

FORUM

Management implications of the Macquarie Island trophic cascade revisited: a reply to Dowding *et al.* (2009)

Dana M. Bergstrom^{*1}, Arko Lucieer², Kate Kiefer¹, Jane Wasley¹, Lee Belbin³,
Tore K. Pedersen^{1,2} and Steven L. Chown⁴

¹Australian Antarctic Division, Department of the Environment, Water, Heritage and the Arts, 203 Channel Highway, Kingston 7050, Australia; ²School of Geography and Environmental Studies, University of Tasmania, Private Bag 76, Hobart 7001, Australia; ³Blatant Fabrications Pty Ltd, Hobart, Tasmania; and ⁴Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

Summary

1. The management of non-indigenous species is not without its complications. In Bergstrom *et al.*'s (2009) study, we demonstrated that feral cats *Felis catus* on sub-Antarctic Macquarie Island were exerting top-down control on the feral rabbit *Oryctolagus cuniculus* population, and that the eradication of the cats led to a substantial increase in rabbit numbers and an associated trophic cascade.

2. Dowding *et al.* (2009) claim our modelling was flawed for various reasons, but primarily that a reduction in the application of the rabbit control agent, *Myxoma* virus, coinciding with cat removal, was a major driver of rabbit population release.

3. We explore this proposition (as well as others) by examining rates of *Myxoma* viral release between 1991 and 2006 (with an attenuation factor for the years, 2003–2006) in association with presence/absence of cats against two estimates of rabbit population size. *Myxoma* viral release was a significant factor in the lower estimates of rabbit population, but the effect was small, and was not significant for higher rabbit population estimates. By contrast, the presence or absence of cats remained highly significant for both estimates.

4. *Synthesis and applications.* We re-affirm our position that top-down control of rabbit numbers by cats, prior to their eradication, was occurring on Macquarie Island. Nonetheless, we agree with Dowding *et al.* (2009) that systems with multiple invasive species represent complex situations that require careful scrutiny. Such scrutiny should occur in advance of, during, and following management interventions.

Key-words: invasive species, rabbits, sub-Antarctic, trophic cascade

Introduction

The management of non-indigenous species is not without its complications. These include direct and indirect impacts of interventions on non-target organisms (e.g. D'Antonio & Vitousek 1992; Courchamp, Chapuis & Pascal 2003; Messing & Wright 2006; Carvalheiro *et al.* 2008). In a previous paper (Bergstrom *et al.* 2009), we note that trophic cascades, as a consequence of management interventions, are not commonly documented, and that even where the potential for such effects is recognized by managers, the outcomes may often play out in unexpected ways. We demonstrated how the eradication of

cats on Macquarie Island led to an increase in rabbit numbers, which subsequently caused landscape-wide effects on vegetation, and that this outcome, though predictable from the previous history of rabbit impacts on the island and so not entirely unexpected, was not fully anticipated (Bergstrom *et al.* 2009, p. 74).

Dowding *et al.* (2009) take issue with our conclusions. They argue on the grounds of citation of other previous work, and with some speculation, that our modelling is flawed and that our conclusions are unsupported. Three key concerns emerge from their commentary.

1. That a causal link between 'cat eradication alone' and increase in rabbit numbers has not been established owing to the form of the *Myxoma* variable used in Bergstrom *et al.*'s (2009) models.

*Correspondence author. E-mail: dana.bergstrom@aad.gov.au

2. Bergstrom *et al.* (2009), ‘Whether intentionally or not...’ appear ‘...to present the current rabbit impacts as unprecedented’ (Dowding *et al.* 2009) and that the effects of climate variability on rabbit populations ‘are not clear’ (Dowding *et al.* 2009).

3. The conclusion, reached by Bergstrom *et al.* (2009) – that the impacts of cat control were not fully anticipated – is not supported by their analysis (i.e. the increase in rabbit numbers is not a consequence of release from top-down control), but nonetheless that the cat abatement plan recognized that such impact may be realized (Dowding *et al.* 2009).

