

Home range, activity and habitat use of European rabbits (*Oryctolagus cuniculus*) in arid Australia: implications for control

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Abstract. The home range, activity and habitat use of wild European rabbits in northern South Australia were compared during winter and summer, and results used to suggest improvements to control techniques. Average home range was significantly smaller in summer (2.1 ha) than winter (4.2 ha) and there was no significant difference between the sexes. Rabbits used both dune and swale habitat but most warrens and more surface fixes were recorded in dune habitat in both seasons. Proportionally more surface fixes were found in swale habitat at night than during the day. The proportion of diurnal fixes on the surface was not significantly influenced by season, averaging 47% in winter and 62% in summer. Only 30% of radio-collared rabbits flushed by humans retreated to warrens. Comparable levels of diurnal surface activity in both winter and summer suggest that the death rate from fumigation or warren destruction may be similar in both seasons. High levels of diurnal surface activity suggest that warren fumigation may be ineffective unless rabbits can first be flushed to their warrens. The use of dogs to flush rabbits before fumigation or ripping should increase the efficacy of control. Activity data suggest that fumigation or ripping should be conducted between 0900 and 1600 hours in winter and 1100 and 1800 hours in summer when radio-collared rabbits were most likely to be down their warrens. Home-range data suggest that the effectiveness of poison baiting may be increased by placing bait lines closer together in summer and, although bait lines should be concentrated in dune habitat, some poison should also be placed in swale feeding areas remote from warrens. The most successful control method for radio-collared rabbits was fumigation with phosphine gas tablets, with 10 of 11 rabbits successfully killed. Pressure fumigation with chloropicrin was also successful but 1080 poisoning and warren destruction using shovels were all relatively unsuccessful.

Introduction

The European rabbit (*Oryctolagus cuniculus*) was introduced to Australia in 1859 and now inhabits ~60% of Australia, including both the arid and semi-arid zones (Myers *et al.* 1989). Rabbits have severely affected native flora and fauna by inhibiting the regeneration of native vegetation (Lange and Graham 1983; Cooke 1987), supporting populations of introduced predators such as the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) (Catling 1988; Bowen and Read 1998) and competing with native animals for food and shelter (Dawson and Ellis 1979; Priddel *et al.* 1995). Consequently, the decline or extinction of many medium-sized mammals, particularly in the arid and semi-arid zones, has been associated with the introduction of rabbits (Calaby 1969; Morton 1990). Competition and land degradation by feral rabbits is now listed as a key threatening process under the Commonwealth Environmental Protection and Biodiversity Conservation Act (2000). Rabbits are considered a known or perceived threat to more than 45 species of threatened native plants and animals (Environment Australia 1999). Prior to the release of rabbit calicivirus disease, South Australia's arid-zone livestock industry suf-

fered an estimated loss of \$17.4 million each year due to rabbits (Cooke 1991).

A variety of methods are used to control rabbits in Australia including warren destruction, fumigation, poisoning and trapping (Williams *et al.* 1995). One of the key objectives of the Threat Abatement Plan for Rabbits (Environment Australia 1999) is to improve the effectiveness and humaneness of rabbit-control techniques. Warren destruction through ripping is highly effective (Parer and Parker 1986; Williams and Moore 1995) but is inappropriate in some arid areas where numerous, small warrens are located in sand dunes under perennial vegetation (Vine and Eldridge 2000; K. Moseby, personal observations). Several studies have investigated the effectiveness and efficiency of poisoning, warren ripping and chemical fumigation by measuring the overall changes in rabbit populations (Foran *et al.* 1985; Williams and Moore 1995; Vine and Eldridge 2000). However, the fate of individual rabbits after control is rarely known and may assist with interpretation of control results. A greater understanding of rabbit behaviour including activity patterns and home range may help to identify appropriate control methods and optimise the spatial and temporal

components of control initiatives. Many species in the arid zone use rabbit warrens for shelter, especially during the hot summer months. By limiting warren destruction to periods when warrens are most likely to contain rabbits, deaths of non-target species through inefficient control will be reduced.

This study used radio-telemetry to determine the influence of season and sex on the home range, activity, warren and habitat-use of rabbits in arid South Australia. At the culmination of the study, a variety of standard control techniques were used to kill the rabbits and retrieve the radio-transmitters. Earlier trials with 'Rid-a-Rabbit', which uses liquid petroleum gas pumped into warrens and ignited, proved ineffective, with four separate warrens trialed and all four radio-collared rabbits dug up alive after treatment. Notes on the comparative success of poisoning with 1080 oats, fumigation with chloropicrin and phosphine tablets and manual warren destruction on the individual rabbits are included. Results are then used to suggest an optimum control strategy for rabbits in sandy arid areas where ripping is not feasible.

