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REVIEW

Pests controlling pests: does predator control lead to greater European rabbit abundance in Australasia?

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ABSTRACT

1. In New Zealand and Australia, rural landowners believe that local predator control to protect indigenous biota exacerbates European rabbit *Oryctolagus cuniculus* problems on their land. We assess the validity of their concerns by reviewing the published literature on effects of predators on rabbit abundance.
2. In New Zealand, where rabbits and their predators are introduced, predators appear to have relatively little effect on rabbit numbers compared with other factors leading to mortality, such as disease, flooding of burrows and burrow collapse. Similarly, in Australia, rabbit numbers are driven primarily by climate and its 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. In the Iberian Peninsula, where rabbits and their predators are indigenous, the effects of predators are unknown, as they are often confounded by other factors. Rabbit numbers are influenced mostly by habitat, food, disease and rainfall. Elsewhere in Europe, predators have their strongest effect when rabbit numbers have been reduced by other factors, but have little effect on high-density rabbit populations.
3. In Australasia, abundance of predators (especially rabbit specialists) can usually be predicted from rabbit abundance, not vice versa. Although predation effects can be limiting under certain conditions, they are minor compared to the roles of climate, food, disease and habitat.
4. A key unresolved question is whether those circumstances where predator control might lead to increases in rabbit populations can be identified with enough certainty to allow reliable predictions to be generated. One approach is to implement robust rabbit, predator and disease monitoring programmes at sites with predator control operations. Data on changes in rabbits, predators, and disease prevalence could be combined with local data on other key factors to facilitate reasonable inference about effects of predators on rabbits. The inclusion of carefully matched non-treatment areas is crucial if such programmes are to succeed.

INTRODUCTION

As predator control programmes aimed at enhancing indigenous biodiversity or game bird populations expand in some regions, landholders with overabundant European rabbits *Oryctolagus cuniculus* (referred to as ‘rabbits’) sometimes argue that predator control on land adjacent to their properties exacerbates their rabbit problems. In New Zealand, where rabbits and their mammalian predators are introduced, some landholders are seeking a financial contribution from local pest control authorities and the government’s Department of Conservation to subsidize 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, non-government organizations and landholders. Public perceptions are critical: many landowners and members of the general public 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 towards addressing this issue, and to update Trout and Tittensor's (1989) overview, we review the published scientific literature on the effects of predators on rabbit populations.

Ecological processes

In addition to being affected by disease, in general terms, the dynamics and abundance of prey populations at any point in time are governed by resources such as food and shelter, and by predation from predators at higher trophic (feeding) levels (Fig. 1). These are referred to in the literature as 'bottom-up' and 'top-down' processes, respectively, and provide a convenient structure for placing effects of predators in the wider context of other factors that influence rabbit populations. Animal populations are rarely governed exclusively by top-down or bottom-up regulation, and the relative strengths of both processes vary with environmental factors (Elmhagen et al. 2010), such as climate

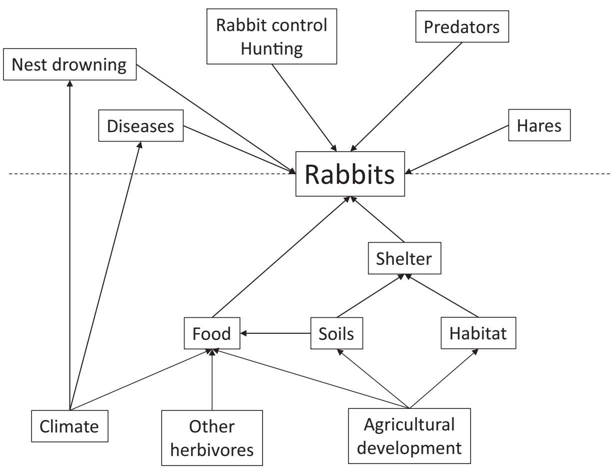

Fig. 1. Some of the key factors that affect rabbit abundance, showing predation as only one of many influences. Those above the dotted line are sometimes referred to as 'top-down' influences, and those below the line as 'bottom-up' influences. Disease includes myxomatosis, rabbit haemorrhagic disease and coccidiosis. There is some evidence for interference competition from hares on low-density rabbit populations (Flux 2008). Agricultural development includes replacement of indigenous vegetation with productive pasture species and the application of fertilizers.

and soil conditions. While we partially address disease, other population drivers, such as competition, are not addressed explicitly in this review.

