

CAN FOXES REGULATE RABBIT POPULATIONS?

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Abstract: I report on the second part of a 2-phase experimental test of the predator regulation hypothesis. I examined the effect of predation by red foxes (*Vulpes vulpes*) on the population dynamics of European rabbits (*Oryctolagus cuniculus*) in montane Australia. Foxes were permitted to reinvade 2 sites where indices of rabbit numbers had increased 10.3- and 23.3-fold after 20 months of fox removal, and compared trajectories of these rabbit populations with those at 2 other sites where fox populations were not controlled. Over 16 months, foxes returned to both removal sites, reaching levels comparable to those on nonremoval sites, but lower than preremoval densities. Rabbit populations declined immediately after foxes reinvaded and remained low for 16 months on one site, suggesting that fox predation was effective at regulating numbers. However, the rabbit population on another higher-density site recovered and increased another 23% over the following 16 months, suggesting they were not regulated by predation. Rabbit numbers at nonremoval sites continued to be suppressed. These results did not provide consistent support for the predator regulation hypothesis, but provided evidence that rabbit populations may escape predator regulation once they exceed a critical density.

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The role of predation in the dynamics of mammalian prey populations continues to invoke controversy (Krebs 1995, Sinclair and Pech 1996). Experimental evidence suggests that predators may play a key role in limiting prey abundance (Newsome et al. 1989, Meserve et al. 1993, Reid et al. 1995, Krebs et al. 1995, Norrdahl and Korpimäki 1995, Banks et al. 1998). However, it is less clear whether predation can act in a density-dependent manner to regulate prey density (Boutin 1995, Krebs 1995, Sinclair and Pech 1996).

Most evidence for predator regulation is correlative, resulting from the search for density dependence in patterns of predator abundance (numerical responses; Korpimäki and Norrdahl 1989, 1991) or diet (functional responses; Korpimäki et al. 1991, Hanski et al. 1991, Pech et al. 1992) during fluctuations in prey densities (Boutin 1995, Sinclair and Pech 1996, Korpimäki and Krebs 1996). Theory suggests that regulation should occur at low prey densities (Erlinge et al. 1984; Hestbeck 1987; Messier 1994, 1995), such as during poor environmental conditions (Newsome et al. 1989, Boutin 1995). Recent evidence also suggests that some invasive species that respond rapidly to improve-

ment in environmental conditions may escape predator regulation (Sinclair et al. 1990, Newsome et al. 1989, Pech et al. 1992), leading to 2 stable states (Hestbeck 1987, Sinclair 1989, Messier 1994, Pech et al. 1995, Sinclair and Pech 1996). However, experimental manipulations of prey densities provide the most convincing tests of predator regulation (Korpimäki and Krebs 1996), but have rarely been performed for mammalian systems (Sinclair 1989, Sinclair and Pech 1996, but see Pech et al. 1992).

To test for predator regulation, Sinclair (1989) suggested that predators be removed and then allowed to reinvade subsequent to prey increase. If predators are able to regulate prey numbers, prey should decline to their preremoval densities when predators return. In this paper, I report on phase II of a 2-part, replicated field experiment to test if fox predation can regulate populations of rabbits in montane Australia. Banks et al. (1998) described phase I, demonstrating that fox removal resulted in a 6.5–12-fold increase in indices of rabbit abundance within 18 months. In phase II, I tested the above hypothesis by allowing predators to reinvade and monitoring responses of predator and prey for 16 months. I expected that if predation regulates rabbit numbers, reinvasion by foxes should cause rabbits to decline and remain at densities prior to fox removal.

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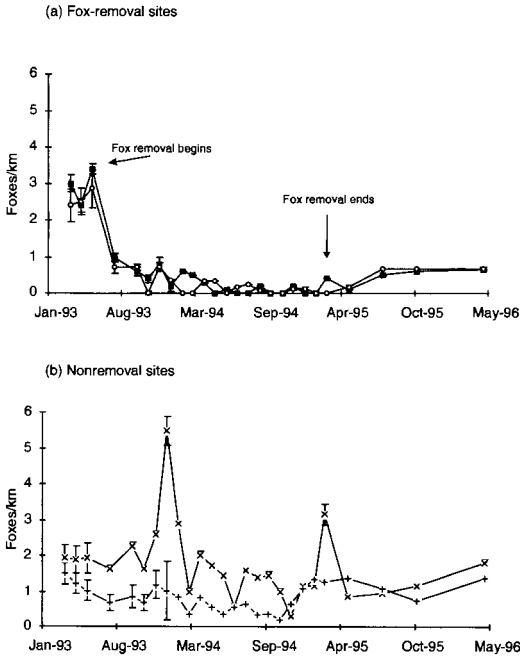


Fig. 1. Numbers of foxes observed from spotlight transect counts on (a) fox removal sites and (b) nonremoval sites in Namadgi National Park. Values represent the mean number of foxes seen per km; (a) -○- = Grassy and -■- = Boboyan; (b) -+- = Orroral and -x- = Glendale. Error bars (\pm SE) indicate the precision in the repeated spotlight sampling. Fox removal in (a) began in July 1993 and ceased in February 1995. Data from April 1993 to January 1995 from Banks et al. (1998) shown here for context.

