ECOLOGICAL COSTS OF FERAL PREDATOR CONTROL: FOXES AND RABBITS

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Abstract: We used a predator removal experiment to examine the role of red fox (*Vulpes vulpes*) predation in suppressing rabbit (*Oryctolagus cuniculus*) population growth in Namadgi National Park in southeastern Australia. At 2 sites, fox abundance was reduced with a 1080 poisoning campaign maintained over 18 months. The responses of rabbit populations in these fox-reduced sites were compared to 2 other sites where fox populations remained intact. In the 2 removal sites, rabbit populations grew to 6.5 and 12.0 times their initial population size within 18 months. In the untreated sites, rabbit populations showed very small population increases over the same period. The experiment demonstrated that 1 introduced pest species suppressed the population growth of another pest species. As fox removal was initially planned to protect native fauna threatened by fox predation, the response of the rabbits represents a serious ecological cost of fox control.

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The red fox (hereafter, fox) was introduced into Australia in the 1850s and quickly became a major pest species across the southern half of the continent (Rolls 1969). This species is implicated in the decline or extinction of 23 species of native small- and medium-sized mammals and currently is listed as a significant threat to 30 species of endangered or vulnerable mammals and birds (Saunders et al. 1995). The fox also is a significant predator of domestic stock, in particular sheep and lambs, and can

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kill up to 30% of the lambs produced in some areas (Lugton 1993). Hence, control of foxes has become a priority for nature conservation agencies and the agricultural industry in Australia.

There is a close relation between the fox and another introduced vertebrate pest in Australia, the European rabbit (hereafter, rabbit). Where rabbits are available, they are consistently the major prey item of foxes, composing up to 100% of the fox diet in some areas (Newsome et al. 1997). The spread of the rabbit less than a decade before the introduction of the fox no doubt assisted spread of the latter species (Rolls 1969); today, the distributions of these 2 pests closely overlap (Wilson et al. 1992). Rabbits apparently support fox populations at elevated levels, which then affect native species via opportunistic predation (Christensen 1980, Lundie-Jenkins et al. 1993). Direct environmental damage caused by the rabbit includes competition with many native species of herbivores as well as domestic stock, and severe land degradation via overgrazing and construction of warrens (Williams et al. 1995). Indeed, the rabbit is recognized as Australia's number 1 vertebrate pest.

There is abundant anecdotal evidence that fox predation suppresses growth of rabbit populations, but there is limited experimental support. In arid New South Wales, Wood (1981) estimated that foxes took up to 75% of newly emergent juvenile rabbits and caused a mortality rate of >85% for rabbits <9 months old. Foxes also prey heavily on adult rabbits in arid environments (Martenz 1971, Bayly 1978, Catling 1988), and Wood (1981) suggested that density-dependent predation by foxes may limit rabbit population growth. This hypothesis was confirmed by Newsome et al. (1989) in a fox removal experiment demonstrating predator suppression of rabbit populations, and Pech et al. (1992) showed further that predators regulated rabbit numbers at low densities through density-dependent predation. In arid environments, the presence of foxes mitigates the effects of rabbits because foxes slow the recovery of rabbit populations after drought (Newsome et al. 1989).

In temperate areas where environments are less variable, the role of predation in suppression of rabbit numbers is less clear. Rabbit population dynamics in cooler climates are strongly influenced by rainfall (Gilbert et al. 1987) and also by nutrient levels (Andrewartha and Birch 1984), but populations do not fluctuate as dramatically as in arid areas. Mortality of juveniles in temperate areas is around 30%, which is lower than arid areas, but appears to be higher in areas with predators (Richardson and Wood 1982). Rabbits remain the staple prey for foxes (Newsome et al. 1997), but the effect of this predation is not known, and it is not clear if this predation suppresses rabbit population growth or is compensatory.

In this paper, we report the responses of rabbit populations to a fox control program designed to protect native fauna in a subalpine area. Hence, we measure the responses of rabbit populations to fox control as a by-product of efforts to protect native wildlife, and discuss the role of fox predation in the suppression of this significant vertebrate pest.

STUDY AREA

The study was conducted in Namadgi National Park, an area of subalpine forest and repossessed open grassy farmland in the Brindabella Ranges, 50 km south of Canberra, Australia (35°40′S, 149°5′E). We chose 4 valleys, each approximately 10 km^2 in area and separated by 7–22 km of mostly sclerophyllous forest. We assumed these distances provided some barrier to fox movement, and thus independence among sites. Rabbits were most abundant in the ecotone between the cleared valley and the remnant timbered areas; foxes were prevalent throughout. The main mammalian prey of foxes is rabbits (40% by occurrence) and kangaroos (*Macropus giganteus*; ≤45%), with native small mammals, invertebrates, and vegetation composing the remainder (P. Banks, unpublished data).