Review structure

Animal population dynamics are complex. The question posed in this review is quite specific and, ideally, requires replicated predator manipulation experiments that test the effects of predation directly by controlling for influences other than predation. Our review focuses on mainland New Zealand and Australia (summarized in Table 1), where rabbits and their associated predators were introduced by European colonists, and where both predators and prey are significant threats to indigenous biota and local production systems. Experiments conducted in New Zealand are reviewed first, followed by descriptive or correlative studies on, for example, rates of predation on rabbits, or links between the natural variability in rabbit and predator abundances. Factors that influence the survival of rabbits, especially juveniles, are likely to 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 in Australia have similar pest status to those in New Zealand, but the guild of mammalian (and avian) predators in Australia that consume rabbits (primarily foxes *Vulpes vulpes*, feral cats *Felis catus* and dingoes *Canis lupus dingo*) is quite different from that in New Zealand (cats, feral ferrets *Mustela putorius furo*, stoats *Mustela erminea*, weasels *Mustela nivalis vulgaris*), and the climatic fluctuations and dryland environments are often more extreme in Australia. Finally, for comparison, we briefly 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. In 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).

METHODS

The literature was searched using the Web of Science (v.5.14) search engine with the keywords 'rabbit' and 'predator'. This produced 1028 papers, book chapters, reports, and conference proceedings published from 1920 to 2014. We narrowed this result down by focussing only on those publications in which demographic responses of predators and prey were considered. We cross-checked and validated our literature set by checking the cited references within each publication.

Table 1. Studies reviewed on the effects of predators on European rabbit populations in New Zealand and Australia. For experimental manipulations, we note whether a non-treatment comparison was reported; for observational studies, this is not applicable (na)

Location	Approach	Main factors addressed	Non-treatment	Predation purported as important?	Reference
Wairarapa, New Zealand	Experimental	Predation Food	No	Yes, coupled with food shortage	Gibb et al. (1978)
North Canterbury, New Zealand	Experimental	Predation Disease	Yes	Yes, coupled with disease	Reddiex et al. (2002)
Central Otago, New Zealand	Experimental	Predation Disease	Yes	No	Reddiex (2004)
Northland, New Zealand	Experimental	Predation	Yes	Yes	Gillies et al. (2003)
Otago, New Zealand	Experimental	Predation	Yes	No	Norbury et al. (2013)
Wairarapa, New Zealand	Descriptive	Parasitism	na	Yes, coupled with parasitism	Tyndale-Biscoe and Williams (1955)
North Canterbury, New Zealand	Descriptive	Predation Nest drowning	na	Yes	Robson (1993)
Wellington region, New Zealand	Descriptive	Predation Food	na	Yes	Gibb and Fitzgerald (1998)
New South Wales, Australia	Experimental	Predation Rainfall	Yes	Yes, coupled with drought	Newsome et al. (1989), Pech et al. (1992)
Western Australia, Australia	Experimental	Predation Rainfall	Yes	Yes, coupled with food	Risbey et al. (2000)
New South Wales, Australia	Experimental	Predation	Yes	Yes	Banks (2000)
New South Wales, Australia	Experimental	Predation	Yes	No	Davey et al. (2006)
New South Wales, Australia	Descriptive	Predation Disease	na	Yes	Parer (1977)
New South Wales, Australia	Descriptive	Predation Disease	na	Yes	Wood (1980)
Australian Capital Territory, Australia	Descriptive	Predation	na	Yes	Richardson and Wood (1982)
New South Wales, Australia	Descriptive	Predation Disease	na	Yes	Moriarty et al. (2000)

NEW ZEALAND

Experimental studies

Gibb et al. (1978) studied a single rabbit population inside an 8-ha fenced enclosure in the Wairarapa district of the North Island over a 10-year period. For the first six years, numbers of rabbits increased until they exhausted their food supply, then numbers collapsed. Numbers of predators (cats and ferrets) lagged behind rabbits, but the authors concluded that predation 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. Numbers of rabbits remained low until predators were removed, and then increased 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 rabbits. 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. it was not 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 reduced predation pressure and the increased availability of food on rabbit population recovery. These kinds of experiments are often vulnerable to a 'fence effect' (enclosed populations can reach unnaturally high densities; Krebs et al. 1969) and a 'pantry effect' (predators in the surrounding area are attracted to the enclosed, high-density prey population – although in this case, predators were mostly deterred from crossing 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 (South Island) at the same time as RHD arrived. Rabbit abundance was measured there and at two other 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 (2004) replicated the experiment at two other South Island sites in Central Otago, where conditions for rabbit survival and growth are more favourable. Again, the experiment coincided with an outbreak of RHD, and although the effect of the disease on rabbits was not quite as pronounced as in North Canterbury, no effects of predator removal were apparent on the rates of rabbit population decline.

