

Damage caused by low-density exotic herbivore populations: the impact of introduced European rabbits on marsupial herbivores and *Allocasuarina* and *Bursaria* seedling survival in Australian coastal shrubland

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Received: 19 November 2010 / Accepted: 24 September 2011 / Published online: 2 October 2011
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Abstract The impact of over-abundant exotic herbivores is well recognised, but their impact at low population densities is poorly understood. This study examined interactions between European rabbits and native herbivores, and their impact on seedling recruitment in coastal South Australia, 2 years after rabbit haemorrhagic disease (RHD) had reduced rabbit density to 4.48 rabbits ha⁻¹. Rabbit density was further reduced to 0.44 rabbits ha⁻¹ in replicated experimental treatments. Rabbit control reduced total grazing pressure by 39% despite compensatory grazing increases of >100% for both western grey kangaroos and common wombats. Rabbit control slowed the rate of grazing and mortality for planted drooping sheoak and sweet bursaria seedlings, but few survived for 12 months: 0 and 3% of sheoak, in untreated areas and rabbit control treatments, respectively, and 3 and 11% of bursaria, respectively. Planted sheoaks survived well if protected by rabbit-proof netting (60%). Within treatments, seedling grazing and survival rates were negatively correlated with rabbit density but kangaroo and wombat density had no measurable effect. We conclude that RHD may briefly have reduced rabbit

densities enough to allow recruitment of bursaria but that sheoak require much lower rabbit densities than those provided by existing biological control agents. If left unaddressed, rabbit grazing could ultimately lead to the loss of sheoaks throughout most of their current range, irrespective of other attempts to conserve them. More generally, these data show how species-specific damage caused by low-density exotic herbivore populations may occur in the presence of more abundant but less-damaging native herbivores.

Keywords Drooping sheoak · Sweet bursaria · Rabbit control · RHD · Seedling survival · Western grey kangaroo · Common wombat

Introduction

Exotic herbivores damage native plant communities, in part, because they preferentially graze on native versus exotic plant species, thereby increasing exotic plant abundance, survival, flower and seed production, canopy cover, height and species richness in plant communities (see multispecies reviews by Parker et al. 2006; Oduor et al. 2010), damaging ecosystem function (Eldridge and Simpson 2002; Stritar et al. 2010) and facilitating further invasion (Simberloff and Von Holle 1999). Exotic herbivores suppress native plants to a much greater extent than do native herbivores (Parker et al. 2006). Although these are well recognised global problems, little is known about the relationship between

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exotic herbivore density and damage (Nunez et al. 2010). Herbivore grazing impacts are often managed on the principle that damage is likely to be incrementally reduced for any reduction in herbivore density, although that principle has been clearly demonstrated in few cases (Hone 2007). However density-damage relationships may be complex. In some circumstances, partial control of exotic herbivores could exacerbate their impacts by reducing grazing on less-palatable exotics without an equal reduction in grazing of palatable native species (Nunez et al. 2008). For the more palatable species in plant communities, there may be a low threshold density above which exotic herbivores profoundly affect their abundance and population structure (e.g. Lange and Graham 1983; Alverson et al. 1988; Allcock and Hik 2004; Denham and Auld 2004; Mutze et al. 2008).

European rabbits, *Oryctolagus cuniculus* L., are a recognised threat to conservation of many Australian native plants (Department of Sustainability, Environment, Water, Population and Communities 2008). The Family *Casuarinaceae* is one group of Australian native trees that has particularly palatable foliage and contains several species at risk from rabbit grazing (Bishop and Venning 1986; Cooke 1988; Denham and Auld 2004; Murdoch 2005). Drooping sheoak, *Allocasuarina verticillata*, is a widespread small tree, 4–10 m high, which occurs as a dominant or sub-dominant component of temperate south-eastern Australian woodlands. Drooping sheoak woodlands are reasonably well conserved in parks and reserves (Neagle 1995) but sheoak trees are relatively short-lived (60–100 years, Bishop and Venning 1986) and the ongoing removal of seedlings by rabbits threatens the species composition and structural integrity of these woodlands even when otherwise conserved (Smith 1963; Bishop and Venning 1986). This is especially so in sandy coastal and sheet-limestone areas, which characteristically support high rabbit densities.

Cooke (1988) concluded that natural regeneration of sheoaks in the Coorong region of South Australia has been restricted, since the arrival of Europeans and their associated livestock and rabbits in the 1800s, to a short period after myxomatosis first reached the area in the 1950s. Furthermore, he found that seedlings emerging during periods of above average rainfall survived only in rabbit-proof fenced exclosures. However, exclosures also limit access by other mammalian herbivores. Western grey kangaroos, *Macropus fuliginosus*,

common wombats, *Vombatus ursinus*, feral goats, *Capra hircus*, and feral fallow deer, *Dama dama*, occur in the Coorong area and might affect seedling survival. To determine whether conventional rabbit control could duplicate the protective effect of exclosures, Cooke subsequently controlled rabbits on approximately 50 ha of the study area. Wombats and kangaroos both increased in abundance on the rabbit control area (Cooke 1998) but a small number of sheoak seedlings emerged and grew outside one exclosure that was isolated from persistent rabbit populations by a band of dense mallee scrub (B. Cooke, unpublished data). In addition, recruitment of sweet bursaria, *Bursaria spinosa*, occurred at the same site but not in rabbit infested areas, indicating that it too was susceptible to rabbit grazing. Bursaria is a large shrub (0.5–5 m tall) that is widely distributed through temperate forests and woodlands of eastern Australia.

