Does control of introduced predators lead to greater rabbit abundance?

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Summary

Project and Client

- As predator control programmes that enhance indigenous biodiversity expand, some landholders with overabundant rabbits believe that predator control that adjoins their properties has exacerbated their rabbit problems. There are a number of cases where landholders are seeking a financial contribution from regional councils or the Department of Conservation to subsidise their rabbit control costs. As a first step at addressing this issue, Landcare Research reviewed the published scientific literature on predator effects on rabbit populations for the Hawke's Bay Regional Council in March 2014.

Objectives

- To determine whether control of introduced predators in New Zealand leads to greater abundance of European rabbits, by reviewing published literature on New Zealand and overseas studies.

Results

- In New Zealand, none of the predator removal experiments provides compelling evidence for predator removal increasing rabbit abundance. Predators appear to have relatively little effect on rabbit numbers compared with other forms of mortality such as disease, drowning in burrows, or collapse of burrows.
- In Australia, rabbit numbers are driven primarily by climate and its subsequent effects on food abundance and quality, and by disease. However, where rabbit numbers are low following drought or major epizootics, predation can limit population recovery.
- On the Iberian Peninsula (where European rabbits are indigenous), rabbit numbers appear to be influenced mostly by favourable habitat, food, disease and rainfall. The effect of predators is unclear as it is often confounded by other factors.
- In other parts of Europe, predators have their strongest effect during and after rabbit numbers have been reduced by other factors, but have little effect on high density populations. Predation appears to be less important than the effects of climate, food and habitat on rabbit numbers.
- Predator abundance (especially for species that specialise on rabbits) can usually be predicted by rabbit abundance, not necessarily vice versa.

Conclusions

- Rabbit abundance is by and large determined by factors other than predation.
- Predation acts as a limiting factor under certain conditions, but in most situations its effects are minor compared with the roles of climate, food, disease and habitat.
- For areas of New Zealand that are highly favourable for rabbits, such as those of the central South Island with continental-type climates, the control of introduced predators

is less likely to lead to greater rabbit abundances than in areas where other forms of rabbit mortality prevail, such as in some high rainfall zones. Any increases in rabbit numbers subsequent to predator control, however, are likely to be small compared with the primary influence of climate, food, disease and habitat.

Recommendations

- If, in some circumstances, predator control leads to rabbit increases, a key unresolved question is whether or not those circumstances can be identified with enough certainty to generate predictions about where and when rabbit increases are likely to occur, and if so, how many extra rabbits can be attributed to predator control? Answers to these questions would be prohibitively expensive and difficult to achieve. A partial solution would be to design and implement a robust and consistent rabbit, predator and disease monitoring programme at sites adjacent to or overlapping predator control operations such that data on changes in rabbit populations could be collected alongside data on changes in disease prevalence and predator abundance. These data could be combined with local data on climate and other conditions to facilitate reasonable inference about predator effects on rabbit abundance. Inclusion of carefully matched non-treatment areas (rabbit populations unaffected by predator control programmes but exposed to similar climate, food supply and disease prevalence) is perhaps the most crucial requirement of such a programme.
- We recommend this concept should be trialled in one region, with others contributing monitoring data to construct a national picture.

1 Introduction

There is an emerging controversy in New Zealand concerning predator control and its effects on rabbit numbers. As predator control programmes that enhance indigenous biodiversity expand, some landholders with overabundant rabbits believe that predator control that adjoins their properties has exacerbated their rabbit problems. There are a number of cases where landholders are seeking a financial contribution from regional councils or the Department of Conservation to subsidise their rabbit control costs. The issue will become increasingly complex as new technologies and ambitious visions of pest eradication over very large scales gain traction (Parkes 2013). Clearly, there is much at stake in terms of relationships between government and landholders. Public perceptions are critical: many landowners and members of the general public will apply the intuitive logic that if predators consume rabbits they must regulate their numbers. However, predator–prey population dynamics are rarely that simple. As a first step at addressing this issue, Landcare Research reviewed the published scientific literature on predator effects on rabbit populations for the Hawke's Bay Regional Council.

2 Objective

- To determine whether control of introduced predators in New Zealand leads to greater abundance of European rabbits, by reviewing published literature on New Zealand and overseas studies.

