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ECOSYSTEMS

Do Exotic Vertebrates Structure the Biota of Australia? An Experimental Test in New South Wales

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ABSTRACT

From 1993 to 2001, we conducted a series of experiments in a mixed grassland–woodland system in central New South Wales (NSW) to quantify the interactions between red foxes and their prey and competitors. Foxes were removed from two areas around the perimeter of Lake Burrendong, and data were collected from these areas and a nearby untreated area before, during, and after the period of fox control. The arrival of rabbit hemorrhagic disease (RHD) in 1996 provided an opportunity to examine the interactive effects of controlling foxes and rabbits. In this landscape, typical of central NSW, (a) the fox population was not affected by a large reduction in the abundance of rabbits, or vice versa; (b) the cat population declined in areas where foxes were removed after the large RHD-induced reduction in rabbit numbers, but there was no consistent response to the removal of foxes; (c) the abundance of some macropod species increased in response only to the combined removal of rabbits and foxes; (d) there were no consistent changes in the abundances of bird species in response to the removal of either foxes or rabbits, but there were clear habitat differences in bird species richness; and (e) there was likely to be an increase in woody plant species after the large reduction in rabbit populations by RHD. We conclude that (a) long-term field experiments (more than 3 years) are required to quantify the indirect consequences of controlling foxes and rabbits, and (b) single manipulations, such as fox control or rabbit control, are not necessarily sufficient for the conservation of remnant woodland communities in southeastern Australia.

Key words: community structure; predator–prey interactions; predator–prey manipulation; functional response; fox removal; rabbit hemorrhagic disease; Australia.

INTRODUCTION

A fundamental concern in ecological theory is the question of how the stability of a community is related to its diversity (MacArthur 1955; May 1973), connectivity (Dunne and others 2002), and compartmentalization (Berlow and others 2004; Krause and others 2003). After the occurrence of non-random extinctions, food web interactions determined the stability properties of a system (Ives and Cardinale 2004). Strongly interacting complex communities may be able to resist the invasion of new species (Case 1990); however, successful invaders have the potential to produce

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synergistic interactions that exacerbate the disturbances to native biota (Simberloff and Von Holle 1999). Inherent to these ideas is the prediction that successful invasions would lead to reduced complexity and a restructuring of the community (Elton 1958; Vitousek and others 1996). In this study, we present an experimental test of the hypothesis that invasive species create a simplified community structure—in this case, a community of exotic mammal predators and herbivores that have effected a simplification of the species composition and abundance of native mammals and birds in the temperate woodlands of central New South Wales.

Much has been written about the impact of exotic species on the habitats of Australia, the community of indigenous species, and the extinction of endemics. For example, red foxes (*Vulpes vulpes*), introduced from Europe in the 1850s, currently threaten 24 mammal, 19 bird, and 10 reptile species (Newsome and others 1997). In past decades, other species have disappeared as foxes spread across the continent (Finlayson 1961; Short and Milkovits 1990; Short 1998). In areas such as Tasmania and on other islands where habitats are still intact and foxes were not established until very recently, many endemic marsupials still exist, whereas they became extinct in the 1850s on mainland Australia. Where foxes have been removed, there have been marked increases in the abundance and range of marsupial species that are of a size vulnerable to fox predation (Kinnear and others 1988, 1998; Friend 1990; Phillips and Catling 1991; Priddel 1991; Morris and others 2003; Saunders and others 1995). However, after the removal of foxes, increases were reported in the number of feral cats (*Felis catus*) (Friend 1990; Christensen and Burrows 1995; Short and others 1995), along with changes in their diet and habitat use (Molsher 1998), with some resultant negative impacts on prey species (Risbey and others 2000).

Some species—for example, ground-nesting birds (Priddel 1991)—are highly susceptible to foxes and cats, but in general the effect of these predators depends on the range and abundance of alternative prey species and abundance (Parer 1977; Wood 1980; Newsome and others 1989; Phillips and Catling 1991; Pech and others 1992). For example, in Namadgi National Park the removal of foxes had no impact on bush rats (*Rattus fuscipes*) (Banks 1999), but fox predation suppressed populations of eastern gray kangaroos (*Macropus giganteus*) (Banks and others 2000) and European rabbits (*Oryctolagus cuniculus*) (Banks and others 1998). The presence of foxes influences the behavior of rabbits and kangaroos, such that both species change their foraging behavior according to predation risk (Coulson 1999; Banks and others 1999; Banks 2001); but for some prey species, the level of risk can be affected by habitat structure (see, for example, Stokes and others 2004).

Exotic herbivores, such as European rabbits, have been abundant in Australian landscapes since the 1800s and have had major impacts on plant communities. Clear evidence of their influence was seen when the disease myxomatosis removed over 95% of the rabbits in the early 1950s (see review in Williams and others 1995) and more recently after the arrival of rabbit hemorrhagic disease (RHD) (Sandell 2002). In addition, rabbits are an important resource for feral cat and fox populations (Catling 1988; Molsher and others 1999) that threaten secondary prey species (Pech and Hood 1998), and they compete with other herbivores (Williams and others 1995), and they may exert an indirect effect on many animal species by altering their habitat.

In general, predators may affect the structure of communities directly through predation or indirectly through competition with other predators or through a change in the behavior of the prey species. Herbivores may affect other herbivores by maintaining high populations of predators (apparent competition) or directly through competition for resources such as food, shelter, or refuge from predators.

Impacts are frequently observed, but they have rarely been quantified. The most conclusive evidence is provided by removal experiments. Although there have been several large-scale experiments in Australia to remove exotic mammals—usually foxes, cats, or rabbits—in almost all cases the effects of the removal of one species are measured against the change in abundance of a few (usually one) other species such as malleefowl (*Leipoa ocellata*) (Priddel and Wheeler 1997), yellow-footed rock-wallabies (*Petrogale xanthopus*) (Sharp 2000), black-footed rock-wallabies (*Petrogale lateralis*) (Kinnear and others 1988, 1998), or brush-tailed bettongs (*Bettongia pencillata*) (Kinnear and others 2002).

We know relatively little about the effects of exotic mammals on the structure of a community as a whole. In this study, we examined the effects of two major perturbations of fox and rabbit populations on the flora and fauna of an area in central New South Wales. The premise is that introduced exotic vertebrates structure communities in mixed grassland–woodland systems by altering the species diversity and abundance of woody plants, mammals, and birds.

Hypotheses and Predictions

Predators. Foxes change the structure of the vertebrate community directly through predation or indirectly by competition with other predators. Therefore, we can test the following predictions by manipulating the abundance of foxes: Fox removal will result in less predation and an increase in the abundance of a subordinate predator, the feral cat (prediction p_1), which competes with foxes or is subject to fox predation. In addition, fox removal will result in an increase in European rabbits (p_2), macropod herbivores (p_3), and ground-feeding birds (p_4). If prediction p_1 is correct, predictions p_2 to p_4 may be affected for prey species susceptible to predation by cats.

Herbivores. Rabbits are the dominant exotic herbivore; they change the structure of the plant community through herbivory and the structure of the vertebrate community through competition or via their function as an important prey species. Therefore, we can test the following predictions by manipulating the abundance of rabbits: A reduction in rabbit numbers—for example, by RHD—will result in a decrease in their major predators (p_5), foxes, feral cats, and wedge-tailed eagles (*Aquila audax*), and an increase in macropod competitors (p_6) and specialist ground-feeding birds (p_7) through the indirect effects of increased herbaceous vegetation. In the long term, low rabbit numbers will lead to changes in the structure of the plant community through enhanced recruitment of woody species (p_8), with subsequent changes in bird species richness (p_9). Prediction p_7 may be affected if the removal of rabbits does not generate a response in vegetation because prediction p_6 is correct or if land managers alter the number of livestock.