The trial reported here was established in 1997 in response to the release of a second rabbit biocontrol agent, rabbit haemorrhagic disease (RHD). RHD reached the Coorong in 1996 and reduced rabbit populations in the following year to 27% of long-term average numbers (Mutze et al. 2002). This study sought (a) to determine whether the impact of RHD was sufficient to allow another period of successful regeneration for sheoak woodlands; (b) to quantify the response of marsupial herbivores to reductions in rabbit numbers; (c) to determine whether control of exotic herbivores in the presence of uncontrolled marsupial grazing could reproduce more widely the limited recruitment of sheoak and bursaria that had been previously observed adjacent to the one exclosure site; and (d) in so doing, to quantify the rabbit density at which sheoak regeneration can occur. Information of this type is essential to inform management decisions in rabbit-infested conservation reserves.

Methods

Study site

The study area was in Coorong National Park about 10 km south of Salt Creek (36°08'S, 139°18'E). The Park is a band of coastal lagoon and fore-dunes, with adjoining shrubland and mallee scrub on the inland side, extending 150 km along the coast of south-eastern South Australia. Experimental sites were

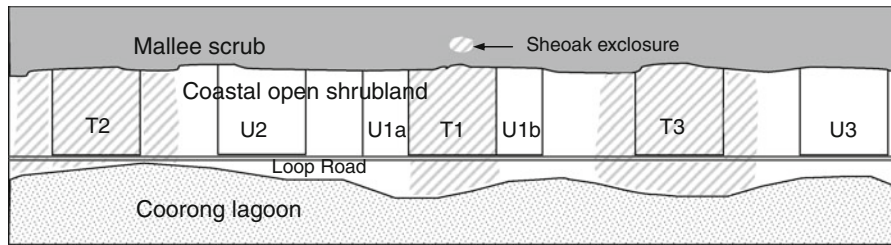


Fig. 1 Schematic diagram showing relative positions of experimental blocks established in the Coorong National Park to measure the impact of RHD and rabbit control on herbivore

located in a narrow (<1 km-wide) band of rabbit-infested open coastal shrubland between the Coorong lagoon and dense mallee *Eucalyptus diversifolia* scrub that supported few rabbits (Fig. 1). The shrubland consists of a mosaic of dense shrubs (approximately 42% cover) in patches of varying size interspersed with open herb/grass/sedgeland (58% cover) (proportions estimated from 1:2,500 aerial photography, September 1995, South Australian Department of Environment and Natural Resources), with occasional emergent pink gums *Eucalyptus fasciculosa* and sheoak. Mean annual rainfall is 480 mm. The climate is Mediterranean, with cool-moist winters and hot-dry summers. Annual plant growth is generally restricted by available soil moisture to late autumn, winter and spring (May–November), with most annual species dying off at the beginning of summer (December–February).

Experimental treatments

Six experimental blocks (three replicates, each of two paired treatments) were established in autumn 1997 to measure flora and fauna changes after the arrival of RHD, and responses to additional rabbit control. Each block was 50–120 ha in area. Rabbits were controlled on treatment blocks T1, T2 and T3 in 1997, 1998 and 1999, but not on untreated blocks U1a, U1b, U2 and U3. One of the rabbit control blocks (T1) was re-established on the 50 ha experimental site that had been subject to previous rabbit control from 1991 to 1993 (Cooke 1998). The untreated replicate in that original experiment consisted of two halves (U1a, U1b) located on either side of, and immediately adjacent to block T1. The close proximity (approximately 100–200 m) of parts of the treated/untreated replicates in the original blocks created some problems in maintaining treatment differences in rabbit numbers: there was infiltration of

numbers and recruitment of drooping sheoak and sweet bursaria. Treatment blocks (T), untreated blocks (U). Areas subject to rabbit control are shown with diagonal hatching

some rabbits into treated areas and also some draw-down influence of treatment on nearby untreated areas. To limit that problem in two additional paired (treated/untreated) replicates established in 1997, untreated replicates were single blocks of similar size and shape to treated blocks, and separated by buffers of approximately 500 m (Fig. 1).

Rabbit control was by conventional methods used for agricultural land in South Australia; poisoning with 375 mg kg⁻¹ sodium monofluoroacetate (1080)-treated oats laid in trails throughout the site, followed by warren destruction and fumigation of any re-opened burrows (Williams et al. 1995, pp 130–139). Warrens were mapped and then destroyed using a twin-tine ripper on a tractor-mounted backhoe. Care was taken to minimise damage to existing trees and shrubs and to avoid treating burrows utilised by common wombats. The area was searched after poisoning and ripping for fresh signs of rabbit and wombat activity (live animals, dung, and digging) and for any evidence of non-target poisoning mortality. Poisoning was repeated in February or March 1998, 1999 and 2001, supplemented throughout the experiment by fumigation of active warrens and shooting when ongoing rabbit activity was observed. Feral goats present in low numbers in 1997 were removed by mustering and shooting, with the aid of Judas goats to locate all animals (Taylor and Katahira 1988).

Herbivore abundance

Herbivore abundance was estimated from weight of dung deposited in fixed quadrats, a technique widely used to census abundance of rabbits and larger herbivores in Australian landscapes (e.g. Wood 1988; Williams et al. 1995; Landsberg and Stol 1996; Mutze et al. 2002; Allcock and Hik 2004). Dung pellets

provide an approximately linear index of rabbit density (Wood 1988) and estimates of goat, sheep and kangaroo density that correspond closely to estimates based on visual sightings (Landsberg and Stol 1996). Given the size of treatment blocks and home range size for each species, it is likely that the estimated changes in rabbit abundance represent changes in density of resident animals (Williams et al. 1995), while changes in marsupial abundance are likely to have been driven primarily by immigration, emigration and foraging patterns of residents with home ranges overlapping the site (Coulson 2008; McIlroy 2008).

