Advances in vertebrate pest control: implications for the control of feral house mice on Marion Island

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We review the options and technologies available to eradicate exotic mammals, especially rodents, from various habitats but in particular from islands. We also recommend possible measures against the house mouse population of Marion Island.

The house mouse as a pest species on Marion Island

Feral populations of house mice, *Mus domesticus* (Fig. 1), occur on many oceanic islands,[1] including the sub-Antarctic Marion Island (46°54'S, 37°45'E) situated 2300 km SSE of Cape Town, South Africa. This population has been living on the island for some 180 years[1,2] and still thrives, despite attempts at population control by introducing cats, *Felis catus*.[3,4]

The house mouse is an opportunistic breeder with a high potential rate of population increase.[5] Breeding on Marion is seasonal, females giving birth to an average of 6.9 pups and producing 7.3 litters during the breeding period.[6] These mice apparently undergo density-dependent population changes, probably related to refuge and/or food availability.[3] The repercussions of changes in climate on mouse numbers, possibly through the relaxation of factors limiting survival and/or reproductive output, served as motivation for a recently completed study on the population. However, ten years of data from 1991 to 2001 indicated no significant annual increase in population. Population numbers do change seasonally, though, in response to seasonal breeding, peaking at the end of summer at densities as high as 300 mice per hectare, most (93–97%) of which die during the winter.

Dietary studies suggest that mice on Marion may influence the plant community structure through seed harvesting.[7,8] However, their principal direct impact may be on the invertebrate community through selective predation.[7–10] On Marion, mice may take 0.7–1% of the daily standing crop of macro-invertebrates.[11,12] Perhaps more important is their indirect effect through the removal of decomposer biomass and subsequent impairment of nutrient mineralization.[11] Their presence and consequences for the island's biota are undesirable, mainly because of Marion's conservation status. Thus, efforts to either control or eradicate mice from the island make conservation sense.

A 1995 workshop[13] concluded that eradication of mice from Marion Island would be beneficial in restoring ecosystem function. However, before instigating a control programme, possible control options and their feasibility need to be assessed. At the time of the workshop, poison baiting appeared to be the most likely management tool.[13] During the 1990s, a number of alternative control options underwent refinement.[14–17] Here we review these options and examine technologies which should become available within the next decade. We also make recommendations for possible population control of house mice on Marion Island.

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Integrated pest management

Many decades of effort have failed to eradicate exotic mammals from all but the smallest islands.[18] Today emphasis is being placed on multiple strategies of population control that are more likely to produce the desired effect.[19,20] For instance, the aim of a fertility control strategy may not be to eradicate a pest species *per se*, but to maintain its numbers at a low density by reducing the birth rate,[21,22] such that the added effects of other control measures may eventually eradicate the population.

Integrated control programmes have been proposed to control British badger (*Meles meles*) populations and the Kaimanawa horses (*Equus* species) of New Zealand, based on a joint culling and immunocontraception operation. The successful eradication of the European rabbit (*Oryctolagus cuniculus*) from Cabbage Tree Island, Australia, involved the serial introduction of themyxoma virus, rabbit haemorrhagic disease and finally a poison-baiting programme.[23] Similarly, an integrated programme successfully eliminated the feral cat population on Marion Island. Initially, feline panleukopenia was introduced in 1977 and when the virus failed to continue spreading effectively through the population after five years, was augmented with alternative control strategies including hunting, trapping and poisoning.[24,25] A common denominator of successful programmes has been a detailed understanding of the habitat use, behaviour, reproductive parameters and population dynamics of the target species.[26–28]

Rodenticides as agents of control

A workshop[13] on the impact and contril of house mice on Marion considered the large-scale application of a rodenticide for their eradication. Successful rodenticide-based control strategies depend on a clear biological understanding on which to build, including a knowledge of bait toxicity, palatability and delivery mechanisms. Variations in these factors, such as changing bait type,[29] can make the difference between ineffective and more efficient methods of targeting rodent pests while avoiding non-pest species.