3 Report structure

Animal population dynamics are complex. The question posed in this report is quite specific and, ideally, requires replicated predator manipulation experiments that test the effects of predation directly by controlling for influences other than predation. Experiments conducted in New Zealand ought to provide the most relevant evidence (and most compelling if the experiment is robust), and so these are reviewed first. The next level of inference comes from descriptive or correlative studies, such as rates of predation on rabbits, or studies that explore links between the natural variability in rabbit and predator abundances. Factors that influence survival of rabbits, especially juveniles, are likely to also influence population dynamics strongly as population growth is most sensitive to this vital rate (Smith & Trout 1994; Norbury & Reddiex 2005). Next, we review the Australian literature. Rabbits there have similar pest status to that in New Zealand, but the guild of mammalian (and avian) predators in Australia that consume rabbits (primarily foxes, cats and dingoes) is quite different to that in New Zealand (cats, ferrets, stoats, weasels), and the climatic fluctuations and dryland environments are often more extreme. Finally, we review the literature from the Iberian Peninsula (where the European rabbit and most of its predators are indigenous) and elsewhere in Europe where the predator guild differs even more. On the Iberian Peninsula, for example, more than 40 species of predators (including raptors) eat rabbits, and interactions within the predator guild can lead to complex ecological outcomes (e.g. Palomares et al. 1995).

4 Ecological processes

In addition to disease, in general terms, the dynamics and abundance of animal populations at any point in time are governed by resources such as food, shelter and climate, and by predation from carnivores at higher trophic (feeding) levels. These are referred to in the literature as 'bottom-up' and 'top-down' processes, respectively, and provide a convenient structure for placing predator effects in the wider context of other factors that influence rabbit populations. Animal populations will rarely be governed exclusively by top-down or bottom-up regulation, and the relative strengths of both processes will vary with environmental conditions, such as climate and soil conditions. While we partially address disease, other population drivers, such as competition, are not addressed explicitly in this report.

5 New Zealand

5.1 Experimental studies

Gibb et al. (1978) studied a single rabbit population inside an 8-ha fenced enclosure in the Wairarapa over a 10-year period. For the first six years, rabbit numbers increased until they exhausted their food supply, and then collapsed. Predator numbers (cats and ferrets) lagged behind rabbits but the authors concluded that they accelerated the rabbit population decline, on the basis of simple estimates of total predator off-take and the following circumstantial evidence: predators were much more abundant than rabbits during the decline phase; all observed rabbit carcasses showed predator sign; and few young rabbits (predators' preferred prey) were observed during the decline period. Rabbit numbers remained low until predators were removed, and then climbed to a higher peak than previously recorded, before crashing again as food supplies were exhausted. The authors argued that during the low rabbit phase, predators held rabbits at a low level or in a 'predator pit' (sensu Pech et al. 1992) because they were able to persist by feeding on other prey besides rabbits, thus maintaining a constant, controlling predation pressure on rabbit numbers. For 20 years this study had been held up as evidence of a regulatory effect by predators on rabbit populations in New Zealand. However, it was based on a single rabbit population (i.e. non-replicated) and non-treatment populations were not included for comparison. Therefore, other factors that affected the dynamics of the rabbit population, such as climate and rainfall, could not be accounted for. Indeed, rainfall increased during the rabbit increase phase so it is impossible to estimate the relative effects of predation (or the lack of it) and the increased availability of food on rabbit population recovery. These kinds of experiments are often vulnerable to a 'fence effect' (i.e. enclosed populations can reach unnaturally high densities) and a 'pantry effect' (i.e. predators in the surrounding area are attracted to the enclosed, high-density prey population – although in this case, predators were mostly deterred from entering the fence). These two effects can lead to very unstable prey population dynamics, which may have amplified the effect of predation on the dynamics of the rabbit population.

More than two decades elapsed before the next predator removal experiment in New Zealand was published, by which time rabbit haemorrhagic disease (RHD) had arrived. Reddiex et al. (2002) removed predators (cats, ferrets and stoats) from two sites in North Canterbury at the same time as RHD arrived. Rabbit abundance was measured there and at another two sites where predators were not removed. Rabbit numbers declined on all sites during the RHD outbreak but the declines were only moderate where predators were removed, and quite dramatic where predators were present. Mortality rates of juvenile rabbits were also higher where predators remained. Reddiex et al. (2004) replicated the experiment in Central Otago, where conditions for rabbit survival and growth are more favourable. Again, the experiment coincided with an outbreak of RHD, but this time no effects of predator removal were apparent on the rates of rabbit population decline.

A more recent predator removal experiment in central and eastern Otago showed no effects of predator removal on rabbit abundance in low-density rabbit populations that were supressed by RHD (Norbury et al. 2013).

