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The effect of rabbit-warren ripping on the consumption of native fauna by foxes in the arid zone of New South Wales

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ABSTRACT

The diet of foxes in an arid zone site in western New South Wales was analysed from the contents of scats collected every three months from October 1986 to July 1989. Fox diet comprised 27% invertebrates, 25% carrion, 17% rabbits, 16.5% reptiles, 10% dasyurids and 4.5% ground-dwelling birds after the digestibility of each category had been accounted for. There was no clear seasonal pattern in dietary composition although fewer rabbits were ingested in autumn and winter. Foxes ate rabbits in direct proportion to their availability while the ingestion of ground-dwelling birds and dasyurids was either independent of, or inversely proportional to, their abundance. There were no significant relationships between fox and prey densities. The impact of a decrease in rabbit density on the diet and abundance of foxes was investigated by ripping all rabbit warrens ($n = 37$) in one site and leaving all warrens ($n = 38$) undisturbed in an untreated site. Fox density did not change significantly in either site. Foxes significantly increased their ingestion of ground-dwelling birds, dasyurids and invertebrates while decreasing their ingestion of rabbits in the ripped site. The diet of foxes in the untreated site did not change significantly. The ability of foxes to switch their prey preferences while maintaining their density could be highly detrimental for secondary prey species and may be the mechanism by which foxes have contributed to the declines of native fauna in the arid zone.

INTRODUCTION

The rate of recent mammalian extinction in Australia is greater than on any other continent (Short & Smith 1994) and fox (*Vulpes vulpes*) predation has been identified as a major contributing factor in these declines (Kinnear *et al*. 1988, 1998; Friend & Thomas 1995; Wyre 2004). The predatory impact of foxes is now recognised nationally as a key threatening process (Department of Environment, Water, Heritage and the Arts 2008). In the arid zone of Australia the rate of mammalian decline is higher than for any other habitat and 11 of the 72 species originally found there are extinct (Burbidge & McKenzie 1989; Dickman *et al.* 1993; Short & Smith 1994; Morton 1990).

The introduction of the rabbit (*Oryctolagus cuniculus*) has also been an important factor in the decline of small mammal populations in Australia (Low 1984). The distributions of the fox and rabbit are similar (Van Dyck & Strahan 2008) and many previous studies of the diet of foxes in Australia have indicated that rabbits are an important prey item (e.g. Catling 1988; Saunders et al. 1995, 2004; Risbey et al. 1999; Molsher et al. 2000; Glen et al. 2006).

Foxes may rely on rabbits as their primary prey (Newsome et al. 1989), and because rabbit populations can reach very high densities this enables fox populations to also reach high densities. A very high ratio of foxes to endemic mammals may result (Johnson 2006). While rabbits are demographically resilient to high intensities of fox and feral cat (*Felis catus*) predation, few marsupials have a reproductive output that rivals that of rabbits (Van Dyck & Strahan 2008) and so they are unable to sustain the increased intensity of predation (Low 1984).

Rabbits have been, and continue to be, an important pest species in Australia (Williams 1995). Consequently there have been intensive and sustained efforts to control their populations and the damage they cause to agricultural and environmental assets. Various control methods have been devised for rabbit control and these involve direct approaches such as poisoning, warren ripping or shooting or indirect methods that include the introduction of diseases such as myxomatosis or rabbit

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calicivirus disease (Williams 1995). Although these methods continue to reduce rabbit densities, control efforts need to be sustained especially in areas of high agricultural or environmental importance (Invasive Animals Cooperative Research Centre 2016).

While rabbit control programs may be beneficial to the protection of crops and wildlife habitat, it is less clear how reducing rabbit densities may affect fox densities and subsequent predation upon vulnerable native prey species. In this study we examined the diet of foxes in the arid zone of New South Wales through scat analysis and then quantified how this and fox abundance changed when rabbit densities were reduced through warren ripping. The subsequent fox–prey interactions and prey-switching were examined to elucidate a potential causal mechanism for fauna declines, even though most of the local extinctions occurred more than a century ago. Although this study was undertaken in the arid zone more than 20 years ago, the results obtained are still relevant throughout Australia today. The postulated mechanisms for faunal decline are discussed in relation to other biomes and current rabbit and introduced predator control programmes.