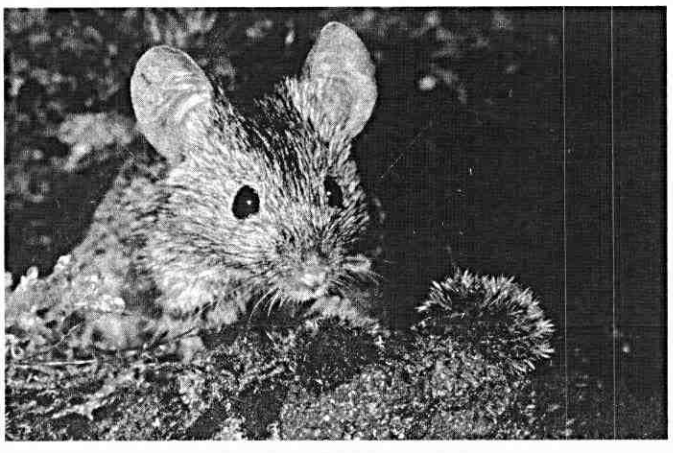

Fig. 1. The house mouse (*Mus domesticus*) has been accidentally introduced to many oceanic islands and is of significant agricultural importance as it often occurs in pest proportions.

Brodifacoum is the most potent of the second-generation anticoagulants that have been developed[30] and has been touted as a possible rodenticide for use on Marion.[13] This follows its use in successful rodent eradication campaigns on a number of smaller islands.[31] Prior to its deployment, the highly toxic nature of brodifacoum needs to be considered, using an environmental risk assessment.[32] The chemical is relatively insoluble and, after a single aerial drop, is less likely than other poisons (such as sodium monofluoroacetate 1080) to accumulate in either aquatic systems or plant material.[32,33] Tests in New Zealand suggest that only small numbers of invertebrates are likely to feed on the bait.[34]

In several previous campaigns, the poisoning of non-target species was not properly addressed.[35] For instance, during baiting operations on Enderby Island (New Zealand), at least two-thirds of the skua population was killed by direct intake of poison bait, while on Montuihe Island, brodifacoum poisoning was responsible for deaths among 10 species of birds, including 60% mortality of the paradise shellduck (*Tadorna variegata*).[36] Ironically, attempts to conserve rare or endangered species on their island habitats, such as the Seychelles magpie-robin (*Copsychus sechellarum*),[37] little spotted kiwi (*Apteryx owenii*)[38] and North Island saddleback (*Philesternus carunculatus*),[39] have been compromised through poisoning of these threatened birds.

While primary poisoning occurs through the direct ingestion of bait,[40] secondary poisoning may arise from the scavenging of mouse carcasses.[35,36,40] At Marion, lesser sheathbills (*Chionis minor*), Subantarctic skuas (*Catharacta antartica*), and Kelp gulls (*Larus dominicanus*), are all likely to take poison bait as well as scavenging poisoned mice; in an Australian field study, 25% of poisoned mice died above ground, making the carcasses available for scavengers.[41] Factors such as bait colour,[30] delivery method, the use of flavourants and timing of an operation should be optimized to allow maximum impact on mouse populations, while minimizing casualties amongst non-target species.

Despite these disadvantages, brodifacoum appears to be one of the better poisons available for rodent control, with a recorded mortality rate of 99% in house mice.[41] Besides its high toxicity, mice do not build up resistance to the poison, a problem associated with first-generation anticoagulants such as warfarin.[30] Ironically, the use of warfarin to control black rats (*Rattus rattus*), on Lord Howe Island (Australia) resulted in its use as an important food source by mice that had grown resistant to its action.[42,43]

Marion is larger (290 km^2) than any other island from which rodents have successfully been eradicated, making it potentially difficult to deliver bait efficiently or cost-effectively. The expense of bait release by helicopter, the most probable delivery method, is likely to be high. For instance, an evaluation of the costs and benefits of controlling house mice on Thevenard Island, Western Australia, provides some sobering statistics.[44] The expenses incurred in conducting a poisoning operation totalled over A$1000 (R5500) ha^{-1}, largely due to the cost of travel and accommodation. The expense of brodifacoum and bait stations alone over the 22-day trial period was A$ 55 (R300) ha^{-1}.[44] Given that mice on Marion are excluded from altitudes of greater than 800 m (van Aarde, pers. obs.), an area of at least 200 km^2 potentially supports mouse populations. Based on Moro's estimates,[44] the cost of a single bait programme over such an area, for poison and bait stations alone, would run to over R6 million.