STUDY AREA

I conducted this study in Namadgi National Park, an area of montane forest and repossessed open grassy farmland in the Brindabella Ranges, 50 km south of Canberra, Australia. As described in Banks et al. (1998), 4 valleys were chosen for the experiment, each approximately 10 km² in area and separated by 7–22 km of mostly sclerophyllous forest. Rabbits were most abundant in the ecotone between the cleared valley and the remnant timbered areas, and were the main prey of foxes (40% of diet; Banks 1997).

METHODS

Background and Phase 1

The methods used to reduce fox numbers during phase 1 of the experiment were reported by Banks et al. (1998). Briefly, foxes were reduced on 2 removal sites (Boboyan and Grassy) by baiting with the toxicant 1080, while fox populations remained intact on 2 nonremoval sites (Orroral and Glendale). Spotlighting surveys

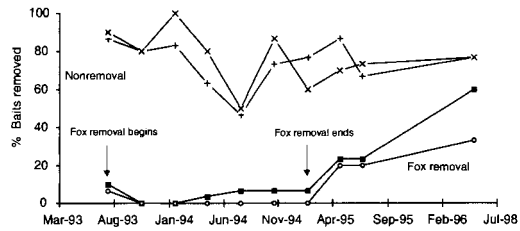


Fig. 2. Monthly percentage of nontoxic baits removed by foxes on removal sites (-○- = Grassy; -■- = Boboyan) and nonremoval sites (-+- = Orroral; -x- = Glendale) in Namadgi National Park. Fox removal started July 1993 and ended February 1995.

were used on 5-km transects to index the density of foxes and rabbits on each site. These began at dusk (Williams et al. 1995), were traversed on 3–4 consecutive nights per month at or near the new moon and were conducted from May 1993 to January 1995. The baiting of foxes from July 1993 to February 1995 caused fox indices to decline to <15% of preremoval levels and 80% lower than the 2 nonremoval sites (Fig. 1). Quarterly estimates of uptake of nontoxic baits (30 per site) and scat counts

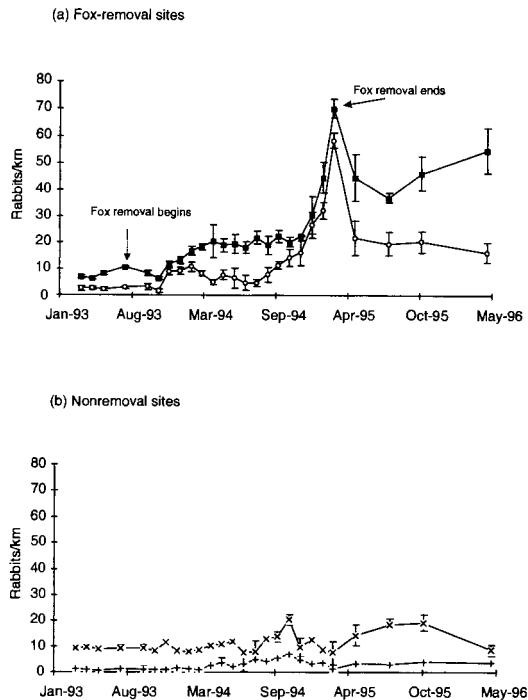


Fig. 3. Mean (\pm SE) number of rabbits observed per 5-km transect on (a) fox-removal sites and (b) nonremoval sites in Namadgi National Park; (a) -○- = Grassy and -■- = Boboyan; (b) -+- = Orroral and -x- = Glendale. Data from April 1993 to January 1995 from Banks et al. (1998) are shown here for context.

along 5-km transects indicated baiting was successful. Banks et al. (1998) reported on the first 18 months of phase I, where rabbits on fox-removal sites increased to 6.5- (Boboyan) and 12-fold (Grassy). The present paper also reports on the final months of phase I when fox removal ended and phase II began.