METHODS

Study area

This study was undertaken at Fowlers Gap, the arid zone research station of the University of New South Wales (31° 05′ S, 141° 43′ E), 110 km north of Broken Hill in north-western New South Wales. The station covers 39,200 ha and at the time of the study was a working sheep station with approximately 7000 head of stock. The climate is generally dry with hot summers and mild winters (Bell 1973) and the productivity of the land is comparatively low (12.2 dry sheep equivalents per 100 ha (W. Tatnell, pers. comm.). The average annual rainfall is 232 mm (Australian Bureau of Meteorology; www.bom.gov.au) and during the study near-average rainfall was received (mean 216 mm). Foxes were not subjected to any control measures and feral cats occurred at low densities (Marlow 1992).

The study area covered 3400 ha and was predominately situated on the Conservation Land System, which is characterised by semi-arid to arid shrubland (<1 m) dominated by the family Chenopodiaceae. The main chenopod species include bladder salt-bush (*Atriplex vesicaria*), blue-bush (*Maireana* spp.) and copper-burrs (*Sclerolaena* spp). Stands of prickly wattle (*Acacia victoriae*) occur in watercourses (Mabbutt 1973).

Study sites

The study area was subdivided into three sites (Fig.1). Site 1 was characterised by the virtual absence of rabbits (<10 single-entrance burrows). It covered an area of 1630 ha and contained 19 km of monitoring transect. Site 2 had relatively high densities of rabbits (38 complex rabbit warren systems; see below). It covered 920 ha and contained 11.5 km of monitoring transect. The rabbit warrens in this site were left intact during the experiment to reduce rabbit density(see below). Site 3 also had relatively high densities of rabbits (37 complex rabbit-warren systems). It covered an area of 850 ha and contained 8.5 km of monitoring transect. All warrens in this site were ripped during the experiment to reduce rabbit density.

Scat analyses

All fox scats observed on monitoring transects within Sites 1, 2 and 3 (total 39 km) were collected every three months from October 1986 to July1989. An additional collection of scats was undertaken in Sites 2 and 3 in November 1988 as part of the rabbit density reduction experiment. The foxes' overall diet was quantified from the contents of scats collected in Sites 1 and 2 from October 1986 to July1989 and from Site 3 from October 1986 to October 1988. The scats collected in Site 3 (where warrens were ripped) from November 1988 to July 1989 were used only in analyses investigating dietary changes when rabbits were removed (see below).

A scat was defined as 'a cohesive intestinal discharge or a limited part thereof' (Lund 1962). The contents of each scat were sorted macroscopically into their constituent categories. The volume (ml) of each category was measured by quantifying the amount of water it displaced in a 100 ml measuring cylinder. Samples were then oven-dried and weighed. The ingested biomass of each category was estimated using the technique described by Lockie (1959), where the digestibility of each food type was calculated and a digestibility correction factor applied. The weight of each item (g) in a scat was divided by the digestibility correction factor to calculate the ingested biomass of that prey type. Lockie (1959) calculated digestibility correction factors for rabbits (34%), small mammals (18%) and small birds (20%). The digestibility correction factors for carrion (50%), invertebrates (10%) and reptiles (18%) were modified from Goszczynski (1974).

The identity of all hair in the scats was determined using the techniques described by Brunner and Coman (1974). Both cuticle scale patterns and cross-sectional characteristics were used. Reference slides were prepared for species not listed in Brunner and Coman (1974), e.g. *Planigale* spp. The remains of feathers were identified to Order using the technique of Day (1966). Reptilian remains were identified by examining the size and shape of scales and assigning them to species known to be present in the study area based on Cogger (1992). Invertebrate remains were sorted to Order using Anderson (1998).

Field abundance estimations

The field abundances of foxes and ground-dwelling birds were estimated using spotlight counts (100 W