METHODS

Study Site

The study site covers approximately 90 km^2 on the east side of Lake Burrendong (32°40′S, 149°10′E) at the confluence of the Macquarie and Cudgegong rivers, about 32 km upstream of Wellington in central New South Wales (Figure 1). It consists of open grassland with scattered mature eucalypt trees and mixed eucalypt–*Callitris* woodland (Allcock and Hik 2003, 2004). Livestock production is regulated at a level deemed by government agencies to be consistent with the requirements of a water catchment area.

The climate is generally temperate, with mild to cool winters (2°–15°C) and warm to hot summers (14°–33°C). Rainfall occurs relatively evenly throughout the year, with a yearly average of 673 mm. During the study period, 1994, 1995, and 1997 were regarded as dry years, with rainfall being 20% below average or lower, whereas 1996 and 1998 had rainfall more than 20% above average.

Treatments

To test the predictions on the role of foxes, we measured the consequences of fox removal on populations of feral cats, rabbits, eastern gray kangaroos, swamp wallabies (*Wallabia bicolor*), wallaroos (*Macropus robustus*), and ground-feeding birds. For feral cat, rabbit, and macropod populations, an untreated area was compared with two other areas before, during, and after fox removal. For the birds, an untreated area was compared to one treated area during and after fox removal.

To test the effects of a reduction in rabbit abundance on predator (fox and cat) populations, we compared periods before and after the arrival of RHD. These treatments were nested within the treatments of fox removal. The response in the diet of wedge-tailed eagles after the arrival of RHD was measured by comparing times of relatively high rabbit numbers with a period of low rabbit numbers. The consequences of reducing rabbit numbers on other mammal herbivores (macropods) were measured by comparisons before and after the arrival of RHD, again nested within the fox treatments. For ground-feeding birds, we compared populations before RHD with those after the arrival of RHD.

The effects of the rabbit population on the structure of the vegetation were examined by measuring the survival of seedling transplants subjected to herbivory by different combinations of rabbits, macropods, and livestock (domestic sheep [*Ovis aries*] and cattle, [*Bos taurus*]). The potential for rabbit-induced changes in vegetation to affect bird species was then determined by calculating species diversity in the four main vegetation types in the study area.

Data collection started in November 1994. From September 1995 through September 1999, the central part of the study site was divided into three contiguous areas. These were a control area of 22 km^2 (Control), where the fox population was not manipulated, and two baited areas where foxes were removed using 1080 poison bait lines along ridge tops and along 4WD trails. Baiting, which followed standard procedures in eastern Australia (Saunders and others 1995), consisted of burying

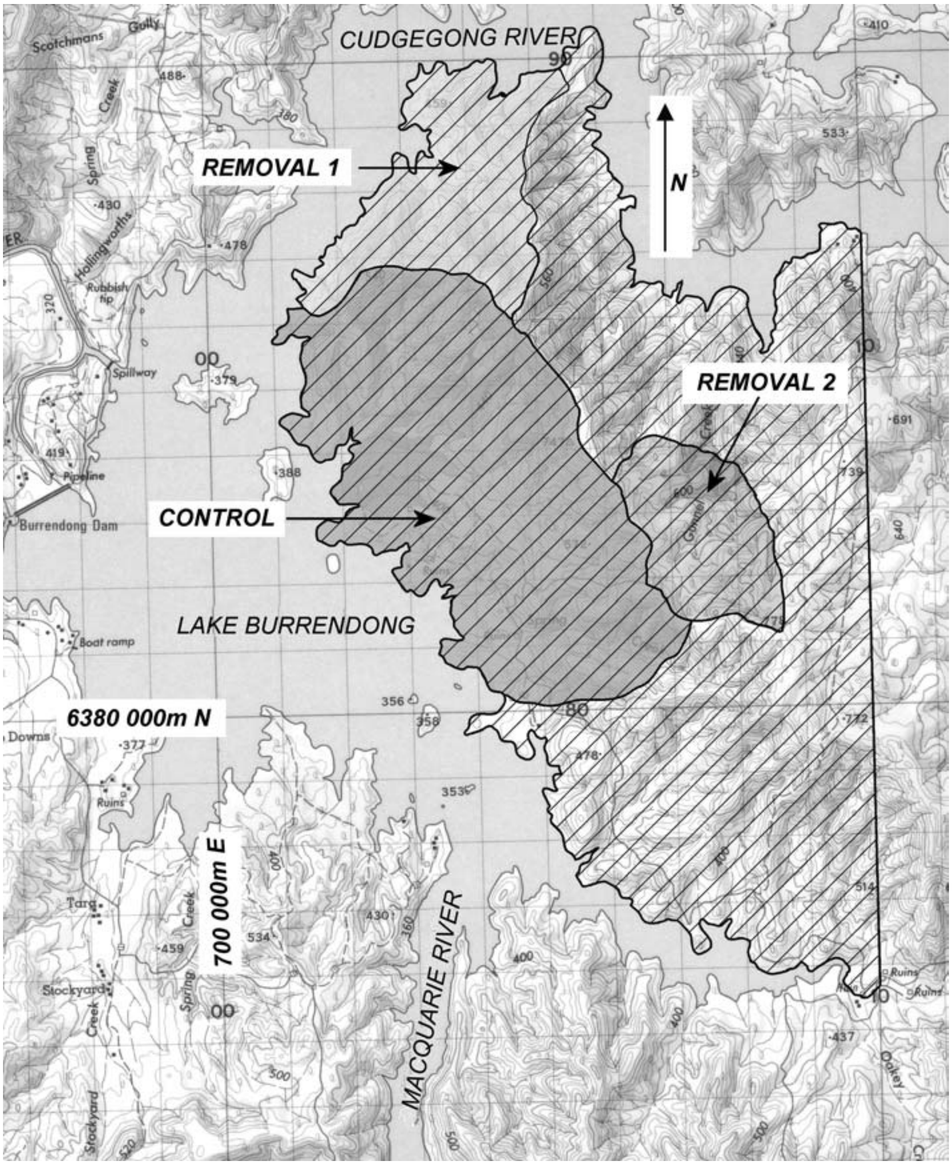

Figure 1. Location of the three fox -treatments (Removal 1, Removal 2, and Control) within the study site (*hatched*) at Lake Burrendong, New South Wales. (Source: map sheet 8732 ''Euchareena,'' 1:100,000, edition 1, 1975).

commercial poison baits (FOXOFF) at 200-m intervals and replacing them when taken, or after 1 month if not eaten. Continuous baiting throughout the Removal 1 area (8 km^2) reduced foxes to a minimum population density, while baiting for a 10-day period every 3 months was designed to produce an intermediate population density of foxes in the Removal 2 area (6 km^2). Baiting ceased in September 1999 and data were collected in all areas until December 2001. In July 1996, RHD arrived in the area (Saunders and others 1999), but its effect on rabbit abundance was not detected in spotlight counts until September 1996. The project therefore involved four periods:

1. T1, from November 1994 to September 1995, when rabbits and foxes were present in high numbers throughout all areas;
2. T2, October 1995–August 1996, when foxes were removed in the two treatment areas, Removal 1 and Removal 2, but rabbit populations remained untreated;
3. T3, September 1996–September 1999, when rabbit numbers were reduced by RHD in all areas and fox removal continued in the two treatment areas; and
4. T4, October 1999–December 2001, when rabbit numbers remained low but baiting ceased and foxes returned to the two removal areas.

Techniques

The abundance of macropods, rabbits, foxes, and cats was surveyed by spotlight counts; indices of bird abundance were obtained by a combination of transect and plot counts. The diets of foxes and cats were assessed from scats; the diet of wedge-tailed eagles was assessed from orts collected around and under nest sites. The vegetation was classified into four main types: grassland, open eucalypt woodland, dense eucalypt woodland, and *Callitris* woodland; however, for some analyses, these types were amalgamated into two broader categories. The impact of herbivory on vegetation was measured with permanent belt transects and a series of exclusion plots; long-term changes were estimated from aerial photographs. *Allocasuarina verticillata* woodland, a relatively minor habitat in the Control area, was included in the belt transects (for details, see Appendix 1, available online at http://www.springerlink.com).