Materials and methods

Study site

The Arid Recovery Reserve (30°29'S, 136°53'E) is a 60-km² enclosure situated 20 km north of Roxby Downs in arid South Australia. A 1.8-m-high rabbit-, cat- and fox-proof netting fence surrounds the reserve and all rabbits, cats and foxes have been removed from the reserve. This study was conducted immediately outside the reserve where quarterly spotlight transects were used to conservatively estimate the natural densities of rabbits during 2002 to be 8–43 km⁻², with an average of 19.5 (WMC (Olympic Dam Corporation) Pty Ltd 2003). The climate of Roxby Downs is arid, failing to reach its long-term average rainfall of 166 mm in 60% of years (Read 1995). Only 44 mm of rain was recorded at the Arid Recovery Reserve in 2002. The dominant landforms include longitudinal orange dunes separated by clay interdunal swales. Dunes are generally between 100 m and 1 km apart. The study area encompasses a range of habitat types including chenopod (*Atriplex vesicaria* and/or *Maireana astrotricha*) shrubland swales, wattle (*Acacia ligulata*), hopbush (*Dodonaea viscosa*) and native pine (*Callitris glauco-phylla*) dunes, mulga (*Acacia aneura*) sandplains and canegrass (*Eragrostis australasica*) swamps.

Radio-tracking

Rabbits were captured opportunistically in both dune and swale habitat. Live-trapping proved ineffective so rabbits were captured at night in nets. A handheld spotlight was used to locate rabbits along tracks around the reserve and a single shot with a 0.22 rifle was fired above their head to stun them, before catching them with nets. The rabbits were weighed, sexed, checked for reproductive status and fitted with mortality-sensitive radio-transmitters (Biotelemetry, SA). Animals were radio-tracked at different times of the day and night, usually only once in a 24-h period. GPS coordinates were recorded for each location, along with the landform (dune or swale) and whether the rabbit was in a warren or on the surface. Previous studies have suggested that more than 30 fixes are required to provide an asymptotic home range for rabbits (Hulbert *et al.* 1996; White *et al.* 2003). Each rabbit was thus radio-tracked for a minimum of 30 fixes over a minimum period of 21 days but the number of unique fixes was sometimes lower as

multiple fixes were often recorded at the same warren. More than 50 rabbits were radio-collared during the study but collar failure and mortality meant that sufficient fixes could be obtained from only 18 rabbits. Ten rabbits (6 male, 4 female) were radio-tracked in summer between January and April 2002 and eight different rabbits (3 male, 5 female) in winter between July and September 2002.

Response to disturbance

Many rabbits were on the surface during diurnal radio-tracking, prompting an investigation into the response of rabbits to disturbance. Rabbits that were flushed by the observer during diurnal radio-tracking were located again after 5 min. The observer remained quietly at the site of the initial fix during the 5-min waiting period. During the second fix the observer recorded whether the rabbit had sought refuge in a warren or was still residing on the surface. The response of diurnal surface rabbits to disturbance was also recorded when the observer was accompanied by a dog. Several different untrained, unleashed domestic dogs were used on six occasions during winter 2002.

Collar retrieval

Live-trapping of rabbits in cage traps to retrieve collars proved unsuccessful (see also Wood 1980), so when sufficient fixes were obtained to accurately plot home range, rabbits were killed and collars retrieved. Standard control methods were used, namely warren destruction, 1080 poisoning, pressure fumigation of warrens with chloropicrin and warren fumigation with phosphine gas. Surface-dwelling rabbits were chased into warrens before fumigation or destruction. When the mortality sensor had been activated, collars were retrieved by digging up the warren. Ten rabbits were killed using each of the four control methods.

Warren destruction by ripping was not feasible as most warrens were in sand dunes under perennial vegetation. Destruction was therefore conducted by collapsing the warren as much as possible using a shovel and piling sand on top of the entrances to a depth of ~0.5 m.

Poisoning was conducted by laying two oat trails of non-poisoned oats 2–3 days apart using a bait layer trailer towed behind an all-terrain vehicle. The oats were laid in a single line along the side of the dune spanning the distance of the rabbit's known home range and extending 100 m either side. One trail of oats poisoned with 1080 (monosodium fluoroacetate) was laid 2–3 days later. Poisoned oats were obtained from the Animal and Plant Control Commission (SA).

Warren fumigation with phosphine gas involved wrapping two Gastion® (Rentokil Initial Pty Ltd, NSW) tablets in a 20-cm length of toilet paper and wedging them into the end of a 1-m length of hollow poly-pipe. The pipe was then placed down the warren entrance and a shovel used to collapse the entrance of the burrow so that only the end of the pipe was exposed. Approximately 150 mL of water was poured down the pipe to activate the tablets and then a ramming rod was inserted to push the tablets out into the warren. The pipe and ramming rod were removed and the entrance covered with sand to a depth of 0.5 m. In cases where warrens had more than one entrance, every second entrance was treated, with other entrances collapsed using shovels.