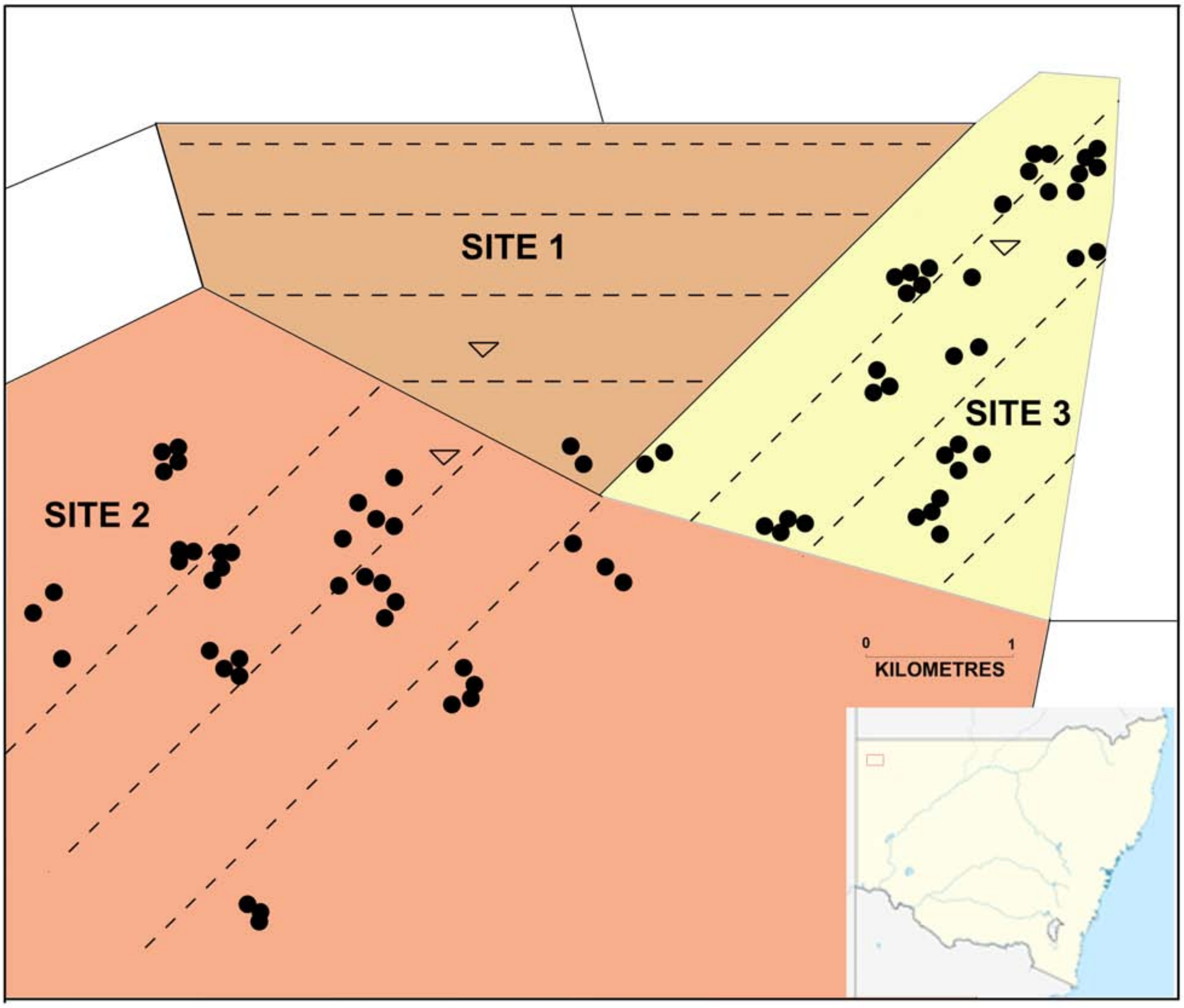

Figure 1. Map of the study area. Dotted lines indicate monitoring transects, circles are the location of rabbit warrens, and triangles indicate the location of pit-fall lines.

spotlight) along the monitoring transects in Sites 1, 2 and 3. Counts were repeated on three consecutive nights every three months. For foxes, the distance and angle of any individual sighted from the vehicle were recorded. Due to the low height of the vegetation (<1 m) visibility was very good and so sightings were truncated at 300 m. Sighting data were analysed using the line-transect methods described in Burnham et al. (1980) and a probability density estimation was calculated. For ground-dwelling birds (stubble quail *Coturnix pectoralis* and little buttonquail *Turnix velox*), density was calculated using the strip-width method. Quail have the distinctive behaviour of flushing with a distinctive rapid, whirring flight, low to the ground (Simpson & Day 1993) and the maximum distance that birds were observed to fly from the vehicle was 20 m.

Rabbit abundance was estimated every three months using the technique described in Parer and Wood (1986). This involved examining all the burrow entrances present at 87 warrens and assessing whether or not each was active. An index to the number of rabbits present in the warren was then calculated. To verify this estimation actual rabbit counts were conducted at 10 warrens for three consecutive evenings for an hour before sundown. This result was averaged for the 10 warrens and the resulting ratio of rabbits observed to active burrows present was extrapolated to other warrens. All rabbit warrens were within 500 m of the monitoring transects.