Data Analyses

Geographical constraints determined the experimental design. Due to the unbalanced replication, our analyses focused on parameter estimation in each time period to identify large effects of treatments. Consequently, we compared population indices of mammals between treatments and time periods using *t*-tests for unequal variances. Power for the tests was calculated from Number Cruncher Statistical Systems 2000 (www.NCSS.com). In addition, we used the nonparametric Wilcoxon matched-pairs signed rank test to compare rates of change in treatment and control areas for the assemblages of bird species. Bailey's method for the 95% multinomial confidence limits (CL) (Cherry 1996) was used for changes in tree canopy cover on aerial photographs.

RESULTS

Fox Removal Experiment

Removal of Foxes. Fox numbers were monitored before (T1), during (T2 + T3), and after (T4) the removal experiment in all three areas (Removal 1, Removal 2, and Control). Numbers of foxes were significantly reduced in both Removal areas compared to those in the Control area (Figure 2a) (one-tailed $t = 5.17$, $P = 0.0001$, Removal 1; t = 3.81, $P = 0.0009$, Removal 2). Foxes returned rapidly to both removal areas when baiting ceased (within 6 weeks in Removal 1 and within 1.5–5 months in Removal 2), and numbers then did not differ from those at the start of the experiment ($t = 0.46$, $P > 0.3$).

Effect of Fox Removal on Feral Cats. Feral cats appeared to be affected by the continuous removal of foxes (Figure 2b). In the Removal 1 area, no cats were observed over the initial year when foxes were present (T1). They appeared consistently once fox removal began (T2), (t = 3.41, $P = 0.005$) and maintained their numbers when foxes returned. In the Control area, the abundance of cats declined significantly by about 60% over the same time periods (t = 2.29, $P = 0.03$). In the Removal 2 area, cats declined in number but less than in the Control area, and this decline was not a significant change over the same time periods. However, given the variation in cat density between the three sites, there was low power to detect an increase in cat numbers; a doubling in numbers produced only a 20% chance of detection.

Effect of Fox Removal on Rabbits. During periods T1 and T2, before the arrival of RHD, rabbit numbers increased on all three areas (Control, Removal 1, and Removal 2) (Figure 2c). This population growth coincided with an increase in rainfall between T1 and T2, with a mean of 48.6 mm per month from November 1994 to September 1995 and a mean of 59.8 mm from October 1995 to August 1996 (long-term monthly mean, 56.4 mm). Rabbit abundance increased less in both areas where foxes were removed compared to where foxes were present, indicating that there was no negative effect of foxes. There was sufficient power to detect such a threefold change in rabbit numbers in fox removal areas if it had occurred (100% chance of detection for a three-fold increase, $n = 2$).

Effect of Fox Removal on Macropods. The population of eastern gray kangaroos showed no significant response to fox removal prior to the arrival of RHD (T1 and T2). Power to detect a 50% change was 90% for $n = 2$ sites, suggesting that the lack of response was real. Numbers remained the same in the Control area and increased only slightly in the two Removal areas (t = 0.72, $P > 0.2$, Removal 1; t = 1.52, $P = 0.08$, Removal 2). There is some indication of a delayed increase in both Removal areas when rabbit abundance was low during periods T3 and T4, even though fox control ceased at the end of T3 (Figure 2d).

No consistent effects of fox removal were observed with swamp wallabies (Figure 2e); as for the eastern gray kangaroos, there was sufficient power to detect a change of 50%. This species was initially uncommon in both Removal areas. In Removal 1 there was an increase, whereas in Removal 2 and in the Control area there was no change. Similarly, there were no detectable effects of fox removal on the number of wallaroos.

Effect of Fox Removal on Ground-feeding Birds. During the course of the study, 130 bird species (excluding waterbirds) were recorded, of

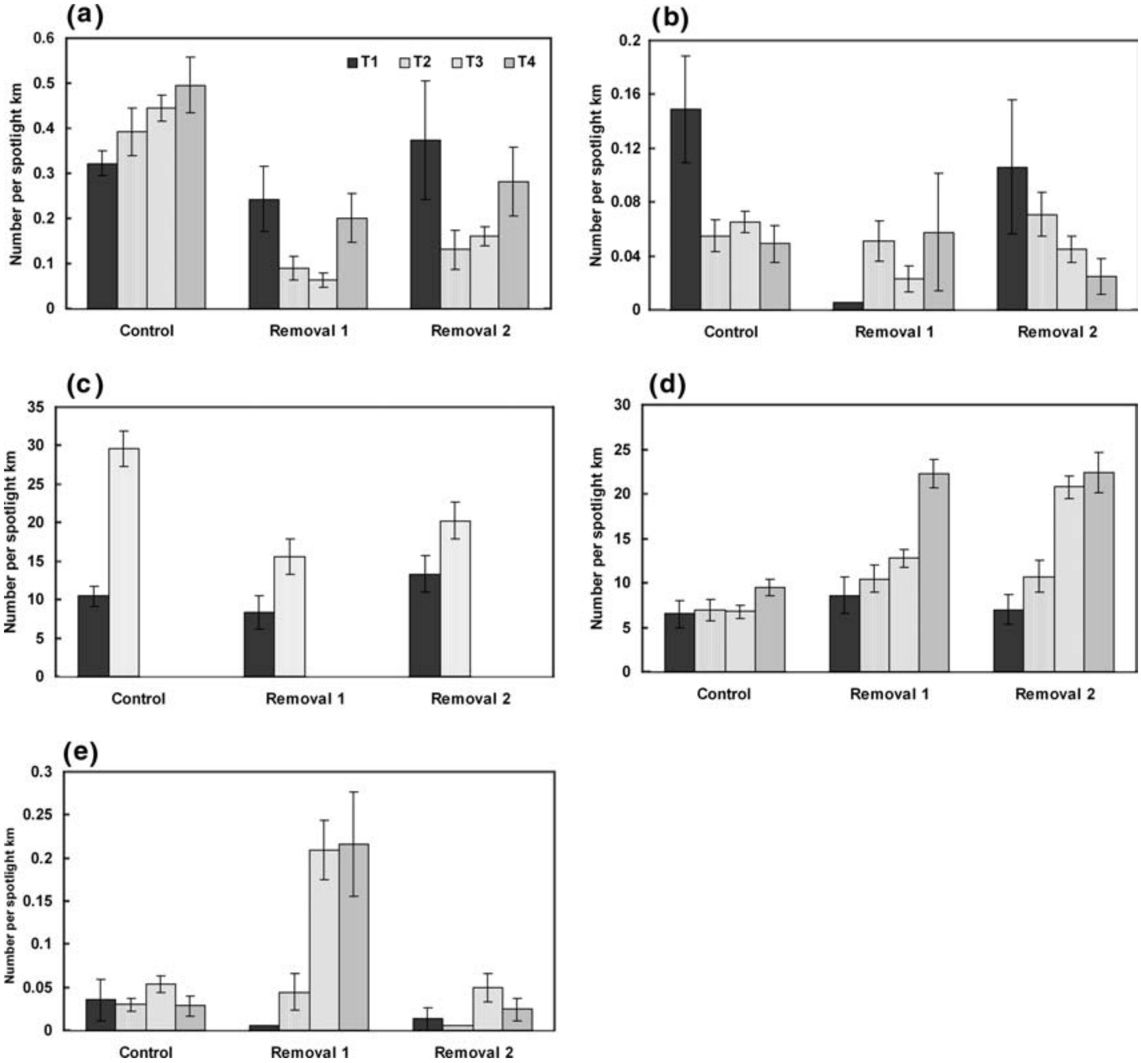

Figure 2. Average fox (**a**), cat (**b**), European rabbit (**c**), eastern gray kangaroo (**d**), and swamp wallaby (**e**) abundance (± SE) within the untreated area (Control) and two fox removal areas (Removal 1, Removal 2) at Lake Burrendong. The sequence of periods was as follows: T1 (foxes present, no rabbit hemorrhagic disease [RHD]), T2 (foxes removed, no RHD), T3 (foxes removed, RHD present), and T4 (foxes returned, RHD present). The number of spotlight sessions was as follows: T1, six in Control, six in Removal 2, five in Removal 1; T2, nine in each of Control, Removal 1, and Removal 2; T3, 25 in each of Control, Removal 1, and Removal 2; T4, eight in each of Control, Removal 1, and Removal 2.

which 29 species were regarded as being prone to fox predation. There were sufficient data on only 22 species to calculate the index of change, I_{Fi} (see Appendix 2, available online at http://www.springerlink.com). Of these, 12 either nested or fed on the ground and so were regarded as of greater risk from fox predation than the remaining 10, which were either very small (so less likely to be attractive prey for foxes) or did not spend the majority of time feeding on the ground.

