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FORUM

Cats, rabbits, *Myxoma* virus, and vegetation on Macquarie Island: a comment on Bergstrom *et al.* (2009)

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Summary

1. Eradication of a single pest species from a multiply invaded island system may have unpredicted and detrimental impacts. Bergstrom *et al.* (2009) describe damage to vegetation following an increase in the number of rabbits on Macquarie Island. They propose that the increase in rabbit numbers was caused solely by eradication of cats.

2. However, their modelling is flawed and their conclusion that cats were controlling rabbit numbers is unsupported. We suggest the increase was because of some combination of four factors: reduced releases of *Myxoma* virus, abundant food after 20 years of vegetation recovery, release from cat predation and climate variability.

3. Recent high numbers of rabbits on Macquarie Island are not unprecedented; vegetation has been damaged in the past but has recovered. Rabbit numbers appear to be in decline again in the absence of both cats and *Myxoma* releases, suggesting that other factors can contribute to regulation of rabbit numbers in this system.

4. We do not agree with the implication that pest management could have been better integrated. Eradication techniques for rodents and rabbits on an island the size of Macquarie were unavailable when cat eradication was deemed necessary. The benefits to seabirds of cat eradication have been rapid. Our analysis further highlights the complexity of multiply invaded island ecosystems.

Key-words: conservation management, ecological models, invasive mammals, island restoration, pest eradication, seabirds, subantarctic

Introduction

Islands are an important resource for preserving biodiversity, but the value of many has been compromised by the accidental or deliberate introduction of invasive species. Recent technical advances mean that it is now possible to remove some pest species from islands. Where one pest species is present and is removed, the effects of removal are often predictable and usually beneficial to indigenous species. Where multiple pests are present however, interactions between them can mean that the impacts of removing only one are less predictable and may be detrimental to indigenous species (Zavaleta, Hobbs & Mooney 2001; Rayner *et al.* 2007).

Four mammalian pest species occurred on subantarctic Macquarie Island: cats *Felis catus* L., rabbits *Oryctolagus cuniculus* L., ship rats *Rattus rattus* L. and house mice *Mus musculus* L. Cats have recently been eradicated. Rabbit numbers have increased and this has resulted in severe damage to the island's vegetation. A recent study by Bergstrom *et al.* (2009) documents this damage and proposes that the rise in rabbit numbers was caused solely by release from cat predation. The study suggests that the impacts were unexpected, and that the decision to undertake cat eradication in isolation was, in hindsight, an error.

While we agree that the removal of rabbits (and rodents) from the island is now a very high priority, we disagree with the conclusion that cats were controlling rabbit numbers. We suggest that other factors, notably changes in release of *Myxoma* virus, were involved.

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Relationship between cats, rabbits and *Myxoma*

Bergstrom *et al*. (2009) set out their primary hypothesis as 'the eradication of cats led to an increase in rabbit abundance' and conclude 'Rabbit numbers on Macquarie Island have returned to pre-control levels…and this can be clearly ascribed to the removal of cats'. We suggest that a causal link between increased rabbit numbers and cat eradication alone has not been established.

We suggest that changes in variables other than cats (notably *Myxoma* virus) may have affected rabbit abundance. *Myxoma* was released almost annually on Macquarie Island from 1978, because unfavourable environmental conditions meant that repeated releases were required (Brothers *et al*. 1982). While the virus was highly effective at reducing rabbit numbers for two decades, the release programme was compromised from 1999 onwards.

Bergstrom *et al*. (2009) note that releases of *Myxoma* ceased in October 2006 'for technical reasons'. In fact, the only reason for cessation of releases was that virus production ceased (Parks & Wildlife Service 2007). Copson (2002) recorded that supply of the virus became irregular, with no new stocks available from early 1999 to late 2000. This limited the release programme and priority was given to parts of the island where rabbits were having high impacts. Copson (2002) also noted that in some areas there were often very few signs of an outbreak. A final batch of virus was produced by the Commonwealth Serum Laboratory in October 2000. Vials from this batch (which had an expiry date of April 2002) were used irregularly over smaller and smaller areas of Macquarie Island until all supplies ran out in 2006.

There was also some evidence that the virus may have become less effective at controlling rabbits. Blood samples taken from live rabbits in 2004 showed that myxomatosis antibodies were widespread, indicating that rabbits had been exposed but had not yet died; it was further suggested that the virus was not being effectively transmitted in parts of the island (J. Kovaliski to G. Copson *in litt*. 7 October 2004). While this does not establish that the virus was becoming attenuated or that resistance was developing, it is at least consistent with experience elsewhere that myxomatosis may decline in overall effectiveness for a number of reasons (e.g. Ross & Tittensor 1986; Williams, Moore & Robbins 1990).

The situation is further complicated by the fact that the effects of predation and *Myxoma* may be more than additive. Rabbits that contract the disease are still active when blinded, and therefore probably more susceptible to predation, so some animals that might otherwise have recovered may have been killed by cats.