METHODS

Reducing Fox Numbers

We reduced fox numbers at the 2 removal sites via 1080 baiting. We buried approximately 60 commercial FOXOFF baits (35 g each) in and around the 2 valleys; each bait contained 0.3 mg of 1080 (sodium monofluoroacetate). To target transient and reinvading animals, we placed baits at 200-m intervals on the main access roads through the sites and on all roads in a 5-km radius around the sites. The baits were buried 10 cm beneath a pile of loose soil that attracted passing foxes.

We initially checked baits over a 10-day period and replaced any baits taken. This schedule was designed to reduce fox numbers as quickly as possible. After this period, fresh baits were placed monthly, checked after 7 days, and removed if not taken. Baiting began in July 1993 and continued to January 1995. Despite a clear decline in local fox activity, baits were continually taken by reinvading foxes, and individual foxes likely took multiple baits before they died.

Monitoring Fox Populations

To ensure that fox numbers were reduced in the removal sites, we used a combination of spotlighting, uptake of nontoxic baits, and scat counts to index the abundance of foxes in each of the 4 areas. We conducted spotlighting counts of foxes (animals/km) for 3–4 consecutive nights each month along 5-km transects at each site. Any foxes seen while spotlighting in the removal sites were shot in the head with a low velocity 0.22-calibre rifle that made minimal noise. Less than 25% of the animals seen were shot, because many animals were too far away or too difficult to shoot. Overall, however, 1080 baiting was the most effective control technique. Once fox numbers had been substantially reduced (late 1993), baiting was used as the primary method of fox control.

We also used nontoxic baits to monitor fox numbers. Prior to using poison baits, we buried 30 nontoxic baits at 200-m intervals along roads at each site. The number of baits removed after 2 days was then used as an index of fox abundance. We conducted this monitoring twice at all 4 sites, 12 and 18 months after fox removal began. The techniques used to monitor fox numbers at the removal sites were identical to those used in the nonremoval sites and are directly compared to nonremoval sites in the results. We also counted scats and removed them from 3-km transects established along roadsides at each site as another index of fox abundance. We made collections bimonthly because few scats were present in the removal sites after the removal campaign began.

Monitoring Rabbit Populations

We monitored changes in rabbit abundance associated with fox removal via spotlight counts (animals/km) on 5-km transects established at each site (Newsome et al. 1989, Pech et al. 1992). Spotlighting is an acceptable and reliable index of rabbit abundance compared to other census methods such as counts of active warren entrances (Pech et al. 1992), and was considered the technique best suited for our local conditions and requirements. Although spotlighting may miss juvenile animals that remain close to the warren (Newsome et al. 1989), counts of active warren entrances would have underestimated the growth in rabbit numbers at the removal sites because many animals apparently were living on the surface.

To spot rabbits, we used a 100 W spotlight from the top of a vehicle travelling <5 km/hr. We drove along spotlight transects on 3–4 consecutive nights/month at or near the new moon. In preliminary surveys, we saw more rabbits on dark, moonless nights compared to moonlit nights (Kolb 1992). Surveys were not conducted on rainy or on windy nights, which reduced weather-related variability in the data (Williams et al. 1995). Spotlighting commenced 1 hr after dusk to coincide with the peak in activity of rabbits (Williams et al. 1995). We conducted surveys for foxes and rabbits on the same nights, but if foxes were shot at the removal sites, we omitted from the dataset the survey for rabbit numbers on that night, due to potential disturbance. We conducted spotlight censuses of rabbit numbers every month from May 1993 to February 1995.

RESULTS

Fox Removal

The removal campaign began in July 1993 and in 6 months resulted in a decline of foxes from 2.8 and 3.4/km to <0.5/km at the 2 removal sites (Fig. 1A). After 12 months, this density was reduced to near zero. Over the same period, numbers in the untreated sites remained relatively steady, with a large peak associated with the appearance of cubs at 1 site, followed by some declines during the second winter (Fig. 1B). Initial fox densities at the control sites were 2.0/km and less than at the removal sites (2.5–3.0 km). However, at 12 and 18 months of fox control, the nontoxic bait indices of fox activity showed substantially more baits taken in the nonremoval sites compared to removal sites. Between 90 and 94% of baits were taken in 2 nights at the nonremoval sites compared to 0 and 5% at the removal sites. Similarly, signs of foxes were substantially reduced at the removal sites, where <3 scats/km were found along transects compared to about 20 scats/km of transect at the nonremoval sites. These data confirm the efficacy of the removal