Dung was collected every 4 months from March 1997 to March 1999 inclusive. In each treatment block, ten fixed quadrats were arranged at approximately 40-m intervals along each of four transects spanning the block. Transects were approximately 200 m apart. Dung was collected from rectangular quadrats with a common baseline of 4 m, 0.25 m wide (areas of 1.0 m²) for rabbits, 1.25 m wide (5.0 m²) for kangaroos and 5 m wide (20 m²) for wombats, goats and deer. The larger sample areas were used to account for the lower density and more patchy distribution of the less common species' dung. All quadrats were placed in open patches of herb/grassland with no shrubs, because previous studies on the site (Mutze et al. 2002, 2008) had shown that very little dung was deposited where quadrats were overgrown by shrubs. Therefore dung density estimated herbivore abundance or usage in the open habitat and over-estimated herbivore density in the open shrubland as a whole.

Dung was dried to constant weight at 40°C and weighed to the nearest 0.01 g. For the purpose of comparing each species' contribution to total grazing pressure we assumed that all species were eating diets with similar proportions of digestible dry matter, even if not with total dietary overlap. The first sample collected (pre-treatment) included any dung that was >4 months old, so contained greater dung mass than subsequent 4-monthly samples. Changes in total grazing pressure due to rabbit control were estimated from relative changes in total dung mass on treated areas (T) compared to untreated areas (U), assuming that if there was no treatment effect then pre-treatment T/U = post-treatment T/U. During some periods dung beetles were observed to consume fresh wombat dung and partially eaten older wombat dung was also found. At no time during this study were dung beetles or beetle damage detected in other species dung, so

wombat dung may be underestimated in this study relative to that of other species. The effects of treatment (T, U), season (July, November, March), replicate and year (1997–1998, 1998–1999) on mean dung densities (g m⁻²) of each species were tested by ANOVA (Statistica 9.1, Statsoft OK) for the 2 years that followed treatment.

Rabbit density was estimated from dung weight in the following manner: average body mass of 360 rabbits shot in the Coorong study area during 1997–1998 for epidemiological studies (Mutze et al. 2002) was 1.554 kg. Daily dry matter intake (DMI) for a 1.554 kg rabbit on native pasture was estimated as 95 g day⁻¹ (Short 1985). Digestibility of DMI varies widely with food quality and we assumed an intermediate value of 60% digestible matter. Rabbit dung is persistent on this site and dung that is >1-year-old may constitute a substantial proportion of dung collected when first clearing a transect (Mutze et al. 2002). Some dung is missed during collection or may be consumed by other animals. We assumed that on average only 5% of dung was consumed or decayed between deposition and collection because dung collected at 4-month intervals showed little sign of weathering or microbial decay. That equates the collection of 1 g m⁻² year⁻¹ rabbit dung (=10 kg ha⁻¹ year⁻¹) if collected, in total, from three 4-monthly samples, to an average rabbit density over the year of 0.76 rabbits ha⁻¹. We assumed a mean body mass of 36.5 kg for kangaroos (Coulson 2008) and 26 kg for wombats (McIlroy 2008). DMI was estimated from published intake:body mass relationships for western grey kangaroos as 1,291 g day⁻¹ (Short 1986) and for wombats as 929 g day⁻¹ (Evans et al. 2003). That equates the collection of 1 g m⁻² year⁻¹ dung to average densities of 0.051 kangaroos ha⁻¹ and 0.070 wombats ha⁻¹.

Rabbit abundance was also estimated from spotlight transect counts along the portion of Loop Road transect (Mutze et al. 2002) within the rabbit control (3.8 km) and no-control (2.2 km) blocks. Counts were conducted on two consecutive nights, approximately monthly, with the aid of a 100 W spotlight from the back of a 4WD utility driven at 12 km h⁻¹. Data were expressed as mean rabbits km⁻¹ during the 4 months between each dung sample to facilitate comparisons with estimates from dung weight. Counts of the larger, less common herbivores were highly variable due to the small transect lengths and were unsuitable for population estimates.

Vegetation biomass

Biomass of herbs, forbs, sedges and grasses was estimated from a permanently marked 0.594 m² sampling plot within each wombat dung sampling quadrat using a variation of the Adelaide technique (Andrew et al. 1976). For each species in the sample plot, a comparable-sized voucher specimen was harvested from nearby. Several different-sized vouchers were used where plant size varied considerably within the plot. The volume of plant material in each plot was estimated as a multiple of nearest-sized hand-held voucher specimen 'units'. Voucher specimens were dried to constant weight and used to calculate dry weight for each species in each plot. Grazing impacts on species composition are to be published in detail elsewhere—the data are used here only to determine whether treatment differences in total biomass were sufficient to influence herbivore response to rabbit control and/or seedling survival through plant–plant competition.

Seedling survival

Sheoak and bursaria seeds were collected from the Coorong study site in 1997 and planted in individual tubes filled with unfertilized local sandy soil in winter–spring 1997. Seedlings were 10–15 cm in height at the time of planting in the study area on 25–27 June 1998, following good autumn rains. Twelve seedlings of each species were planted without tree-guards in each of the six blocks. Within each block, paired sheoak and bursaria seedlings were planted 2 m apart at 12 sites, each site separated by ≥ 30 m. Sites were selected to match environmental conditions (soil type, slope, aspect and vegetation) in paired sites from adjacent treated and untreated blocks. An additional guarded sheoak seedling was planted at 5 of the 12 sites within each of the six blocks. Each guarded seedling was protected by a wire netting guard, 400 mm wide and 900 mm high with 40 mm diameter mesh size. In addition nine sheoak seedlings that remained after establishing the above treatments were planted within the treated areas and each surrounded by a pile (approximately 0.4 m high by 1 m wide) of dead fallen branches from nearby shrubs or trees, of sufficient density to make access for any herbivore difficult but not impossible. Seedlings were watered at the time of planting only.