Before we address these concerns, two other significant issues need to be highlighted. Bergstrom *et al.* (2009) is not about the importance of the impacts of cats on seabird populations relative to the significance of vegetation impacts, nor is it about whether or not the eradication of cats should have taken place. We highlighted the rationale of cat eradication and that it was much-needed (Bergstrom *et al.* 2009, pp. 74, 79), noting that ‘The eradication of cats was positioned in a commendable, integrated pest management framework...’, and acknowledged the conservation importance of eradication of cats and other invasive alien species on other islands (see also Frenot *et al.* 2005). Furthermore, it is widely accepted that landscape-scale changes to the vegetation have been caused by the rabbit population increase (Miller 2007; Scott & Kirkpatrick 2008), as demonstrated by Bergstrom *et al.*’s (2009) analysis of satellite imagery.

Cats, *Myxoma* and rabbits

Dowding *et al.* (2009) speculate that the increase in rabbit numbers was because of a combination of factors; release from cat predation, changes in vegetation, climatic conditions, and particularly changes in the release of *Myxoma* virus.

Dowding *et al.* (2009) also suggest that ‘there appears to be little evidence that cats ever controlled rabbits effectively’. The basis for their argument is twofold: that in the 1860s, rabbits established in the presence of cats; and that prior to *Myxoma* virus release in 1978, observations of high population densities of rabbits indicate consistently poor top-down control by cats. Such an argument neglects the consequences of seabird populations being very much larger at the time of rabbit arrival, allowing their establishment on the island at a time when cats had abundant alternative prey. Seabirds were still a significant component of cat prey in the early 1970s (Jones 1977). Subsequently, this seabird prey resource disappeared (Brothers 1984; Brothers, Skira & Copson 1985; Scott 1996), and by 1997, rabbits were the only dominant food item of cats, although rat and mouse components were on the increase (Copson & Whinam 2001, fig. 3).

Taking a broader perspective, top-down control of mammal populations by predators, and/or increases following experimental or serendipitous predator removal, have been widely documented in a range of other systems (Trout & Tittensor 1989; Hanski *et al.* 2001; Sinclair *et al.* 2001; Terborgh *et al.* 2001; Korpimäki *et al.* 2002, 2004; Krebs *et al.* 2003; Hambäck *et al.* 2004). It has also been shown that herbivore populations

may increase dramatically in the absence of predators, but that this increase may be transient until bottom-up control takes effect (McLaren & Peterson 1994; noting this for large herbivores). In consequence, top-down control is not an unrealistic expectation, particularly for an island system (Bramwell 1979). Nonetheless, that other factors might play a role is certainly an expectation well-founded on evidence from some other systems (see, e.g. discussion in Sinclair & Krebs 2002; Krebs 2009).

Clearly the most significant concerns raised by Dowding *et al.* (2009) are about the use of *Myxoma* virus as a categorical variable in Bergstrom *et al.* (2009)’s models. We adopted the categorical approach because we expected the release of the *Myxoma* virus to have a considerable impact on the rabbits, based on previous reports (Brothers & Copson 1988; Copson & Whinam 1998). The best fit model – PWS Models (a) and (b) in Table 1 of Bergstrom *et al.* 2009 – did indeed include *Myxoma* as a variable, with a significant and substantial effect. Our generalized linear models indicate that release of the virus explained changes of about 50 000 in the mean population size of rabbits. We did not neglect *Myxoma* in our second set of models, but rather it was carried constant. A full model with interactions was not estimable because no data are available for a period without cats and without the *Myxoma* virus. In addition, we were concerned with what the effects of cat removal had been in the presence of the *Myxoma* virus.

The *Myxoma* virus has been released annually since 1978 (Brothers *et al.* 1982; Copson & Whinam 2001). To fully model its effects requires data on the prevalence and incidence of the virus, the extent to which its effects might have attenuated, and the extent to which additional annual viral releases were being made. These data are not available. Although Dowding *et al.* (2009) speculate that the virus was becoming less effective, they provide no data to show that this is the case.

Since our original paper, data on the number of viral releases (number of rabbits hit by air gun pellets soaked in *Myxoma* virus) over the period 1981–2006, have been provided by PWS (Fig. 1). This shows a drop in the number of releases in 2000. However, the number of releases in subsequent years were generally within or higher than the range prior to 2000 (see also Copson 2002). We have re-estimated our models using data on rabbit population estimates (PWS Models 1 and 3 in Bergstrom *et al.* 2009), presence or absence of cats and number of viral releases for the period 1991–2006 (years with a

Table 1. Best-fit generalized linear models [showing Akaike Information Criterion (AIC) values and Akaike weights (w_i)] of the relationship between \log_{10} rabbit abundance, the presence or absence of cats, viral release (hits) (a continuous variable – see text) and autumn precipitation, for the period 1991–2006