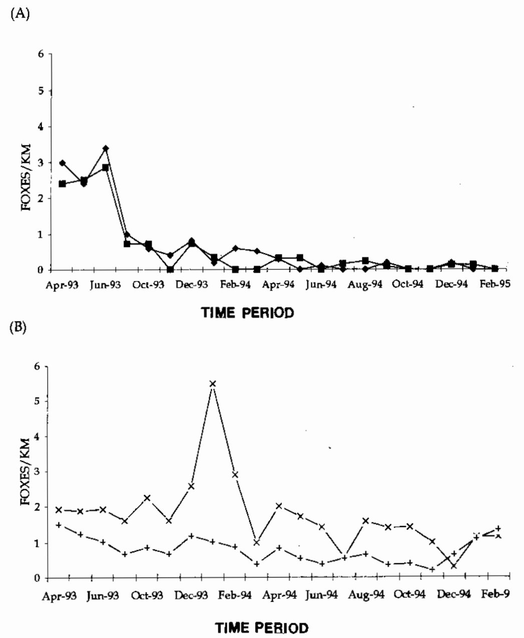

Fig. 1. Numbers of foxes observed from spotlight transect counts in (A) fox removal sites and (B) nonremoval sites. Values represent the mean number of foxes seen per spotlight kilometer averaged over at least 3 consecutive nights spotlighting each survey. In (A), (—♦—) = removal site 1 and (—■—) = removal site 2. In (B), (—+—) = nonremoval site 1 and (—x—) = nonremoval site 2.

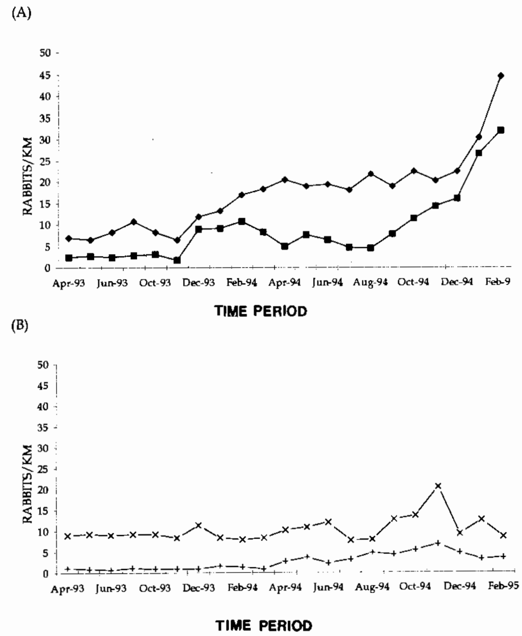

Fig. 2. Numbers of rabbits observed from spotlight transect counts in (A) fox removal sites and (B) nonremoval sites. Values represent the mean numbers of rabbits seen per spotlight kilometer averaged over at least 3 consecutive nights spotlighting each survey. In (A), (—♦—) = removal site 1 and (—■—) = removal site 2. In (B), (—+—) = nonremoval site 1 and (—x—) = nonremoval site 2.

campaign and point to a clear and consistent difference in the abundance of foxes between the removal and nonremoval sites.

Responses of Rabbits

Prior to removal of foxes, rabbit numbers in all 4 sites were between 2 and 8/km. Small increases were seen at the removal sites within 1 month of the initiation of fox removals (Fig. 2A). However, these increases diminished over October and November 1993 when a rabbit control campaign was initiated by the National Parks staff. Numbers dropped to slightly less than preremoval levels but increased immediately during the month following breeding. Rabbits continued to increase in fox removal sites to 6.5 and 12.0 times their initial population sizes after 18 months of fox control. This increase represents an instantaneous rate of increase, r, (Caughley 1977) of 1.3 and 1.7/year. Numbers at 1 of the nonremoval sites increased from very low densities to almost 2-fold over the same period, while numbers declined slightly at the other site (Fig. 2B). This change constituted instantaneous rates of increase of 0.46 and 0.03/year. Rabbit numbers were higher at the removal sites after 18 months ($t_2 = 4.7$, $P < 0.05$) and were still increasing when the experiment ended.

DISCUSSION

The 1080 poisoning was very effective in reducing the abundance of foxes at the removal sites. Other nontarget predators of rabbits (e.g., feral cats, dingos [*Canis familiaris*], wedgetailed eagles [*Aquila audax*]) appeared unaffected by the fox baiting. Compared to foxes, these 3 species were at very low densities throughout the study. At all sites, feral cats were seen very infrequently (<1 animal every 2 months), dingos were trapped by National Parks staff and rarely encountered, and wedgetails were infrequent visitors. Moreover, FOXOFF contains chemical attractants specifically targeting foxes. Thus, although the active compound "1080" is toxic to cats and dingos, both species continued to be seen in the removal sites after baiting began, and <2% of baits taken could not be attributed to foxes. Hence, foxes were by far affected most by the removal campaign, where-by the abundance of foxes was the only clear difference between removal and nonremoval sites that was attributable to the poisoning.