Seedlings were monitored for evidence of grazing damage and to determine survival rates, at 2 week intervals for the first 2 months after planting, monthly from 2 to 8 months and 1 and 10 years after planting. Seedlings were classified as dead when no green plant tissue was visible above ground. Moisture stress was taken as the cause of death when during summer the seedling remained ungrazed but had browned and died, and surrounding annual grasses had also dried off and died. Grazing impact was considered to have killed seedlings when all that remained was root material or a short stub of dead stem, and no dead stem material was found in the surrounding litter. Grazing impact could not be differentiated between herbivore species for small seedlings because, in many cases, insufficient stem material remained for identification of bite marks.

For seedlings surviving beyond 1 year, rabbit damage was characterised by chisel-like 45° cuts on stems at up to 0.45 m height and 7 mm diameter, beyond which stem height/diameter plants escaped rabbit grazing. Damage was attributed to large herbivores (kangaroos, goats, deer or wombats) where seedlings had ragged breaks in stems of <20 mm diameter at heights of up to 1.5 m. Deer damage on older juvenile sheoak (up to 3 m height) was further characterised by ringbarking of larger stems at heights of 0.2–1.0 m as a result of antler rubbing. The height/diameter characteristics of trees that remained vulnerable to such damage could not be clearly established.

The effect of treatment, and herbivore abundance and pasture biomass within treatments, on the time until each seedling was grazed (days) and its survival time (days) was tested using log-normal regression survival models, with censored data for individuals that survived throughout the measuring period (Statistica 9.1, Statsoft OK). Fitted models incorporated treatment as a discrete grouping variable with two levels (rabbit-control, no-control), with plant biomass and dung density of each herbivore species at the adjacent dung collection point as continuous variables within groups. Preliminary analyses indicated that kangaroo and wombat dung density had similar effects (i.e. coefficients similar in sign and magnitude) so the data were re-fitted with kangaroo plus wombat dung combined as a single variable to simplify models. Models were fitted with all continuous variables and reduced by deleting non-significant terms, and results are presented only for terms that remained significant in at least one analysis.

Results

Herbivore abundance

Rabbits proved difficult to control on parts of treatment block T2 during 1997, and rabbit density remained above that in the other two treatment blocks until autumn 1998. Also, the poisoning trails laid during 1997 on T1 were too close to the untreated areas and rabbit numbers were partially suppressed on the untreated block U1 from July to November 1997. Notwithstanding those effects, and minor but significant seasonal variability ($F_{2,17} = 3.9$, $P < 0.05$) (Fig. 2a), treatment was highly effective ($F_{1,17} = 265$, $P < 0.001$) with no significant differences in mean rabbit densities between years ($F_{1,17} = 1.3$, $P > 0.26$). Importantly, rabbit control maintained an approximate tenfold difference in mean rabbit density between the untreated areas (4.48 ± 0.58 SE rabbits ha^{-1}) and the treatment areas (0.44 ± 0.15 SE rabbits ha^{-1}) during the seedling experiment (Fig. 2a). Rabbit spotlight counts in untreated areas were initially twofold higher than on treatment blocks and were 17-fold higher for the 12 months after seedlings were planted (Fig. 3). Although limited to a small part of the treated areas, the spotlight counts indicate that treatment effects persisted throughout the experiment.

Rabbit control reduced total grazing pressure, as estimated from total dung mass, by 39.6% in 1997–1998 and by 39.4% in 1998–1999 (Table 1). Within that overall decrease, compensatory increases in grazing pressure by native herbivores occurred where rabbits were controlled (Table 1). Kangaroo grazing pressure doubled in the first few months and remained at that elevated level (Fig. 2b), with no significant variation between seasons ($F_{2,17} = 0.03$, $P > 0.24$) or years ($F_{1,17} = 0.01$, $P > 0.93$). Kangaroo density during the seedling experiment was 0.047 ± 0.009 SE kangaroos ha^{-1} in the untreated areas and 0.105 ± 0.015 SE kangaroos ha^{-1} in the rabbit control treatments. Wombat grazing pressure trebled, but more gradually, with significantly higher levels in the second year ($F_{1,17} = 12.3$, $P < 0.003$), and a more pronounced treatment effect in summer than in earlier seasons (treatment \times season $F_{2,17} = 9.87$, $P < 0.002$) (Fig. 2c). Wombat density during the seedling experiment was 0.020 ± 0.004 SE wombats ha^{-1} in the untreated areas and 0.066 ± 0.020 SE wombats ha^{-1} in the rabbit control