Phase II: Predator Reintroduction

I first allowed foxes to reinvade removal sites in late February 1995 when the fox-control program ended. I expected that dispersing foxes from surrounding areas would rapidly establish a substantial population on removal sites during main dispersal periods (Mar–May). Similar events have hampered attempts to control foxes in other areas (Kinnear et al. 1988, Newsome et al. 1989, Short et al. 1995) and continuous reinvasions necessitated persistent baiting during phase I of the Namadgi experiment (Banks et al. 1998).

I continued monitoring rabbits and foxes quarterly (excluding Mar 1996) using spotlighting and nontoxic bait uptake for foxes as described above, until May 1996. This sampling represented 16 months of fox reintroduction and 2 recruitment periods for both foxes and rabbits.

Statistical Analyses

I used Randomized Intervention Analysis (RIA; Carpenter et al. 1989) to determine if abundance indices on the 2 removal sites had similar trajectories after the end of fox removal compared to phase I. I used Monte Carlo methods in SPSS (1996) to determine significance of these comparisons.

RESULTS

Fox Decline and Reinvansion

Fox numbers crashed following the initiation of baiting and remained low for the next 16 months (Fig. 1A; Banks et al. 1998). Foxes slowly increased after February 1995 as a result of 2 dispersal periods following fox removal. Surveys indicated that fox numbers had not reached preremoval levels (Fig. 1A), but were comparable to nonremoval sites in the second year after baiting (Fig. 1B). Uptake of nontoxic bait also confirmed the return of foxes (Fig. 2).

Rabbit Responses

In the last months of phase I, abundance indices of rabbits in Grassy and Boboyan contin-

ued to increase beyond the levels reported by Banks et al. (1998) to 70.2 and 58.3 rabbits/km, or 10.3 and 23.3 times preremoval levels (Fig. 3A). Immediately following the end of fox removal, rabbit numbers in Boboyan and Grassy declined to 44.2 and 21.6 rabbits/km, respectively (Fig. 3A). In <2 months, numbers had decreased to levels similar to those observed before the 1994–95 breeding season, and continued to decline to July 1995. After this initial decline, rabbit indices at Boboyan increased again in the following breeding season and by May 1996 had increased to 54.7/km, or 23% higher than May 1995 (Fig. 3A). In contrast, spotlight counts of rabbits remained stable on Grassy after the initial decline, with small decreases over the following 16 months to 16.3 rabbits/km. This difference in population trajectories on the 2 removal sites was significant (RIA mean pre–post removal difference = 17.2, $Z = -3.02$, $P = 0.03$). Rabbits on nonremoval sites showed little change over this 16-month period (Fig. 3B), remaining at low levels throughout and without any decline in numbers in March 1995 as evident on removal sites.

DISCUSSION

The end of fox removal efforts led to the return of small numbers of foxes to both removal sites and an almost immediate decline in abundance indices of rabbits. Declines were not observed in areas where fox populations remained intact. Invading foxes have caused declines in island populations of arctic hares (Marström et al. 1989) and probably arid-zone rabbits (Pech et al. 1992), although for cyclic prey, predators are not thought to initiate cyclic declines (Krebs et al. 1995, Korpimäki and Krebs 1996). Part of the apparent decline of rabbits observed at Namadgi was likely due to changes in habitat use (and consequent detectability by spotlight) of rabbits in response to reinvansion of foxes (Banks et al. 1999). Notably though, rapid decreases in fox numbers following their initial removal did not lead to immediate increases in numbers of rabbits (Fig. 3A).

Declining per capita resource availability resulting from large increases in rabbit abundance may have influenced the subsequent crash in abundance that coincided with the end of fox removal. Rabbits at their peak density in fox removal sites had larger caeca and longer overall guts compared to rabbits in nonremoval sites, indicative of a poorer quality diet and suggest-

ing the increase in rabbit density reduced the quality of the available forage (Banks et al. 1999). However, they were in better condition than rabbits in control sites at this time, and hence, did not appear to be suffering a critical food shortage of a magnitude likely to precipitate a rapid crash in density (Banks et al. 1999).

To have caused the decline at Namadgi, foxes would have had to prey heavily on rabbits (Catling 1988, Newsome et al. 1997). Saunders et al. (1995) and Pech et al. (1992) estimated that a fox consumes 500 g of meat per day, or roughly 1 rabbit per day (Catling 1988). Therefore, a decline in rabbit abundance from 70 to 45/km in 1 month due to predation was realistic given the observed numbers of foxes.