There appears to be little evidence that cats have ever controlled rabbits effectively on Macquarie Island. We note that rabbits were able to establish (and flourish) in the presence of cats, which had been present for about 60 years before rabbits were introduced (Copson & Whinam 2001). This indicates that cats were unable to control a low-density rabbit population at that time. The high densities of rabbits present before *Myxoma* release in 1978 clearly indicate that numbers were not being effectively controlled by cats then either. Predator–prey studies in semi-arid Australia have demonstrated that low-density rabbit populations can be regulated by predators (Pech *et al*. 1992), but if rabbits can escape this low-density state, they can no longer be regulated by predation. Myxomatosis might have allowed such regulation on Macquarie Island by reducing rabbit densities to the point where cats could control them during the 1980s and 1990s, but there is no evidence for or against this hypothesis; unfortunately, the time at which cats were eradicated coincides closely with reduced *Myxoma* releases.

The models presented in the study are therefore overly simplistic, as they treat *Myxoma* as a categorical variable, i.e. they can only consider it either present or absent, and if present, it is assumed to be uniformly effective. The models do not take into account the reduction in the amount of virus released from 1999 or its possible decline in effectiveness. Given the coincidence in timing of cat removal and reduction in the spread of *Myxoma*, we conclude that a direct causal link between the increase in rabbit numbers and cat eradication alone has not been established.

Table 1 of Bergstrom *et al*. (2009) presents the results from two datasets described as 'slightly different'. While these datasets differ little in terms of the time covered (33 vs. 29 years), there are major implications resulting from the inclusion or exclusion of the short pre-*Myxoma* period (1974–1978) in their models. When the entire dataset is included, the presence of *Myxoma* and precipitation emerge as the best predictors of rabbit abundance. Cats are a significant predictor only when *Myxoma* is removed as a variable.

In their discussion, Bergstrom *et al*. (2009) note 'Rabbit numbers on Macquarie Island have returned to pre-control levels (Fig. 2)…'. However, we note that the highest population estimates they show (red columns in Fig. 2) are only achieved when counts from additional plots added to the sampling regime after 2004 are included; when counts from the original plots only are compared (blue columns), levels in 2005 and 2006 are about half those in 1978, immediately before *Myxoma* was introduced. We also note that subsequent counts from 2008 and 2009 (Terauds 2009) indicate that rabbit numbers (measured on either set of plots) are declining again, in the absence of both cats and recent *Myxoma* releases. This decline is consistent with rabbit numbers being regulated at least in part by available vegetation, a suggestion that has been made previously (Scott 1988).

Rabbit counts before and after virus release in 1978 suggest that myxomatosis was highly effective at controlling rabbits for about two decades, and Model 1 in the study (using the 1974–2006 dataset) confirms this. Importantly, we note that there is no attempt in the study to explain why myxomatosis did not continue to control rabbits after removal of cats. However, the fact that it did not is entirely consistent with the reduction in releases of the virus previously described.

Bergstrom *et al*. (2009) also claim that cat diet data provide additional support for the results of their models. Their calculations suggest that the cat population was capable of eating 4000–13 700 rabbits, i.e. all or most of those present

on the island. However, this analysis does not take account of rabbit productivity. During the 1974–75 breeding season, an average of 19·3 rabbit kittens were produced per breeding female (Skira 1978). At this rate, a surviving population of only 2000 adult female rabbits would produce almost 40 000 rabbit kits annually. We conclude that the diet data do not support the conclusion that cats were controlling rabbits. The same argument (that there is no account taken of productivity) applies to the suggestion that 103 000 mice and 36 600 rats have entered the system since cat eradication. In fact, no evidence is provided that cats were limiting rodent numbers.

Rabbits and vegetation

Whether intentionally or not, the study appears to present the current rabbit impacts on vegetation as unprecedented, and as a recent phenomenon, related only to the removal of cats. In fact, cycles of high rabbit numbers (and consequent damage to vegetation) have occurred periodically, and their current density is not unprecedented.

Rabbits were introduced to Macquarie Island in 1878. Records collected by Scott (1988) indicate that densities have varied markedly in different parts of the island at different times, and that total numbers have fluctuated. Before the introduction of *Myxoma*, total numbers varied up to threefold (50 000–150 000) between 1956 and 1978 (Copson, Brothers & Skira 1981), and there were notable peaks in 1950 (Taylor 1955), 1965–1966 (Sobey *et al.* 1973) and 1977–1978 (Copson *et al.* 1981). It is important to note that rabbit numbers have only recently returned to near pre-*Myxoma* levels and that the pre-*Myxoma* period was also a time when cat numbers were not managed.

The available records suggest that the vegetation on Macquarie can recover from high rabbit densities. There was damage to vegetation before the introduction of *Myxoma* (Taylor 1955; Jenkin 1975), but there was also local recovery at different times (e.g. Selkirk *et al.* 1983; Scott 1988) before the impact of *Myxoma* became widespread. There was large-scale recovery during the prolonged period of low rabbit numbers after the virus became effective (Copson & Whinam 1998; Scott & Kirkpatrick 2008). We note that photographs in Figure 4(a,c) of Bergstrom *et al.* (2009) show vegetation in 2001 that is likely to have recovered (probably several times) from rabbit densities as high as (or higher than) those currently present. Exclusion plots have shown that recovery of native vegetation is rapid on Macquarie once grazing stops, and threatened plants are now fenced at a number of sites to ensure their recovery following rabbit eradication (Parks & Wildlife Service 2007).