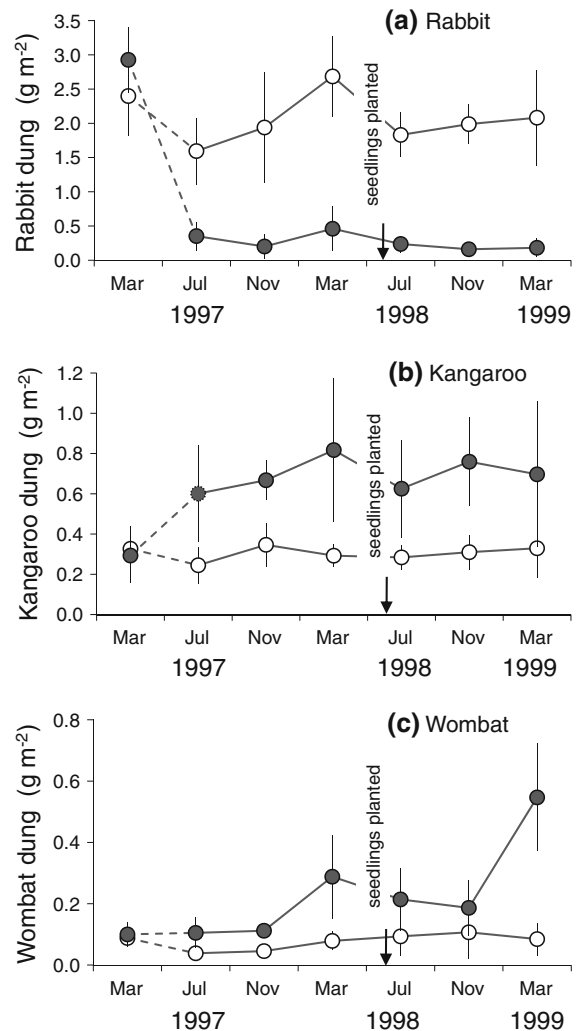


Fig. 2 Seasonal changes in dung weight index of abundance for rabbits, western grey kangaroos and common wombats in Coorong National Park following rabbit control treatment. Rabbit control, *closed symbols*; untreated, *open symbols*; mean \pm SE, $n = 3$. Pre-treatment samples were collected immediately before treatment in March 1997, post-treatment samples at 4-monthly intervals thereafter

treatments. Treatment effects also varied between replicates for both kangaroos and wombats (treatment \times replicate $P < 0.01$); both species responded strongly on the original block T1 that had been subject to previous rabbit control, kangaroos responded more strongly on T3 than T2, and wombats more strongly on T2 than T3.

No evidence of non-target mortality was found when the site was searched during and after rabbit control.

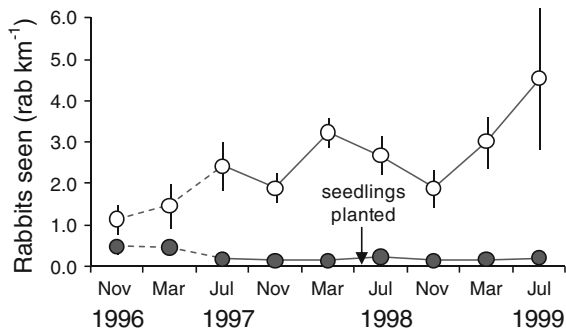


Fig. 3 Spotlight transect counts of rabbits in Coorong National Park following rabbit control treatment in March 1997. Rabbit control, closed symbols; untreated, open symbols; 4-monthly mean \pm SE

A small mob of feral goats was commonly seen during field work in 1997, but no goats were seen after that mob was removed in late 1997. Thereafter combined goat and deer dung decreased from $0.03 \text{ g m}^{-2} \text{ year}^{-1}$ in 1997 to nil during the seedling experiment in 1998–1999 (Table 1).

The proportional contribution of each herbivore species to total dung weight in the untreated blocks remained fairly constant (Table 1). That indicates that the methodology used to estimate the effect of rabbit control on total grazing pressure and relative abundance of herbivore species was reasonable. Pre-treatment grazing levels in the rabbit control blocks in Table 1 are drawn only from the two new treatment blocks—T1 was not suitable for a pre-treatment baseline because of intermittent rabbit control between 1991 and 1994. Nevertheless, grazing levels in 1991 when the experiment was first established (91% rabbit, 7% kangaroo, 0.3% wombat, 1% goat, Mutze and Cooke 1998) were

proportionately similar to pre-treatment grazing levels on the three untreated blocks and the two new treated blocks presented in Table 1, if allowance is made for higher pre-RHD rabbit numbers.

Vegetation biomass

Mean biomass of herbs, forbs, sedges and grasses in untreated plots was $\geq 348 \text{ kg ha}^{-1}$ in all sample periods, and exceeded mean biomass in rabbit control plots in all sample periods (Table 2).

Seedling survival

All nine sheoak seedlings growing through piles of fallen branches, and 60% of sheoak seedlings protected by netting guards survived for at least 12 months. Moisture stress was the main cause of death in guarded seedlings; most were lost in summer and none were browsed (Fig. 4a, b). By contrast, only one unguarded sheoak seedling survived for 12 months after planting (Fig. 4b). Two unguarded sheoaks died in spring with no evidence of grazing, possibly due to insect or fungal attack, and a further ten seedlings died, ungrazed, of moisture stress during summer, but severe grazing damage was responsible for most seedling mortality (80%). In the rabbit control treatments, sheoak seedlings remained ungrazed for longer than those in untreated areas, and within treatments, sheoaks remained ungrazed for longer where rabbit dung was less prevalent (Table 3a; Fig. 4a). Many sheoaks survived grazing in spring and produced new shoots, but most were killed by grazing during summer, so there were no significant effects of treatment on sheoak

Table 1 Relative abundance of herbivores in Coorong National Park following rabbit control in March 1997

	March 1997 (before treatment)		July 1997–March 1998 (after treatment)		July 1998–March 1999	
	Rabbit control	Untreated	Rabbit control	Untreated	Rabbit control	Untreated
Total dung mass	2.81	3.38	1.20	2.43	1.20	2.37
Rabbit	2.40 (85%)	2.93 (87%)	0.34 (28%)	2.07 (85%)	0.19 (16%)	1.97 (83%)
Kangaroo	0.29 (10%)	0.33 (10%)	0.70 (58%)	0.29 (12%)	0.69 (58%)	0.31 (13%)
Wombat	0.10 (3%)	0.09 (3%)	0.17 (14%)	0.05 (2%)	0.32 (26%)	0.10 (4%)
Goat/deer	0.03 (1%)	0.04 (1%)	0.003 (0.2%)	0.005 (0.2%)	Nil	Nil

Data shown as the density of herbivore dung per transect (g m^{-2}) and the contribution by species to the treatment total. The March 1997 pre-treatment sample included old dung (i.e. >4-months old) but excluded data from the treatment replicate (T1) that had been subject to rabbit control in earlier years. Subsequent post-treatment data represent mean density of dung collected in three 4-monthly samples from three replicates

Table 2 Total biomass of herbs, forbs and grasses in Coorong National Park following rabbit control in March 1997

Date	Rabbit control (kg/ha \pm SE)	No control (kg/ha \pm SE)
June 1997	205 \pm 28	417 \pm 67
November 1997	401 \pm 50	487 \pm 23
April 1998	255 \pm 33	348 \pm 17
November 1998	503 \pm 49	562 \pm 18
November 1999	427 \pm 17	517 \pm 39

survival (Table 3b; Fig. 4b). During the first 12 months of the seedling experiment, no rabbit dung was found on the dung transect point closest to the surviving sheoak, indicating very low rabbit densities in that vicinity.

