BIOLOGICAL CONTROL OF VERTEBRATE PESTS

R. P. PECH, CSIRO Wildlife and Ecology, GPO Box 284, Canberra, ACT 2601, Australia.

ABSTRACT: Biological control of vertebrate pest species has evolved from classical "release and forget" strategies to current programs of integrated management, which in the future may include the use of genetically modified organisms. Key stages in the use of biocontrol are illustrated with the history of managing rabbits (*Oryctolagus cuniculus*) in Australia. Two pathogens have been successfully released, myxoma virus in the 1950s and rabbit haemorrhagic disease (RHD) virus in 1995, and both have been highly effective in suppressing rabbit populations. The rapid attenuation of myxoma virus, as well as bioclimatic constraints on its distribution, and the development of resistance in wild rabbits prompted the later release of insect vectors and highly virulent strains of the virus. The evolution of the current rabbit-myxomatosis-RHD-predator system is still being monitored, and research is in progress to add immunocontraceptive strains of myxoma virus to the suite of rabbit control techniques. Increased attention to measuring the outcomes of pest management resulted in a nationwide program to document the economic and environmental consequences of RHD. This program was conducted much more systematically than for introduction of myxoma virus or its vectors, and similar monitoring is likely to be mandatory for future biocontrol agents.

KEY WORDS: biological control, European rabbit, myxomatosis, rabbit haemorrhagic disease, immunocontraception

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INTRODUCTION

Apart from some early introductions of predators, biological control of vertebrate pests has usually but not exclusively relied on pathogens that increase mortality rates (Fenner and Fantini 1999). The application of these biocontrol agents has increased in sophistication with better knowledge of the epidemiological factors that affect their performance, and current management guidelines usually recommend integration with conventional techniques such as poisoning and habitat manipulation. In Australia, society's expectations of biocontrol have also evolved, being influenced by some spectacular successes, for example with myxomatosis and RHD. These expectations have been modified in recent years by heightened awareness of ethical and social issues and the wide range of indirect agricultural and environmental impacts. These considerations are likely to become more important in the future, particularly with moves towards the use of genetically modified organisms.

The history of using biological agents to control the European rabbit (*Oryctolagus cuniculus*) in Australia will be reviewed briefly, and then used to illustrate general issues for the future use of pathogens for pest control.

BIOLOGICAL CONTROL OF RABBITS IN AUSTRALIA

The release of myxoma virus in the 1950s decimated rabbit populations that had reached plague proportions over two-thirds of the continent. This provided immediate relief for embattled farmers, an opportunity for the recovery of native plant communities and a legacy of unrealistic expectations for future biological control of vertebrate pests. However, the hoped for final solution to the rabbit problem did not eventuate. Instead, moderate control of resistant rabbit populations was achieved by a complex assortment of strains of predominantly intermediate virulence. Then followed a series of attempts to enhance the impact of myxomatosis with the release of virulent strains of virus, for example Lausanne, and new insect vectors, the European rabbit flea (*Spilopsyllus cuniculi*) in the late 1960s and the arid-adapted Spanish flea (*Xenopsylla cunicularis*) in the 1990s (Williams et al. 1995).

There is no evidence that the Lausanne, or similar strains, survived competition from field strains of myxoma virus (Williams et al. 1995). The European rabbit flea enhanced the spread of myxomatosis particularly in higher rainfall areas, although with unforeseen indirect consequences for the conservation of native fauna in southwest Western Australia, where a decline in the secondary poisoning of foxes resulted in increased predation on native fauna (King et al. 1981). The most recently added vector, the Spanish rabbit flea, was released throughout much of the drier parts of the rabbit's range (Cooke 1995; Robertshaw and Gould 1995) but any opportunity to assess the benefits was lost with the introduction of RHD in 1995.

A pre-release assessment of the ecological consequences of rabbit control was conducted as an essential element of the impact assessment process for RHD (Newsome et al. 1997). This included information from earlier biocontrol in Australia and overseas, as well as multi-species population models to predict the long-term effects of rabbit control. After the virus inadvertently spread from quarantined island trials to mainland Australia in 1995 to 1996, a two-year program of national monitoring and surveillance was implemented to measure the agricultural and environmental outcomes, as well as record the direct impact on rabbit populations and collect epidemiological data.

