” Fencing was government sponsored and at the height of the fence construction boom there were 320,000 kilometres of rabbit proof-fence across Australia. The longest spanned 3,256 kilometres north to south across Western Australia.

As part of the rabbit fencing boom, colonial parliaments passed legislation to make it compulsory for landholders to destroy all rabbits on their farms and stations and made it illegal to aid the spread of rabbit.

The Museum notes that fencing failed for many reasons and by the late 1940s the rabbit population had increased to 600 million due to a number of high rainfall years but also because WWII reduced manpower for trapping and fence maintenance.

At the same time as the country was fighting rabbit plagues, families benefited from the availability of rabbits as a free source of meat during the Great Depression and itinerant ‘rabbitohs’ or rabbiters found employment in the capture and sale of rabbits.

In the more prosperous years following WWII, the consumption of rabbits and employment of of rabbitohs largely disappeared. A small meat rabbit breeding industry developed mainly to source restaurant demand based on New Zealand white rabbits due to their high feed to meat ratio and fine bones.

There is also a small pet industry for rabbits in some states. Queensland has legislation which makes the keeping of a rabbit as a domestic pet illegal. In states where rabbits can kept as pets, breeds attractive to children are largely used.

The existence of the small meat and pet rabbit industries mean that introduced biocontrols for wild rabbits need to ensure protections for farmed and pet rabbits, largely through the availability of vaccines.

HISTORY AND BENEFITS OF RABBIT BIOCONTROL IN AUSTRALIA

Australia has introduced four biocontrol agents for rabbits over the past 60 years: two viral diseases (myxoma virus – MV and rabbit haemorrhagic disease virus – RHDV1) and two flea vectors (Spilopsyllus cuniculi and Xenophsylla cunicularis) to aid their transmission. A third viral agent, RHDV2, was detected in Australia in 2014, but it is not known how the virus entered the country. A new strain of RHDV1, K5, was released nationally in 2017. A detailed timeline showing the history of biocontrols is shown in Table 1.

Biological control agents have been the most successful method of reducing rabbit abundance in Australia by far. The initial impact of the MV reduced rabbit numbers by as much as 99 per cent and RHDV1 by up to 98 per cent in arid areas. The general trends in rabbit numbers since 1945 and projected numbers through to 2029 and beyond are illustrated in Figure 8.

The general trend across Australia following the release of a new biocontrol or vector has been a rapid and substantial decline in rabbit abundance, followed by a gradual recovery in numbers. Despite such increases, rabbit abundance has generally not reached the pre-biocontrol release levels.

Table 1: A historical timeline of rabbit biocontrols in Australia.

1857–60	The primary rabbit releases at Barwon Park (Vic), Anlaby Station (SA) and Point Lowly (SA) for hunting become established. Some farms abandoned as early as 1881.
Late 1940s	The rabbit population increases to 600 million due to a number of high rainfall years and because of reduced manpower for trapping and fence maintenance during WWII.[1]
1950	The world's first vertebrate pest biocontrol — myxoma virus (MV) — released, killing 99.8% of infected rabbits.
1951–52	Rapid selection of genetically resistant rabbits leads to weakened forms of myxomatosis.
1969	Rabbit flea species (Spilopsyllus cuniculi) approved for release to act as an improved vector to spread MV in areas with low mosquito levels.
1993	Spanish rabbit flea (Xenophsylla cunicularis) adapted for arid conditions approved for release and improves transmission of MV.
1995	The rabbit population returns to about 300 million with populations continuing to rise.[2]
1995	Rabbit haemorrhagic disease virus (RHDV1) introduced, killing up to 98% of rabbits in arid areas.
2000s	Rabbits begin to develop resistance to RHDV1 infection. Increasing resistance results in increasing rabbit numbers being observed.
2009	Benign endemic rabbit calicivirus (RCV-A1) discovered and characterised.[3] RCV-A1 confers partial protection to lethal RHDV1 infection and therefore impedes effective RHDV based biocontrol.
2009+	To counteract RCV-A1, new naturally occurring RHDV1 strains from overseas are imported from Europe and Asia and evaluated as part of the RHD Boost project to increase the effectiveness of RHDV1 based biocontrol.
2012	Invasive Animals CRC develops 20-year rabbit biocontrol pipeline strategy and strategic rabbit biocontrol research program to boost RHDV1 effectiveness, assess feasibility of new potential rabbit biocontrol candidates, and increased capabilities to promote integrated rabbit control at a regional level.
2014	Rabbit haemorrhagic disease virus 2 (RHDV2) arrives in Australia and spreads to all rabbit populations across Australia within 2 years. Rabbit populations reduced by 60% on average and up to 80% in some populations, including a proportion of rabbits with immunity to RHDV.
2017	The first nationally coordinated release of a new RHDV1 strain, RHDV1-K5, in 20 years (based on former Invasive Animals CRC program). Delivers a 34% national average knockdown at release sites but is outcompeted by RHDV2 at a landscape scale.[4]
2016–18	RHDV2 becomes the dominant strain in the Australian landscape.[5]
2017	Centre for Invasive Species Solutions formed as successor to IA CRC and continues to advance rabbit research, including the assessment of RHDV2 as a biocontrol agent.
2018	Scientists discover that rabbits that survive MV have a 10% poorer survival rate when subsequently infected with RHDV1. The interaction between biocontrols provides additional benefit.[6]
2019	Intestinal Eimeria rabbit parasites assessed as an additional control agent but found to be unsuitable as virulent Eimeria parasites are already widespread across Australia.[7]

[1]National Museum of Australia (2021). [2]Ward (2011), [3]Strive et al (2009). [4]Cox et al (2019). [5]Ramsey et al (2020). [6]Barnett et al (2018). [7]Peacock et al (under review) Source: Adapted from the Victorian Department of Environment and Primary Industries (2011). See Appendix 1 for description of each biocontrol technique mentioned above.

This pattern is reflected in rabbit abundance in the arid pastoral area of north-eastern South Australia following with the introductions of MV, RHDV1, the arrival of RHDV2 and then the release of RHDV1-K5 (Figure 9). The horizontal red line on the graph shows the relative rabbit abundance above which recruitment of palatable native vegetation does not occur.

Other control measures, such as poisoning and warren ripping were not often applied in this region so population variations can be primarily attributed to the biocontrol agent. As mosquitoes are generally scarce in the region, the release of European rabbit fleas (Spilipsyllus cuniculus) in 1969 enhanced the spread of MV (Cooke et al. 2013).