Bursaria seedlings fared only a little better than sheoaks: rabbit control treatment reduced the rate of grazing damage and mortality, and within treatments, grazing and mortality rates were higher where more rabbit dung was present (Table 3c, d), but by the end of summer most seedlings were dead (Fig. 4c, d). Moisture stress killed 21% of bursaria seedlings with no evidence of grazing, but grazing damage killed 74% of seedlings. Two seedlings remained ungrazed in the rabbit control treatments after 12 months. Two further seedlings in the rabbit-control and one seedling in the no-control treatments were grazed but survived for more than 12 months. The densities of rabbit dung found on the dung transect points closest to the five surviving bursaria were substantially lower than treatment means, equivalent to mean rabbit densities of 0, 0, 0.16, 0.32 rabbits ha⁻¹ (in treated areas) and 0.36 rabbits ha⁻¹ (in untreated areas).

There were no statistically significant within-treatment effects of kangaroo, wombat or combined kangaroo + wombat dung on seedling grazing rates or survival in any model that included the other significant terms. The effect of kangaroo + wombat dung on bursaria grazing rate approached statistical significance (t value = 1.71) but had a positive coefficient, indicating a weak but non-significant trend towards lower seedling grazing rates where marsupial densities were higher. There were no effects of plant biomass on seedling grazing rates or survival when considered as the sole explanatory variable or in models with other significant variables included.

During the last 9 years of the seedling experiment, three guarded sheoak seedlings that survived through

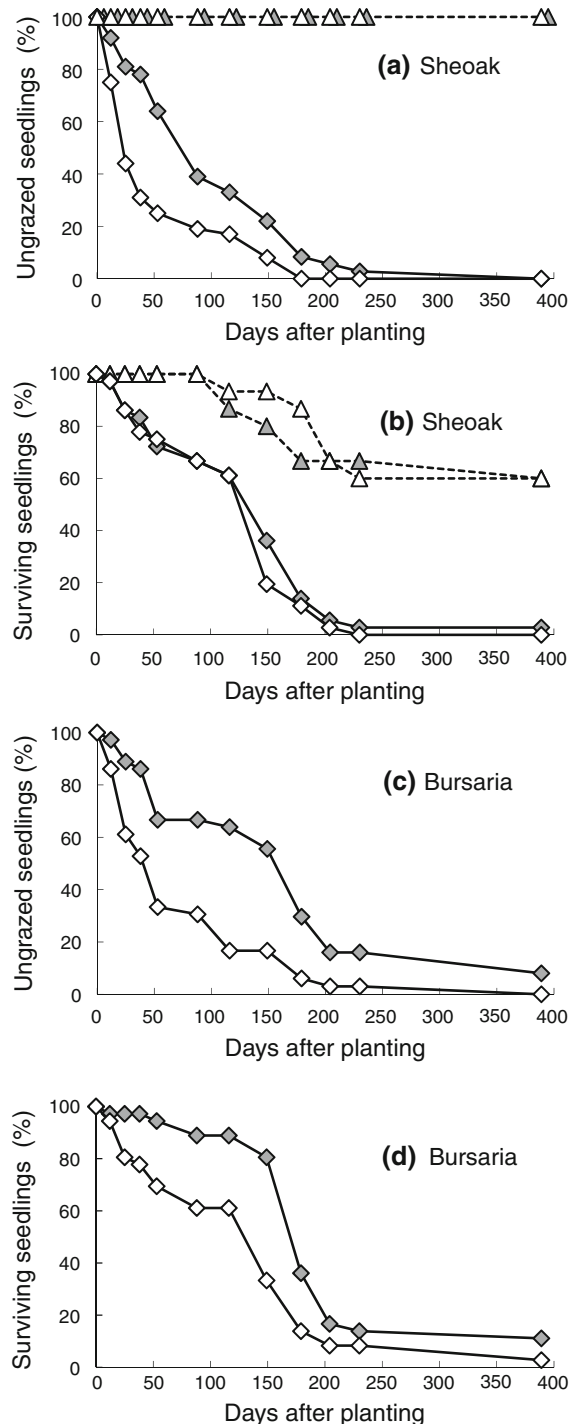


Fig. 4 Grazing and mortality schedules for drooping sheoak and sweet bursaria seedlings in Coorong National Park, subject to different levels of protection against rabbit grazing. Seedlings were planted 25–27 June 1998. Rabbit control, *closed symbols*; untreated, *open symbols*; with tree-guards, *dashed line*; without tree-guards, *solid line*

Table 3 Log-normal regression survival analysis for 12-month grazing and survival rates of bursaria and sheoak seedlings in Coorong National Park, in relation to rabbit control treatment (\pm) and residual grazing intensity index of rabbits (g dung m⁻² year⁻¹) within treatments