The abundances of small mammals and reptiles were estimated using pitfall traps at three sites. The pit-lines were positioned in a triangular arrangement and each pit was 45 cm deep. The pit-lines contained 11 pits, each 10 m apart with three sets of pit-lines at each of three sites (i.e. 33 pits per site and 99 in total). A 30-cm high fly-screen fence buried into the ground connected the pits. The pitfall sites were positioned within 100 m of the monitoring transects. The pits were opened for 10 consecutive nights every three months from October 1986 to July 1989. The number of individuals caught in the pits was converted to a density (ha^{-1}) by calculating the area of the pitfall trap site and converting it to hectares. The dasyurid species monitored were *Sminthopsis crassicaudata* (fat-tailed dunnart), *S. macroura* (stripe-faced dunnart), *Planigale gilesi* (paucident planigale) and *P. tenuirostris* (narrow-nosed planigale). Mice (*Mus domesticus*) occurred at very low densities during this study (<10 individuals caught). *S. crassicaudata* was the most commonly monitored dasyurid followed by *P. tenuirostris* and then *P. gilesi*. *S. macroura* was rarely captured (<10 individuals). The reptilian species monitored included *Tympanocryptus lineata* (lined earless dragon), *Morethia boulengeri* (Boulenger's skink), *Ctenotus uber* (spotted ctenotus), *Diplodactylus byrnei* (Byrne's gecko) and *D. tesselatus* (tessellated gecko).

The abundance of invertebrates was estimated using light traps which comprised a tank of water, 1 m in diameter and 45 cm deep, with an ultraviolet light suspended above it. Two light traps were used and each was employed for ten consecutive days every three months from October 1986 to July 1989. The two traps were positioned within 100 m of the monitoring transect. Each morning invertebrate remains were collected, dried in an oven and then weighed to obtain a biomass estimate (kg/trap). All invertebrates were sorted to Order and the most commonly collected taxa were coleopterans (mainly green carabid beetles, *Calosoma* spp.) and orthopterans, especially the plague locust *(Chortoicetes terminifera)*.

The field availability of carrion was estimated by calculating kangaroo and sheep mortality rates that were obtained from a concurrent study by Edwards et al. (1995) on sheep–kangaroo interactions undertaken within the same study area. The carrion available to foxes included red and western grey kangaroos (*Macropus rufus* and *M. fuliginosus*, respectively) and sheep (*Ovis aries*).

Statistical analyses

The average composition of the foxes' diet was calculated from the volume of each dietary category within each scat using the descriptive statistics module within the SPSSx statistics package (Norusis 1985). The interaction effects between the dietary categories and field abundances were calculated using canonical correlation analysis in the MANOVA program within the SPSSx statistics package (Norusis 1985). For this analysis the data matrix included a field abundance estimate for each category for each sampling period and site so that there was a corresponding field abundance for every dietary volume entry. The data were tested using Bartlett's test of sphericity to determine if they were inter-related and therefore needed to be analysed using multivariate analysis (Norusis 1985). The distributions of the variables were tested for homoscedascity and normality of variance using both Cochrans *C* and the Bartlett–Box *F* tests. The variance of the data was not homoscedasctic and all data were log-transformed and converted to z-scores. This last transformation enabled the field abundances of different prey types to be compared directly even though they were measured at different scales.

Canonical correlation analysis was used to explain as much variance as possible within the dependent variable set (the dietary occurrences) from the independent variable set (the field abundances). It derives a linear combination from the two sets of variables so that the correlation between the two is maximised. It thus tries to account for the maximum amount of relationship between the two sets of variables (Nie et al. 1975). The procedure selects the first pair of canonical correlates so that they have the highest inter-correlation possible. The factors that load most heavily on the first canonical variate are the most important with the strongest relationships being identified by loadings with an absolute value greater than 0.6. A second set of canonical variates is then selected to account for the maximum amount of relationship between the two sets of variables left unaccounted for by the first canonical correlates. This process is repeated until all the variance has been accounted for. Because each successive set of canonical variates accounts for the residual variance it produces combinations of variables that are uncorrelated with one another (Norusis 1985).

The quantity of each prey species in the diet of foxes was regressed against the field availability of that species to determine if any prey preferences occurred. The abundance of foxes was regressed against the field availability of each prey item to determine if fox populations were sustained by any specific prey item. The numerical responses of foxes with rabbits, dasyurids, ground-dwelling birds, reptiles and invertebrates were calculated by plotting the rate of increase of the fox population as a function of the density of the prey species. The rate of increase of the fox population was also compared with the field abundance of carrion. The rates of increase for foxes were calculated by dividing the fox density estimate obtained during each sampling period by the density estimate for the previous period.