During pressure fumigation with chloropicrin, smoke generated from diesel or high-grade medicine oil was blown into the main warren hole to identify other entrances. A shovel was used to collapse all but one warren entrance and entrances were covered in sand to a depth of 0.5 m. Smoke was blown for a further 30 s to check that all entrances were identified and covered before the last open entrance was closed. Rural Larvacide® (SA Rural Agencies Pty Ltd, SA) was then administered for 60 s using a petrol-powered fumigator at a rate of ~1 drop per second. The fumigator was then removed and the main hole collapsed with a shovel and covered with sand to a depth of 0.5 m.

Collars were retrieved opportunistically over several months during both summer and winter. Control methods were conducted by a variety

of different operators, all of whom had been trained in each control method. At least two radio-collared rabbits were not killed during each collar-retrieval episode to control for the possibility of natural mortality. In total, 10 rabbits were used as controls over the study period. Control rabbits were killed when 40 fixes were obtained or when other rabbits were captured that could act as controls.

Statistical analyses

Home-range calculations were performed using RANGES V (Kenward and Hodder 1996) and were calculated by the Minimum Convex Polygon method (MCP) using 95% of fixes. Individual warren fixes were included once only. Increment area analysis was performed on the fixes for each animal to determine the minimum number of unique fixes required to estimate the home range (Kenward and Hodder 1996). A two-way crossed ANOVA was performed on home range to test for main effects and interaction of season and sex. To determine whether a relationship existed between weight and home-range size, a regression was also performed comparing rabbit weight with home-range size. A Student's *t*-test was used to determine whether there was a difference in the number of burrows used by rabbits in summer and winter and to compare diurnal surface fixes between seasons. Statistical analyses were performed using either Systat 8.0 (SSPS Inc. 1998) or Microsoft Excel 2000. In all cases α was 0.05.

To determine the influence of season and daylight on the use of dune and swale habitat by radio-collared rabbits, a generalised linear mixed model was fitted using the methodology of Schall (1991) using a binomial distribution, log-link and Wald tests for fixed effects. Each surface fix was recorded as either summer or winter, nocturnal or diurnal and in dune or swale habitat. Night fixes were taken between 2000 and 0600 hours in summer and 1800 and 0700 hours in winter. A generalised linear mixed model was also used to determine the influence of season and time of day on activity patterns. The 24-h day was divided into 10 even periods and the number of surface and warren fixes for each rabbit was compared between periods. The effect of season on activity patterns was also included. Radio-collared rabbits were fitted as a random effect to account for intraspecific differences in activity patterns. The GenStat statistical package was used to conduct the generalised linear models.

Results

Home range

Between 32 and 50 fixes were collected for each rabbit. The number of unique fixes required to achieve home-range asymptote ranged from 24 to 37, averaging 32 over an average period of 31 days (Table 1). Home ranges were circular or elliptical and varied from 0.77 ha to 9.18 ha, averaging 2.1 ha ($n = 10$) in summer and 4.2 ha ($n = 8$) in winter. Although the smallest rabbit had the smallest home range there was no significant correlation between home-range size and weight ($r^2 = 0.09$, $F = 1.584$, d.f. = 1,16, $P = 0.2262$). A two-way ANOVA found no interaction between sex and season on home range ($F = 0.2748$, d.f. = 1,14, $P = 0.6083$). Data were then pooled within season and home ranges were significantly larger in winter than in summer ($F = 6.2297$, d.f. = 1,16, $P = 0.0239$). Breeding rabbits were captured in both winter and summer. Although average home ranges of females were slightly larger than those of males in both summer (females, 2.38 ± 0.68 ha; males, 1.96 ± 0.43 ha) and winter (females, 4.75 ± 1.23 ha; males, 3.39 ± 0.96 ha) there was no significant difference between the home ranges of males ($n = 9$) and females ($n = 9$) when data were pooled within sex ($F = 1.81$, d.f. = 1,16, $P = 0.1972$).