Parameter	χ^2	df	P	Coefficient	SE	t value
(a) Sheoak grazing rate						
Treatment group	9.20	3	0.027			
Regression	5.51	1	0.019			
Rabbit				-0.059	0.025	-2.39
Constant				4.089	0.126	32.6
Sigma				0.927	0.077	12.0
Censored observations n = 0						
(b) Sheoak mortality rate						
Treatment group	0.81	3	0.848			
Regression	2.60	1	0.107			
Rabbit				-0.034	0.021	-1.63
Constant				4.715	0.106	44.4
Sigma				0.783	0.066	11.9
Censored observations n = 1						
(c) Bursaria grazing rate						
Treatment group	9.94	3	0.019			
Regression	5.89	1	0.015			
Rabbit				-0.064	0.026	-2.48
Constant				4.47	0.131	34.06
Sigma				0.968	0.082	11.74
Censored observations n = 2						
(d) Bursaria mortality rate						
Treatment group	11.30	3	0.010			
Regression	4.50	1	0.034			
Rabbit				-0.049	0.023	-2.15
Constant				5.017	0.117	42.95
Sigma				0.854	0.075	11.39
Censored observations n = 5						

Censored observations are those that were ungrazed or survived throughout the experimental period

the initial 12-month period subsequently died during a severe drought in 2006–2007, four survived and had been repeatedly browsed by large herbivores at the limit of the tree-guard, two large sheoaks (2.5 and 3 m in height) had their tree guards broken away and had been ringbarked and killed by deer antler rubbing, but nine others had retained their tree-guards and become well-established young trees of 2.5–4.5 m height. The only surviving unguarded sheoak was browsed repeatedly by rabbits, survived until 2007 without reaching escape size from rabbit damage, and was dead in 2008. Three of the five surviving unguarded bursaria survived for 10 years but had been kept to short stubs of <3 cm height by repeated rabbit grazing. All had been overgrown and partially hidden by the outer leaves of nearby grass tree, *Xanthorrhoea semiplana*, tussocks.

Discussion

The impact of rabbits on marsupial herbivores

This study demonstrates the ability of rabbits at only moderate population densities to competitively suppress large marsupial herbivore numbers in conservation reserves. Kangaroo numbers increased rapidly following rabbit control and were maintained at the higher level in all subsequent samples (Fig. 2). This contradicts predictions based on functional-response grazing models (Short 1985) that competition between rabbits and larger herbivores may be limited to periods of low food availability (Choquenot 1992). Total pasture biomass exceeded levels which greatly limit food intake of kangaroos (Short 1985, 1986) and was higher in areas not subject to rabbit control, so

competition based on available pasture biomass should not have occurred, or if at all, only during summer and early autumn, when annual forage had died off or been consumed, and reproduction consequently declined in rabbits (Mutze et al. 2002). We conclude that rabbits compete with kangaroos during periods of high feed availability by selectively removing the more nutritious plant species and plant tissues from native pasture, as they do in livestock pasture (Myers and Poole 1963; Wood et al. 1987).

Wombat numbers increased in response to rabbit control by an even greater margin than kangaroos, but more gradually. This is probably due to their dietary reliance on perennial native grasses and sedges (Mallett and Cooke 1986; McIlroy 2008) which, in this area, recover gradually over several years following effective rabbit control (Cooke 1998). Wombat numbers were also suppressed by rabbits at all times, but to a much greater extent in summer (Fig. 2c). This result could be explained by greater dietary overlap during summer: i.e. by rabbits switching from a diet predominantly of annual forbs and grasses during winter/spring to a diet that concentrated on perennial dicots, sedges and grasses in summer/autumn (as they do switch in south-western Australia, Martin et al. 2007), while wombats in this region favour perennial sedges and grasses throughout the year (Mallett and Cooke 1986). Although the numerical response of both marsupials was primarily driven by immigration and changes in foraging range, it follows that total marsupial abundance is also likely to increase gradually if limiting food resources become more available. That is particularly true for common wombats, whose populations are generally limited by food availability (McIlroy 2008), particularly, in this area, during summer (Mallett and Cooke 1986; Cooke 1998). Grazing responses of kangaroos and wombats varied considerably between replicates in this study, possibly because of differences in abundance of sedges, and the role of pasture composition is the subject of ongoing investigation.

Dietary competition is likely to be extreme between rabbits and smaller marsupial herbivores with more limited foraging ranges and dispersal capacity, and the direct role of competition in the demise of small mammal populations in southern Australia is probably underestimated, as opposed to the role of introduced predators, and of rabbits in maintaining high predator numbers (Johnson 2006). Unfortunately, many of these species are now too rare within the rabbits' range in

Australia for meaningful studies. It is also interesting to note that although common wombats are theoretically susceptible to 1080 poisoning from rabbit bait and fumigation of jointly used burrows, rabbit control had no short-term impact on wombat abundance, and dramatically increased their abundance over the following years. Rabbit control appears, on our data, to be a critical component of wombat conservation efforts.

The impact of rabbits on seedling survival

Vegetation damage by introduced European rabbits has been recorded in a vast array of habitat types and plant communities, ranging from desert shrublands (Lange and Graham 1983) to mesic subantarctic (Chapuis et al. 2004) and subtropical islands (Coyne 2010), and has been extensively reviewed by previous authors (e.g. Williams et al. 1995). In low-productivity desert ecosystems, severe damage occurs even at low rabbit density (≤ 1 rabbit ha^{-1} : Lange and Graham 1983; Donlan et al. 2002; Denham and Auld 2004; Mutze et al. 2008). Rabbits remove seedlings of some uncommon, highly palatable species within a few days (Lange and Graham 1983), so quickly that their impact cannot easily be studied by any means other than planted seedling experiments. In more-productive mesic landscapes these effects have generally been documented only at moderate-high population density (e.g. ≥ 3 rabbits ha^{-1} : Cooke 1988; Leigh et al. 1987; Chapuis et al. 2004). Possibly the lowest-density record from such areas is that of Davey et al. (2006) who recorded rabbit damage to *Casuarina glaucophylla* seedlings when spotlight transect counts averaged 2.1 rabbits km^{-1} , although Allcock and Hik (2004) suggest seedling impact within that study was measured where rabbit counts were 5 rabbits km^{-1} . By comparison, damage continued at the Coorooong in rabbit control areas where counts were an order of magnitude lower (Fig. 3). This study sets a new low-density benchmark for the damaging impact of rabbits on Australian temperate-zone flora, highlighting what is likely to be a more widespread but little-recognised threat posed by low-density exotic herbivore populations to key components of highly productive vegetation communities.