In the most recent developments in biocontrol for vertebrate pests in Australia, the Pest Animal Control Cooperative Research Centre (PAC CRC) is developing immunocontraceptive agents for rabbits, foxes (*Vulpes vulpes*) and house mice (*Mus domesticus*) (Tyndale-Biscoe 1994). The potential benefits of fertility control for rabbits have been tested using surgical sterilization to mimic vaccines in large-scale, replicated field experiments

in eastern and western Australia (Williams and Twigg 1996; Twigg and Williams 1999). In addition, spatial and non-spatial epidemiological models have been used to compare the benefits of sterilizing strains versus existing lethal strains of myxoma virus (Hood 2000). The research for the new technology is still in progress with each stage of development subjected to detailed scrutiny by the Australian Genetic Manipulation Advisory Committee.

DEVELOPMENT PATHWAY FOR BIOLOGICAL CONTROL

The historical route of biological control of rabbits in Australia is an outcome of the influence of scientific, social and economic pressures, typical of agricultural development in general (Norton 1988). Beginning with the suggestion in 1919 by H. B. Aragão that myxoma virus could be used to control rabbits in Australia (Fenner and Fantini 1999), rabbit biocontrol has progressed from release and enhancement of naturally occurring pathogens and their vectors to the current research on genetically engineered immunocontraceptive viruses. This process can be divided into six stages of development.

Pre-selection of Candidate Biocontrol Agents

In principle, candidate biocontrol agents for vertebrate pest species should be safe, humane, effective and realistically cheap. For example, technical criteria to meet these requirements guided the selection of mouse cytomegalovirus as a vector for immunocontraception (Shellam 1994). Spratt (1990) listed the essential features of biocontrol agents for mammals:

1. Increased mortality rather than decreased fecundity because this is more likely to provide effective control (but see for example, McCallum (1993) on the outcomes of fertility control using macro- and micro-parasites),
2. Density-dependent mortality, infertility or pathogenicity,
3. A direct life cycle,
4. Transmission via aerosol or a highly mobile vector,
5. Environmental persistence,
6. High host specificity,
7. Suitability for laboratory study and mass production,
8. Ability to pass quarantine regulations.

Myxoma virus and rabbit haemorrhagic disease virus satisfy most of these although, for example, density-dependence has not been quantified for either virus. In addition, as a New Zealand inquiry demonstrated (Anon 1987), it is not certain that myxomatosis would satisfy modern standards for humaneness.

The list by Spratt (1990) is not exhaustive. For example the liver nematode *Capillaria hepatica* met all the criteria but, in large-scale field trials, had limited impact on populations of house mice, probably because the rate of increase of the host under favorable conditions outstripped the regulatory ability of the parasite (McCallum and Singleton 1989). Virological and ecological screening of candidate biocontrol agents for vertebrate pests can still be attempted, as for example in the recent research on cane toads (Anon 1998). However, both myxomatosis and RHD were assessed for use in Australia because of their devastating and somewhat serendipitous impact on *O. cuniculus* overseas, rather than as the result of a systematic search.

Pre-release Epidemiology and Safety

Species-specificity is usually a prerequisite for a candidate biocontrol agent and may result from a narrow host range or from ecological factors that prevent contact with non-target susceptible species. In some cases the requirement for species-specificity might be relaxed; for example, in New Zealand it may be useful if a future biological control agent for stoats (*Mustela ermina*) also suppresses other species of introduced mustelids. Data from the geographical source of the biocontrol agent may suggest a likely level of species-specificity but tests will be required for non-target species potentially in contact with the agent. In the case of the European rabbit in Australia, there are no closely related native species, the economic benefit from harvesting rabbits is low relative to impact costs, and techniques are available to protect high-value rabbits used as pets or laboratory animals. Nevertheless, species-specificity was one of the most important concerns to be addressed for the use of RHD in Australia. High security laboratory trials were conducted to demonstrate that domestic species and representative species of native animals are not susceptible to the virus (Lenghaus et al. 1995). The criteria for selecting test species included representation of major taxonomic groups (e.g., macropods, marsupial carnivores), and economic (livestock) and cultural (e.g., koalas, *Phascolarctos cinereus*) value. The results from these trials with RHD were unambiguous, with no adverse effects on non-target animals (Anon 1996). However the long-term species-specificity of the virus remained contentious even though the probability of acquisition of new host species through mutation appears low (Robinson 1999). For both myxomatosis and RHD, the issue of species-specificity was confined essentially to Australia and New Zealand. However, resolution of this issue for the current research into genetically-engineered myxoma virus for controlling rabbits, and similar research for the biocontrol of brushtail possums in New Zealand, must take into account the potential risks to the target species in all parts of their global distribution (see for example, Nettles 1997; Stöhr and Meslin 1997; and Williams 1997).