In grassy–open woodland, eight predation-prone species were disadvantaged by the return of foxes to the Removal 1 area as predicted, whereas 12 benefited, contrary to prediction (see Appendix 2a http://www.springerlink.com). Four species that were greatly disadvantaged after the return of the fox (T4) were the pied currawong $I_{Fi} = -5.40$, apostlebird $I_{Fi} = -7.06$, brown treecreeper $I_{Fi} = -7.52$, and the rufous songlark $I_{Fi} = -8.68$. The species that showed the greatest benefit after the return of foxes were the peaceful dove $I_{Fi} = 2.26$ and the crested pigeon $I_{Fi} = 2.76$. The willie wagtail $I_{Fi} = 0.04$ and noisy miner $I_{Fi} = 0.13$ were not affected. In dense woodlands, eight predation-prone species were disadvantaged, whereas 10 benefited from the return of foxes (see Appendix 2b at http://www.springerlink.com). The most disadvantaged species were the magpie-lark

$I_{Fi} = -6.91$ and the eastern rosella $I_{Fi} = -8.09$. Those that benefited most were the crested pigeon $I_{Fi} = 4.02$, the peaceful dove $I_{Fi} = 4.81$, and the southern whiteface $I_{Fi} = 7.14$. The two former species benefited in both habitat types.

The Wilcoxon matched-pairs test was used to determine whether the rate of change for each species in the Removal 1 area was less than the rate in the Control area when foxes returned to the removal site. Separate comparisons were made for the bird assemblages in the grassy–open woodland and the dense woodland. In both groups, the results were not significantly different from a null hypothesis of no effect of fox reduction on bird numbers (grassy–open woodland, Wilcoxon T = 117, $n = 22$, $P = 0.36$; dense woodland, T = 68, $n = 18$, $P = 0.23$).

Removal of Rabbits by Rabbit Hemorraghic Disease

Impact of Rabbit Hemorrhaghic Disease on the Abundance of Rabbits. After the first detection of RHD in July 1996, there was a major change in rabbit abundance throughout the study area. Numbers dropped by approximately 90% from an average of 19.2 per spotlight km for the period T1 + T2 to 2.1 per spotlight km by November 1996. After the initial epizootic, numbers remained relatively stable, ranging from 0.25 to 5.3 per spotlight km, with no obvious seasonal pattern.

Prior to the arrival of RHD in July 1996, about half of the 200-m sections (90 of 178) along the bird survey transects were classified as having high numbers of rabbits, with the remainder being low. Areas of high rabbit numbers were dispersed throughout the study area irrespective of fox treatments. The average number of rabbits pre-RHD in these sections was 18.7 (± SE 3.26) per 200 m; this figure dropped by 87% to an average of 2.4 (± SE 0.23) after the arrival of RHD. Those sections designated as having low rabbit numbers dropped by 74% from 3.3 (± SE 0.52) to 0.85 (± SE 0.11) rabbits per 200-m section.

Effect of Rabbit Removal on Foxes. In the Control area, fox numbers increased throughout the study, and there was no effect of the reduction of rabbits (Figure 2a). In the Removal 1 and Removal 2 areas, the number of foxes returned to pretreatment levels (T1) after baiting ceased (T4) despite the fact that rabbit numbers were then only about 10% of the initial densities.

Measures of the volume of rabbit in the diet of foxes (Figure 3) show that rabbits were an important prey item when they were abundant in winter and spring, with foxes having a type II functional response to rabbits at that time. At low rabbit numbers, carrion (from macropods and livestock), insects, and fruits made up the diet. In summer and autumn, foxes had a higher intake of insects and fruit (Molsher 1999), and there was no clear conventional functional response to rabbits.

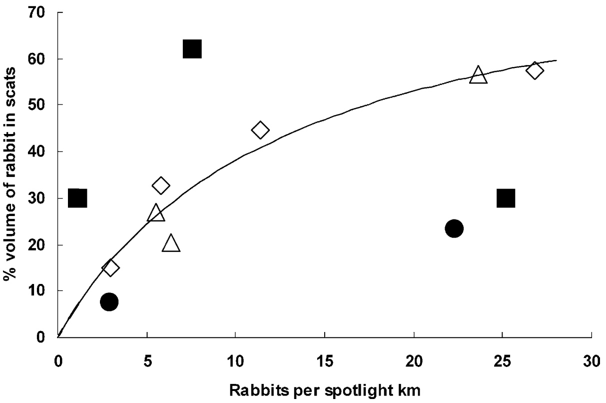

Figure 3. Dietary response of foxes to changes in rabbit abundance in winter (◇), spring (Δ), summer (●), and autumn (■). The type II functional response curve was fitted to the winter and spring data. The equation is % volume = 87 × N / (13 + N), where N is the index for the rabbits in units of number per spotlight km. Data are from 321 scats collected by Molsher (1999).

Effect of Rabbit Removal on Feral Cats. In the absence of foxes (during T2 and T3 in Removal 1 and Removal 2), feral cat numbers declined after the RHD-induced reduction of rabbits (Figure 2b). The decline in each area approached significance; for counts over the combined Removal areas, this decline was significant (one-tailed t = 2.10, $P = 0.02$). However, the effects of rabbits were confounded by the change in the abundance of foxes because they can depress cat numbers (see above). In the Control area, cats had already declined markedly between periods T1 and T2, prior to the arrival of RHD, and there was no apparent effect of the reduction in rabbits on cat numbers. Similarly, no consistent effect of rabbits on cat numbers was evident after foxes returned to the Removal areas. Based on data from scats collected during T1, T2, and the first part of T3, rabbits were the main component of the cat diet, and they remained so for a wide range of rabbit population densities (Figure 4).

Effect of Rabbit Removal on Wedge-tailed Eagles. No data were obtained on the diet of wedge-tailed eagles before the arrival of RHD. Therefore dietary data from 1999, when there was an average of 5.33 rabbits per spotlight km in September over the entire study area, were compared with data from 2001, when rabbits were measured at 1.12 per

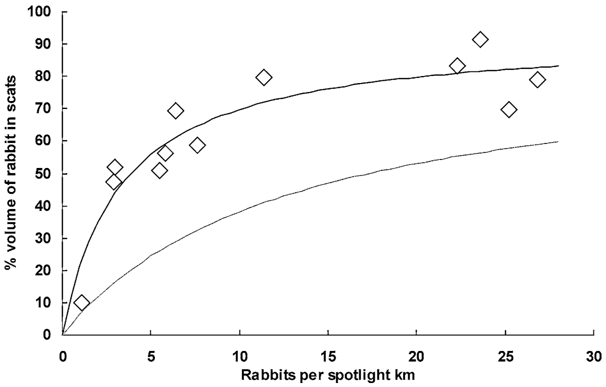

Figure 4. Dietary response of cats to changes in rabbit abundance. The equation for the type II functional response curve (*solid line*) is % volume = 93 × N / (3.5 + N), where N is the index for rabbits in units of number per spotlight km. Data are from 436 scats collected by Molsher (1999). The fox functional response (*dotted line*) from Figure 3 is shown for comparison.

spotlight km in September. These years represent extreme values compared to the average abundance of 2.57 rabbits per spotlight km during T3 and T4. In October 1999 and October 2001, food remains were collected from under 11 nests. When rabbit numbers were relatively high, a greater proportion of the pellets contained rabbit material and a greater proportion of the bones were from rabbits than when the numbers were very low. In 2001, there were higher proportions of macropod hair and bones, and to some extent material from possums and sheep or goats, compared to 1999 (Table 1).