Model	Variables and their estimates (significance in parentheses)	AIC	w_i
PWS Model 1	Cat absence, +0.165 (0.004) <i>Myxoma</i> hits, –0.00034 (0.033)	–9.89	0.53
PWS Model 3	Cat absence, +0.248 (0.007) <i>Myxoma</i> hits, –0.00039 (0.11)	3.88	0.39

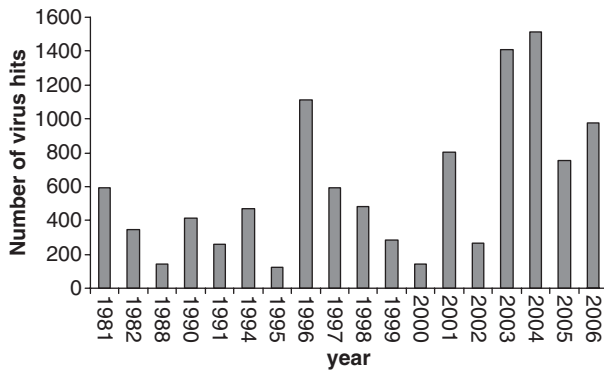


Fig. 1. Annual *Myxoma* virus hits to live rabbits over the period 1981–2006, as provided by Tasmanian Parks and Wildlife Service. Axis is not continuous; additionally, years 1981–1990 are annual numbers from October of the previous year to September of year represented.

consistent temporal reporting span on viral releases). While acknowledging that not every hit may be effective, we made the assumption that for the period 1991–2002, efficacy was constant over time. Acknowledging Dowding *et al.*'s (2009) concerns that the last batch of *Myxoma* virus supplied to the island had an expiry date of 2002, we set viral release values to 1 for the period 2003–2006 (i.e. assuming the virus was still present, but not supplemented and therefore that its effects were minimal).

The outcomes (using either the data from PWS Model 1 assessments of abundance, or PWS Model 3) varied somewhat depending on the model used, but this variation only concerned whether or not *Myxoma* virus hits entered the model significantly (Table 1). In PWS Model 1, *Myxoma* virus release was significant (at $P = 0.033$), but its effect size was small (-0.00034). By contrast, the presence or absence of cats remained significant ($P = 0.004$, effect $+0.165$; Table 1), indicating that an increase of *c.* 20 000 rabbits across the period can be attributed to the removal of cats. Using PWS Model 3 data, the number of *Myxoma* virus releases was not significant. Cat presence/absence was again highly significant, and the effect of their eradication amounted to a difference of *c.* 40 000 rabbits. In consequence, taking into account changes of *Myxoma* virus hits, the eradication of cats had a population-level effect similar in size to the introduction of *Myxoma* virus originally (see above). These analyses, taking *Myxoma* virus release changes into account, further support our view that cats were exerting top-down control on the rabbit population prior to their eradication.

Nonetheless, these analyses also beg the question of whether PWS Model 3 data should be used. Dowding *et al.* (2009) are concerned that only when these model data are used do counts increase to pre-control levels, and also note that in a new report (Terauds 2009), rabbit numbers are decreasing again. Terauds (2009, p. 9) provides an independent, cogent argument for the use of the new estimates [Bergstrom *et al.*'s (2009) PWS Model 3]. Using these data, rabbit numbers have indeed shown a decline in the past 2 years. In the absence of cats, rabbits may well now be experiencing food limitation, as has been recorded

for this and other species elsewhere (see above), but such a conclusion awaits supporting data.

Vegetation and climate variability

In their discussion of rabbits and vegetation, Dowding *et al.* (2009) argue that 'Whether intentionally or not...' Bergstrom *et al.*'s (2009) paper '...appears to present the current rabbit impacts as unprecedented' (Dowding *et al.* 2009). This is not the case. On three occasions we refer to previous observations of the effects of past grazing. For example, on p. 74 Bergstrom *et al.* (2009) write: 'Extensive grazing by rabbits was documented at least by the early 1950s (Taylor 1955) and by 1960, the effects were catastrophic, with a prediction that the "...grassland vegetation on Macquarie Island is doomed to destruction" (Costin & Moore 1960)'.