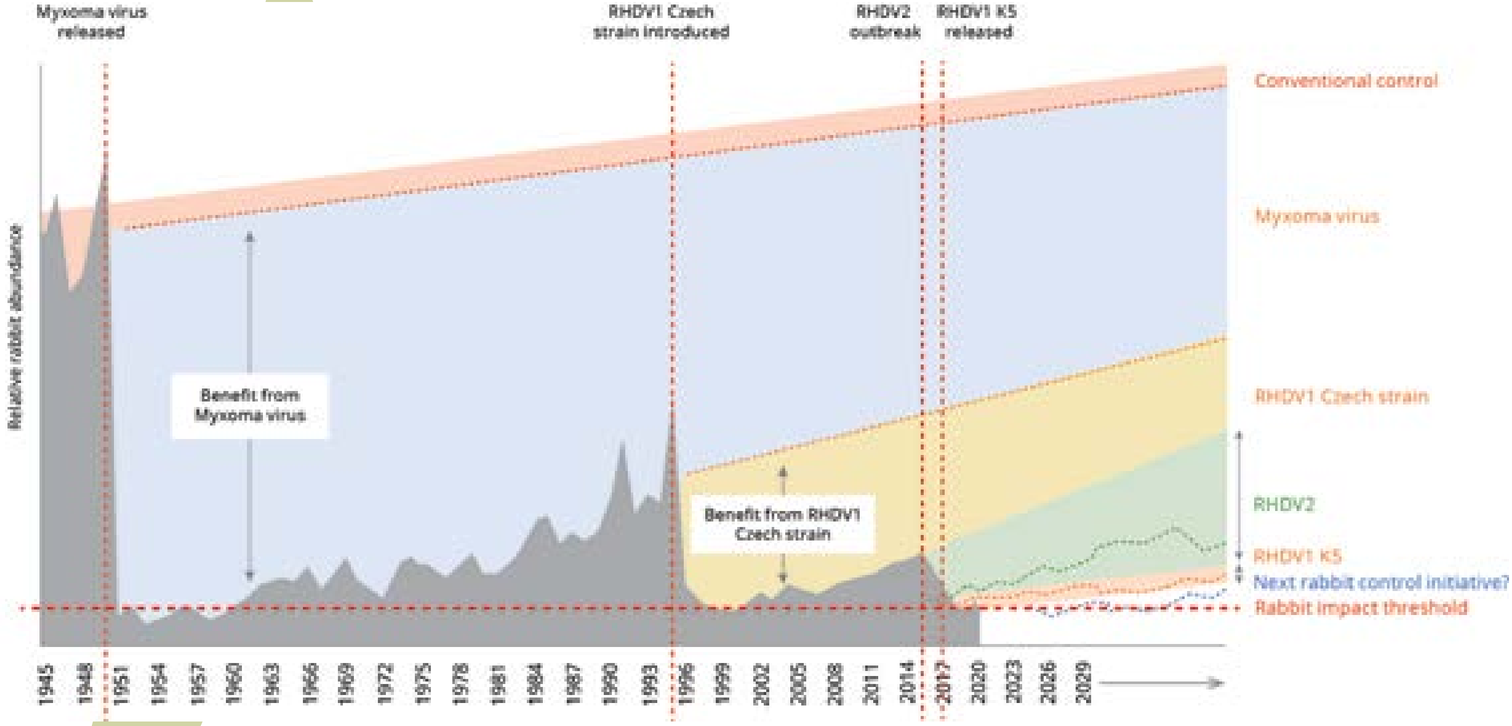


Figure 8: Illustration of general trends in rabbit numbers since the release of myxomatosis (1950) and projected benefits of subsequent releases of biocontrol agents into the Australian rabbit population. The rabbit impact threshold shown is for illustration purposes only as impact thresholds vary for different landscapes, ecological communities and species. In reality, rabbit numbers as low as 1 rabbit per 2 ha can have significant detrimental impacts to the environment. It is important to note that conventional rabbit control is essential to maintaining low rabbit levels and capitalising on the impact of biocontrol (Modified from Saunders et al 2010, Cox et al. 2013, Cooke 2018, Strive & Cox 2019)

A LONG-TERM RABBIT BIOCONTROL PIPELINE STRATEGY

The Centre for Invasive Species Solutions (CISS) — and its predecessor, the Invasive Animals Cooperative Research Centre (IA CRC) — together with its members and partners, recognise the environmental, economic and social benefits of long-term sustainable rabbit control. These organisations have championed a multi-pronged, long term strategic approach to harness the unique opportunities and potential high returns on investment that successful biocontrol initiatives can provide. This approach is detailed in the Rabbit Biocontrol Pipeline Strategy, 2012–2027 (CISS 2021, in production). A summary of rabbit biocontrol pipeline activities undertaken since the 1960s is presented in Figure 9.

Phase 1, IA CRC foundational activities 2007 to 2012

The foundational activities of the rabbit biocontrol pipeline strategy were undertaken between 2007 and 2012 by the IA CRC. The primary focus of these activities was on the RHDV strains already present in Australia and understanding the geographic variation in their efficacy.

CSIRO research through the IA CRC was the first to uncover the presence of an endemic, non-pathogenic form of calicivirus — Australian rabbit calicivirus (RCV-A1) (Strive et al 2009) — and showed that it was able to provide transient and partial immunity to lethal RHDV1 infection (Strive et al 2013). Experimental infection studies showed that while some rabbit populations were developing genetic resistance to infection with RHDV1, the virus was partially compensating for this by evolving towards relatively increased virulence.

Following this work, over the past decade, governments and industry have co-invested in two five-year R&D plans, driving forward the long-term rabbit biocontrol pipeline strategy.

Phase 2, 2012 to 2017

The 'RHD Boost' project was conceived when it became apparent that the prevalence of RCV-A1 was impeding the performance of the initial RHDV1 strain (Czech 351) in cool, high rainfall areas of the continent (Strive et al. 2010; Liu et al. 2014). RHD Boost aimed to identify, evaluate and select any suitable naturally occurring overseas strains of RHDV that might be able to outcompete RCV-A1 and increase the effectiveness of RHDV in higher production, temperate areas of Australia.

Once 38 RHDV variants and RHDV-like viruses had been imported and evaluated by RHD Boost, the Korean K5 strain (RHDV1-K5) was selected as the biocontrol agent for release. This was based on its increased ability to overcome partial cross protective immunity provided by the non-pathogenic RCV-A1 and its increased ability to infect genetically resistant wild rabbits (IA CRC 2014). A complementary study confirmed the efficacy of a common commercial RHDV1 vaccine on RHDV1 K5 (Read and Kirkland 2017).

Approval for the use of RHDV1-K5 was given be the Australian Pesticides and Veterinary Medicines Authority (APVMA) and other government regulators prior to its nationwide release in March 2017. Before its release, increased surveillance efforts put in place by RHDV Boost identified the exotic RHDV2 in Australia in 2015, and later demonstrated it had arrived earlier in 2014. RHDV2 spread rapidly within the Australian rabbit population — within 18 months it had mostly replaced the existing RHDV1 strain and become the dominant calicivirus in the Australian landscape. The impact of RHDV2 on rabbit populations varied but achieved an average reduction in rabbit numbers of 60% (Ramsey et al 2020).

An 'RHD Accelerator' approach was adopted to facilitate 'in the lab' accelerated natural selection of RHDV variants able to overcome immunity to naturally circulating strains, or outperform them. This delivered proof-of-concept that virus variants with altered immunological properties can be selected for and remain highly virulent in rabbits. However, no variants were produced during this period mainly as a consequence of the need to carry out selection and growth in experimentally infected animals. The approach has been paused until substantial progress has been made in the development of culture systems that allow the cultivation of RHDV in vitro. This is being pursued through a joint Meat & Livestock Australia and CSIRO Phase 3 project which aims to develop organoid tissue culture systems for rabbits (see below).

Bioprospecting was chosen as the preferred method for a systematic review of known rabbit pathogens, with assessments undertaken through expert consultations and stakeholders to determine their potential as suitable biocontrol agents/biocides.

Current phase 3, 2017 to 2022

Phase 3 has continued to monitor the spread, evolution and interactions between the various virus strains in Australian wild rabbit populations and is focussing on the case for RHDV2 to be registered as an additional tool for the rabbit biocontrol pipeline. This involves undertaking a thorough characterisation of RHDV2 to assess its suitability as an additional biocide and generating the data needed for an application to the APVMA for its registration.

A current CISS project is exploring the potential use of genetic biocontrol technologies as an alternative long-term, non-lethal means of managing invasive animals (including rabbits) in Australia. These technologies often involve genetic modifications to skew the sex bias of the offspring towards all-male, leading to the eventual collapse of the target population.

Meat & Livestock Australia and CSIRO are also co-funding a series of projects informed by and closely aligned with the rabbit biocontrol pipeline to accelerate implementation of this phase of the pipeline strategy. Major project components include the development of organoid tissue culture systems for rabbits and assessment of its suitability for the cultivation of rabbit caliciviruses ex vivo; bioprospecting of lagomorph (rabbit and hare) pathogens within Australia and abroad; and modelling using population genomics data to investigate whether emerging genetic control technologies may feasibly assist in the control of rabbits in Australia.

Phase 4, 2022 to 2027

Based on consideration of the first three phases of the implementation of the long-term biocontrol R&D pipeline, this report provides a framework and recommendations to move forward into Phase 4.