Rabbits were reduced to <50% of their pre-RHD levels when RHD reached the Coorooong, promoting significant recovery in some elements of the local flora (Mutze et al. 2008). Following further reduction by mechanical/chemical control treatments, to <0.5

rabbits ha^{-1} , rabbits were contributing $<20\%$ of mammalian grazing pressure in the treated areas but continued to suppress seedling survival. By contrast, no effect on seedling survival was detected for the two common endemic marsupial herbivores which were jointly responsible for $>80\%$ of mammalian grazing pressure in the treated areas.

Seedling survival rates indicated that RHD might just have reduced rabbit densities sufficiently, if only for a short time (Mutze et al. 2002), for some natural recruitment of bursaria. This conclusion is supported by casual observations early in the experimental period of sparse bursaria recruitment in an untreated patch of grass-tree tussocks, sufficient only to replace natural mortality of adult bursaria during the following 10 years. However, sheoak are more sensitive to rabbit grazing and rabbits have already recovered substantially from the initial effects of RHD (Mutze et al. 2002, 2008). Regardless of the possible role of other herbivores, it is clear that the existing biological control agents alone will not reduce rabbit numbers to the level where sheoak regeneration might occur in coastal woodlands.

We were unable to reduce rabbit density sufficiently to achieve positive recruitment rates for sheoak (objective (d) of this study) but this work confirms previous findings that sheoaks will regenerate if grazing is controlled adequately (Cooke 1988). While some seedlings may have died from the combined effects of grazing and moisture stress, most seedlings protected by tree-guards survived, suggesting that sheoak seedlings can usually tolerate moisture stress in the absence of grazing. By matching seedling planting sites between treatments, we minimised any influence of variable plant–plant competition and soil moisture stress on variation between treatments in seedling survival of shrubs, but survival versus biomass analyses suggest that plant–plant competition had no measurable effect within treatments. Outside of tree-guards, the few sheoak seedlings that were protected by planting inside dense piles of fallen branches all survived. We presume that dead annual vegetation retained by the fallen branches in summer, and the branches themselves, provided a micro-habitat with sufficient shade and mulch to maintain soil moisture, but a properly designed experiment is needed to identify the critical factors. Germination of sheoak seedlings in this type of microhabitat may be an important factor influencing natural recruitment.

Implications for conservation management

The impact of low-density rabbit populations is of particular concern for the future of sheoak woodlands because so many of them have been reduced to scattered trees in rabbit-infested reserves or livestock pastures. Sheoaks are palatable to livestock, indeed they were often left standing during land clearing operations last century because of their fodder value, and lopped during drought to feed stock (Bishop and Venning 1986). It seems unlikely that any natural regeneration of sheoak will occur in livestock pastures, or in vegetation reserves when rabbits are present at or above densities of $0.5 \text{ rabbits ha}^{-1}$. These data suggest that rabbit grazing, if left unaddressed, could ultimately lead to the loss of sheoaks throughout most of their current range, irrespective of other attempts to conserve them.

The effect of rabbits on sheoak regeneration is mirrored in buloke, *Allocasuarina luehmannii*. Herbaceous pine-buloke woodland in Hattah-Kulkyne National Park is listed as a threatened habitat under the Victorian Government *Flora and Fauna Guarantee Act* of 1998. After RHD reduced rabbit numbers in 1996, to a much greater extent than in the Coorong (Sandell 2002), regeneration of buloke seedlings was recorded at Hattah-Kulkyne for the first time in many decades, despite below average rainfall (Murdoch 2005). Recovery of rabbit populations in recent years has seen all but the largest of those recruits killed by rabbit grazing where rabbit populations are above $0.6 \text{ rabbits ha}^{-1}$ (F. Murdoch, unpublished data, 2009).

Despite the reduction in rabbit numbers brought about by RHD, the threat posed by residual low-density rabbit populations to tree and shrub recruitment is being recognised for an increasing number of species as more data are gathered (e.g. Denham and Auld 2004; Mutze et al. 2008). It is likely to be widespread in many other species that have been less-extensively studied but occur in habitat occupied by rabbits. In particular, other species of *Casuarinaceae* may be threatened by this process, which could seriously affect nationally vulnerable fauna such as glossy black-cockatoos, *Calyptorhynchus lathami*, that feed almost exclusively on the seeds of *Allocasuarina* (Higgins 1999). Indeed, research conducted from this perspective to identify edaphic factors limiting the distribution of remnant *Allocasuarina* (Cameron 2006) may, in part, have identified factors

affecting the distribution of sparse rabbit populations—we suggest this is an area of research worthy of further attention. Furthermore, the Coorong data indicate that *Allocasuarina* seedling recruitment might be prevented by rabbits at densities so low that the presence of rabbits, let alone their effect on seedling survival, is barely noticeable to conservation managers.

More generally, this study highlights the risk that severe species-specific damage caused by low-density exotic herbivore populations may easily be overlooked. It is particularly likely to go unnoticed in highly productive environments, in the presence of more abundant endemic herbivores, where there is considerable dietary overlap between exotic and endemic herbivores, and/or where the total grazing pressure varies little with partial control of exotic herbivores because of compensatory increases in endemic species.

Acknowledgments We would like to thank Brian Cooke who established the rabbit control experiments at this site in 1991 and Roger Roberts and the Tiver families for assistance during field work at Salt Creek. Chris Holden and anonymous referees provided helpful comments on earlier drafts of the manuscript. This work was conducted with funding support from the Australia and New Zealand Rabbit Calicivirus Disease Program.

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