Gillies et al. (2003) described the effects of a predator control operation in a northern kauri *Agathis australis*–podocarp forest and adjoining grasslands on both predator and prey populations. At the predator control site, indices of rabbit abundance derived from spotlight counts increased, but they were highly variable during the post-control period. The indices were also higher than at a nearby non-treatment site. Unfortunately, the study design makes it impossible to account for the effects of potential drivers of rabbit abundance other than predation. For example, there was no pre-treatment monitoring of rabbit numbers at the non-treatment site, which may have had fewer rabbits anyway (due perhaps to RHD or lower resource availability) irrespective of predator abundances. In addition, the marked variability in post-control rabbit abundance indices at the predator control site suggests that other factors, as well as any release from predation, are likely to have driven rabbit numbers (e.g. RHD, changes in food supply, release from competition from brushtail possum *Trichosurus vulpecula*, which were also controlled). Scale and resourcing frequently limit replication in predator-prey studies, so these issues are common to many studies.

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

None of the experiments carried out to date in New Zealand provides compelling evidence for a top-down effect of predators on rabbit abundance. RHD is now endemic in New Zealand, so the study by Gibb et al. (1978) is arguably less relevant to present circumstances and, as noted above, the conclusions of this study were weakened by limitations in experimental design. The studies by Reddiex et al. (2002) and Reddiex (2004) showed overwhelming effects of the initial RHD epizootics, which were lessened to some extent by predator removal at one site. The studies by Gillies et al. (2003) and Norbury et al. (2013) represent the present endemic condition of RHD in New Zealand, but they were either limited by experimental design or they failed to demonstrate an effect of predator removal on rabbit abundance.

Other studies

Although other researchers working in New Zealand 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, mortality caused by other factors, such as disease, flooding of burrows, or burrow collapse, seems to be of equal or greater importance (Tyndale-Biscoe & Williams 1955, Robson 1993, Gibb & Fitzgerald 1998). High rainfall is generally associated with these other causes of mortality. In drier areas, 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 for bottom-up effects of rabbit numbers on predator abundance is more compelling than the evidence for top-down effects of predators on rabbit abundance, at least in the rabbit-prone areas of Central Otago and the Mackenzie Basin (all South Island; Norbury & McGlinchy 1996, Norbury 2001, Cruz et al. 2013). Rabbit populations are also driven by bottom-up effects: favourable environmental conditions enable them to maximize their reproductive output (Robertshaw 1992, Gibb & Williams 1994) as does pasture development through the replacement of indigenous vegetation with productive pasture species and the application of fertilizers (Norbury et al. 2013). Predator populations in rabbit-prone areas respond indirectly to this increase in primary productivity by responding to increases in rabbit productivity and hence the availability of young rabbits (Gibb & Fitzgerald 1998). Consequently, compared with this strong bottom-up influence, predators appear to have relatively little top-down effect on rabbits.

AUSTRALIA

Many studies conducted outside New Zealand include the effects of foxes, reptiles and a greater suite of raptors. Foxes are generalist predators that do not rely on rabbits as a primary source of prey, apart from when rabbits are abundant (Delibes-Mateos et al. 2008a).

Experimental studies

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 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 suggest 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) showed subsequently that when predators were allowed back into the same predator-removal areas, rabbit populations continued to increase and did not decline to the density in the untreated area, where predators had remained uncontrolled throughout. 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 that, when rainfall increased, numbers of rabbits increased at fox control sites but remained low on untreated sites. Banks (2000) recorded 10.3- to 23.3-fold increases in rabbit numbers in subalpine forest-grassland habitats following 20 months of fox removal at two sites, compared with relatively little change in rabbit numbers at sites where foxes were not removed. When fox control stopped, rabbit numbers declined at both sites. They remained suppressed for 16 months at one site (but at a greater level than prior to fox control) but recovered at the other site where fox reinvasion was slower, thus allowing rabbit productivity to outstrip predation. Robley et al. (2004), reviewing these and other Australian studies, concluded that predation may have a regulatory effect on rabbit populations that are suppressed to low densities by poor environmental conditions (e.g. drought), but that this regulatory effect is weakened when conditions improve.

Not all experiments conducted in Australia, 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 found no effect of fox removal. In fact, the greatest response of rabbit populations 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: rabbit numbers continued to fluctuate seasonally, suggesting that environmental conditions were the primary driver of population changes.

Other studies

Significant levels of predation by cats and foxes on juvenile (Parer 1977, Wood 1980, Richardson & Wood 1982) and adult (Moriarty et al. 2000) rabbits have been reported in Australia. Soil type can affect the vulnerability of juvenile rabbits in burrows to predation by foxes, as sandy soils are more easily excavated (Wood 1980). Newsome et al. (1989), Risbey et al. (2000), Davey et al. (2006) and Fordham et al. (2012) demonstrated clearly that rabbit populations in Australia are driven primarily by climate and its 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 under certain conditions, where rabbit numbers are low following drought or epizootics, predation can limit population recovery. The response of rabbits at any particular site may represent a fine balance between bottom-up and top-down regulation, as exemplified by the contrasting responses of rabbits to the reinvasion of foxes at Banks's (2000) treatment sites.