As well as determining species-specificity, epidemiological data are essential to understand the function of a candidate biocontrol agent in individual animals, to determine whether or not the disease it causes is inhumane, and to predict its impact in field populations. Difficulties arise for lethal biocontrol agents because estimates of mortality rates are required but experimental studies must meet animal welfare standards. In the case of RHD, high-security laboratory experiments provided basic aetiological data but field studies were required to estimate key parameters such as transmission rates. The design of field trials is inevitably a compromise between maintaining stringent containment protocols and selecting environmental conditions representative of the ecological niche of the pest species. A semi-arid offshore island was chosen for RHD trials because it is representative of some mainland areas where rabbits are chronic, and occasionally eruptive, pests. However, the size of the

island constrained the scale of experiments, as did cost, and ultimately the sea barrier to the mainland was breached, almost certainly by insect vectors. The problem of conducting ecologically-realistic trials under contained conditions remains a major hurdle for future candidate biocontrol agents.

Pre-release Predictions of Performance and Impact

An efficient, self-sustaining delivery system is one of the primary attractions of biocontrol over other forms of control such as shooting, trapping and poisoning. In Australia the potential for rapid penetration of the target population was demonstrated by myxomatosis in the 1950s (Fenner and Ratcliffe 1965) and by RHD in the 1990s (less than two years to spread over half the continent) (Kovaliski 1998). In each case, the rabbit population was totally susceptible to the new biocontrol agent. The outcome is likely to be less certain if a new biocontrol agent has to compete with existing field strains. For example, virulent strains of myxoma virus have often been released for rabbit control with little evidence of persistence (Williams et al. 1995). This is consistent with the predictions of non-spatial epidemiological models (e.g., Anderson and May 1982; and Dwyer et al. 1990) and computer-based spatial simulation models (Hood 1999). In a recent experiment, a genetically identifiable strain of similar virulence to current field strains was used in a pilot study for the future use of immunocontraceptive myxoma virus (Robinson et al. 1997). The releases were made at an optimal time in the breeding season and established with a success rate similar to the predicted 50% (Hood 1999).

Standard modelling techniques can be used to predict the direct impact of a candidate biocontrol agent, provided epidemiological and demographic data are available. Preliminary models for RHD in Australia suggested that the disease should not persist, although the addition of a reservoir of virus, perhaps in rabbit carcasses, and relatively stable free-living virus did help to generate a more realistic pattern of disease outbreaks (Barlow 1998). Pech and Hood (1998) used empirical simulations of the likely intensity and frequency of RHD epizootics in a detailed interactive model that included rainfall-driven pasture dynamics, and populations of rabbits, a generic similar-sized native herbivore, and foxes. Data and functional relationships to construct the model came from measurements of the response to grazing by vegetation in semi-arid rangelands (Robertson 1987), from graze-down trials with rabbits (Short 1985) and a predator-removal experiment in western New South Wales (Newsome et al. 1989). The model predicted that with RHD epizootics occurring in a way similar to semi-arid areas overseas, there would be an increase in pasture biomass, more effective predator-regulation of rabbits despite a lower abundance of foxes, and a reduction in predation pressure on native mammals. A more comprehensive assessment based on published and unpublished material, including anecdotal reports from Australia and overseas, was prepared by Newsome et al. (1997). They compared the distributions of feral predators with those of vulnerable and endangered mammals, birds and reptiles and concluded that additional predator control was warranted to protect some native species from predation during the initial RHD epizootic. The long-term impact of fox predation in semi-arid areas could be predicted with the model developed by Pech and Hood (1998) but data were insufficient to assess the consequences of reduced rabbit abundance in temperate areas, or to estimate likely changes in the abundance and impact of feral cats and native predators, such as wedgetailed eagles. Newsome et al. (1997) recommended a monitoring program stratified by the factors: bioclimatic region, the eruptive or chronic nature of rabbit populations, land tenure, and the existence of prior data to compare with post-RHD measurements. This recommendation was adopted, with minor modifications, in the national monitoring program established later by Federal and State governments.