Fox predation upon native fauna was quantified by comparing the relative occurrence of a prey species in the foxes' diet in relation to its field abundance. If foxes were ingesting a species disproportionately to its availability, this would indicate a potentially critical impact on that species. If fox density was unrelated to, or inversely related to, the density of a particular prey species, then fox predation upon that species could be greater than it was able to withstand (Holt 1984).

Rabbit control techniques and subsequent analyses

The 37 rabbit warrens located in Site 3 were ripped in November 1988. Rabbit-warren ripping is a very effective method for reducing rabbit densities (Mutze 1991) but any individual rabbits remaining above ground after warrens are ripped may be very susceptible to fox predation. Warrens were ripped by a 1920 Case FWA tractor dragging a single tyne Jarrett ripper that had a maximum penetration depth of 75 cm. Two warrens reopened after being ripped but these were ripped again and had not reopened by the end of the experiment (July 1989). The 38 warrens identified in Site 2 were left intact. The average composition of the foxes' diet in both sites, both before and after warren ripping in Site 3, was calculated using the descriptive statistics module within the SPSSx statistics package (Norusis 1985).

Canonical correlation analysis was used to compare the diet of foxes in Site 3 before and after warrens were ripped there in November 1988. The diet and prey field abundances for April, June and October 1988 were compared with those obtained in November 1988 and January and April 1989. The data matrices for these analyses contained an entry for the volume of each dietary category in each scat before rabbit removal and afterwards. The MANOVA program within the SPSSx statistics package was used for both these analyses.

To determine if fox density changed in Site 3 when warrens in that site were ripped, the fox densities in Sites 2 and 3 both before (January, April, June and October 1988) and after (November 1988, January, April and July 1989) warren ripping occurred in Site 3 were compared using a 2-way ANOVA.

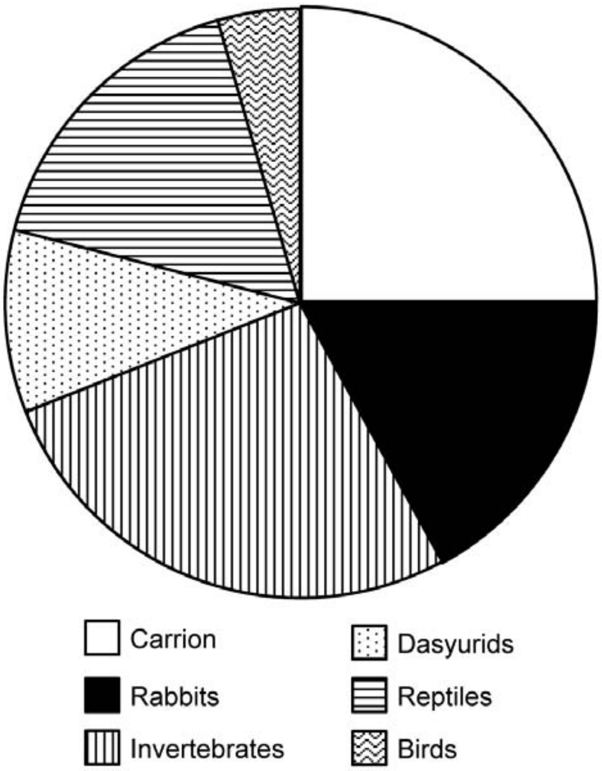

Figure 2. The composition of fox diet corrected for the digestibility of each category. Data from 931 scats collected in Sites 1 and 2 from October 1986 to July 1989 and Site 3 from October 1986 to October 1988.

RESULTS

Fox dietary analysis before rabbit density reduction

The analysis of 931 scats collected in Sites 1 and 2 from October 1986 to July 1989 and Site 3 from October 1986 to October 1988 showed that foxes ate a variety of vertebrate and invertebrate items (Table 1). When digestibility correction factors were applied, the average composition of the foxes' diet was invertebrates (27%), carrion (25%), rabbits (17%), reptiles (16.5%), dasyurids (10%) and ground-dwelling birds (4.5%; Fig. 2). Plant material and inorganic matter were insignificant and there was no clear seasonal pattern in dietary composition except fewer rabbits were ingested in autumn and winter (Fig. 3). The average density of foxes was not significantly different between sites (Site 1, $\bar{x} = 11.9 \pm 10.2$ SD; Site 2, $\bar{x} = 9.0 \pm 4.5$ SD; Site 3, $\bar{x} = 9.5 \pm 4.3$ SD foxes km^{-2}, respectively).