A strong proactive approach should be taken in Phase 4 that considers the available and potential short, medium and long-term options, and balances the risks and likelihood of success with the potential benefits. The approach must maintain critical capability and the ability to quickly react to new opportunities (pathogens or technologies) as they arise.

Phase 4 should highlight the importance of maintaining the underpinning scientific capability and infrastructure, as well as the need to continue to improve integration of biocontrol applications with conventional control methods for maximum impact.

Rabbit biocontrol innovation pipeline.

Achieving sustainable landscape scale rabbit management.

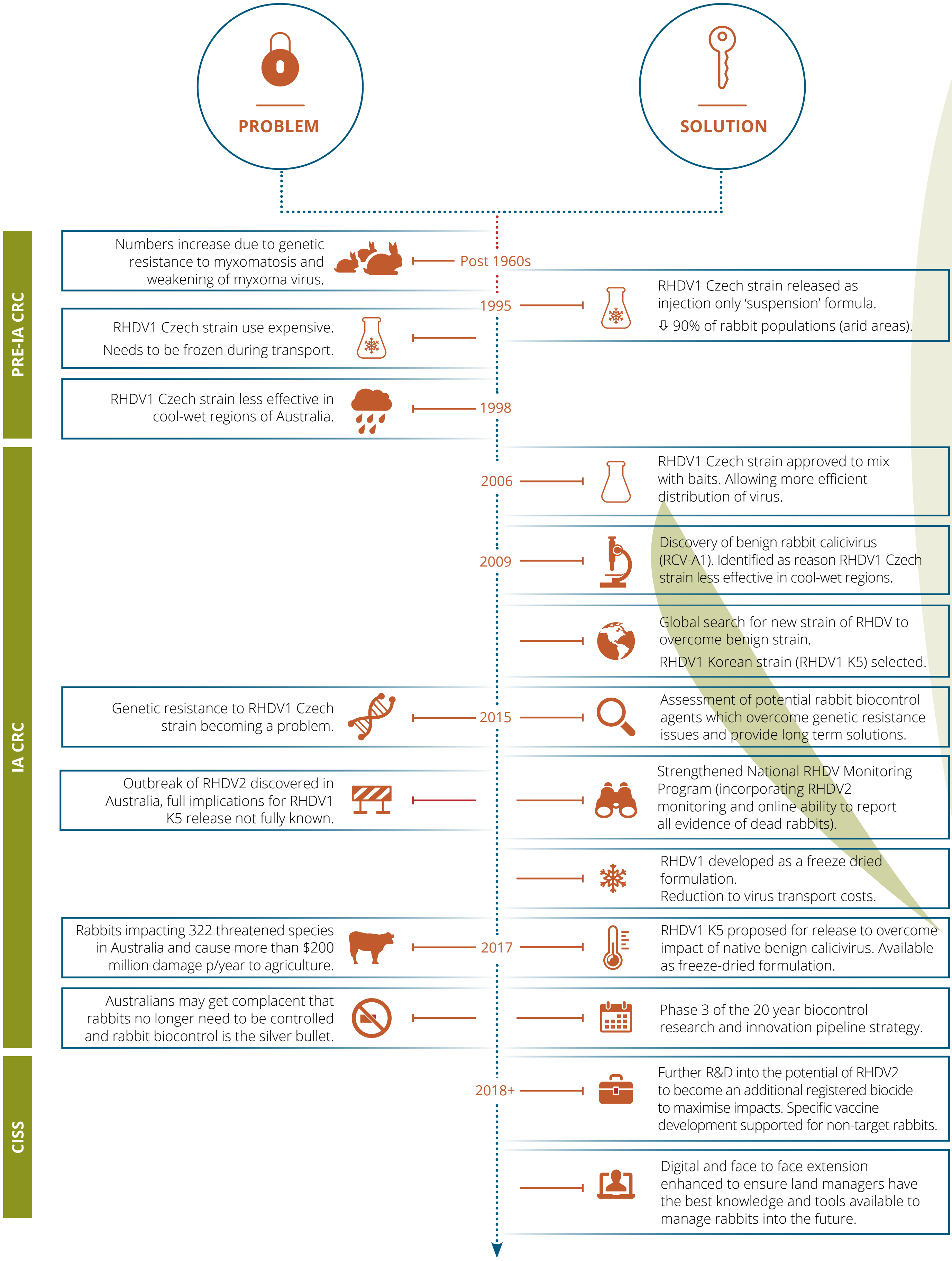


Figure 9: Rabbit biocontrol innovation pipeline.

The self-disseminating nature of pathogenic biocontrols means that recurrent outbreaks are a significant advantage to rabbit management at a landscape scale, particularly in remote areas. The suppressive effect of biocontrol agents provide has also greatly improved the results of conventional control techniques such warren ripping, baiting and fumigation in a more cost efficient and effective manner.

The benefits of rabbit biocontrol are not uniform across Australia (see Figure 10). RHDV1 has generally been more effective in drier, lower rainfall areas and less effective in areas of higher rainfall. Rabbit abundance decreased on average by two-thirds (67.3%) in low rainfall areas but only by a quarter (27.5%) in high rainfall areas (Neave 1999).

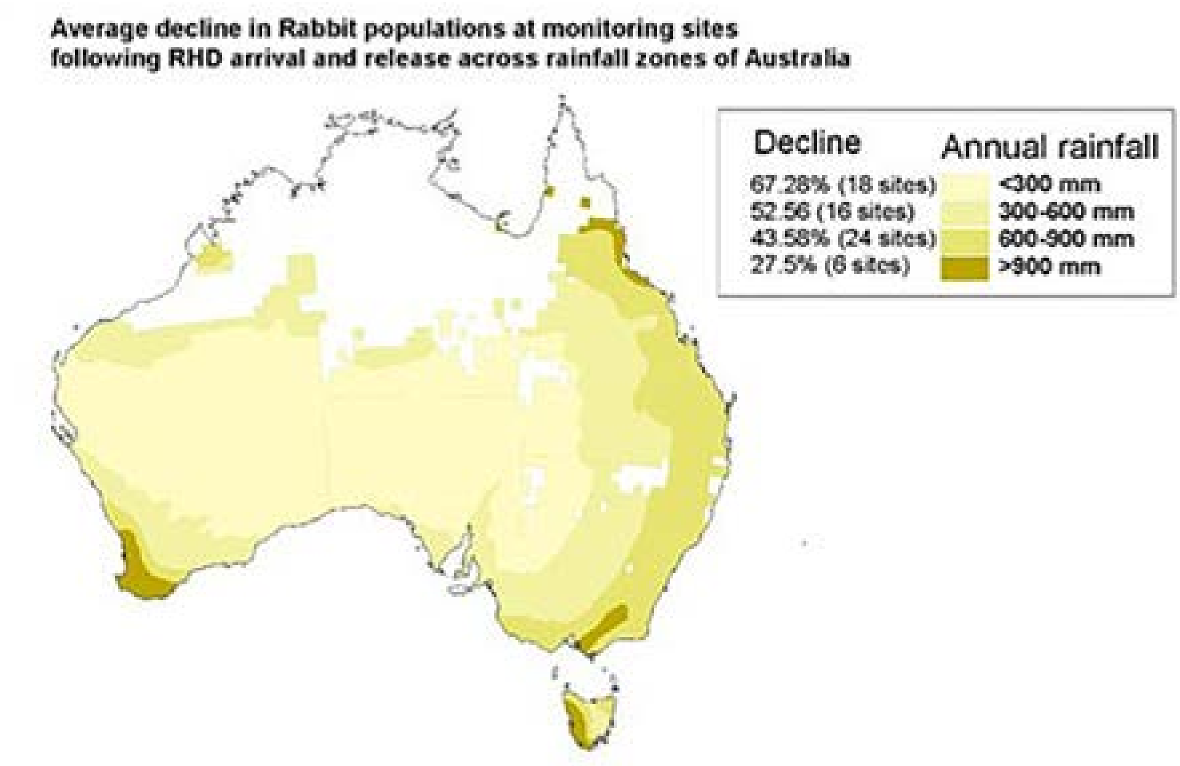


Figure 10: Average decline in rabbit populations by rainfall zone after the arrival of RHDV1 (Neave 1999).