More recently, a programme was devised to eradicate Norway rats (*Rattus norvegicus*), from Campbell Island, New Zealand.[45] Given the island's relatively large area (117 km^2) and similar latitude to Marion, this programme has the greatest relevance to the situation on Marion. In 2001, a single brodifacoum-based bait drop was performed, at 6 kg ha^{-1}, with a 50% drop overlap (to eliminate gaps), the success of which is still to be assessed. The Campbell Island protocol included 70 hours flying time, using three helicopters, over a three-month period.[45] If the area of Marion that would need to be baited is approximately 1.5 times that of Campbell Island, the cost of bait alone for a single drop (approximately R140/kg[44]) would amount to over R14 million. In addition, a maximum of just two helicopters would be available, corresponding to a flying time of 105 hours over 6 or 7 months.

Effective baiting

Simple baiting operations may be undermined when the reduction in population density achieved over a short period fails to influence long-term population dynamics. High mortality in a population of rodents is compensated for in many species by changes within their social structure, or natural regulation of numbers through changing density dependence in survival and reproductive output.[46] Strategic follow-up baiting campaigns are often necessary to maintain low population densities.[26]

Thus, total eradication of a rodent population would have to be achieved both to prevent recolonization and obviate costly subsequent baiting campaigns. To date, poisoning operations have successfully eradicated rodents from at least 41 islands around New Zealand.[47] Most of these campaigns, however, have been directed at the eradication of rats.[31,33,38,48–54] The largest of the islands so targeted is Langara Island (Canada), that covers an area of only 31 km^2,[51] roughly one tenth that of Marion. On an island the size of Marion, the probability of eradicating a mouse population through poisoning would be less than on a smaller island, making poison-baiting operations an expensive and potentially ineffective means of control. The Department of Conservation in New Zealand acknowledges that house mice are the most difficult small mammals to eradicate from islands.[55] Even so, mice have been eliminated from a number of islands,[56–60] the largest of which is the 7-km^2 Enderby Island.[61]

The use of rodenticides such as brodifacoum,[39,40] or sodium monofluoroacetate 1080[62] to control mouse populations may easily be compromised, as the survival of even a few mice will lead to their rapid re-establishment. Thus, if the recorded mortality rate for mice when using brodifacoum is 99%,[41] the survival rate is 1%. Indications that poison-baiting may fail as a technique to eradicate house mice come from choice tests conducted on food containing brodifacoum and non-poison control diets. In these trials only 90% of mice actually consumed poison over a 14-day period,[63] suggesting bait uptake may be a key issue. Veitch[56] recorded the presence of a mouse on Browns Island 18 days after a poison drop; this eradication programme could be considered successful only following the death of this individual. If a single mouse can survive on an island the size of Browns (0.6 km^2), the possibility of multiple survivors could be predicted for Marion.

Biological control

Biological control may be achieved using agents which induce lethal infection of target species, or agents which reduce breeding performance in the target species, either through natural infection or impaired fertility. Pest species usually maximize reproductive rate by producing many large litters, show early onset of sexual maturity and have a low life expectancy. As such, they are more sensitive to reductions in fecundity than increases in mortality.[64–67] Further, dispersal and social structure can counteract simple forms of pest control through mortality.[68] We consider these in turn.

Lethal infection

The most effective lethal control of a feral mammal followed the 1950 introduction of the myxoma virus against the feral rabbit population in Australia. The initial mortality rate was 99.9%, but fell to 95% by 1954.[69] Myxoma control was followed by the introduction of rabbit calicivirus, the agent of rabbit haemorrhagic disease (RHD), into wild Australian rabbit populations in 1995. Like the myxoma virus, rabbit calicivirus has been responsible for a significant decline in the rabbit population.[70] As with myxamotosis, rabbit populations appear to build up resistance to RHD and it can be predicted that populations will shortly begin to recover from the epidemic. Thus, these epidemics have not managed to eradicate this pest species.