Activity

Although rabbits were captured opportunistically, more rabbits were captured in swale habitat as rabbits were more visible and easier to chase there than in the more densely vegetated dunes. However, only five of the 59 warrens used by the 18 rabbits were located in swales, with the remaining 54 in the dunes. Four of the five swale warrens were used by one

Table 1. Attributes and home-range size of rabbits radio-collared in summer and winter
Period refers to the length of time that each rabbit was radio-tracked

Rabbit no.	No. of unique fixes	Sex	Season	Weight (g)	Reproductive status	95% home range (ha)	Period (days)	No. of warrens used
W1	36	Female	Winter	1.500		4.71	32	3
W4	24	Female	Winter	1.800	Pregnant	1.74	27	2
W5	32	Female	Winter	1.675		9.18	26	1
W7	30	Female	Winter	1.250		3.49	40	1
W8	29	Female	Winter	1.300		4.62	30	3
W3	31	Male	Winter	1.375		5.17	36	3
W9	32	Male	Winter	1.150		1.89	31	3
W10	30	Male	Winter	1.400		3.10	29	2
S1	35	Female	Summer	1.450	Lactating	4.06	24	7
S2	30	Female	Summer	1.400	Lactating	2.16	21	4
S3	37	Female	Summer	0.740		0.77	54	1
S9	31	Female	Summer	1.775	Pregnant	2.54	21	6
S4	28	Male	Summer	1.200		1.08	22	2
S5	36	Male	Summer	1.760		2.76	30	5
S6	36	Male	Summer	1.350		2.33	29	5
S7	31	Male	Summer	1.350		3.50	30	2
S10	35	Male	Summer	1.775		0.94	25	4
S11	27	Male	Summer	1.005		1.13	25	5

individual that also used two dune warrens. Radio-tracked rabbits used up to seven warrens; the number was significantly greater in summer (mean = 4.1, s.e. = 0.49) than winter (mean = 2.25, s.e. = 0.55) ($t = 2.52$, d.f. = 16, $P < 0.05$).

Fixes were taken randomly throughout the day and night in both seasons but more daylight hours in summer meant that 68% of the total fixes were taken during daylight hours in summer compared with 47% in winter. Warren fixes accounted for less than 50% of fixes for every radio-collared rabbit. Total warren use per rabbit did not vary between winter and summer and averaged 26% of total fixes (range 3–42%) during both seasons. Nocturnal use of warrens was rare, averaging 5% in winter and less than 1% in summer. In all, 47% of diurnal winter fixes were on the surface ($n = 211$, range = 30–76) compared with 62% in summer ($n = 268$, range = 44–96) but results were not significantly different ($t = 1.82$, d.f. = 16, $P > 0.05$). Even during peak periods of warren use, more than 20% of total fixes were recorded on the surface (Fig. 1).

Rabbit surface activity varied significantly over a 24-h period (Wald statistic = 89.63, d.f. = 9, $P < 0.001$) and followed a cyclical pattern. Surface activity was highest at night and lowest in the middle of the day. There was no significant seasonal effect on activity patterns (Wald statistic = 0.76, d.f. = 1, $P = 0.384$) but a significant interaction between time of day and season (Wald statistic = 39.73, d.f. = 9, $P < 0.001$) indicated a shift in the 24-h activity pattern between seasons (Fig. 1). During winter, rabbits were more likely to be found in their warrens between 0900 and 1600 hours, but in summer were more likely to be found in their warrens between 1100 and 1800 hours (Fig. 1). Rabbits were rarely found in warrens between 2300 and 0600 hours during the summer, but would occasionally be in their warrens at these times during winter.

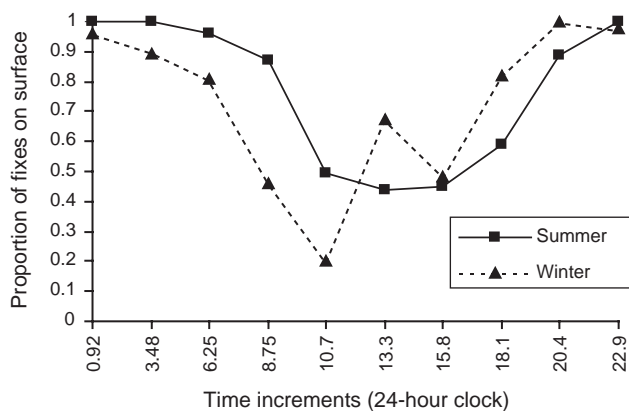


Fig. 1. The proportion of fixes recorded on the surface for all radio-collared rabbits during summer and winter. Time increments indicate the start of the 2.4-h block.

Habitat use

Rabbits used both dune and swale habitat but more surface fixes were recorded in dune habitat in both seasons (Fig. 2). Results from the generalised linear model indicated that daylight significantly influenced habitat use (Wald statistic = 57.17, d.f. = 1, $P < 0.001$). Proportionally more surface fixes were recorded in swale habitat at night than during the day (Fig. 2). Although there was no significant effect of season on habitat use (Wald statistic = 0.63, d.f. = 1, $P > 0.05$) there was a significant interaction between season and daylight (Wald statistic = 8.91, d.f. = 1, $P = 0.003$), suggesting that the day/night effect was smaller in summer than in winter (Fig. 2).