Vegetation change is a further complicating factor in assessing the relative importance of the different factors affecting rabbit numbers. In our view, it is almost certain that the rapid increase in rabbit numbers after 2000 was assisted by the presence of an abundance of palatable plant species, following widespread recovery of vegetation during two decades of low rabbit densities.

Management decisions

Bergstrom *et al.* (2009) state that 'risk assessment of management interventions must explicitly consider and plan for their indirect effects, or face substantial subsequent costs. On Macquarie Island, the cost of further conservation action will exceed AU$24 million'. This has been widely interpreted to mean that remedial action, additional to that required for eradication, will cost a further A$24 million. However, it was planned that eradication and/or long-term control of rabbits, rats and mice would occur when suitable techniques were available (Department of Parks, Wildlife and Heritage 1991). The action now planned is therefore not an additional cost attributable directly to cat eradication. We also note that the cost of eradicating rabbits and rodents is based largely on the cost of bait, transport and delivery, and would be similar whether cats were present or not (and to a large extent irrespective of rabbit density).

In their discussion, Bergstrom *et al.* (2009) state 'The scenario on Macquarie Island suggests that funding of larger but more holistic conservation measures, as opposed to smaller, stepwise measures may, in the long run have been more successful and cost-effective'. While simultaneous eradications are often desirable, stepwise eradication was the only feasible option at the time cat eradication was planned. Even had funding for simultaneous eradications been available, rabbit and rodent eradication techniques for an island the size of Macquarie were not available when eradication of cats was deemed necessary (e.g. Copson & Whinam 2001).

The study also describes the consequences of the cat eradication as 'unintended'. In fact, the possibility of an increase in rabbit numbers (with potential effects on vegetation) was clearly recognized in the cat abatement plan (Scott 1996). The plan budgeted for *Myxoma* virus and stated the intention to use rabbit control 'as a tactical part of the cat eradication program' (Scott 1996). The plan included rabbit control as a goal precisely because eradication techniques had not been developed at that time. The need for long-term control of rabbit numbers was also explicitly recognized by Brothers & Copson (1988).

Bergstrom *et al.* (2009) also suggest that the trophic cascade they describe was not fully anticipated because of 'inadequate recognition of top-down control of rabbits'. In fact, the scale of the rise in rabbit numbers was not anticipated because it was not known at the time cat eradication began that *Myxoma* virus would be unavailable after 2000. We also believe that because a number of factors were potentially regulating rabbit numbers, it has not been established that 'top-down' control of rabbits by cats actually occurred.

Benefits of cat eradication

Bergstrom *et al.* (2009) have emphasized the damage to the vegetation of Macquarie Island, and concluded that the cat eradication was indirectly responsible. The study does not however consider the benefits of the cat eradication. Cats were implicated in the extinction of two endemic land birds and the threatened status of six seabird species (Scott 1996), and were estimated to be killing about 60 000 seabirds per year (Jones 1977).

The benefits of cat eradication for seabirds were rapid. Grey petrels *Procellaria cinerea* Gmelin were confirmed breeding on the island in May 2000 after an absence of over 80 years (Schulz, Robinson & Gales 2005). Cape petrels *Daption capense* L. have been recorded breeding for the first time, soft-plumaged petrels *Pterodroma mollis* Gould appear to be colonizing for the first time, and blue petrels *Halobaena caerulea* Gmelin and fairy prions *Pachyptila turtur* Kuhl are re-colonizing from refugia on off-shore stacks (Brothers & Bone 2008).

While Bergstrom *et al*. (2009) highlight the recent damage to the island's vegetation, there is no recognition of the fact that there would have been continuing damage of a different type (to seabird populations) had the cat eradication not occurred.

Potential effects of climate change

The potential effects of climate variability on rabbit numbers are not clear. However, Bergstrom *et al*. (2009) acknowledge that autumn air temperatures were higher than average in 4 of the 6 years after 2001, which may have allowed higher rabbit kitten survival and contributed to the rise in numbers.

Conclusions

Rabbits have clearly caused major damage to Macquarie Island's vegetation since 2000. While the technology is now available to quantify the changes accurately, severe damage to vegetation has apparently occurred periodically over more than a century. The recent impacts are dramatic, but not unprecedented. Given the obvious benefits to seabirds and the fact that vegetation is likely to recover, we do not agree with Bergstrom *et al*. (2009) that the substantial conservation investment in the island to date has 'largely been lost' as a result of cat eradication.

Our analysis further highlights the complexity of multiply invaded island ecosystems. We agree with Zavaleta *et al*. (2001) that detailed pre- and post-eradication assessments of such systems are important. Unfortunately, in the case of Macquarie Island, two potential rabbit-control agents (cats and *Myxoma* virus) were effectively removed simultaneously, thus compromising post-eradication assessment of the effects of removing either agent alone.

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