Given their wide distribution across Australia biocontrol is the most cost-effective way of managing rabbits and their impacts.

Environmental benefits

The recovery of native vegetation

Rabbit biocontrols have major environmental benefits for native plants, animals and ecosystems. A broad range of evidence following the release of RHDV1 in 1995 provides greater understanding and insight into these benefits. It is likely that similar benefits followed the release of MV in 1950, however, little data of this was collected at the time. However, the initial decline in rabbit abundance from MV is comparable to RHDV1. As such it likely resulted in similar environmental benefits.

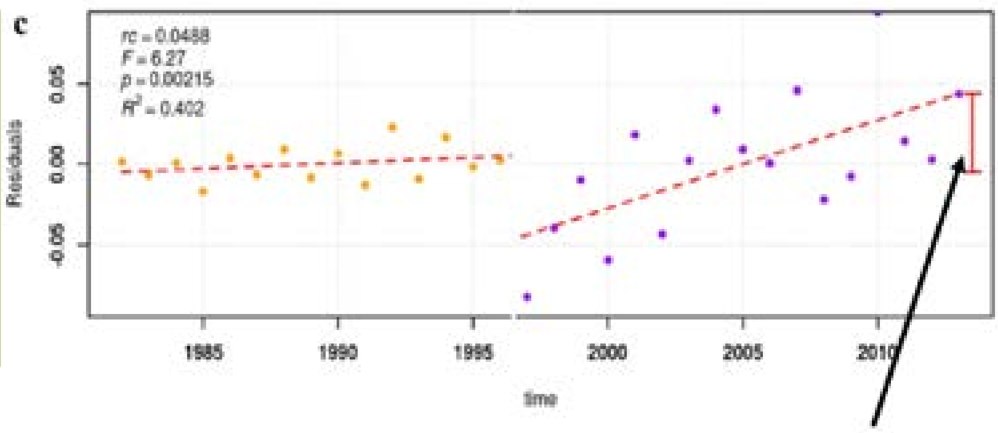
Reports of native vegetation recovery after MV are limited but include bladder saltbush (Atriplex vesicaria) (Hall et al. 1964), rangeland vegetation (Fenner and Ratcliffe 1965), and an extensive list of rangeland native plants including mulga (Acacia aneura) and native pine (Callitris columellaris) (Lord 2000, quoting pastoralist Alan Bartholomaeus). The same, or comparable, native plant species had significant post-RHDV1 recoveries, especially in semi-arid areas despite those regions having below average rainfalls during those recovery periods (Sandell 2002, Murdoch 2005, Mutze et al 2008, Bird et al. 2012, Mutze 2016).

Some case examples are illustrated below. Figure 11 highlights the distinct recovery of vegetation at Thackaringa Station, Broken Hill between 2000 and 2012 using photographs taken from the same location. The recovery cannot be attributed solely to RHDV1 as conventional rabbit control measures were also used. Significantly this degree of regeneration happened despite sporadic periods of drought.

A reduction in rabbit abundance from biocontrol to below 0.5 rabbits per hectare allows native plant seedlings to survival and grow in a way that is impossible to achieve with higher rabbit densities. Estimates of green photosynthetic vegetation biomass were generated for the arid shrublands in northern South Australia after RHDV1 was established in 1995 using time series Landsat satellite imaging and graphing the normalised difference vegetation index (NDVI). Figure 12 shows how NDVI increased significantly across these shrublands after 1995 when rabbit abundance reduced by 95 per cent (Burrell et al. 2017).

Figure 11: Rabbit control from RHDV1 and conventional measures led to significant regeneration of vegetation on Thackaringa Station, Broken Hill despite sporadic drought conditions (Photos: David Lord).

Landscape scale recovery of native vegetation with suppression



Normalised Difference Vegetation Index (NDVI) shows significant increase after RHDV1 establishes in 1995.

Figure 12: Recovery of arid shrublands in northern South Australia as detected by Landsat satellites (Burrell et al. 2017, Pho Peacock).

Figure 13 shows the regeneration of native species at Turretfield, South Australia, in October 2017 as a direct result of the rabbit density falling below 0.5 / ha post-RHDV2. Turretfield had been regularly monitored since 1996 (Bird et al. 2012).

Figure 13: Regeneration of native species at Turretfield, South Australia, October 2017. post-RHDV2. Top left: Christmas bush, (Bursaria spinosa). Top right: Drooping sheoak (Allocasuarina verticillate). Bottom left: Drooping sheoak (A. verticillate). Bottom right: unidentified Acacia); (Photos: David Peacock).

Figure 14 shows how native orchid numbers increased once RHDV1 established in the Coorong National Park of South Australia. An estimated 60 million native orchids were added to the 1,000-hectare creek area by 2002 (Bird et al. 2010).

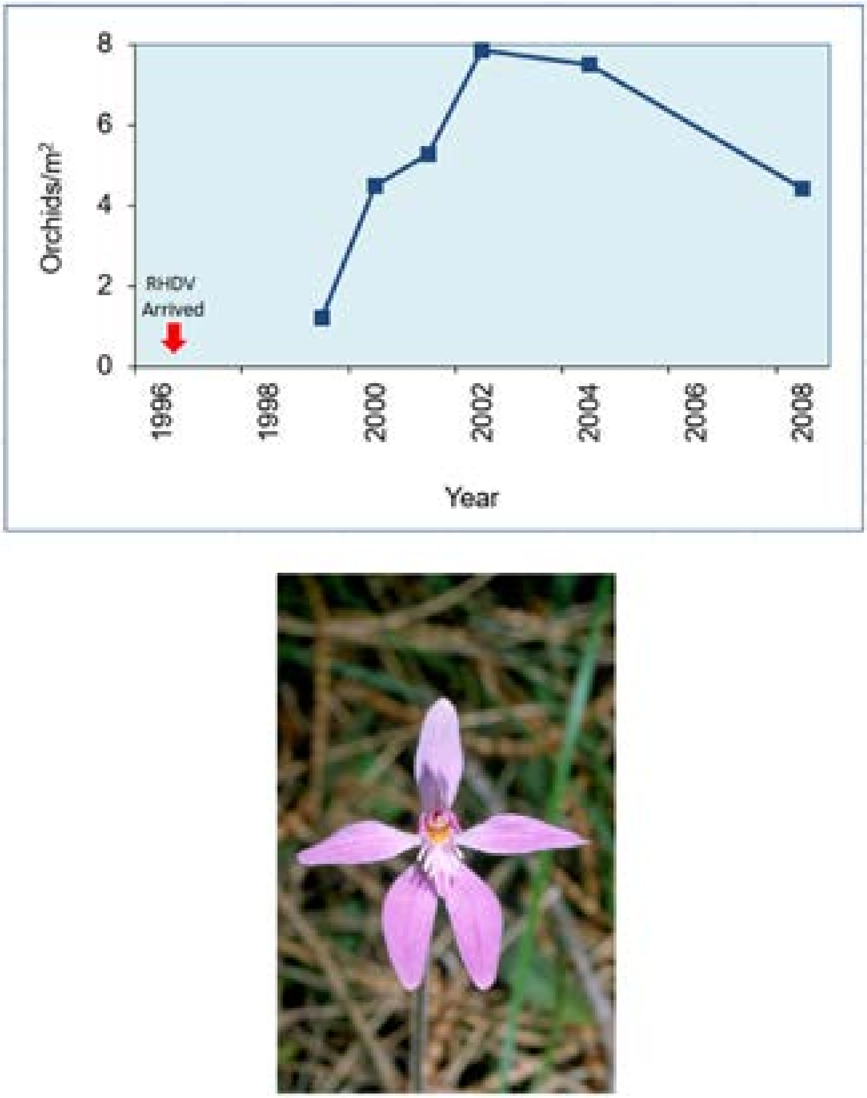


Figure 14: Increase in the native orchid population in the Coorong National Park following the establishment of RHDV1 and the suppression of rabbit numbers (Bird et al. 2010, Photo by Peter Bird).