Response to disturbance

Rabbits retreated into warrens ~30% of the time when they were disturbed by an observer during the day in both summer and winter ($n = 110$) (Fig. 3). At night during winter rabbits flushed into warrens less than 5% of the time ($n = 119$). Rabbits flushed into their warrens 100% of the time ($n = 6$) when the observer was accompanied by a dog during daytime in winter (Fig. 3).

Control methods

The most successful control method for radio-collared rabbits was fumigation with phosphine gas tablets, which led to the deaths of 10 of the 11 rabbits treated (Table 2). Pressure fumigation with chloropicrin was also successful in 8 out of 10 cases but collapsing burrows using a shovel and 1080 poisoning were generally unsuccessful. Unsuccessful shovelling and fumigating attempts ended in the rabbit digging out of the warren and still being alive one week after treatment.

Discussion

Considerable diurnal surface activity of rabbits was recorded in both summer and winter, as has been documented in other

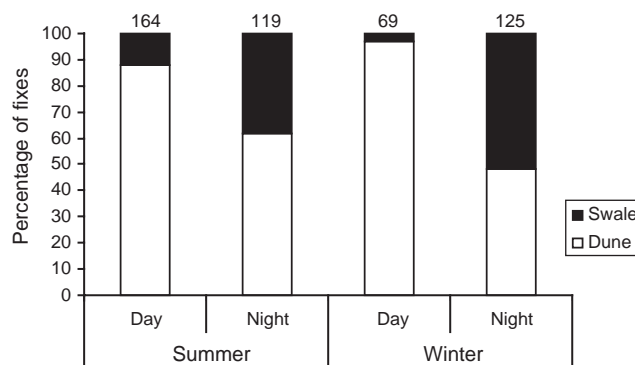


Fig. 2. The percentage of surface fixes recorded in each habitat type during the day and night for all rabbits combined. The total number of fixes is presented above each bar.

studies (Wheeler *et al.* 1981; Kolb 1991). High levels of diurnal surface fixes were found by Wheeler *et al.* (1981) (76%) in Western Australia, where rabbits were found sheltering on the surface even during heavy rain and strong winds. However, finding nearly 50% of diurnal fixes on the surface in mid-afternoon during summer was unexpected considering that the daily maxima exceeded 35°C on 21 days during the study. Surface-activity patterns changed very little between summer and winter, suggesting that temperature, breeding and food availability all have little influence on activity patterns. This contrasts with a study conducted in Scotland by Kolb (1991), who found a higher proportion of the population, mainly young rabbits, on the surface in summer than in winter. It is important to note that the high surface activity of radio-collared rabbits in our study may be partly attributed to the sampling method used. All rabbits were initially caught above ground at night, which may have led to a bias towards sampling those rabbits that either spend more time of the surface generally or more nocturnal hours on the surface. Although live-trapping of rabbits was attempted to reduce this bias, it proved ineffective.

Rabbits in our study could not easily be separated into surface-dwelling or warren-dwelling individuals, as in some Australian rabbit studies such as White *et al.* (2003). The percentage of warren fixes per rabbit varied considerably, with some rabbits using warrens more than others but no clear demarcation between the two categories. We concur with Wheeler *et al.* (1981) that living above ground is a natural tendency when suitable surface shelter is available. Diseases such as myxomatosis have selected against warren-dwelling rabbits in the United Kingdom (Lloyd 1970) and both myxomatosis and rabbit calicivirus disease may select against warren-dwelling rabbits in Australia (Wheeler *et al.* 1981; White *et al.* 2003). Control methods such as warren ripping and fumigation could also select against warren-dwelling rabbits. The reluctance of flushed rabbits to retreat to warrens when disturbed has been noted by other researchers and is thought to be an adaptation to avoiding predation by stoats (Kolb 1991). Although in arid South

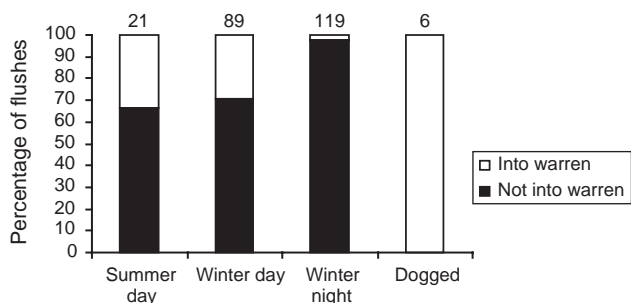


Fig. 3. The percentage of time a rabbit ran into its warren or stayed above ground after being disturbed by a human during the summer (day) or winter (day and night), or with the aid of a dog during daytime in winter.