Dowding *et al.* (2009) do not present any data to show that the sites in fig. 4 of Bergstrom *et al.* (2009) had recovered or been damaged prior to the change we demonstrate. We acknowledge that vegetation can recover in the absence of rabbits (and did so previously, Bergstrom *et al.* 2009, p. 74), and we do not dispute any experimental exclusions of rabbits that demonstrate this point. Nonetheless, the current vegetation losses on the island may well be unprecedented as two separate reports make clear (Scott & Kirkpatrick 2008; Terauds 2009). Moreover, four plant species have now been listed on Tasmania's threatened species list as endangered. Thus, we are wary of the conclusion that no permanent damage through grazing has occurred to Macquarie Island ecosystems with this current population release of rabbits.

Dowding *et al.* (2009) also argue that the potential effects of climate variability on rabbit numbers are not clear. The models examined by Bergstrom *et al.* (2009) included a wide variety of climate variables, and we discussed the association of autumn precipitation and rabbit numbers at length and also examine the likely effects of autumn temperature change.

Management implications

Both our earlier work and the current analyses indicate that cats were exerting top-down control on the rabbit population, and that the eradication of the cats led to a substantial increase in rabbit numbers, with subsequent landscape-wide effects. We argued previously that although the trophic cascade was predictable and not entirely unexpected the extent was not fully anticipated (Bergstrom *et al.* 2009, p. 79).

Dowding *et al.* (2009) re-emphasized that the possibility of an increase in rabbit numbers was recognized in the cat abatement plan. We agree with the latter statement, but with the exception of a single sentence to this effect in the plan (Scott 1996, p. 19), the main concern was with the effect of a continuation of rabbit control in the absence of cat control and the subsequent impact on remaining seabird populations, which explains the need for rabbit control being a tactical part of the cat abatement plan (e.g. Scott 1996, pp. 6–8, 12). Likewise, in other works it is assumed that the recovery of the vegetation would continue (e.g. Copson & Whinam 2001).

Had the substantial effect of cat eradication on rabbit numbers been anticipated, much greater effort may have been given to deploying other control methods as soon as it became known that *Myxoma* virus production would be halted, whilst eradication methodologies were developed (see Copson 2002). In addition, it might have been expected that full funding for a control programme would have been made available far sooner than what it was (see Miller 2007). Rather, it appears that the prevailing view was very similar to that held by Dowding *et al.* (2009) – that although some top-down control by cats may have been taking place, it was relatively unimportant. Our analyses suggest otherwise.

Conclusion

In conclusion, we stand by our earlier statements. Our new analyses also provide further grounds for doing so. However, we agree with Dowding *et al.* (2009) that systems with multiple invasive species represent complex situations that require careful scrutiny. Such scrutiny should occur in advance of, during and following management interventions. In this regard, we appreciate the openness with which the Tasmanian Parks and Wildlife Service staff have approached the current debate and have made their data available for further analysis and consideration.

Acknowledgements

The authors thank Noel Carmichael of the Tasmanian Parks and Wildlife Service for the *Myxoma* hits data, and Justine Shaw, Dian Spear and Martin Riddle for comments on an earlier version of the manuscript.