Native mammal recovery

The management of rabbits at a landscape scale using biocontrol not only allows native plant species to recover, but also aids the recovery of many rare and threatened native mammal species. For example, populations of spinifex hopping mice (Notomys alexis) and plains mice (Pseudomys australis), common wombats (Vombatus ursinus), red kangaroos (Macropus rufus) and western grey kangaroos (M. fuliginosus) all showed signs of recovery following the introduction of RHDV1 (Read 2003, Mutze et al. 2008, Bird et al. 2012).

Based on long-term monitoring, Pedler et al. (2016) concluded:

> “In arid inland Australia, the release of the rabbit biocontrol agent RHDV has been the single most important and cost-effective conservation action for small, threatened mammals (and a range of other taxa and ecosystems) in recent decades.
>
> The dusky hopping-mouse (Notomys fuscus), spinifex hopping mouse (Notomys alexis), plains mouse (Pseudomys australis), and the crest-tailed mulgara or ampurta (Dasycercus cristicauda) increased their abundance by up to 365 per cent following the arrival of RHDV1 in the arid zone (Pedler et al. 2016).”

Figure 15 illustrates the recovery of threatened desert mammals at a landscape scale in north-east South Australia with recorded detection and range size represented by coloured dots and shading. The orange dots are pre-RHDV1 release and the blue dots are post-RHDV1 release.

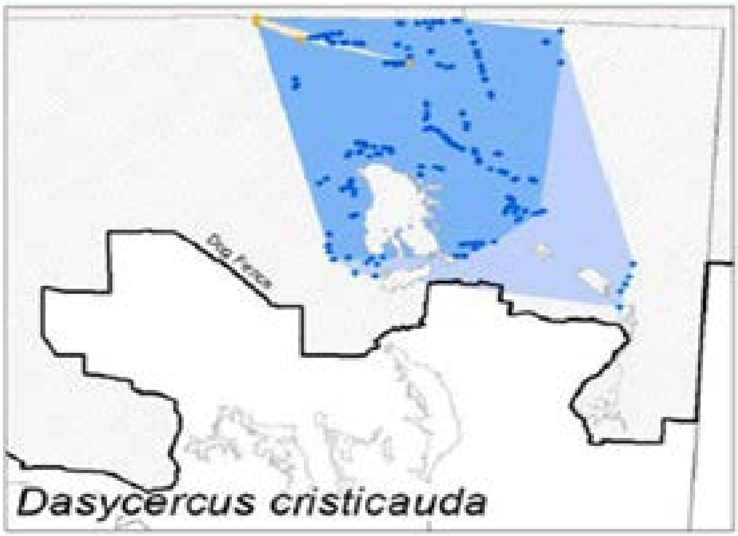


Figure 15: Landscape scale recovery of threatened desert mammals following the release of RHDV1. Map shows the north east 1/3 of South Australia. Yellow dots and yellow shading indicate records of detection and range size from 1970 to 1995. Dark blue dots and shading indicate expansion of records of detection and range from 1996 to 2010. Light blue dots and shading indicate expansion of records of detection and range from 2010 to 2014. (Pedler et al. 2016, Photo by Reece Pedler)

The recovery of these native animals is intrinsically linked to the recovery of their habitat and food resources following the reduction in rabbit abundance. An additional benefit further enhancing their recovery was the reduction in the abundance of foxes (Vulpes vulpes) and feral cats (Felis catus) that was directly attributed to the removal in their primary prey animal, the rabbit (Cooke & Soriquer 2016).

Fox and feral cat numbers were shown to have decreased in the Ikara-Flinders Ranges National Park (South Australia) after the rabbit population had been reduced by 85 per cent following the introduction of RHDV1 (Holden & Mutze 2002). A similar decline in feral cat populations was also reported at Roxby Downs in South Australia after the arrival of RHDV1 (Read and Bowen 2001) with evidence of increased hunger and reduced cat survival following the significant reduction in rabbit abundance (McGregor et al. 2020). This impact is illustrated in Figure 16.

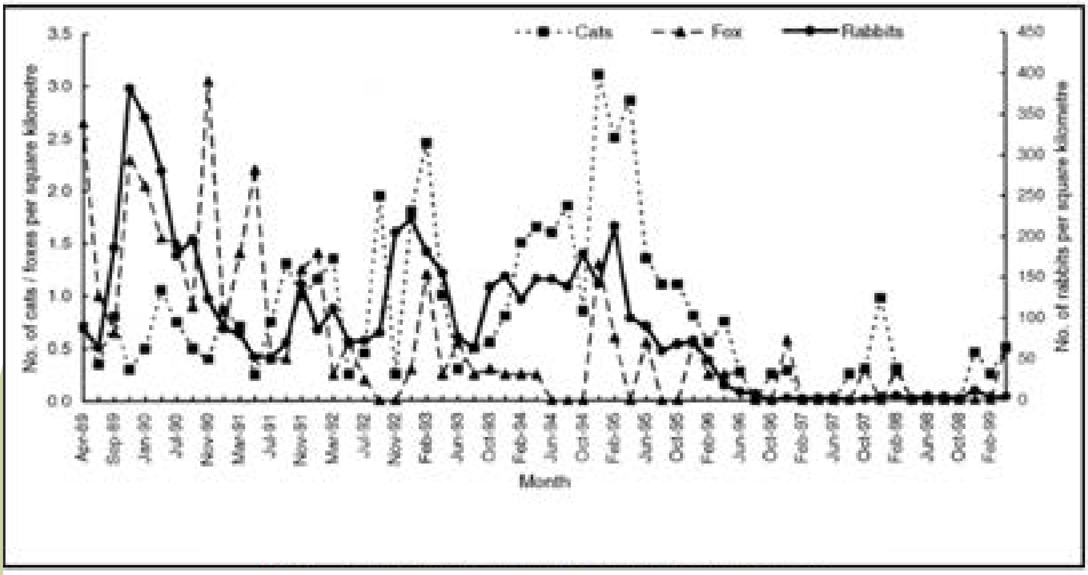


Figure 16: The landscape scale suppression of rabbits, foxes and feral cats in 1989–90 at Roxby Downs, South Australia, following the arrival of RHDV1 (Read and Bowen 2001; Photo by Scott Jennings).

Although the data is limited, it is likely that declines in feral cats and foxes, together with subsequent benefits to native fauna also occurred following the introduction of MV which saw rabbit abundance decline by up to 99 per cent across Australia.

There is a clear link between the prevalence of mange and nutritional stress in many animals including wombats (V. ursinus) (Skerratt et al. 1998) and other species (Pence & Ueckermann 2002). In 1952, an Australia-wide increase in the incidence of manage in foxes led to a major decline in their condition and abundance (Rolls 1969). It is likely that the sharp decline in rabbit numbers that followed the release of MV in 1950 led to this outbreak of mange in the fox population.

Bottom-up rabbit trophic cascades — where animal population abundance is governed by available food and nutrition — are important drivers of the sustainability and recovery of the Australian environment. Widespread suppression of rabbits not only enables the direct recovery of susceptible native vegetation and the fauna that rely on it, but it also benefits native fauna through increased habitat and food resources and the suppression of feral cat and fox abundance.

Carbon benefits through biosequestration

Biosequestration refers to the capture and storage of the atmospheric carbon dioxide, largely through increased rates of photosynthesis resulting from increased vegetation biomass and revegetation. There is a strong temporal relationship between ground cover and vegetation biomass and soil organic carbon levels for given climatic conditions and soil types.

The introduction of RHDV1 in 1995–96 saw declines in rabbit populations of up to 98 per cent (Mutze et al. 1998) with a corresponding increase in standing biomass observed by satellites (Burrell et al. 2017). Therefore, continued investment in biocontrol agents to reduce rabbit numbers is likely to provide environmental benefits resulting from an increase standing vegetation biomass and, consequentially, carbon sequestration (Hardaker & Chudleigh 2020).