The most suitable pathogen to control mice may be the ectromelia virus, which causes mousepox.[71,72] This virus can kill up to 80% of infected mice,[73] though wild Australian mouse populations exhibit innate resistance to ectromelia.[71] Similarly, many wild populations of *Mus* species show genetically determined resistance to flaviviruses,[74] which potentially makes them unsuitable as a viral control agent. As the Marion Island mice have been isolated from other populations for almost 200 years,[1] however, it would be worth investigating their resistance to both ectromelia virus and flaviviruses. The recent screening of the Marion mouse population produced positive titre results for mouse adenovirus-2 (72% infection), parvovirus (56% infection), reovirus (51% infection) and cytomegalovirus (100% infection; G.R. Singleton, *in litt.*), though their epidemiology or pathogenicity have not been investigated.

There are three potential problems with the use of lethal infection agents. First, the use of a lethal agent may select for a genetically resistant pest population. Second, a fecund pest animal can rapidly repopulate a depleted population, Third, the effectiveness of the virus may be reduced by the emergence of isolates with reduced virulence in the field.[75] Thus, while infection agents may have an initial impact on the pest species, alternative methods of maintaining or reducing pest numbers may become necessary after a relatively short time.

Natural infection

Some naturally occurring biological agents, whilst rare, are capable of impairing breeding performance as a result of infection.[72] For instance, the nematodes *Capillaria hepatica*[76] and *Heligmosomoides polygyrus*[77,78] reduce breeding in laboratory mice.[79] *Capillaria hepatica* has been considered an agent to control for Australian mouse plagues,[80,81] though both enclosure-based[14] and field trials suggest it has a minimal effect on breeding and population growth.[82,83]

Fertility control

Over the last 16 years, fertility control has gained in popularity as a population management tool.[84] While hormonal chemosterilants have been tested[15] and used successfully to limit animal populations,[85] immunosterilants are being investigated as the latest advance in fertility control.[16,86,87] Immunocontraception in particular has been touted as a promising long-term, cost-effective biological control strategy.[88,89] Importantly, as animal ethics are being given even greater consideration, reducing recruitment into the population via fertility control is seen as a more humane alternative to population control than exterminating excess individuals via increased mortality.[90–92] Several pest species, including the brushtail possum (*Trichsurus vulpecula*),[67,93] rabbit and European red fox (*Vulpes vulpes*),[94] have been targeted for immunocontraception programmes.

Immunocontraception as a management tool

Potential target sites of immunocontraceptives

Whereas the central endocrine control system and sperm/testes have been considered as target sites for immunocontraceptives,[21,95–99] the ovary has received the most attention, specifically the zona pellucida (ZP), the extracellular glycoprotein matrix surrounding mammalian oocytes, ovulated eggs and developing embryos. Antibodies coating the mature oocytes can prevent fertilization by inhibiting sperm-binding to ovulated eggs or penetration of sperm through the ZP. The region is relatively conservative in mammals and antigens from one species will normally produce antibodies in another.[100] Thus, porcine ZP has been used to induce infertility in a wide range of wild species.[100–105] In mice the ZP3 glycoprotein has been intensively studied as a target antigen for immunocontraception. Indeed, monoclonal antibodies directed against ZP3 have been used to inhibit fertilization by passive immunization.[106,107] Synthetic peptides encoding a ZP3 epitope have resulted in a variable period of immuno-fertility of from zero to eight months,[108,109] whereas mice infected with a recombinant ectromelia virus, expressing the ZP3 glycoprotein, caused infertility for 5–9 months. Similarly, rabbits infected with a recombinant myxoma virus, expressing the ZP B glycoprotein, showed 25% infertility that was increased to 80% following booster inoculations.[110]

Delivery methods

Oral delivery. Oral delivery may affect both target and non-target species, as both may feed on the same bait. It is imperative that orally delivered immunocontraceptive baits are either species-specific or that they do not cause infertility in non-target species. Both recombinant viral[111] and bacterial[112] vectors have been developed for oral delivery, though they have been used in immunization and not sterilization campaigns.