Australia rabbits that flee to sand-dune burrows may be dug out by foxes, rabbits that remain on the surface are also at high risk of predation from foxes, cats and raptors (K. Moseby, personal observations)

White *et al.* (2003) found larger home ranges in autumn for surface-dwelling rabbits (3.14 ha) than for warren dwellers (1.74 ha). Average home ranges in our study were comparable and were influenced by season, possibly owing to differences in food availability or increased activity during the breeding season. We concur with White *et al.* (2003) that sex did not influence home-range size, but differences have been recorded by several researchers, including Cowan (1987) who recorded 0.71 ha for males and 0.44 ha for females, and Fullagar (1981) who recorded 0.22 ha and 0.67 ha for males and 0.16 ha and 0.39 ha for females at two study sites respectively. These figures are considerably smaller than our estimates and are probably due to differences in resource availability.

Our records of multiple warren use by rabbits were consistent with other studies (Wood 1980; Wheeler *et al.* 1981; Cowan 1987; White *et al.* 2003), with White *et al.* (2003) recording an average of 2.9 warrens per rabbit in winter compared with our average of 2.5. Our study concurs with Kolb (1991), who found no difference in warren use between the sexes. Although the proportion of time spent in burrows was the same in each season, rabbits used a larger number of burrows in summer than in winter. Although some rabbits were found breeding during both study seasons, the peak breeding season for rabbits at Roxby Downs is from late winter to early summer (Bowen and Read 1998). During the winter breeding season rabbits may maintain stronger ties to a particular burrow when raising a litter. Dispersal of juveniles and re-establishment of territories may be higher in summer. Mykytowycz and Gambale (1965) found that rabbits from different warrens interchanged and established new territories only during the non-breeding season. The preference for warren construction on sandy substrate has been documented elsewhere (Parker *et al.* 1976; Gilbert *et al.* 1987) and is likely to be due to ease of digging in sandy soils.

Implications for control

Several studies have highlighted the need for integrated control methods as an effective means of controlling rabbits (Cooke 1981; Foran *et al.* 1985; Williams and Moore 1995).

Table 2. The number of radio-collared rabbits that were successfully killed using each control method

Method	No. of rabbits treated	No. of rabbits that died during treatment
1080 poison oats	8	1
Shovelled	10	3
Phosphine tablets	11	10
Chloropicrin gas	10	8
Control	10	1

Williams and Moore (1995) found that the most effective combination was poisoning with 1080 followed by ripping then fumigation with chloropicrin and then maintenance control with phosphine fumigation.

Although 1080 poisoning appeared ineffective on the individual rabbits tested in this study, earlier broadscale baiting has substantially reduced rabbit numbers (K. Moseby, personal observations). However, reduction of rabbit populations through use of 1080 is short-lived unless followed by other control methods (Foran *et al.* 1985). Home-range and habitat-use data suggest that 1080 baiting should not necessarily be restricted to dune habitat but that nocturnal use of swale habitat could justify laying of bait in both habitat types. Other studies have also highlighted the importance of poisoning feeding grounds that may be remote from burrows (Rowley 1958). Baiting with 1080 is likely to be most effective during dry conditions and at times of lowest food availability, usually in the summer months. Baiting during the non-breeding season has also been recommended (Fraser 1988) because there are fewer young rabbits confined to warrens. Rabbits usually remain close to their warrens (Myers and Schneider 1964) although they occasionally roam further than 300 m (Parer 1982). All rabbits in our study used warrens and the maximum home-range size was 9.2 ha, suggesting that baiting will be most useful within a 300-m radius of a warren. Larger home ranges in winter may increase the chances of rabbits encountering bait lines and bait lines may need to be closer together in summer than winter to increase the effectiveness of baiting.

Warren fumigation with phosphine and chloropicrin were both highly effective at killing rabbits known to be in warrens. Phosphine was just as effective as chloropicrin at killing individual rabbits and is safer for the operator, cheaper (Vine and Eldridge 2000), easier to transport and administer and possibly more humane (Williams and Moore 1995; Williams *et al.* 1995). The slightly lower success rate with chloropicrin may be due to increased chance of human error during dose administration. Rabbits spent the equivalent amount of time in warrens during both summer and winter, suggesting that the death rate from fumigation may be similar in both seasons. In all, 30–96% of the diurnal fixes of individual rabbits were on the surface, suggesting that warren fumigation without successfully flushing rabbits to their warrens may be ineffective. Despite the low sample size, the use of dogs to flush rabbits down warrens appears to be highly effective. Dogs would be required to traverse the dunes only as diurnal swale activity was negligible. Home-range data suggest that dogs should traverse a 300-m buffer zone around warrens to ensure that all resident rabbits are flushed. Radio-tracking data suggest that fumigation (or ripping) is likely to be most effective when conducted between 0900 and 1600 hours in winter and between 1100 and 1800 hours in summer when rabbits are most likely to be down warrens. However, there is a possibility that radio-collared rabbits may not accu-

rately reflect true population activity as all collared rabbits were captured at night on the surface.