Economic benefits

Prior to the release of the myxoma virus, the financial impact of rabbits on agriculture was some $2 billion a year. Rabbit biocontrol based on the myxoma virus and RHDV1 Czech 351 strain reduced this impact to about 15% of the pre-release cost (Cox et al 2013). Based on their review of the available literature and the application of a loss-expenditure frontier model with and without biocontrol scenarios, Cooke et al. (2013) conservatively estimated the cumulative benefit of MV and RHDV1 to Australia's livestock and farming industries at approximately $70 billion from 1950 to 2011. This value is expressed in 2011-dollar terms and is made up of around $54 billion from MV on its own and an additional $16 billion from MV and RHDV1 together. Expressed in 2020-dollar terms, this equates to a cumulative benefit of $81.8 billion over six decades(Reserve Bank of Australia, 2022).

The Cooke et al. analysis was undertaken prior to two further major events that have impacted rabbit populations. In May 2015 a new variant of RHDV was detected in New South Wales and serological studies showed it had been present in Australia since at least the Spring of 2014. It was a highly virulent RHD virus, known as RHDV2, that spread rapidly across all Australian states and territories within two years of its arrival. It was estimated to have reduced average rabbit abundance by approximately 60 per cent (Ramsey et al 2020).

The other development post-2011 was the 2017 release of the K5 strain of RHDV1. The appearance of RHDV2 in Australia has been shown to have severely suppressed the potential benefits of the release of RHDV1-K5 (Ramsey et al 2019) and the Centre for Invasive Species Solutions commissioned Hardaker and Chudleigh (2020) to evaluate the impact of RHDV1-K5 for control of rabbits in Australia. The evaluation aimed to estimate:

- the projected potential impact of RHDV1-K5 (without the emergence of RHDV2), based on available data for RHDV1-K5 and RHDV2 impacts; and
- the current impact of RHDV1-Czech-351, RHDV1-K5 and RHDV2 together, and then assess the actual impact attributable to RHDV1-K5.

Hardaker and Chudleigh's economic analysis calculated the estimated Present Value of Benefits for RHDV1-K5 over 30 years using a 5 per cent discount rate (see Table 2). Their analysis produced the following results:

Table 2: Estimated present value of benefits for RHDV1-K5 under different scenarios regarding the presence of RHDV2. Source: Hardaker and Chudleigh (2020).

RDDV1-K5 evaluation scenario	Present value of benefits over 30 years with a 5% discount rate
1) Potential impact of RHDV1-K5 in the **absence** of RHDV2	$86.4 million
2) Combined impact of all additional biocontrol after 2014 (RHDV2, RHDV1a and RHDV1-K5)	$4 billion
3) Estimated actual impact of RHDV1-K5 only given the presence of RHDV2.	$54.3 million

The Hardaker and Chudleigh estimates are subject to a number of qualifications, namely that:

- the analysis did not consider the significant future rabbit biocontrol RD&E costs incurred to release RHDV1-K5 over a 15-to-20-year period, and
- the only actual data available for the impact of RHDV1-K5 is with the background of RHDV2 presence. Consequently, inferring estimates of the potential impact of RHDV1-K5 in the absence of RHDV2 is difficult.

The results of the Cooke et al. (2013) and Hardaker and Chudleigh (2020) studies, although using different methodologies, together provide a quantification of the economic benefits of rabbit biocontrol from 1950 to the present. While the actual impact of the release RHDV1-K5 in 2017 cannot be conclusively calculated due to the serendipitous appearance and spread of RHDV2 in Australia, the Hardaker and Chudleigh study confirms that RHDV1-K5 now forms an integral part of landscape-scale integrated rabbit management practices. The economic benefits alone justify the value of ongoing investment in rabbit biocontrol RD&E and the implementation of biocontrol agents when release criteria are met.

Social benefits

There are no significant scientific studies on the social benefits derived from rabbit biocontrol in Australia. Some of the studies and records that do exist are described in Section Two. These catalogue the considerable social impact of rabbit plagues on farmers, indigenous peoples and rural communities particularly following the successful release of rabbits on mainland Australia in 1857 to 1860 and prior to the release of MV in 1950 and the later releases of RDHV. In effect, social benefits derive largely from the environmental and economic benefits that support the welfare of individuals and communities.

A holistic picture of the benefits of rabbit control

The integrated nature of environmental, economic and social benefits of rabbit control were illustrated diagrammatically by Rabbit Free Australia in correspondence from Rabbit Free Australia to the Commonwealth Minister for the Environment date 30 April 2021 (see Figure 17).

BENEFITS OF RABBIT RABBIT BIOCONTROL

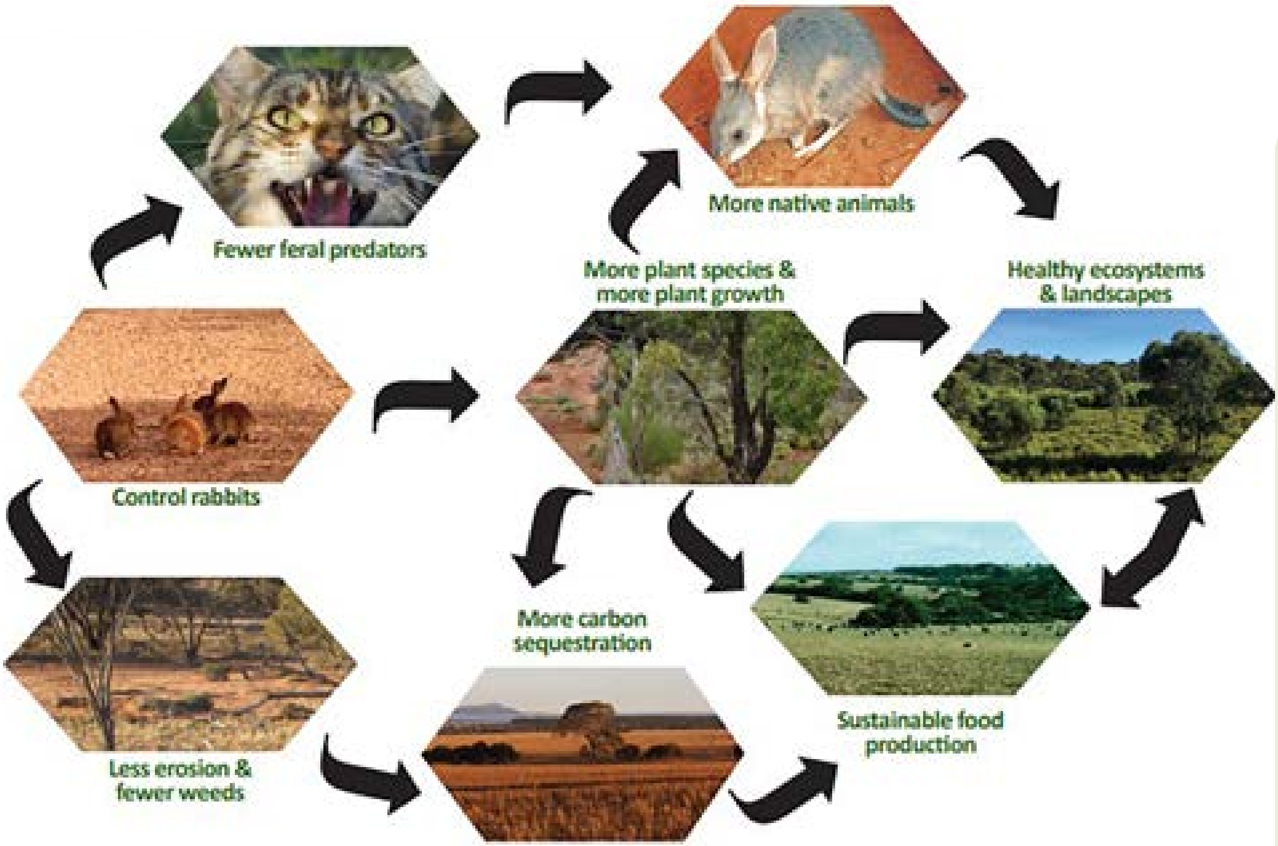


Figure 17: How the benefits of control of rabbits are integrated. Source: Rabbit Free Australia (2021) Unpublished.