Rabbit populations on the 2 removal sites showed trajectories of different magnitudes over the 15-month period after baiting. Rabbits in Boboyan recovered from initial declines during the next breeding season, when 3 times the monthly average rainfall was recorded. This recovery does not support the hypothesis that predation was regulatory after rabbits increased. By contrast, rabbits at Grassy did not recover following the reinvasion of foxes and remained constant (15–20 rabbits/km) over the next 16 months. Although this density was considerably higher than preremoval densities, the stability in numbers despite improved rainfall (and increases at Boboyan suggesting conditions were suitable for increase) gives general support to the hypothesis that predation was regulating the abundance of rabbits. Fox and rabbit abundances in the nonremoval sites also showed little fluctuation over this time.

The proximity of the 2 sites makes differential myxomatosis outbreaks in the sites an unlikely cause of the observed differences (Williams et al. 1973) and rabbit calici virus disease had not yet reached the region. Similarly, it is unlikely that differential rainfall led to poorer pasture conditions on 1 site but not others. Rabbits at Grassy experienced the greatest proportional increases following fox removal (23.3-fold vs. 10.3-fold at Boboyan). Density-dependent food shortages should have exerted the strongest influences on rabbits in the higher-density population, but analysis showed no differences in diet quality among these 2 sites (Banks et al. 1999). Similarly, there were no differences in body condition of rabbits between removal sites 1 month before the large population declines (Banks et al. 1999). Also, whereas behavioral re-

sponses of rabbits to fox reinvasion may have influenced the initial decline in rabbit observations, it is unlikely that differences in rabbit behavior were solely responsible for the differential trajectories in rabbit counts in removal sites.

Pech et al. (1992) argued that rabbit populations in semi-arid Australia existed in a 2-state system (Sinclair 1989). They found that the end of predator removal appeared to cause initial rabbit declines but rabbit abundance did not fall below the predicted critical limiting density, allowing them to escape predator regulation and increase rapidly to resource regulation following improvement in pasture conditions (Sinclair et al. 1990, Pech et al. 1992). My observations support this interpretation and I conclude that responses of rabbits and foxes at Namadgi appear to provide further evidence that rabbit populations may escape regulation by fox predation.

Foxes reoccupied Boboyan more slowly than Grassy relative to the abundance of rabbits. Therefore, it is likely that predation pressure was relatively lower at Boboyan than Grassy, which permitted the growth of rabbit populations in response to increased rainfall. A higher predator-prey ratio at Grassy may have led to more intense predation pressure and population regulation at a lower density. In terms of this 2-state model for population regulation (Sinclair and Pech 1996), I propose that rabbits at Boboyan escaped the upper limit for predator regulation; rabbits at Grassy did not and remained at a lower density due to reinvasion of foxes and despite conditions that allowed increases elsewhere. Moreover, fox and rabbit indices of abundance at Grassy were similar to control sites after fox removal, suggesting similar predator-prey ratios at these 3 sites. However, it is not clear if the limit to predator regulation depends upon a threshold density of rabbits or a critical predator-prey ratio.

Although this experiment was designed to test the predator regulation hypothesis, the contrasting responses of these sites support predictions from the 2-state model of predator regulation. Because only 2 sites were manipulated, several caveats must apply to these interpretations. First, information on diets and predation rate of foxes (Reid et al. 1995) would help resolve this hypothesis. Second, support for a 2-state system would have been strengthened had fox populations returned to preremoval densities and trajectories of rabbit populations re-

mained unchanged. In my study, the 16-month recolonization period covered only 1 breeding season for foxes (Saunders et al. 1995), and rapid immigration into the removal sites may have been hampered by previous removal efforts. Finally, whereas diets and gut morphologies of rabbits at peak densities (Banks et al. 1999) suggested no differences in quality or quantity of food eaten on removal sites, resource availability was not monitored during phase II of the experiment and its influence on the different trajectories of rabbit populations is not known. Further work in this field should endeavor to continue experiments long enough to clearly identify the upper limits to predator and prey densities, and hence clearly identify an escape from predator regulation. Moreover, specific experimental tests of the 2-state model using the predator removal-reinvasion approach (Sinclair 1989) should include replication of high- and low-prey densities as well as appropriate controls for the predator removal (unmanipulated) and predator reinvasion phases (continued removal).

MANAGEMENT IMPLICATIONS

Several authors have suggested introduced predators may play a role in the suppression of introduced prey densities (Newsome 1990). Banks et al. (1998) demonstrated that fox removal causes large increases in rabbit densities and potentially severe ecological damage. Results from the current experiment indicate that fox predation may only suppress rabbit populations at lower densities, such as subsequent to rabbit control efforts. These data suggest further that if rabbits are allowed to increase, the utility of fox predation as a rabbit control agent is likely to be diminished, and conventional rabbit management techniques (e.g., warren destruction, baiting) will be necessary to reduce their numbers.

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