Future proposals to introduce biological control agents into Australia will have to provide evidence that the economic, environmental and social benefits outweigh costs. This was expected to be a legislative requirement for RHD, for example according to the provisions of the Environment Protection (Impact of Proposals) Act 1974 (Williams and Munro 1994), but was pre-empted by the escape of the virus during pre-release trials. The research plans for the PAC CRC include benefit-cost studies to support the development of immunocontraceptive myxoma virus, and virus- or bait-delivered immunocontraceptive vaccines for foxes and house mice. The principles of benefit-cost estimates for vertebrate pest control are well established in Australia (Braysher 1993; Hone 1994), although limited data are available for most pest species, and detailed economic assessments of pest control are rare (but see Choquenot et al. 1998 for a bioeconomic model of rabbit management with conventional techniques). Similarly, data for modelling the indirect ecological consequences of biocontrol agents are available for only a few well-studied species.

Post-release Assessment of Performance and Impact

The significant level of rabbit control achieved after the rapid spread of myxomatosis in 1950 to 1953 was documented at a national scale up until about 1956 (Fenner and Fantini 1999). However, by the late 1960s, the co-evolution of myxoma virus and its host was apparent with the emergence of resistant rabbits and low to moderate virulence strains of virus. Nevertheless, rabbits were still considered to be at about 20% of the pre-myxomatosis levels, at least in Victoria (Douglas 1965). The release of the European rabbit flea resulted in a seasonal shift in outbreaks of myxomatosis, though the impact on rabbit numbers varied between regions and across years (Cooke 1983). The benefits of introducing Spanish flea were never properly evaluated due to the release of RHD in 1995. In 1996, a national RHD program was established with two years of Federal and State Government funds for a detailed epidemiological study (Cooke 1999) and a network of ten intensive monitoring sites, plus several subsidiary studies. These were used to record the agricultural and environmental consequences of RHD-induced changes in rabbit abundance.

Some of the best evidence of environmental change has come from sites with research in progress prior to the arrival of RHD. For example at long-term experimental sites in the Flinders Ranges in semi-arid SA there has

been a substantial improvement in the numbers of palatable perennial plants (Mutze et al. 1998). In addition the broadscale control achieved by biocontrol prevented the aggregation of kangaroos that has occurred previously in response to increased food availability after localized, conventional rabbit control. At a more mesic site in central western NSW, rabbit numbers declined by over 80% in the initial RHD epizootic in 1996 and have been maintained at low levels since by a combination of predation, RHD and myxomatosis (A. Newsome, D. Hik and R. Pech, unpublished data). Measurements in a series of selective animal exclosures have demonstrated that since the arrival of RHD, grazing by eastern grey kangaroos has superseded that of rabbits as an important factor determining the species richness of woodland understorey and the percentage cover of perennial grasses. However, the remaining rabbits can still effectively suppress the recruitment of key perennial plants such as *Callitris* species (Allcock et al. 1999).

From 1996 to 1998, the benefits of RHD to agriculture were primarily through increased pasture production and reduced expenditure on conventional control methods, particularly poisoning with 1080 (sodium monofluoroacetate) baits (Saunders and Kay 1999). The effects of reduced grazing pressure were probably widespread in semi-arid Australia with recruitment of perennial plant species providing pastoralists with improved reserves of drought resistant forage. The impact of RHD on rabbit populations was more patchy in temperate areas of southeastern Australia (Saunders et al. 1999) and concerns have been expressed that the decline in the use of 1080 baits signals an over-reliance by farmers on RHD and myxomatosis (Saunders and Kay 1999). Negative consequences appear to have been minimal, mostly confined to an increase in unpalatable woody species in rangelands.