None of the experiments carried out to date in New Zealand provide compelling evidence for a top-down effect of predators on rabbit abundance. Rabbit haemorrhagic disease is now endemic in New Zealand, so the Gibb et al. (1978) study is arguably less relevant to present circumstances and, as noted above, the conclusions of this study were weakened by poor experimental design. The Reddiex et al. (2002) and (2004) studies showed overwhelming effects of the initial RHD epizootics, which were lessened to some extent by predator removal at one site. The Norbury et al. (2013) study represents the present endemic condition of RHD in New Zealand, but it failed to detect an effect of predator removal on rabbit abundance.

5.2 Other studies

Although other New Zealand studies have not measured the effects of predation on rabbit numbers directly, they have measured predation rates on juvenile rabbits and inferred the potential consequences of these for the rabbit populations. While losses of young rabbits to predation can sometimes be high, other forms of mortality such as disease, drowning in burrows, or collapse of burrows seem to be of equal or greater importance (Tyndale-Biscoe & Williams 1955; Robson 1993; Gibb & Fitzgerald 1998). High rainfall is generally associated with these other sources of mortality, constraining rabbit populations in comparison with drier areas where seasonal pulses of high productivity and lower juvenile mortality are thought to allow rabbits to reach higher densities, but also to cause numbers to fluctuate widely according to conditions (Gibb & Williams 1994).

The evidence is more compelling for bottom-up effects of rabbit numbers on predator abundance, rather than the other way around, at least for the rabbit-prone areas of Central Otago and the Mackenzie Basin (Norbury & McGlinchy 1996; Norbury 2001; Cruz et al. 2013). In turn, rabbit populations are also driven bottom-up by favourable environmental conditions that enable them to maximise their reproductive output (Robertshaw 1992; Gibb & Williams 1994) and, similarly, by pasture development through replacement of indigenous vegetation with productive pasture species and the application of fertilisers (Norbury et al. 2013). Predator populations in rabbit-prone areas respond indirectly to this increase in primary productivity through increases in rabbit productivity and hence the availability of young rabbits. Consequently, compared with this strong bottom-up influence, predators appear to have relatively little top-down effect on rabbits.

6 Australian studies

Note: many studies outside New Zealand include the effects of foxes. Foxes are generalist predators that do not rely on rabbits as a primary source of prey. While these studies provide important guiding principles for our review, the specific outcomes will not necessarily apply to New Zealand.

In Australia, Parer (1977) and Wood (1980) reported significant levels of predation on juvenile rabbits by cats and foxes. Indeed, most predator manipulation experiments in Australia show some effect of predation on rabbits, but this only appears to moderate the overwhelming effects of environmental conditions and food supply on rabbit population growth. Newsome et al. (1989), for example, showed that drought conditions reduced rabbit populations dramatically in a semi-arid grass/shrubland in western New South Wales. Predation by foxes and cats held rabbit numbers at low levels for longer periods than where predators were removed. When the drought ended, rabbits recovered up to four times faster at the predator-removal sites, than at sites where predators remained. Newsome et al. (1989) cite other studies elsewhere in Australia where rabbit irruptions occurred in response to favourable environmental conditions, despite the presence of predators. They suggested that predation is unable to stop climate-induced rabbit irruptions because predators are seasonal breeders, whereas rabbits can breed throughout the year if suitable conditions prevail. Pech et al. (1992) subsequently showed that when predators were allowed back into the predator-removal areas, rabbit populations continued to increase and did not decline to the density in the untreated area. They proposed a two-state predator–prey system for this semi-arid ecosystem: rabbits at low density are constrained by a combination of poor environmental conditions and predation, but are able to escape the effects of predation when environmental conditions improve. Risbey et al.'s (2000) experiment in Western Australian shrubland confirmed this by showing increased rabbit numbers at fox control sites compared with untreated areas when rainfall increased. Banks (2000) recorded 10.3- to 23.3-fold increases in rabbit numbers in subalpine forest/grassland habitat following 20 months of fox removal at two sites, compared with relatively little change in rabbit numbers at non-removal sites. When fox control stopped, rabbit numbers declined and remained low for 16 months on one site, but recovered at another site where fox reinvasion was slower, thus allowing rabbit productivity to outstrip predation. Robley et al.'s (2004) review of these and other Australian studies concluded that predation may have a regulatory effect on rabbit populations that are supressed to low densities by poor environmental conditions (e.g. drought), but that these regulatory effects are weakened when conditions improve.