References

- Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K. & Chown, S.L. (2009) Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology*, **46**, 73–81.
- Bramwell, D. (ed.) (1979) *Plants and Islands*. Academic Press, London.
- Brothers, N.P. (1984) Breeding, distribution and status of burrow-nesting petrels at Macquarie Island. *Australian Wildlife Research*, **11**, 113–131.
- Brothers, N.P. & Copson, G.R. (1988) Macquarie Island flora and fauna management – interpreting progress and prediction for the future. *Papers and Proceedings of the Royal Society of Tasmania*, **122**, 129–135.
- Brothers, N.P., Eberhard, I.E., Copson, G.R. & Skira, I.J. (1982) Control of rabbits on Macquarie Island by myxomatosis. *Australian Wildlife Research*, **9**, 477–485.
- Brothers, N.P., Skira, I.J. & Copson, G.R. (1985) Biology of the Feral Cat, *Felis catus* (L.), on Macquarie Island. *Australian Wildlife Research*, **12**, 425–436.
- Carvalho, L.G., Buckley, Y.M., Ventim, R., Fowler, S.V. & Memmott, J. (2008) Apparent competition can compromise the safety of highly specific biocontrol agents. *Ecology Letters*, **11**, 690–700.
- Copson, G. (2002) Integrated vertebrate pest management on subantarctic Macquarie Island: 1997–2002. *Report for the Natural Heritage Trust Grant Scheme, National Feral Animal Control Program*, 31 p.
- Copson, G. & Whinam, J. (1998) Response of vegetation on subantarctic Macquarie Island to reduced rabbit grazing. *Australian Journal of Botany*, **46**, 15–24.
- Copson, G. & Whinam, J. (2001) Review of ecological restoration programme on subantarctic Macquarie Island: pest management progress and future directions. *Ecological Management and Restoration*, **2**, 129–138.
- Courchamp, F., Chapuis, J.-L. & Pascal, M. (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, **78**, 347–383.
- D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.
- Dowding, J.E., Murphy, E.C., Springer, K., Peacock, A.J. & Krebs, C.J. (2009) Cats, rabbits, *Myxoma* virus, and vegetation on Macquarie Island: a comment on Bergstrom *et al.* (2009). *Journal of Applied Ecology*, **46**, 1129–1132.
- Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M. & Bergstrom, D.M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, **80**, 45–72.
- Hambäck, P.A., Oksanen, L., Ekerholm, P., Lindgren, A., Oksanen, T. & Schneider, M. (2004) Predators indirectly protect tundra plants by reducing herbivore abundance. *Oikos*, **106**, 85–92.
- Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. (2001) Small-rodent dynamics and predation. *Ecology*, **82**, 1505–1520.
- Jones, E. (1977) Ecology of the Feral Cat, *Felis catus* (L.) (Carnivora: Felidae) on Macquarie Island. *Australian Wildlife Research*, **4**, 249–262.
- Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N.C. (2002) Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. *Proceedings of the Royal Society B*, **269**, 991–997.
- Korpimäki, E., Brown, P.R., Jacob, J. & Pech, R.P. (2004) The puzzles of population outbreaks and cycles of small mammals solved? *BioScience*, **54**, 1071–1079.
- Krebs, C.J. (2009) Population dynamics of large and small mammals: Graeme Caughley's grand vision. *Wildlife Research*, **36**, 1–7.
- Krebs, C.J., Danell, K., Angerbjörn, A., Agrell, J., Berteaux, D., Bråthen, K.A., Danell, O., Erlinge, S., Fedorov, V., Fredga, K., Hjäältén, J., Högestedt, G., Jónsdóttir, I.S., Kenney, A.J., Kjellén, N., Nordin, T., Roininen, H., Svensson, M., Tannerfeldt, M. & Wiklund, C. (2003) Terrestrial trophic dynamics in the Canadian Arctic. *Canadian Journal of Zoology*, **81**, 827–843.
- Mclaren, B.E. & Peterson, R.O. (1994) Wolves, moose and tree rings on Isle Royale. *Science*, **266**, 1555–1558.
- Messing, R.H. & Wright, M.G. (2006) Biological control of invasive species: solution or pollution? *Frontiers in Ecology and the Environment*, **4**, 132–140.
- Miller, C. (2007) Rabbits lay waste to Macquarie Island. *Frontiers in Ecology and the Environment*, **5**, 5.
- Scott, J.J. (1996) *A Feral Cat Threat Abatement Plan for Macquarie Island*. Tasmanian Parks and Wildlife Service, Department of Environment and Land Management, Hobart, Tasmania.
- Scott, J.J. & Kirkpatrick, J.B. (2008) Rabbits, landslips and vegetation change on the coastal slopes of subantarctic Macquarie Island, 1980–2007: implications for management. *Polar Biology*, **31**, 409–419.
- Sinclair, A.R.E. & Krebs, C.J. (2002) Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society B*, **357**, 1221–1231.
- Sinclair, A.R.E., Krebs, C.J., Fryxell, J.M., Turkington, R., Boutin, S., Boonstra, R., Seccombe-Hett, P., Lundberg, P. & Oksanen, L. (2001) Testing hypotheses of trophic level interactions: a boreal forest ecosystem. *Oikos*, **89**, 313–328.
- Terauds, A. (2009) *Changes in Rabbit Numbers on Macquarie Island*. Tasmanian Parks and Wildlife Service, Hobart, Tasmania.
- Terborgh, J., Lopez, L., Nuñez V.P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. & Balbas, L. (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1925.
- Trout, R.C. & Tittensor, A.M. (1989) Can predators regulate wild rabbit *Oryztolagus cuniculus* population density in England and Wales? *Mammal Review*, **19**, 153–173.

Received 3 August 2009; accepted 11 August 2009
Handling Editor: Marc Cadotte