Need for future rabbit biocontrol agents

While a silver bullet for the eradication of wild rabbits remains elusive, biological control over the vast range of rabbit distribution in Australia has been highly successful. However, biocontrol remains an ongoing process: rabbit populations continue to have the ability to build resistance to introduced pathogens and for their abundance to increase.

The response of rabbit populations to the release of MV in 1950 indicates that rabbit populations will initially fall dramatically in response to the release of new pathogens but then gradually increase over time. As Figure 8 illustrated, the introduction of each new biocontrol then drives the abundance index lower. It is important to note that sustaining low rabbit populations is also dependant on conventional rabbit control, the two working synergistically together.

However, many land holders across Australia believe that investment in conventional controls such as rabbit warren ripping is not feasible in many areas (e.g. in sand hill country). Any production gains or other benefits are unlikely to meet the control costs except in high value agricultural areas where these costs can be recouped.

Consequently, the demand for persistent use of biological control agents — as the only viable solution to current rabbit problems in these vast areas — remains strong. Furthermore, biological control agents are usually the only feasible means of limiting damage from rabbits in conservation areas due to the high cost of conventional rabbit control and the potential damage caused by their application.

By its very nature, research on biological controls is high risk — potential new pathogens need to undergo extensive safety and efficacy testing in line with stringent regulatory and biosecurity requirements. However, the reward from the successful release of new pathogens — across economic, environmental and social dimensions — can be huge.

The key benefits of continued, ongoing investment into biocontrol research were illustrated in Figures 8 and 17, and have been described by Agtrains Research (2009) as:

- increased pasture biomass for animal production
- decreased effort and cost associated with traditional rabbit control measures
- increased ground cover leading to decreased soil erosion
- improved health of native vegetation and associated habitats and biodiversity and
- increased carbon sequestration

Ongoing, effective and safe biological control of rabbits is the most cost-effective way of conserving biodiversity when analysed against all other mechanisms (Morton et al. 2002, Possingham et al. 2002). This could involve improvements to existing biocontrols, the identification of new pathogens deemed suitable for release as biocontrols, and the exploration of other emerging technologies such as genetic biocontrol. The safety and efficacy for each of these approaches would need to confirmed prior to their application.

New or additional agents could supplement existing agents (MV, rabbit fleas and RHDV1/RHDV2) and avoid a serious resurgence of rabbits in a timely way. One of the objectives in the 'Threat abatement plan for competition and land degradation by rabbits' (DAWE 2016) is the improvement of efficacy, target specificity, integration and humanness of rabbit control. Research to maximise the effectiveness of existing biocontrols, and the investigation of new biocontrols are high priority, long term actions under the plan. This includes potential non-lethal genetic biocontrol technologies that aim to disrupt the reproduction of pest animal populations by skewing sex ratios or leading to sterile off-spring (Ruscoe et al 2021).

If investment in biocontrol dries up, then rabbits will evolve resistance to current biocontrols, their numbers will increase, and the recent gains from the appearance of RHDV2 in 2014 and the release of RHDV1-K5 in 2017 will be squandered.

Additional resources are essential to protect and advance the environmental, economic and social benefits gained from suppression of pest rabbits.

In the short-term additional resources are critically important for:

- the scientific assessment and roll out of RHDV2 as a potential additional biocide for land managers
- the monitoring of current biocontrols to determine whether they have the capability to overcome the ability of rabbit populations to develop genetic resistance
- the monitoring and assessment of pathogens as new biocontrol agents that may bolster the suppression of rabbits.

These conclusions are reinforced by the *National Biosecurity Research and Development Capability Audit* which determined that Australia should invest more heavily in the long-term funding of biological control programs, including monitoring of field effectiveness (IGABRDEWG 2012).

They are further reinforced by the *Inter-Governmental Agreement on Biosecurity* which identifies that a national framework for biocontrol investment and application, including the use of biotechnologies, is a priority action. Given the huge economic, environmental and social impacts from rabbit biocontrol research and innovation the CISS national rabbit biocontrol pipeline strategy — delivered through its long-standing government-industry partnership — should be integral to this framework.

Maintaining a strategic approach will ensure the Centre's national rabbit biocontrol pipeline strategy delivers on its objective to release a new rabbit biocontrol agent every 8 to 10 years to keep rabbit impacts in check.

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APPENDIX 1: BACKGROUND INFORMATION ON RABBIT BIOCONTROL AGENTS

Myxomatosis

Following the rabbit plagues of the late 1800s and early 1900s, efforts were made to find a way to more effectively control rabbits on a large scale. MV was discovered in infected laboratory rabbits in Uruguay in 1896 and Australia was made aware of its potential as a biocontrol in 1919 (Fenner & Fantini 1999).

In its natural host, the South American jungle rabbit (Sylvilagus andinus nee brasiliensis), MV causes benign, localised fibromas. However, in the European rabbit MV causes myxomatosis —a pustule forming disease that affects the lymphoid tissue leading to profound immunosupression and generalised systemic disease (Best and Kerr 2000a, b, Jeklova et al. 2008). Death can occur within 8–12 days in acute cases, or 3–5 days after clinical signs develop.

In 1950 the myxoma virus (MV), a poxvirus (family: Poxviridae, genus: Leporipoxvirus) was released into the rabbit population in the higher rainfall areas of Australia (Myers 1954). The impact of MV on the Australian rabbit population in the first year was dramatic: up to 99% reductions in some areas. However these declines were short lived, and host-virus co-evolution led to the emergence of less virulent field strains of MV as well as genetic resistance to myxomatosis in wild rabbits.

Subsequent attempts to introduce new, more virulent strains of MV failed, as the new strains never became established in the field (Kerr 2012). Despite the loss of its initial virulence, MV is still an effective biocontrol agent, particularly in the wetter areas of Australia, primarily because "in the ongoing arms race between myxoma virus and wild rabbits in Australia ... a novel disease phenotype" emerged in the 1990s which "induced a highly lethal immune collapse syndrome similar to septic shock" (Kerr et al. 2017).

Recently it was discovered that MV causes physiological and/or immunological impacts on rabbits such that survivors have a 10% lower survival when subsequently infected by RHDV (Barnett et al. 2018).

Since the 2016 arrival of RHDV2 at the long-term Turretfield rabbit study site in South Australia, the population has struggled to recover with a major factor being spring outbreaks of virulent MV and the repeated loss of the young each year, and occasionally adult rabbits as well (unpublished data).

Rabbit fleas

The natural spread of MV through the Australian rabbit population was originally facilitated by mosquitoes, particularly Culex annulirostris. However in areas where mosquito activity was low (such as arid areas, or areas with naturally low mosquito numbers), the impact of MV was also low (Williams et al. 1995). To boost the effect of MV, two species of fleas, Spilopsyllus cuniculi and Xenophsylla cunicularis were imported and released across the country.

S. cuniculi is the main vector of MV in Britain and parts of Europe. Its introduction to Australia greatly increased the impact of myxomatosis in semi-arid and coastal areas where mosquitoes were scarce (Cooke 1983). However, S. cuniculi did not survive in the more arid areas of Australia where the annual rainfall was <200 mm (Cooke 1984). Native stickfast fleas (Echidnophaga gillinacea) are abundant in the arid zone and while capable of transmitting the disease they tend to be poor vectors as they do not readily move from rabbit to rabbit but 'stick fast' to one individual.

The Spanish rabbit flea, X. cunicularis, is adapted to hot, arid conditions, and was introduced to facilitate the spread of MV in arid areas (Cooke 1990). It is likely that the release of X. cunicularis into the Australian rabbit population boosted MV effectiveness in arid areas, however research on the impact of its introduction was limited due to the escape of RHDV in 1995 and the dramatic reductions in arid zone rabbit populations before fleas became widely established.