Not all Australian experiments, however, have demonstrated an effect of predator removal. Davey et al. (2006) confirmed the bottom-up effect of rainfall on rabbit numbers in a temperate grass/woodland system, but they found no effect of fox removal. In fact, the greatest response of rabbits to rainfall occurred where foxes were present. They also found that the impact of RHD, at least for several years after its arrival, completely overwhelmed any effects of predation or food supply. Also, Robley et al. (2004) cite Thompson and Shepherd's (1995) unpublished data from Western Australia where no significant increase in rabbit numbers followed fox control, and rabbits continued to fluctuate seasonally thereafter suggesting, again, that environmental conditions were the primary driver of population changes.

Newsome et al. (1989), Risbey et al. (2000), Davey et al. (2006) and Fordham et al. (2012) demonstrated clearly that rabbits in Australia are driven primarily by climate, and its subsequent effects on food abundance and quality (Williams et al. 1995), and by disease (primarily coccidiosis in wetter areas, myxomatosis since the 1950s, and RHD since the mid-1990s). Rabbits, in turn, drive the abundance of predators (Mutze et al. 1998; Holden & Mutze 2002; Cooke 2012). Bottom-up effects, therefore, appear to dominate rabbit–predator interactions in Australia, although where rabbit numbers are low following drought or epizootics, predation can limit population recovery.

7 European studies: Iberian Peninsula

Studies of predator impacts on indigenous rabbits on the Iberian Peninsula (primarily Portugal and Spain) are difficult to interpret because rabbit survival and reproduction are driven by a variety of other factors (e.g. disease, hunting by humans, habitat quality). Most populations are therefore at undesirably low levels for conservation purposes across much of the region. Moreover, predator manipulations are difficult to implement because most predator species are indigenous and are usually not controlled. Game estates, however, undertake some predator control (generally of introduced predators), including illegitimate control of indigenous species in some cases. While studies have shown greater rabbit abundance on game estates, the effect of predator removal is often confounded by other actions that benefit rabbits, such as habitat improvement (Delibes-Mateos et al. 2008b, 2009b). Delibes-Mateos et al. (2008a) showed that foxes, being generalist predators that can persist by feeding on a range of prey types, can regulate low- to medium-density rabbit populations, but that this regulation is insufficient once environmental conditions allow rabbit numbers to flourish. Delibes-Mateos et al. (2009a) cautioned that it is still unclear whether control of generalist predators on the Iberian Peninsula allows rabbit populations to increase. As in New Zealand and Australia, rabbits on the Iberian Peninsula appear to be influenced mostly by bottom-up processes such as favourable habitat, food, rainfall and shelter (Calvete et al. 2004; Ferreira & Alves 2009; Ferreira et al. 2013) and disease. Rabbits appear to drive the abundance of some predator species (Ferreras et al. 2011), rather than the other way around.

8 Other European studies

No predator manipulation experiments on rabbits have been reported from other areas of Europe, reflecting the species' complex management status as often-threatened indigenous wildlife or as 'vermin' on traditionally-managed game estates. Trout and Tittensor (1989) reviewed the evidence for predator impacts on rabbits in the United Kingdom and elsewhere in Europe, and found higher rabbit numbers were generally associated with low predator abundance (again, this is uncontrolled for other influences). They suggested that predators have their strongest regulatory effect during and after rabbit numbers have been reduced by other factors, and that predators have little effect on high density populations. Similarly, Petrovan et al. (2011) and Kontsiotis et al. (2013) concluded that although predators influence rabbit abundance, predation is less important than the bottom-up effects of food and habitat. Rödel and Dekker (2012) found, from hunting records in the Netherlands and Germany, that the long-term dynamics of rabbit populations were adequately explained by temperature and rainfall alone. Further evidence of bottom-up effects comes from Erlinge et al. (1984) who noted that rabbits maintain populations of generalist predators in Europe.

9 Generic patterns: top-down or bottom up?

The question of whether or not predators drive prey abundances has received much attention from ecologists over the years. Early work suggested that predators consumed only the ‘doomed surplus’ prey, i.e. individuals that could not be supported by available resources (Errington 1946). Attention then shifted to the role that top predators play in systems by controlling the abundances of stronger competitors, thus allowing greater diversity of species within communities (Terborgh et al. 1999). Miller et al. (2001) reviewed the importance of carnivores in structuring ecosystems and communities and concluded that ecosystems reflect a balance between top-down and bottom-up regulation (Krebs 2013), and that the relative strengths of these processes vary with environmental conditions (see also Meserve et al. 2003). For primary prey species, like rabbits, population growth eventually declines as resources diminish but may lead to increased predator numbers at high prey densities. Eventually, rapidly-reproducing prey, such as rabbits, reach such high densities that resources are insufficient to maintain growth (Parer 1977; Newsome et al. 1989), leading to density-dependent declines in their numbers. Predator numbers grow more slowly than prey, but, at some point become abundant enough that their effects are additive to resource limitation, thus accelerating the prey population crash. Therefore, rabbits are influenced primarily by resources, and while predators have some effect, they tend to ‘ride the back’ of rabbit abundance (predators are ‘passengers, not drivers’, as expressed by White (2013)).