Virus-vectored delivery. The use of recombinant-microorganism vectors to deliver reproductive antigens has been proposed in cases where species need to be targeted efficiently over relatively large and inaccessible areas.[21,113] These vectors may be spread through the target population by sexual transmission, contagion, orally or via an arthropod carrier.[21] A viral vector must be capable of carrying DNA encoding a reproductive immunogen[86] as well as promoters to express the foreign gene and cytokines to enhance its effectiveness.[114,115]

In Australia, the mouse-specific murine cytomegalovirus (MCMV) is considered a suitable vector for immunocontraception.[72] Within wild Australian house mouse populations, 80–90% of individuals have tested seropositive to MCMV. It is a large DNA virus that establishes persistent non-lethal infection which could be used in a recombinant form to induce an immunocontraceptive response. Further, it is acquired through close contact between individuals and transmitted via bodily secretions (for example, saliva, sexual contact).[72] MCMV is also species specific,[116] one of the most important criteria for a suitable viral vector. Based on the Australian initiative, MCMV could prove an effective vector for immunocontraceptive control of the Marion Island mouse population. Serological tests have shown MCMV to be widespread amongst the island's mice (G.R. Singleton, in litt.).

To date, neither orally nor virally delivered immunocontraceptives have been tested under field conditions,[117] though Spanish workers were recently able to produce a recombinant virus to immunize rabbits against both RHD and myxamotosis.[118] Not only did this recombinant virus protect rabbits

against myxamotosis and RHD, but it was readily transmitted to uninoculated rabbits.[119]

Will fertility control lead to a long-term reduction in population numbers?

The role of fertility control in reducing the population of a widespread vertebrate pest has not been demonstrated in the field and we can predict the outcome of such treatment only through computer-based population models[120] and large-scale field experiments using surgically sterilized adults. These models support the idea that, over the short term, mammal pests could be kept at low density by fertility control.[66,121,122] However, the long-term effects have not been monitored and opinions differ about its effectiveness. Field trials using surgically sterilized individuals suggest that a female sterility rate of 65% would be needed to control mouse populations growth effectively.[123]

As with poisoning, it is probable that suppressing fertility may lead to compensatory breeding within the population.[17] For instance, a reduction in birth rate following immunocontraception may be compensated for by changes in juvenile and adult mortality.[18,124] If juvenile mortality is reduced to the same extent as birth rate, there will be no corresponding reduction in recruitment to the population.[18] Such compensation has been demonstrated in rabbits.[125] Compensation can also occur by increased numbers of offspring by females unaffected by fertility control measures. In trials using populations of surgically sterilized mice, Chambers *et al.*[17] recorded an increase in the litter size and the number of females bearing litters amongst non-sterilized individuals.

Can a species-specific, long-acting immunocontraceptive be developed?

Fertility studies show that species immunized with a recombinant-derived antigen may only induce an immune response only for a period of months.[86,126] Booster immunization is required to maintain antibody levels, or even enhance them.[101,105] Thus, depending on the longevity of the initial immune response, periodic re-infection of the population may be necessary through either a virally vectored or oral route in order to maintain infertility. Recent research on dogs, however, suggests that vaccination with purified ZP glycoproteins can lead initially to immunocontraception and then, irreversibly, to immunosterilization.[89]

The use of a vector already present at Marion Island, such as MCMV, needs to take account of competition between the genetically modified vector and its field strain. Using a modelling approach, Barlow[121] suggested that the persistence of a vector strain within the host is enhanced by the local absence of a wild strain of the same carrier agent. It may therefore be necessary to consider introducing mouse-specific vectors that are present in other *Mus* populations, but absent from Marion Island.