We conclude that fox predation suppressed population growth of rabbits in this subalpine environment. In the removal sites, rabbit populations increased at least 6.5 times within 18 months following fox control. Further, if rabbits had not been reduced by National Parks Service control efforts, the population growth could have been significantly larger. In the areas where foxes remained, the numbers of rabbits remained steady and grew only 10% over the same period. Much of the population growth occurred in the latter half of the experiment, which was during the second breeding season. After pasture improvement in arid New South Wales, rabbit populations that were reduced by drought increased 11.7 times after 14 months of predator control at a fox-removal site compared to 2.8 times at the nonremoval site (Newsome et al. 1989). This initial response was much quicker than occurred in the present study where populations increased 1.5 times within just 6 weeks. At Namadgi, where there were no major fluctuations in environmental conditions during the study, foxes appeared to strongly suppress rabbit population growth.

There has been little other experimental work investigating the role of predator suppression on rabbit populations. Trout and Tittensor (1989) reviewed an abundance of anecdotal evidence, analyzing patterns of rabbit abundance under varying degrees of predator control in rural England. They concluded that predators did play a role in the suppression of rabbit numbers. However, rabbit populations continued to fluctuate and, in some instances, only the magnitude of fluctuation was affected by predation. Experimental evidence provided by Newsome et al. (1989) and the present study confirms these predictions. At Namadgi, rabbit numbers remained stable over the study period at the sites with foxes, and there were only small and rapidly subsiding rises during the breeding season. However, it was not possible to confirm that this small decline was due to fox predation.

MANAGEMENT IMPLICATIONS

The fox control program outlined here was initiated primarily to quantify the direct effect of fox predation on native mammal species. However, a by-product of this control was an increase in another vertebrate pest species and creation of potentially greater environmental problems than in the areas where foxes remained. The environmental damage caused by rabbits can be severe (see reviews by Sumption and Flowerdew 1985, Williams et al. 1995). In particular, overgrazing can lead to increased competitive pressure upon the very native herbivores (Cooke 1993, Lundie-Jenkins et al. 1993) that the fox control program is designed to protect.

Foxes may have a role to play in management of rabbit populations, but this role needs quantification (Williams et al. 1995). Rabbit recovery following control programs might be significantly faster if predators are removed. Therefore, control techniques with less potential for secondary poisoning of predators may be more effective in the long-term management of rabbits. Clearly, if foxes had not been removed, the rabbit population would not have increased to the observed levels in such a short period. In the absence of foxes, the rabbit control program initiated in November 1993 was essentially redundant within 3 months; after 18 months, the rabbit problem was 5 times worse. This response represents a clear and potentially great ecological cost of fox control.

This scenario is likely to be repeated in many areas where rabbits and foxes coexist, in particular where foxes are controlled to relieve predation pressure on alternate or opportunistically eaten native species of prey (Lundie-Jenkins et al. 1993). Where rabbits are present, no native prey species has been taken more frequently than rabbits, and there is some evidence that foxes may take rabbits selectively (Brunner et al. 1975, Seebeck 1978). Although native prey species that are very infrequent prey items for foxes may still be limited by this low level of predation, any significant population growth resulting from fox control will likely be slower and less obvious than the response by rabbits. Recovery times for native species are likely longer than for rabbits because native species generally have lower initial densities (e.g., Kinnear et al. 1988) and lower intrinsic rates of increase compared to rabbits (Dickman 1996), and there is a greater likelihood that predation pressure will be much higher and potentially more limiting for rabbits than native species. As a result, control of foxes will result in a rabbit problem long before native species show signs of significant recovery. This inevitable result is an important consideration for land managers.

Overall, this study shows that foxes can suppress populations of other vertebrate pests and have a role to play in effective management of rabbits (Newsome 1990). Protection of native species threatened directly by fox predation via control of foxes may therefore result in significant and potentially large increases in rabbit numbers. This unwarranted ecological cost of fox control must be weighed against the benefits to native prey species. Where fox control is imperative, integrated programs that control foxes and rabbits simultaneously will be necessary, and the economic costs of rabbit control must be included in costs of removing foxes to protect native fauna. Alternatively, where potential native prey for foxes are not threatened, long-term control of both rabbits and foxes might best be achieved with rabbit control techniques that do not immediately affect foxes (e.g., warren destruction). This approach would allow for persistence of some foxes to maintain predation pressure upon rabbit populations and suppress rabbit population growth for an extended period (King et al. 1981).

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