Effect of Rabbit Removal on Macropods. Eastern gray kangaroos increased significantly when rabbit numbers were reduced during T3 and T4 but only in the Removal areas (Figure 2d) (t = 3.24, $P = 0.001$ Removal 1; t = 7.05, $P < 0.0001$ Removal 2). Similarly, swamp wallabies increased significantly after the arrival of RHD and only in the fox removal areas (Figure 2e) (t = 5.50, $P < 0.0001$ Removal 1; t = 2.69, $P < 0.005$ Removal 2). Neither species of macropods increased when rabbits were removed in the presence of foxes. In contrast, there was no effect of rabbit removal on the number of wallaroos in any area.

Effect of Rabbit Removal on Ground-feeding Birds. The 200-m transect sections were classified as high or low rabbit abundance based on the pre-RHD data. The length of contiguous sections with low rabbit abundance was 1.34 ± 0.37 km (mean ± SE); the length of contiguous sections with high rabbit abundance was 1.47 ± 0.34 km. The abundance of 26 species likely to be affected by changes in food supply due to rabbit removal was recorded during T2, T3, and T4 (see Appendix 3 at http://www.springerlink.com). Of these, seven granivorous species were identified as most likely to benefit due to an increase in seed abundance as a consequence of reduced grazing pressure by rabbits. Of the 26 species, only the following six showed an increased presence on the high rabbit removal areas relative to the low rabbit removal areas: crested pigeon $I_{Fi} = 0.05$, Australian raven $I_{Fi} = 0.17$, eastern rosella $I_{Fi} = 0.34$, Australian king-parrot $I_{Fi} = 0.52$, white-winged chough $I_{Fi} = 0.88$, and restless flycatcher $I_{Fi} = 2.63$. The other 20 bird species were apparently disadvantaged by the change in rabbit abundance (see Appendix 3 at http://www.springerlink.com). The Wilcoxon matched-pairs test showed that there were significant differences in the rates of change in this assemblage of 26 species of birds (that is, comparing the rate of change pre- and post-RHD in areas with low rabbit abundance versus high rabbit abundance, Wilcoxon T = 74, $n = 26$, $P < 0.005$).

However, the differences in rates of change of bird abundances were opposite to those we predicted. Change was greatest where rabbit abundance was initially low—whereas we had predicted that change would be greatest in areas where rabbit abundance was initially high—and then dropped to low levels after the arrival of RHD. Thus, both the eastern yellow robin and the masked lapwing showed significant increases in the low rabbit areas (eastern yellow robin, t = −3.63, $P = 0.001$; masked lapwing t = −2.92, $P = 0.005$), but non-significant changes in the high rabbit areas. Only the restless flycatcher showed a change in the predicted direction—namely a non-significant decrease in low-rabbit areas but a significant increase in high-rabbit areas (t = −2.18, $P = 0.02$).

Effect of Rabbit Removal on Vegetation. We detected no increase in herbaceous vegetation cover in the permanent transects with the reduction of rabbit population densities after the arrival of RHD (Figure 5a, and b). A repeated-measures mixed-effects model (SAS systems procedure MIXED with a REPEATED statement) indicated highly significant differences in vegetation cover between years and between habitats ($P < 0.0001$), as well as a highly significant habitat by year interaction ($P < 0.0001$). In particular, grassland transects showed a substantial shift through time, as vegetation cover in 1998 and 1999 was reduced by approximately 50% compared to 1996 and 1997. This finding may

Table 1. Proportions of Hair and Feathers in Pellets and Proportions of Bones Found under Wedge-tailed Eagle Nests in October 1999 When Rabbit Abundance was Relatively High and October 2001 When Rabbit Abundance was Relatively Low

	Pellets		Bones	
Species	1999 (*n* = 49)	2001 (*n* = 22)	1999 (*n* = 114)	2001 (*n* = 69)
Rabbit	0.78	0.45	0.75	0.54
Feathers	0.22	0.23	—	—
Macropod spp.	0.06	0.77	0.08	0.19
Pig (*Sus scrofa*)	0.27	0.09	0.01	0.01
Sheep (*Ovis aries*), Goat (*Capra hircus*)	0.04	0.2	0	0.17
Possum spp.	0.02	0.18	0.01	0.04

n = number of pellets or bones.

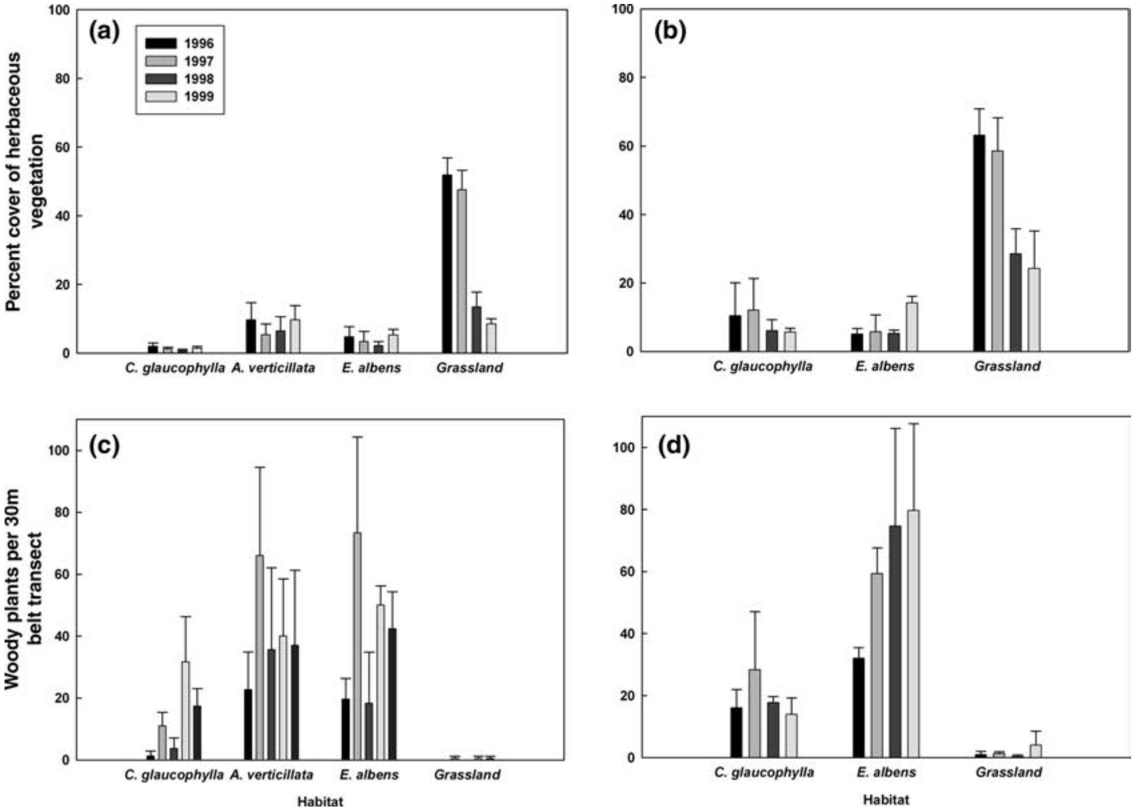

Figure 5. Herbaceous vegetation cover measured by line intercept (**a, b**) and density of woody plants (shrubs, shrub seedlings and tree seedlings) (**c, d**) for transects in four habitats (open *Eucalyptus albens* woodland, *Callitris glaucophylla* woodland, *Allocasuarina verticillata* woodland, and grassland) in the Control area (**a, c**) and three habitats (open *E. albens* woodland, *C. glaucophylla* woodland, and grassland) in the Removal 2 area (**b, d**) from 1996 to 1999. Error bars are SD. Rabbit hemorrhagic disease (RHD) arrived at the site after sampling in 1996.

reflect the effects of a prolonged period of below-average rainfall in 1997, prior to the 1998 sampling.