Although less destructive to vegetation and non-target species than ripping, warren destruction using shovels was not generally effective in controlling rabbits as most rabbits dug out of collapsed warrens. All warren-destruction attempts were in sand habitat, which is an easy substrate to dig. Warren destruction in harder substrate may be more successful. Despite the low success rate, collapsing burrows may be useful after poisoning with 1080. Collapsing warrens with a shovel does not destroy all the mammal and lizard holes that are associated with rabbit warrens, allowing many non-target animals to escape. Only warrens re-opened by rabbits would require fumigation thus leading to more efficient fumigation and fewer non-target deaths.

Although most warrens used by rabbits in this study were on the dunes, studies have shown that large, deep warrens located in harder ground can become refugia during drought and act as sources for recolonisation of sandy areas after rain (Myers and Parker 1975). Therefore, control of swale warrens by ripping may be a key to long-term control. Despite the reduction of rabbit numbers due to rabbit calicivirus disease, humane and efficient rabbit control continues to be an important management consideration for land managers in arid South Australia. Such management should take into account the variation in diurnal and seasonal activity of rabbits and the efficacy of different control techniques.

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References

- Bowen, Z., and Read, J. (1998). Population and demographic patterns of rabbits (*Oryctolagus cuniculus*) at Roxby Downs in arid South Australia and the influence of rabbit haemorrhagic disease. *Wildlife Research* **25**, 655–662. doi:10.1071/WR98004
- Calaby, J. H. (1969). Australian mammals since 1770. *Australian Natural History* **16**, 271–275.
- Catling, P. C. (1988). Similarities and contrasts in the diets of foxes, *Vulpes vulpes*, and cats, *Felis catus*, relative to fluctuating prey populations and drought. *Australian Wildlife Research* **15**, 307–317.