EUROPE

Iberian Peninsula

Studies of the impacts of predators on indigenous rabbits in 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 of rabbits, and the predators that specialize on them, are at undesirably low levels for conservation purposes in much of the region (Delibes-Mateos et al. 2009a). Moreover, predator populations are difficult to manipulate because most predator species are indigenous and legally protected, and therefore are usually not controlled. In some game estates, however, quite intensive predator control is undertaken, at least in central and southern Spain (Delibes-Mateos et al. 2013. This is mostly targeted at indigenous predators. Some, such as foxes, are legally controlled, while others are illegally controlled (Barrull et al. 2011). 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. Rouco et al. (2008) found no significant effects of predator exclusion on the fate of translocated rabbits, but other experimental factors may have obscured these effects. Delibes-Mateos et al. (2009a) cautioned that it is still unclear whether control of generalist predators in the Iberian Peninsula allows rabbit populations to increase. As in New Zealand and Australia, rabbit populations in the Iberian Peninsula appear to be influenced mostly by bottom-up processes such as habitat, food, rainfall and shelter (Calvete et al. 2004, Ferreira & Alves 2009, Ferreira et al. 2013), and by disease (Moreno et al. 2007). Rabbits appear to drive the abundance of some predator species (Ferreras et al. 2011), rather than the other way around.

Other parts of Europe

To our knowledge, no published predator manipulation experiments involving rabbits have taken place in other parts of Europe, reflecting the species' complex management status: rabbits are threatened indigenous wildlife in some areas but are considered 'vermin' in other areas and on some traditionally managed game estates. Trout and Tittensor (1989) reviewed the evidence for impacts of predators on rabbit populations in the United Kingdom and elsewhere in Europe and found that high rabbit numbers were generally associated with low predator abundance (without control 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 of rabbits. 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.

GENERIC PATTERNS: TOP-DOWN OR BOTTOM-UP?

The question of whether or not predators drive the abundance of their prey has received much attention from ecologists over the years. Early work suggested that predators consumed only the 'doomed surplus', i.e. individuals that could not be supported by the available resources (Errington 1946). Attention then shifted to the role that top predators play in systems by controlling the abundances of stronger competitors at lower trophic levels, thus allowing greater diversity of species to exist 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, and that the relative strengths of these processes vary with environmental conditions (see also Meserve et al. 2003 and Krebs 2013). For primary prey species such as rabbits, population growth eventually declines as resources diminish, but high densities may lead to increased predator numbers. Eventually, rapidly reproducing prey species, such as rabbits, reach such high densities that resources are insufficient to maintain population growth (Parer 1977, Newsome et al. 1989), leading to density-dependent declines in their numbers. Numbers of predators increase more slowly than those of prey, but predators may become so abundant that their effects on prey populations are additive to the effects of 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'; White 2013).

Salo et al. (2010) concluded that most predator manipulation studies show that predators have an effect on prey populations, but the effect is small or non-existent for resource-driven prey dynamics. Similarly, White (2013) reviewed the evidence for predator regulation of prey populations 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 contribute to extinctions of naive indigenous prey with which they did not evolve, as in many New Zealand and Australian systems. The predators we have discussed so far in this review co-evolved with European rabbits either over millions of years, or more recently over thousands of years, since people introduced rabbits into other parts of Europe. Rabbits and their predators have presumably adapted their behaviours to co-exist (e.g. Barrio et al. 2010); 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 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 specialize on rabbits) can usually be predicted by rabbit abundance, not necessarily vice versa.

CONCLUSIONS

It is important to emphasize 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) but do not necessarily drive populations towards any particular state (Reddiex et al. 2001). The evidence reviewed here is reasonably consistent: predation is a limiting factor for populations of 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 effects 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 circumstances, 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 populations recover.

RESEARCH RECOMMENDATIONS

Key unresolved questions are: if, in some circumstances, predator control leads to increases in numbers of rabbits, can those circumstances be identified with enough certainty to generate predictions about where and when rabbit populations are likely to increase, and if so, what proportion of the population increase is attributable to predator control? Answers to these questions will inform the debate between concerned landholders and pest control agencies, and, in theory, lead to fairer and more equitable outcomes. The data needed to answer the questions, however, are unlikely to be available without a large number of carefully controlled experiments conducted in a variety of different land types and under various climatic conditions (see Reddiex & Forsyth 2006). This would be prohibitively expensive and difficult to achieve. A partial solution would be to implement a robust rabbit, predator and disease monitoring programme where predator control operations take place. 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 as a control method is waning in some areas, leading to increased rabbit numbers (e.g. Parkes et al. 2008). Crucially, such effects need to be accounted for by including carefully matched non-treatment areas (where rabbit populations are unaffected by predator control programmes but are exposed to similar climate, food supply and disease prevalence). Without non-treatment areas, little or no inference can be made about the effects of predator control.

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