There was a significant increase in woody plant density along the permanent transects after the arrival of RHD (Figure 5c, and d). A repeated-measures mixed-effects model (SAS systems procedure MIXED with a REPEATED statement) showed significant effects for year ($P < 0.0001$) and habitat ($P < 0.0001$) and no significant year by habitat interaction ($P = 0.33$) when underlying differences between sites were accounted for. Eucalypt woodland habitats showed the greatest increase in woody plant density; most of this increase was due to recruitment of two shrub species—sticky daisy bush (*Olearia eliptica*) and hopbush (*Dodonaea viscosa*). There was little woody plant recruitment into grassland habitats; however, in one of the areas (Removal 2), woody plant recruitment into open habitats appeared to increase slightly in the later years of the study (Figure 5d).

Impact of Herbivores on Grassland and Woodland Vegetation in T3 and T4. In both habitats (grassland and open eucalypt woodland), exclusion of grazing animals caused increases in standing plant biomass in spring and summer throughout the course of the study (Figure 6a–d). Repeated-measures mixed-effects models (SAS procedure MIXED with REPEATED statement) for spring and summer data separately showed significant effects of treatment ($P = 0.01$ in spring and $P = 0.0001$ in summer), habitat ($P < 0.0001$ in both seasons), and time ($P < 0.0001$ in both seasons). Spring plant biomass also showed a significant time by habitat interaction ($P = 0.02$). Frequently, exclusion of stock resulted in increases in standing biomass relative to the unfenced plots, with little additional change with exclusion of macropods or rabbits; however, in some cases exclusion of macropods also resulted in increased standing biomass. Comparison of plots with large herbivores excluded and complete exclosures indicated that exclusion of rabbits in the absence of other herbivores had no effect on standing plant biomass (Figure 6).

As detailed in Allcock and Hik (2004), exclusion of herbivores had a substantial impact on the survival and projected establishment rates of *C. glaucophylla* and *E. albens* (Figure 7a and b), and different exclusion treatments affected survival differently for the two species. For *C. glaucophylla*, there was a decrease in survival with increasing standing plant biomass, and survival in unfenced plots was lower than that in complete exclosures. In general, there was a trend toward increasing survival with increasing herbivore exclusion (although not all differences were statistically significant), indicating that rabbits had a negative impact on *C. glaucophylla* seedlings. For *E. albens*, exclusion of stock resulted in a substantial increase in survival, with no differences evident among the fenced treatments, indicating that rabbits did not appreciably reduce *E. albens* survival.

An investigation of the number of seedlings showing damage by particular herbivore groups revealed that rabbits browsed substantially more *C. glaucophylla* seedlings (28% in grasslands and 60%–80% in woodlands) than *E. albens* seedlings (14%–20% in grasslands and 27%–60% in woodlands). In addition, stage-based matrix models used to create establishment projections for the two species indicated that excluding rabbits could enable a substantial increase in *C. glaucophylla* establishment (leading to a doubling of establishment in grassland and a tripling in woodland), whereas it had a minimal impact on *E. albens* (Allcock and Hik 2004).

Long-term Changes in Plant Communities. Of the 490 points used to estimate vegetation change from the aerial photos, 98 were assessed as having tree cover in 1965, with nine undecided; the corresponding results for 1995 were 224 and 16. The tree canopy cover increased from 20% (CL 15%–24%) to 45% (CL 40%–51%). Ground assessment in 2004 showed that, of the 162 points with tree cover not present in 1965, the new canopy cover consisted of 48% *E. albens*, 40% *Callitris* spp., 8% *D. viscose*, and 2% for both pepper tree (*Schinus areira*) and *O. eliptica*.

Association of Plant and Bird communities. Rarefaction analysis of the plot survey data for birds enables a comparison of observed species numbers between habitats of unequal sample size. Standardized at 500 individuals for all four major habitat types, our observations (± SD) show that most bird species occur in dense eucalypt woodland (63.9 ± 2.9), followed in decreasing order by open eucalypt woodland (54.8 ± 6.0) and *Callitris* woodland (49.3 ± 7.6). Grassland had the lowest number of species, with an expected richness of about 33.6 ± 2.5 species per 500 individuals.

DISCUSSION

There is a substantial body of evidence to show that introduced exotic mammals have altered Australian habitats and changed the species composition of other trophic levels, mainly through top-down effects of predation and herbivory. As well, there is some evidence for bottom-up effects in the case of rabbits sustaining populations of introduced and native predators. Against this background, we have conducted experiments to explore the consequences for other trophic levels of removing introduced predators and herbivores (Table 2). Although there was only one control and two treated replicates, some of the comparisons between control and treatments were qualitatively opposite to our predictions, and these comparisons provided sufficient power to interpret the results. Similarly, some of the comparisons where no sig-

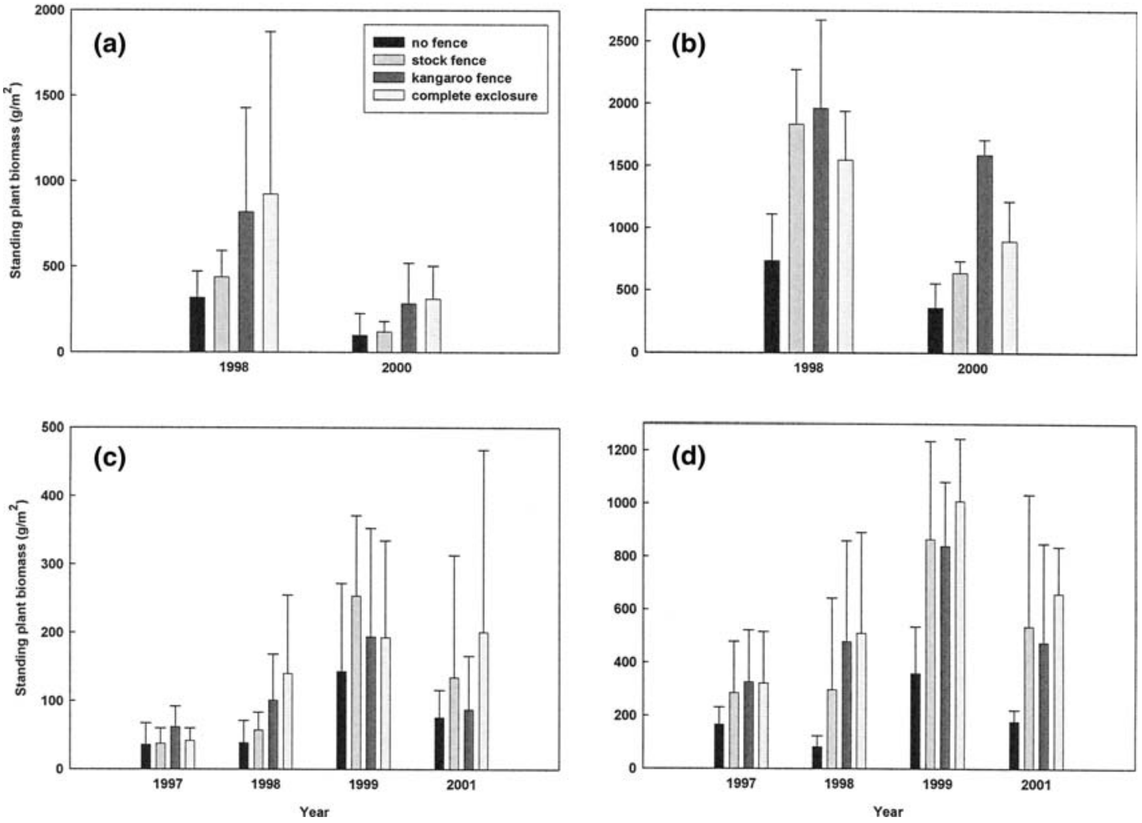

Figure 6. Standing plant biomass in exclusion plots in spring (**a, b**) and summer (**c, d**) in open eucalypt woodland (**a, c**) and grassland (**b, d**) habitats. Note the differences in scale on the y-axes. Error bars are SD.