The factors that most influenced dietary composition were identified from the results of canonical correlation analysis. The first canonical variate accounted for 70% of the dietary variance and had a canonical correlation of 0.43 (Table 2). It showed a highly significant inter-relationship between the composition of the diet and the field abundances of all the dietary categories ($p < 0.001$; Table 2). The loadings upon the first canonical variate indicated that the presence of rabbits (0.75) and the absence of dasyurids (–0.61) were the most important dietary factors (Table 2). The most important field category associated with these dietary influences was the presence of rabbits (0.76). The second canonical variate only accounted for a further 17% of the variance and so the factors that influenced this variate were of less significance.

Fox-prey interactions before rabbit density reduction

There was a significant relationship between the dietary occurrence and the field abundance of rabbits (Fig. 4a) and there was an inverse relationship between the ingestion of dasyurids (Fig. 4b) and ground-dwelling birds (Fig. 4c), although these relationships were not significant. The ingestion of invertebrates, reptiles and carrion was unrelated to their field abundances. The numerical response of the fox population was not significantly related to the density of any prey type though the correlations between fox abundance and the field abundances of all prey categories except ground-dwelling birds were positive (Table 3).

Fox dietary analysis and prey interactions after rabbit density reduction

A total of 157 scats was collected at Site 3: 79 scats during the three sampling periods before rabbit removal (29 scats in April 1988, 23 in June 1988 and 27 in October 1988) and another 78 scats after rabbit removal (20 scats

Table 1

Dietary items identified within fox scats (N = 931).

Mammals	Reptiles	Birds	Invertebrates
Oryctolagus cuniculus	*Ctenotus uber*	*Coturnix pectoralis*	Chilopoda
Sminthopsis spp.	*Tympanocryptus lineata*	*Turnix velox*	Orthoptera
Planigale spp.	*Diplodactylus* spp.		Hemiptera
Mus domesticus	*Morethia boulengeri*		Coleoptera
Ovis aries (carrion)	*Pseudonaja textilis*		Scorpionidea
Macropus rufus (carrion)	*Tiliqua rugrosus*		
M. fuliginosus (carrion)			

Table 2

Results of canonical correlation analysis comparing species availability and dietary occurrence. Data are from 931 scats collected in Sites 1 and 2 from October 1986 to July 1989 and in Site 3 from October 1986 to October 1988

Root No	Percent variance	Cumulative variance (%)	Canonical correlation	*p*
1	70	70	0.43	<0.001
2	17	87	0.23	<0.05
3	9	96	0.17	ns
4	3	99	0.09	ns
5	1	100	0.04	ns
Correlations	**Diet 1**	**Diet 2**	**Field 1**	**Field 2**
Rabbit	0.75	0.10	0.76	0.55
Dasyurid	–0.61	0.25	–0.02	0.43
Bird	–0.48	0.43	0.15	–0.45
Invertebrate	–0.34	–0.83	0.26	–0.53
Reptile	0.09	–0.33	0.50	–0.69
Carrion	–0.06	0.12	0.30	0.21

Table 3

Correlations between fox and prey abundances. Data are from Sites 1 and 2 (October 1986 to July 1989) and Site 3 (October 1986 to October 1988).

	Fox	Rabbit	Dasyurid	Birds	Reptile	Invertebrate	Carrion
Fox	1						
Rabbit	0.39	1					
Dasyurid	0.32	0.70	1				
Birds	–0.36	–0.02	0.41	1			
Reptile	0.47	0.50	0.82	0.21	1		
Invertebrate	0.41	0.70	0.57	–0.06	0.82	1	
Carrion	0.67	0.32	0.54	–0.37	0.75	0.66	1

collected in November 1988, 32 in January 1989 and 26 in April 1989).

Following the ripping of the warrens in Site 3, the incidence of rabbit in the foxes' diet decreased from 30% to 19%, ground-dwelling birds increased from 2% to 12%, and dasyurids increased from 9 to 12% (Fig. 5). There was no significant change in fox density ($F_{3,15}$=2.07, p=0.17).

When the foxes' diet after rabbit density reduction was analysed using canonical correlation, a highly significant first variate resulted and this accounted for 75% of the dietary variance (Table 4). The most important factors were a decline in the ingestion of rabbits and a high consumption of ground-dwelling birds. These factors had loadings on the first canonical variate of –0.86 and 0.60 respectively (Table 4). The field abundance that most influenced the composition of the diet was the absence of rabbits and its loading on the first canonical variate was –0.84 (Table 4). In contrast, canonical correlation analysis of fox diet in Site 2, where warrens had not been ripped, showed that the first variate was highly significant (0.57) and accounted for 99% of the dietary variance (Table 5). No prey category loaded significantly more heavily on this variate than any other.