Salo et al. (2010) concluded that most predator manipulation studies showed an effect on prey populations but the effect was small or non-existent for resource-driven prey dynamics. Similarly, White (2013) reviewed the evidence for predator regulation of prey and concluded that co-evolved predator–prey dynamics are generally driven bottom-up. This contrasts with non-co-evolved dynamics where the top-down effects of introduced predators may lead to extinctions of naive indigenous prey with which they did not evolve, as happens in many New Zealand systems. The predators we have discussed so far in our review co-evolved with European rabbits either over millions of years, or more recently over thousands of years as people introduced rabbits into other parts of Europe. Rabbits and their predators have presumably adapted their behaviours to co-exist; co-evolution and co-existence imply that predators would be unlikely to suppress rabbit numbers continuously to very low levels. Instead, they should theoretically co-exist in a ‘stable-limit’ cycle (sensu May 1972), as appears to be the case in the wild. That does not mean to say that removal of predators cannot lead to increased rabbit numbers (as occurs in some circumstances), but it supports the idea that rabbit abundance is by and large determined by factors other than predation, and that predator abundance (especially for species that specialise on rabbits) can usually be predicted by rabbit abundance, not necessarily vice versa.

10 Conclusions

It is important to emphasise the difference between regulating factors, which drive populations towards some long-term average density, and limiting factors, which cause changes in vital rates (e.g. productivity, or survival of some component(s) of the population) but do not necessarily drive the population towards any particular state (Reddiex et al. 2001). The evidence reviewed here is reasonably consistent: predation acts as a limiting factor on rabbits, primarily through its effects on juvenile survival, and on rabbit abundance and population dynamics under certain conditions, but its effects are minor compared with the roles of climate, food, disease and habitat. Rabbit population dynamics are typically driven by processes other than predation, and there is good evidence that in many circumstance rabbit abundance drives the abundance of predators. When rabbit populations are in decline, or are regulated by bottom-up pressures, predation may act to accelerate the decline or to limit the rate at which they recover. The question posed in this report is whether control of introduced predators leads to greater abundance of European rabbits in New Zealand. Based on the evidence, this seems less likely for areas that are periodically highly favourable for rabbits, such as in the continental-type climates of the central South Island, and more likely where other forms of rabbit mortality prevail (Reddiex et al. 2002), such as in some high rainfall zones (Tyndale-Biscoe & Williams 1955; Robson 1993; Gibb & Fitzgerald 1998). Any increases in rabbit numbers after predator control, however, are likely to be small compared with the primary influence of bottom-up processes and disease.

11 Future research recommendations

A key unresolved question is: if in some circumstances, predator control leads to rabbit increases, can those circumstances be identified with enough certainty to generate predictions about where and when rabbit increases are likely to occur, and if so, how many extra rabbits can be attributed to predator control? Answers to these questions will greatly inform the debate between concerned landholders and pest control agencies, and in theory, lead to fairer and more equitable outcomes. Such data, however, are unlikely to be available without a large number of carefully controlled experiments conducted in a variety of different land types and climatic conditions (see Reddiex & Forsyth 2006). This would be prohibitively expensive and difficult to achieve. A partial solution would be to design and implement a robust and consistent rabbit, predator and disease monitoring programme at sites adjacent to or overlapping predator control operations such that data on changes in rabbit populations could be collected alongside data on changes in the other processes likely to have major impacts on rabbit population dynamics. For example, the effectiveness of RHD is waning in some areas, leading to increased rabbit numbers (Parkes et al. 2008). These effects need to be accounted for in any predator control programme. These data would facilitate reasonable inference about predator effects on rabbit abundance. Inclusion of carefully matched non-treatment areas (rabbit populations that are unaffected by predator control programmes but are exposed to similar climate, food supply and disease prevalence) is perhaps the most crucial requirement of such a programme. Without this, little or no inference can be made about the effects of predator control. Although the establishment of a widespread monitoring programme of this type may seem onerous, we suggest that the concept could be trialled in one region, with others contributing monitoring data to construct a national picture.

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