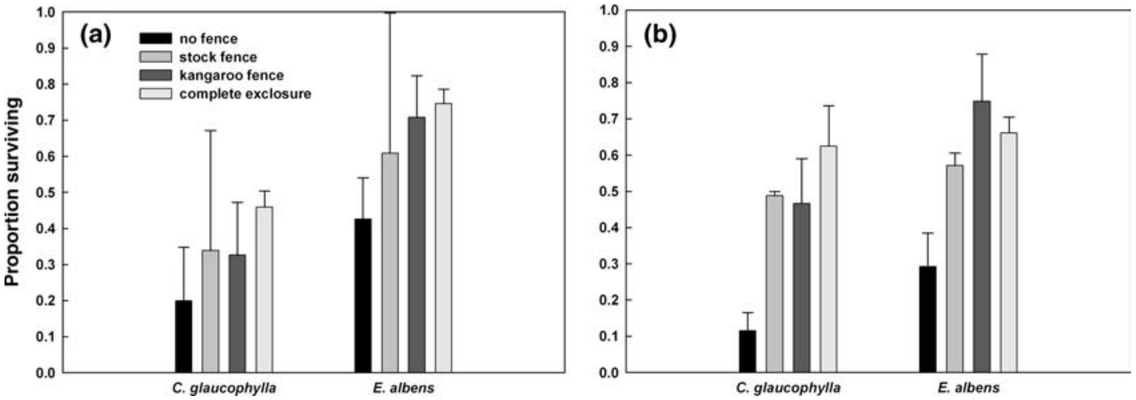

Figure 7. Survival ± SE after 3 years of *Callitris glaucophylla* and *Eucalyptus albens* seedlings planted in four herbivore exclusion treatments in (**a**) grassland and (**b**) woodland habitats.

nificant change took place had sufficient power to detect a change if it had occurred, indicating that the lack of change was real.

Fox Removal

There was an inconsistent effect of fox removal on the main subordinate terrestrial predator, the feral cat (prediction p_1). Feral cat numbers either increased (Removal 1) or did not change significantly (Removal 2) when foxes were removed; by comparison, we observed marked drop in numbers in the Control area. However, when foxes returned to the Removal 1 area, cat numbers remained high. The equivocal results probably reflect the difficulty of assessing cat population densities with spotlight

Table 2. Summary of Predicted and Observed Responses to Reductions in the Abundance of Foxes and Rabbits

Treatment	Prediction	Observed Response
Removal of foxes	p_1: Increase in abundance of feral cats	Mixed response; cats increased in abundance when foxes were removed but persisted when foxes returned after baiting ceased
	p_2: Increase in abundance of rabbits	No response
	p_3: Increase in abundance of macropods	No initial response by eastern gray kangaroos but a delayed increase following the RHD-induced decline in rabbit numbers; no consistent response by swamp wallabies; no response by wallaroos
	p_4: Increase in abundance of ground-feeding birds	No consistent response
Removal of rabbits	p_5: Decrease in abundance of predators	No affect on foxes; mixed response by cats, partly confounded by fox removal, but dietary data indicate cats are more dependent on rabbits than are foxes; alternative prey used by wedge-tailed eagles to provision nestlings
	p_6: Increase in abundance of macropods	Increase in numbers of eastern gray kangaroos and swamp wallabies but only in fox-removal areas; no affect on wallaroos
	p_7: Increase in the abundance of ground-feeding birds	No consistent response
	p_8: Enhanced recruitment of woody plant species	Historical data and transect data indicate increased recruitment of trees and shrubs; data from exclosures and predictions of stage-based models indicate increased establishment of *C. glaucophylla* but no change for *E. albens* seedlings; minimal impact of rabbits on standing plant biomass since the arrival of RHD
	p_9: Bird species richness determined by habitats that, in turn, respond to rabbit abundance	Higher bird species richness in habitats with more trees and shrubs

RHD, rabbit hemorrhagic disease.

counts (Mahon and others 1998; Molsher and others 1999) and the low densities recorded. There are no data available to assess the impact of fox removal on other predators in the area, which include raptors and the lace monitor (*Varanus varius*).

This system no longer has ground-living marsupials in the weight range most vulnerable to foxes. In general, none of the potential mammalian herbivore prey (rabbits, macropods) showed a consistent and significant increase when foxes were reduced relative to unmanipulated areas. Rabbit numbers were low due to the severe drought during period T1, but they increased in all areas under the favorable climatic conditions in T2. The comparatively slow postdrought increase in fox numbers, similar to that observed previously when rabbit abundance increased rapidly in western NSW (Pech and others 1992), probably accounts for the failure of predation to reduce rabbit numbers in the Control area compared to the areas where foxes were removed (contrary to prediction p_2). However, the number of eastern gray kangaroos was beginning to increase in the fox removal areas relative to the Control area before the arrival of RHD (prediction p_3); this trend was reinforced when the disease reduced rabbit populations from their original high density. The greatest increase in kangaroos occurred after foxes returned to the Removal 1 area, possibly due to a lag in the response to fox control, because foxes can limit juvenile recruitment of eastern gray kangaroos (Banks and others 2000).

If foxes removed birds to any extent, then it was predicted that, as foxes reinvaded during T4, numbers on the manipulated areas would decline to a greater degree, or increase less, than on unmanipulated areas. However, the results from grassy–open woodland (grassland and open eucalypt woodland) and from dense woodland (dense eucalypt woodland and *Callitris* woodland) were not significantly different from a null hypothesis of no effect of fox reduction on bird numbers (prediction p_4). Some increases and decreases were observed in bird species irrespective of how prone they were to fox predation. There were no species unique to Removal 1 and Removal 2 during the period of fox control. In general, the removal of foxes did not change the structure of the bird community.

Rabbit Removal

After the low rainfall of 1995 and before the arrival of RHD in July 1996, rabbit populations increased in all areas, most likely due to favorable weather conditions that generated ample food. In the Control area, there was no change in the sightings of foxes when rabbit abundance was reduced by about 85% by disease at the start of T3, in contrast to prediction p_5. When rabbits were numerous, they were a major component of fox diet, and they were supplemented by a wide range of other items, including carrion, insects, and vegetation, particularly in spring and summer, when these alternative food sources were more available (Molsher 1999; Molsher and others 2000). Therefore, in the grassy woodlands of central New South Wales, foxes appear to be efficient generalists and can use prey other than rabbits without measurable population-level impacts. This finding is in contrast to predictive models (Pech and Hood 1998) and observations (Holden and Mutze 2002) for semi-arid areas of southern Australia.

In contrast to foxes, cat numbers appeared to decline after the reduction of rabbits during T3 in the Removal 1 and Removal 2 areas, but not in the Control area (prediction p_5). However, cat numbers again appeared to be high during T4 in the Removal 1 area, despite continuing low counts of rabbits and the return of foxes to that area. As with foxes, rabbits were the main component of the cat diet, and they remained so for a wide range of rabbit densities. It was not until rabbits reached very low numbers that alternative prey became more evident in the diet, one of which was the exotic house mouse (*Mus domesticus*) when that species was present (Molsher and others 1999). In semi-arid systems, cat numbers decline after large reductions in rabbit populations (Read and Bowen 2001; Holden and Mutze 2002), and the diet data from Burrendong suggest that cats may be specialists in this system and hence may have declined after the impact of RHD, but our spotlight results are equivocal.