- Cooke, B. D. (1981). Rabbit control and the conservation of native mallee vegetation on roadsides in South Australia. *Australian Wildlife Research* **8**, 627–636.
- Cooke, B. D. (1987). The effects of rabbit grazing on regeneration of she-oaks, *Allocasuarina verticillata* and saltwater ti-trees, *Melaleuca halmaturorum*, in the Coorong National Park, South Australia. *Australian Journal of Ecology* **13**, 11–20.
- Cooke, B. D. (1991). Rabbits – indefensible on any grounds. *Search* **22**, 193–194.
- Cowan, D. P. (1987). Aspects of the social organisation of the european wild rabbit (*Oryctolagus cuniculus*). *Ethology* **75**, 197–210.
- Dawson, T. J., and Ellis, B. A. (1979). Comparison of the diets of yellow-footed rock-wallabies and sympatric herbivores in western New South Wales. *Australian Wildlife Research* **6**, 245–254.
- Environment Australia (1999). Threat abatement plan for competition and land degradation by feral rabbits. Department of the Environment and Heritage (Biodiversity Group), Canberra, ACT.
- Foran, B. D., Low, W. A., and Strong, B. W. (1985). The Response of rabbit populations and vegetation to rabbit control on a calcareous shrubby grassland in central Australia. *Australian Wildlife Research* **12**, 237–247.
- Fraser, K. W. (1988). Reproductive biology of rabbits, *Oryctolagus cuniculus* (L.), in central Otago, New Zealand. *New Zealand Journal of Ecology* **11**, 79–88.
- Fullagar, P. J. (1981). Methods for studying the behaviour of rabbits in a 33-ha enclosure at Canberra and under natural conditions at Calindary NSW. In 'Proceedings of the World Lagomorph Conference, Guelph Ontario 1979'. (Eds K. Myers and C. D. MacInnes.) pp. 240–254. (IUCN: Switzerland.)
- Gilbert, N., Myers, K., Cooke, B. D., Dunsmore, J. D., Fullagar, P. J., Gibb, J. A., King, L. R., Parer, I., and Wood, D. H. (1987). Comparative dynamics of Australasian rabbit populations. *Australian Wildlife Research* **14**, 491–503.
- Hulbert, I. A. R., Iason, G. R., Elston, D. A., and Racey, P. A. (1996). Home range size in a stratified upland landscape of two lagomorphs with different feeding strategies. *Journal of Applied Ecology* **33**, 1479–1488.
- Kenward, R. E., and Hodder, K. H. (1996). 'Ranges V: An Analysis System for Biological Location Data.' (Institute of Terrestrial Ecology, Furzebrook Research Station: England.)
- Kolb, H. H. (1991). Use of burrows and movements by wild rabbits (*Oryctolagus cuniculus*) on an area of sand dunes. *Journal of Applied Ecology* **28**, 879–891.
- Lange, R. T., and Graham, C. R. (1983). Rabbits and the failure of regeneration in Australian arid zone *Acacia*. *Australian Journal of Ecology* **8**, 377–381.
- Lloyd, H.G. (1970). Post-myxomatosis rabbit populations in England and Wales. *European Plant Protection Organisation Publication Series A* **58**, 197–215.
- Morton, S. R. (1990). The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proceedings of the Ecological Society of Australia* **16**, 201–213.
- Myers, K., and Parker, B. S. (1975). Effect of severe drought on rabbit numbers and distribution in a refuge area in semiarid north-western New South Wales. *Australian Wildlife Research* **2**, 103–120.
- Myers, K., and Schneider, E. C. (1964). Observations on reproduction, mortality, and behaviour in a small, free-living population of wild rabbits. *Wildlife Research* **9**, 138–143.
- Myers, K., Parer, I., and Richardson, B. J. (1989). Leporidae. In 'Fauna of Australia. Volume 1B'. (Eds D. W. Walton and B. J. Richardson.) pp. 917–931. (CSIRO Publishing: Melbourne.)
- Mykytowycz, R., and Gambale, S. (1965). A study of the inter-warren activities and dispersal of wild rabbits, *Oryctolagus cuniculus* (L.), living in a 45-acre paddock. *Wildlife Research* **10**, 111–123.
- Parer, I. (1982). Dispersal of the wild rabbit *Oryctolagus cuniculus* at Urana in New South Wales. *Australian Wildlife Research* **9**, 427–441.
- Parer, I., and Parker, B. S. (1986). Recolonisation by rabbits (*Oryctolagus cuniculus*) after warren destruction in western New South Wales. *Australian Rangeland Journal* **8**, 150–152.
- Parker, B. S., Myers, K., and Caskey, R. L. (1976). An attempt at rabbit control by warren ripping in semi-arid western New South Wales. *Journal of Applied Ecology* **13**, 353–367.
- Priddel, D., Carlile, N., Davey, C., and Fullagar, P. (1995). The status of Gould's petrel, *Pterodroma leucoptera leucoptera*, on Cabbage Tree Island, New South Wales. *Wildlife Research* **22**, 601–610.
- Read, J. L. (1995). Recruitment characteristics of the white cypress pine (*Callitris glaucophylla*) in arid South Australia. *Rangeland Journal* **17**, 228–240.
- Rowley, I. (1958). Behaviour of a natural rabbit population poisoned with "1080". *Wildlife Research* **3**, 32–39.
- Schall, R. (1991). Estimation in generalized linear models with random effects. *Biometrika* **78**, 719–727.
- SSPS Inc. (1998). 'SYSTAT 8.0 Statistics.' (SSPS Science Marketing Department: USA.)
- Vine, A., and Eldridge, D. (2000). Busting the bunnies: evaluating re-invasion of warrens. *Range Management Newsletter* **00/3**, 11–12.
- Wheeler, S. H., King, D. R., and Robinson, M. H. (1981). Habitat and warren utilization by the european rabbit *Oryctolagus cuniculus* (L.), as determined by radio-tracking. *Australian Wildlife Research* **8**, 581–588.
- White, P. C. L., Newton-Cross, G., Gray, M., Ashford, R., White, C., and Saunders, G. (2003). Spatial interactions and habitat use of rabbits on pasture and implications for the spread of rabbit haemorrhagic disease in New South Wales. *Wildlife Research* **30**, 49–58. doi:10.1071/WR01106
- Williams, C. K., and Moore, R. J. (1995). Effectiveness and cost-efficiency of control of the wild rabbit, *Oryctolagus cuniculus* (L.), by combinations of poisoning, ripping, fumigation and maintenance fumigation. *Wildlife Research* **22**, 253–269.
- Williams, K., Parer, I., Coman, B., Burley, J., and Braysher, M. (1995). 'Managing Vertebrate Pests: Rabbits.' (Bureau of Resource Sciences & CSIRO Division of Wildlife and Ecology & Australian Government Publishing Service: Canberra.)
- WMC (Olympic Dam Corporation) Pty Ltd (2003). Environmental Management and Monitoring Report: Jan-Dec 2002. WMC Resources Ltd., Roxby Downs, South Australia.
- Wood, D. H. (1980). The demography of a rabbit population in an arid region of New South Wales Australia. *Journal of Animal Ecology* **49**, 55–79.

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