Rabbit haemorrhagic disease

Even though MV was still an effective biocontrol agent, and the introduction of the two rabbit fleas were aiding its spread, after almost ten years of good winter rainfall over most of Australia following the 1982 drought, rabbit numbers once again increased. This prompted the investigation of a recently emergent virus, Rabbit Haemorrhagic Disease Virus (RHDV). The highly virulent RHDV was first identified in China in 1984 where it killed 140 million domestic rabbits in less than 12 months (Liu et al. 1984, Xu 1991). The virus was later confirmed in European rabbitries and soon spread to wild populations where it caused a major decline in wild rabbit numbers (Cooke and Fenner 2002). An investigation of the virus revealed it to be a calicivirus (family: Caliciviridae, genus: Lagovirus).

In 2010 a new serotype of RHDV (called RHDV2 or GI.2 or RHDVb) emerged in Europe (Le Gall-Reculé et al. 2011) and spread rapidly (Le Gall-Reculé et al. 2013). RHDV2 was detected in Australia in 2015 (Hall et al. 2015) but likely arrived in 2014 (Strive et al. 2020). It spread very rapidly across the country (Mahar et al. 2017) and reduced many rabbit populations by 60–80% (Mutze et al. 2018, Ramsey et al. 2020).

Currently recombinant variants of RHDV2 are killing most rabbits in Australia (Ramsey et al. 2020), with some rabbits being killed in south-eastern Australia by some RHDVa recombinants (Mahar et al. 2018).

RHDV, RHDVa and RHDV2 are considered virus serotypes of lagomorphs (rabbits and hares), with their origin still unclear (Esteves et al. 2015, Lavazza et al. 2015). While RHDV has been shown to be species specific and only infect European rabbits, RHDV2 also infects and kills the Sardinian Cape hare (Puggioni et al. 2013), the Italian hare, (Camarda et al. 2014) and the European brown hare (Velarde et al. 2016), including the introduced European brown hare here in Australia (Hall et al. 2017).

RHDV2 appears to be a disease that will only cause disease in lagomorphs (rabbits and hares) (Urakova et al. 2019). RHDV generally kills fewer young rabbits than adult rabbits. Young rabbits are innately resistant to lethal disease from RHDV but can become infected, resulting in a comparatively mild infection of the liver and subsequent life-long immunity to RHDV. The reasons for this innate resistance to lethal disease from RHDV appear to relate to heightened innate immune responses, but RHDV2 appears capable of down-regulating these responses, causing the higher infection and mortality seen in young rabbits (Neave et al. 2018).

Fully susceptible adult rabbits usually die within 72 hours following infection; however prolonged courses of the disease have also been reported (Kerr and Strive 2012). Rabbits with terminal RHD often develop fever, show lethargic behaviour and can die suddenly. Outwardly, animals that have died from RHDV appear healthy. The cause of death is usually liver failure due to a severe hepatitis and the formation of blood clots throughout the body. Recent research on the long-term Turretfield (SA) rabbit study dataset showed that rabbits that survive MV have a 10% poorer survival when subsequently infected by RHDV (Barnett et al. 2018). Thus, the interaction between MV and RHDV is providing an additional 10% benefit.

RHDV was brought into Australia to assess its usefulness as a future biocontrol agent in 1993. Following host specificity testing in quarantine facilities at the Australian Animal Health Laboratories, RHDV escaped from an island research facility onto mainland Australia in October 1995 and spread rapidly (Kovaliski 1998).

As with MV, RHDV had an immediate and devastating impact on the Australian rabbit population, particularly in the arid and semi-arid areas (Henzell et al. 2002), reducing the populations in these areas by as much as 98%. Its landscape-scale benefits have now been recognised as including the significant recovery of native vegetation (Burrell et al. 2017) that would benefit carbon sequestration and climate change, and enabled sustained recovery of threatened desert mammals (Pedler et al. 2016).

Notably unlike MV, RHDV did not attenuate rapidly but appeared to maintain its relative virulence. Before RHDV2's emergence in Australia, studies showed that wild Australian rabbits were beginning to develop some resistance to RHDV infection (Nyström et al. 2011, Elsworth et al. 2012), with research showing selection for genes such as associated with the major histocompatability complex (MHC) (Schwensow et al. 2016, 2017, 2020). This is a likely cause of the observed post-RHDV increase in rabbit numbers (Mutze et al. 2015). However, RHDV2 (and MV) have recently driven down these recovering rabbit populations (Mutze et al. 2018). Though it is likely they will again somewhat recover, the continuous and rapid recombination of the serotypes in Australia, such as RHDV2 (Kovaliski et al. 2014), may provide a much more prolonged suppression. In Italy the more recent strains of RHDV2 have proved more virulent than the earlier strains (Capucci et al. 2017).

Virally-vectored immunocontraception

Between 1992 and 2005 research efforts of the Cooperative Research Centre for Biological Control of Vertebrate Pest Populations (a predecessor of the Invasive Animals CRC) focused on the development of non-lethal biocontrol options specifically aimed at reducing the fertility and fecundity of rabbits. Recombinant MVs were constructed that induced an auto-immune response to components of the reproductive tract, resulting in infertility. While the work succeeded in producing viruses that reduced the fertility of female rabbits by up to 100%, the approach was abandoned as high levels of infertility were not maintained over the long term (van Leeuwen and Kerr 2007). In addition, there was concern that a recombinant strain would not disseminate sufficiently in the field, as it was unlikely to outcompete existing field strains of MV. There were also concerns about public acceptance regarding the release of a genetically modified virus into the environment (Henderson and Murphy 2006).

Eimeria parasites (an option recommended by the Rabbit Biocontrol Business Case)

Research shows beneficial rabbit control interactions between parasites and myxomatosis (Bertó-Moran et al. 2013, Boag et al. 2013), and between myxomatosis and rabbit haemorrhagic disease (Barnett et al. 2018). In addition to some species being capable of causing death, especially in juveniles, increasing the parasite burden of rabbits could reduce their numbers by reducing fitness, which then impacts on fecundity, and increasing their susceptibility to diseases such as myxomatosis.

A primary group of rabbit parasites are the Eimeria parasites. Currently 16 valid species of Eimeria are recognised as parasitising Oryctolagus cuniculus: E. coecicola, E. exigua, E. flavescens, E. intestinalis, E. irresidua, E. magna, E. matsubayashii, E. media, E. nagpurensis, E. neoleporis, E. oryctlagi, E. perforans, E. piriformis, E. roobroucki, E. stiedai and E. vejdovskyi (Duszynski and Couch 2013). An additional new species, E. kongi n. sp., has also now been described in farmed rabbits in Hebei, China (Cui et al. 2017). All but one of these parasites are intestinal, with E. stiedai a parasite of the rabbit's liver.

Many of these Eimeria species can be a major issue in farmed rabbits (Duszynski and Couch 2013). Species have been individually tested and categorised from non-pathogenic (E. coecicola) to highly pathogenic (E. flavescens, E. intestinalis), but recognising that strain, coinfections, including with Escherichia coli, dose and hot conditions can impact pathogenicity (Coudert et al. 1995).

As the two most pathogenic Eimeria species, E. intestinalis and E. flavescens, had only been detected at Wellstead in south-west Western Australia (Hobbs and Twigg 1998), and not at other mainland sites (Mykytowycz 1956; Stodart 1968, 1971) a study was undertaken to examine other sites and confirm this limited distribution, with the option to utilise E. intestinalis and E. flavescens as additional agents of rabbit control at locations where they are absent.

Contrary to previous reporting, E. flavescens was detected at all 23 effectively sampled sites and E. intestinalis at only about half of these sites (Peacock et al. Under Review). As virulent Eimeria parasites are already widespread across Australia, they are considered unsuitable as an additional control agent to complement existing viral biocontrol agents.

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