Information on the diet of wedge-tailed eagles was not available when there were very high rabbit numbers before RHD arrived at the study site. However, after 1996, there was still substantial (five fold) between-year variation in the abundance of rabbits when wedge-tailed eagles were provisioning their young. When rabbit numbers were very low in 2001, they comprised approximately half of the eagles' diet; whereas at the higher rabbit numbers of 1999, they accounted for 75%–80% of the diet. It is likely, therefore, that before RHD, when rabbit abundance was an order of magnitude higher (20–30 per spotlight km), they comprised most of the eagles' diet. When rabbits were scarce, they were replaced in the eagles' diet largely by macropods. The dietary data are supported by observations of the behavior of wedge-tailed eagles during the bird transect surveys (A. Sinclair and C. Davey unpublished). Over a 10-month period prior to RHD, an average of 0.12 wedge-tailed eagles km^{-1} were seen feeding on rabbits; after RHD, these observations declined to 0.03 km^{-1}. The difference in the number of transect observations before and after the decline in rabbit abundance could be due to either a greater reproductive success before RHD or a change in observability due to altered hunting patterns. Although the number of territories remained the same between October 1999 and October 2001, the proportion of pairs breeding dropped from 84% to 73%, and the breeding success (number of fledged young) dropped from 1.0 to 0.82 per breeding territory (C. Davey unpublished). This response is similar to that of the great horned owl (*Bubo virginianus*) in northern Canada. When snowshoe hare (*Lepus americanus*) numbers declined during the 10-year cycle, owl numbers remained constant but breeding success was proportional to hare abundance (Rohner and others 2001).

In general, the bird community did not increase in abundance in response to a decline in rabbit numbers as predicted (p_7); only six of 26 species showed a positive response. In contrast, the majority of birds increased more in areas of initially low rabbit abundance and where there was relatively little change in rabbit numbers.

Synergistic Effects of Fox and Rabbit Removal

Eastern gray kangaroos increased significantly after RHD arrived but only in the fox removal areas, indicating either that this response was simply a delayed effect of fox removal (prediction p_3) or an interaction with the removal of rabbits (prediction p_6). The latter is the more likely because when rabbits were present there was little or no increase in Removal 1 and only a small, nonsignificant increase in Removal 2. Once rabbits declined, however, the increase in kangaroos was much greater on both removal areas whereas the Control area showed no increase. Thus, foxes appear to reduce the abundance of kangaroos in the absence of rabbits, and rabbits can inhibit the increase of kangaroos in the absence of foxes (Figure 2d). Furthermore, when foxes were allowed back into the Removal areas, kangaroos continued to increase at a faster rate there than in the Control area, indicating a lag effect of fox removal: It appears that a pulse of young animals escaped predation, then continued to contribute to the population. Therefore, we suggest that both exotic species have a depressive effect on the kangaroo population's rate of increase, and when both species are present there is a synergistic depressive effect on kangaroo population densities.

Similar to eastern gray kangaroos, numbers of swamp wallabies increased significantly after the appearance of RHD and only in the fox Removal areas (Figure 2e). Swamp wallabies did not increase when rabbits were removed in the presence of foxes or when foxes were removed in the presence of rabbits. Therefore, it appears that the presence of either exotic species was sufficient to control the rate of increase of this wallaby. In contrast, there was no effect of fox or rabbit removal on wallaroos in any area. Wallaroos tend to live in steep, rocky terrain and may be less vulnerable to foxes or less affected by competition from rabbits.

In general, both foxes and rabbits can depress at least some macropod species. When both are present, there is a synergistic interaction that is greater than the effect of the two separately. These effects probably act through a combined top-down action of predation, most likely on juvenile kangaroos (Banks and others 2000), and bottom-up control through interspecific competition for grass food.

Long-term Effects of Rabbit Removal on Vegetation and Bird Communities

For herbaceous plants, the effect of year was opposite in direction to that expected if the elimination of rabbits reduced grazing pressure; in T3 and T4, the exclusion of rabbits had a minimal impact on standing biomass, with far more biomass being taken by livestock and kangaroos. In contrast, the increase in the recruitment of woody plants was consistent with prediction p_8. Even at low numbers, rabbits had the potential to substantially reduce woody plant survival, particularly *C. glaucophylla* seedlings. However, although rabbits did occasionally browse *E. albens* seedlings, their impact on this species was minimal, and *E. albens* establishment was predicted to be more dramatically affected by the activities of livestock and kangaroos than by rabbits (Allcock and Hik 2004).

Photo interpretation of changes in vegetation over a 30-year period from 1965 shows a significant increase in the tree canopy cover. Ground assessment indicates that trees of different ages have appeared since 1965, primarily due to the recruitment of white box and *Callitris*, suggesting a continual increase rather than a single pulse of recruitment for both species. Prior to the completion of Lake Burrendong in 1968, the Soil Conservation Service of New South Wales undertook major restoration work in the early 1960s. Livestock were removed and a 1080 poisoning campaign around the foreshores was initiated to control rabbits. Also, the poisoning might have resulted in a reduction in the abundance of macropods. It is likely that reduced grazing pressure on eucalypt seedlings by livestock and eastern gray kangaroos and on *Callitris* seedlings by rabbits during and after the 1960s enabled the establishment of woody vegetation. The present level of herbivory appears to be insufficient to prevent the gradually increasing dominance of white box and *Callitris* in the landscape. Therefore, we could assess the long-term effects of rabbit removal by comparing the richness of bird species in these young regenerating woodlands with that of the semi-natural and degraded open eucalypt woodland and grassland with a few scattered mature trees.

Rarefaction analysis indicates that there were approximately 20% more bird species present in dense eucalypt woodland than in the open eucalypt woodland and the *Callitris* woodlands. In contrast, the bird community in the *Callitris* woodland did not differ significantly in species richness from that in open eucalyptus woodland, although many of the species differed in abundance between the two habitats. In general, the long-term restructuring of the vegetation due to the suppression of rabbits by RHD should enable a significant increase in the biodiversity of birds (prediction p_9). This effect may be offset by the impact of kangaroos on the regeneration of eucalypt woodland, depending on whether kangaroo populations are reduced by culling or future levels of fox predation.

CONCLUSION

We examined the impact of exotic predators and herbivores on native fauna and flora through the control of foxes by poison baiting and the reduction of rabbits by a new disease in Australia, RHD. Removal of the top introduced predator, the fox, produced mixed changes in the abundance of a subordinate introduced predator, the feral cat, and no immediate changes in the abundance of a suite of native or introduced primary prey. Also, there were no consistent changes in a suite of potentially susceptible bird species. Removal of an abundant introduced herbivore, the European rabbit, affected the abundance of a specialist predator, the feral cat, more than two more-generalist predators, the fox and the wedge-tailed eagle. There was no evidence for strong, direct competition between rabbits and native herbivores. However, rabbits had a significant effect on the regeneration of *Callitris* but not on white box eucalyptus. Thus, over the last 50 years, rabbits (together with livestock) appear to have strongly influenced the structure of the landscape, and their continued suppression by RHD is likely to increase the recruitment of *Callitris*. Based on current habitat associations, this change will alter the composition of the bird community but not the total diversity of bird species.

The response by indigenous herbivores to fox or rabbit removal can be explained by a combined top-down action of predation and bottom-up control via interspecific competition. There was an increase in the abundance of macropods only when both exotic species were removed. The results from the Burrendong study demonstrate that there are complex interactions of the exotic species at all trophic levels. Generalist predators are more resilient to environmental perturbations and are potentially more dangerous to rare endemic species (Pech and others 1992; Sinclair and Pech 1996; Sinclair and others 1998) than specialist predators. Exotic herbivores can have major impacts on the plant community, but the environmental consequences of removing abundant herbivores such as rabbits may not be evident in time frames of less than a decade. Finally, single-species removal experiments that do not take synergistic effects into account could lead to erroneous conclusions. In general, there is evidence that invasive species have restructured part of the community (the plants and, possibly indirectly, the birds in the long term), but not other parts (the herbivores) due to counteracting effects between invasives.

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