One intention of the RHD monitoring program was to document the outcomes of biocontrol in a much more comprehensive way than in the past. The limited duration of the program combined with additional pest control programs and climatic variability has meant that in many cases the benefits of rabbit biocontrol alone are not clear. However, the program's national perspective in recording the epidemiology of the disease, its impacts on rabbits and the outcomes for agriculture and conservation have set new standards for vertebrate pest management in Australia.

Post-release Epidemiology

The rapid shift to strains of myxoma virus with low to moderate virulence, as well as selection for resistant rabbits, that occurred in Australia in the 1950s and 1960s has been well documented (Fenner and Ratcliffe 1965; Fenner and Fantini 1999). Later tests using field strains collected in 1977 and 1978 showed a substantial increase in the innate resistance of wild rabbits since the 1950s, with a tendency for higher resistance in rabbits from regions with warmer climates (Parer et al. 1994). The importance of co-evolution in this host-disease system has been confirmed in a recent detailed comparison of a highly virulent strain and an attenuated strain of myxoma virus in wild and laboratory rabbits (Best and Kerr 2000). Also three of four field isolates collected in southeastern Australia from 1991 to 1994 were highly virulent in laboratory rabbits but had little effect in wild-derived outbred rabbits (P. J. Kerr, personal communication, in Fenner and Fantini 1999). On theoretical grounds (Anderson and May 1982), similar evolution should be expected for RHD although so far there appears to have been minimal genetic change in Australian strains of the virus (Asgari et al. 1999). In the few years since release, RHD has become established throughout the range of the rabbit with regional variations in epidemiology that are beginning to be understood from detailed studies in the Flinders Ranges of South Australia, supported by serological data from other widely dispersed sites (Cooke 1999). The complexity of the current system, with both RHD and myxomatosis operating in rabbit populations, will provide a challenge for understanding the epidemiology of future biocontrol agents, such as immunocontraceptive myxoma virus.

Performance Enhancement

The history of rabbit management in Australia has included several attempts to maintain or improve the effectiveness of myxoma virus. Some of these, such as the introduction of the European rabbit flea, were successful but others had limited impact or the outcomes are unknown (e.g., the introduction of the Lausanne strain). The lack of a detailed knowledge of how strains of myxoma virus compete and persist is part of the difficulty in directly manipulating the virus in the field. Epidemiological models can predict how virulence and demography will affect host-virus interactions and the dynamics of genetically manipulated strains (Hood 1999), but molecular techniques are only just beginning to provide the relevant field data (Kerr et al. 1995). However, the problem of cross-strain immunity that operates with myxoma virus may not apply to all host-virus systems. For example, cross-immunity is considered unlikely to block the transmission of immunocontraceptive mouse cytomegalovirus in house mice (Shellam 1994).

With the increasing sophistication of molecular biology, the genetic manipulation of biocontrol agents, or in some cases the pest species itself (see for example Davis and Fulford 1999; and Davis et al. 1999), is likely to become an increasingly important issue in vertebrate pest management. The prospect of genetically engineered viruses has already generated public debate of the associated social and ethical issues within Australia, as well as overseas (Williams 1997). Future debate will include the potential direct and indirect impacts of genetically modified organisms, and will be better informed when the effort on epidemiological and ecological research is increased to match the rate of advance of genetic technology.

CONCLUSION

In the past there have been high expectations and almost universal public acceptance of biological control of pest species in Australia. The history of myxomatosis in Australia illustrates the pathway of development of a biocontrol agent, from initial epidemiological studies through to attempts to enhance its performance, most recently with genetic manipulation techniques.

Experience with RHD and the development of immunocontraceptive myxoma virus indicates that high standards of accountability will be demanded in all aspects of the future use of biological control techniques. Advances in biotechnology are likely to increase the options for biocontrol beyond the search for natural enemies of the pest species, though additional complications will arise from international concerns about genetically enhanced biocontrol agents. However, biological control is likely to remain high on the agenda of countries like Australia where vertebrate pest species are widespread, often in accessible terrain, or in areas with limited opportunities for intensive management.

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