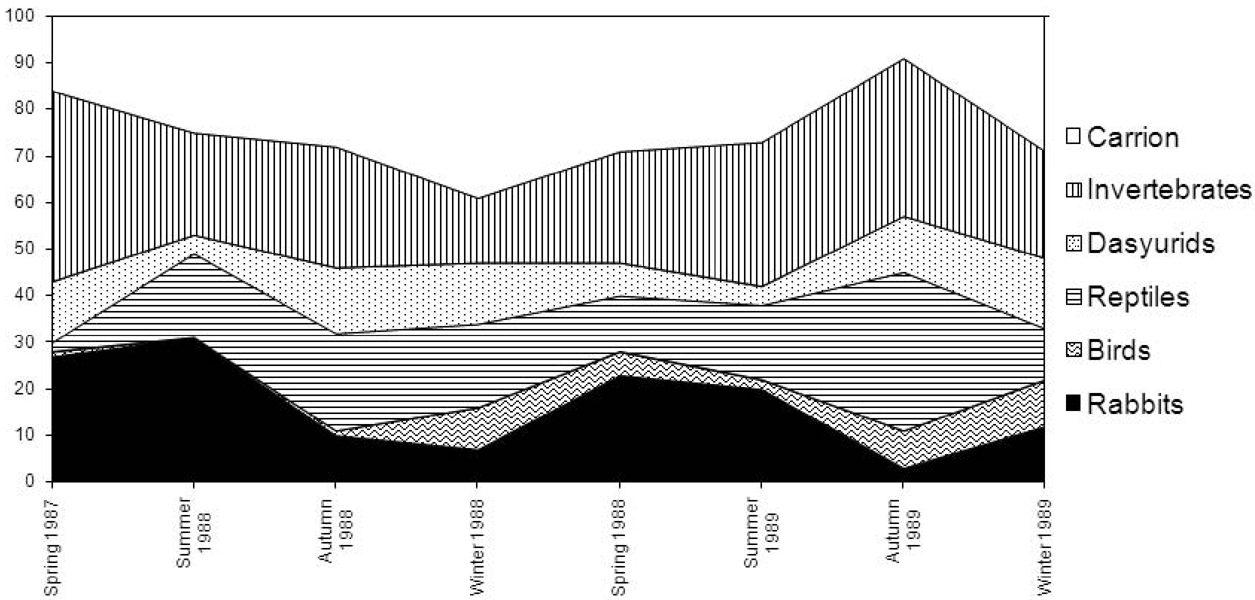

Figure 3. Seasonal composition of fox diet at the study site. Data averaged for all sites and sampling periods except Site 3 from November 1988 to June 1989.

DISCUSSION

The composition of the diet of foxes in the arid zone of western New South Wales was influenced strongly by the abundance of rabbits. Rabbit abundance determined the contribution of all other items to the diet and when rabbit abundance increased more rabbits were ingested. The proportion of ground-dwelling birds and dasyurids in the diet of foxes increased significantly when rabbit warrens were ripped, even though the field availability of these prey species was stable or decreasing. This change of prey preferences with a change in rabbit availability has been previously reported (Holden & Mutze 2002; Read & Bowen 2001) and a similar inverse density-dependent ingestion of prey species has been observed (Scott & Klimstra 1955; Kruuk 1972; Green & Osbourne 1981; Paltridge 2002).

Fox density was positively related to the field abundance of all prey types except ground-dwelling birds but none of these relationships was statistically significant. There was no change in fox density following the ripping of rabbit warrens. The capacity of foxes to prey upon a particular species was consequently not limited by the density of that species because fox density was independent of the density of any individual prey item. This observation is consistent with the conclusions of other studies where the relationship between predator abundance and the impact on prey species

Table 4

Results of Canonical Correlation Analysis comparing composition of fox scats collected in Site 3 for three sampling periods before (N = 79) and after (N = 78) rabbit removal (n.s. = not significant).