Shellam[72] suggests that pre-existing immunity to a viral vector may not be a significant barrier to transmission, as there is good evidence of the circulation of several virus variants in immune populations as well as the isolation of multiple variants from a single individual. In a field experiment, Robinson *et al.*[126] released a readily identifiable strain of virus into several rabbit populations to test the idea that it could compete with wild strains and demonstrated that the new strain was able to spread through the population.

Another potential problem with a viral vector may be low transmission rates at low population densities.Use of a sexually transmitted virus, however, such as a herpes-type virus, would eliminate such density-dependent effects, as sexual activity and viral transmission are directly related.[67]

Immunocontraception: the ethical debate

Immunocontraception appears to have been accepted by some as a management tool of both free-ranging and zoo animals, using remote delivery via darts.[101,127] Oral delivery via a bait has also met with international acceptance, as in the immunization of foxes against rabies in Europe. At present oral bait delivery is the only available method when dealing with rodents and has been used successfully in the past to deliver immunosterilants.[85] It has also been considered for immunocontraceptive control populations of introduced grey squirrel (*Sciurus carolinensis*).[128]

The main ethical debate over immunocontraceptives is the use of recombinant pathogens as a vector. The potential risks of a virally vectored immunocontraceptive are widely acknowledged[19,126,129–131] by researchers, governments and the general public. While some parties advocate ending further trials immediately, others believe they should proceed with extreme caution.[21,92] Even if the release of genetically modified vectors into the environment is finally approved, it will be a long time before the consequences of such actions can be assessed.

At present a widespread fertility control programme via immunocontraception remains a novel concept with an uncertain outcome and considerable risk.[93] Furthermore, the World Health Organisation (WHO) recommends that vectors under consideration for the delivery of contraceptive antigens must be non-transmissible, given the potential for international exportation of affected animals. Together, the WHO and the Office International des Épizooties (the veterinary equivalent of WHO) consider that if contraception is to be used in wild species its actions must be reversible and species specific.[94,132,133] There is no system presently available that satisfies concerns over the risks linked to the release of a transmissible contraceptive virus in wildlife populations.[134] Once introduced into a population, a viral-vectored agent cannot be recalled.[19,91] This was poignantly demonstrated recently by the rapid spread of the RHD virus from Wardang Island to mainland Australia.

Towards the effective control of feral mice on Marion Island

It is clear that, while immunocontraception may provide an alternative approach to wildlife management, our understanding of its application is in its infancy. However, this technology is evolving rapidly. To produce a suitable immunocontraceptive may take many years and cost millions of rands,[67] though as the relevant technology becomes more refined, we can anticipate that the associated costs will decline. Compared to the potential costs of repeated poison-baiting campaigns, techniques such as viral-vectored immunocontraception may provide a long-term, relatively cost-effective solution to pest-related problems. In addition there is already a substantial research programme under way in Australia to examine ways of controlling *Mus musculus* populations. While the aim of this may be to prevent rodent plagues, it is obviously relevant to the Marion Island rodent management programme.

A viral-vectored mechanism may be the only appropriate method of fertility control for house mouse populations.[135] Population models developed for other species suggest that an integrated pest management strategy, based on fertility control in conjunction with a secondary control agent such as poisoning, may be the best way of either eradicating or controlling such populations, including the mice on Marion. From an ecological perspective, the eradication of mice from the island is highly

desirable. We suggest that the following steps be taken to understand the potential efficacy of population control measures:

1. Develop a series of field trials to assess the consequences of lethal control, through poisoning, for mouse populations. This should examine the effects on both target and non-target species.
2. Determine the feasibility of using lethal control to eradicate mice from an island as large as Marion, possibly testing this via a full-scale eradication programme on a smaller South African island first.
3. Develop a field trial on Marion Island, using surgically or chemically sterilized mice to examine the effect(s) of varying intensities of fertility control on population density, reproductive output, reproductive compensation and survival.
4. Use reproductive and life-history variables monitored in the above trials to model the effects of fertility control, lethal control, or a combination of both treatments in order to examine the best method of eradicating or controlling the mouse population on Marion.

We hope that, by the time these questions have been properly answered, scientific advances in the field of immunocontraception will make this a humane and effective way of contributing to the control of Marion's mouse problem.

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