Root No	Percent variance	Cumulative variance (%)	Canonical correlation	p
1	75.05	75.05	0.60	<0.001
2	14.08	89.13	0.31	<0.05
3	7.49	96.62	0.19	n.s.
4	3.36	99.98	0.15	n.s.
5	0.02	100.00	0.01	n.s.
Correlations	**Diet 1**	**Diet 2**	**Field 1**	**Field 2**
Rabbit	–0.86	–0.31	–0.84	–0.29
Bird	0.60	–0.22	–0.25	–0.41
Dasyurid	0.30	–0.53	–0.33	–0.11
Invertebrate	–0.24	0.71	0.19	0.35
Reptile	–0.36	0.12	–0.19	–0.22
Carrion	0.30	0.33	0.22	0.28

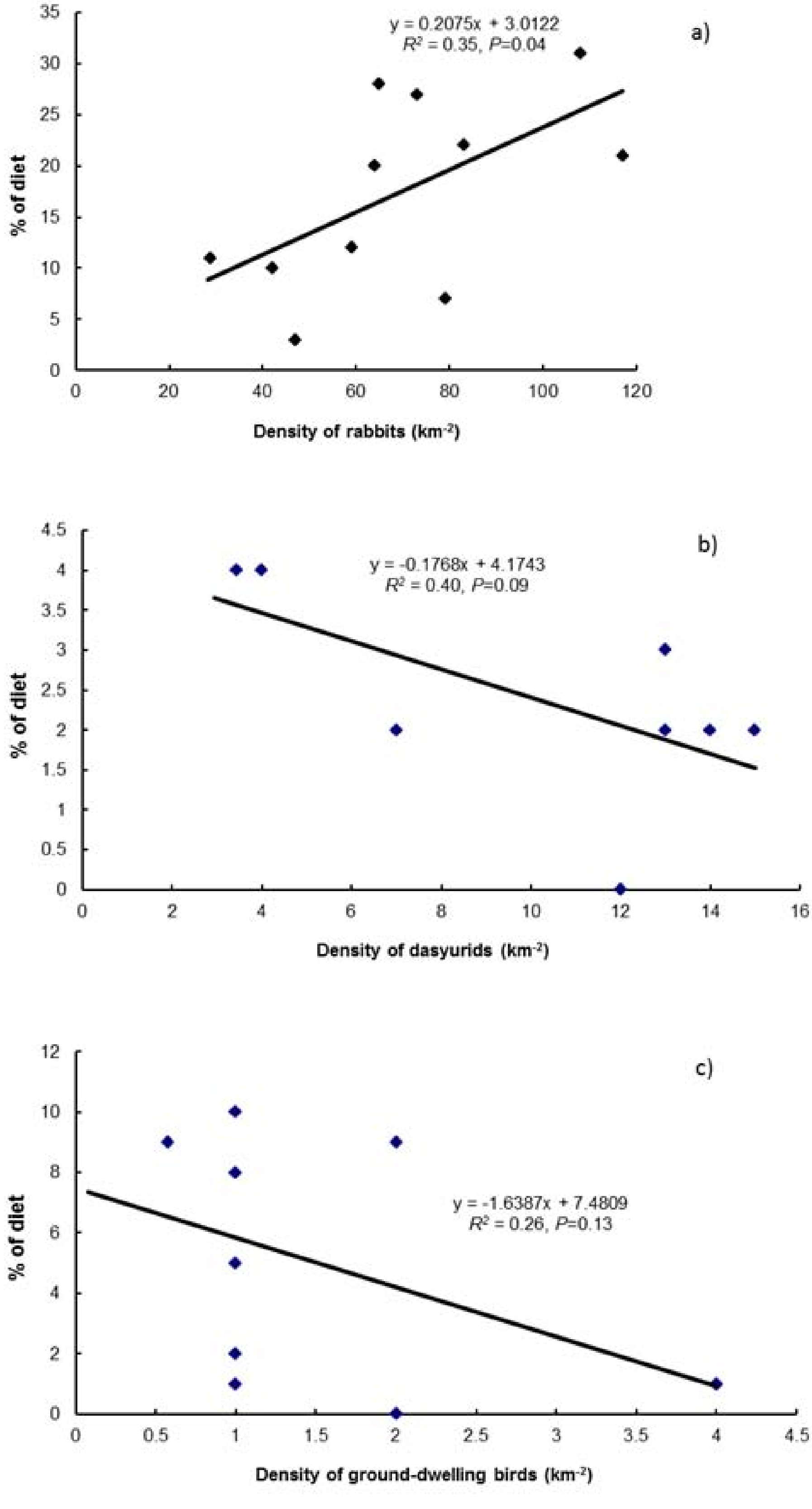

Figure 4. Relationship between the abundance of (a) rabbits, (b) dasyurids and (c) ground-dwelling birds and their occurrence in the foxes' diet. Data from all sites and sampling periods except Site 3 from November 1988 to June 1989. Note change of scale on x axis in each panel.

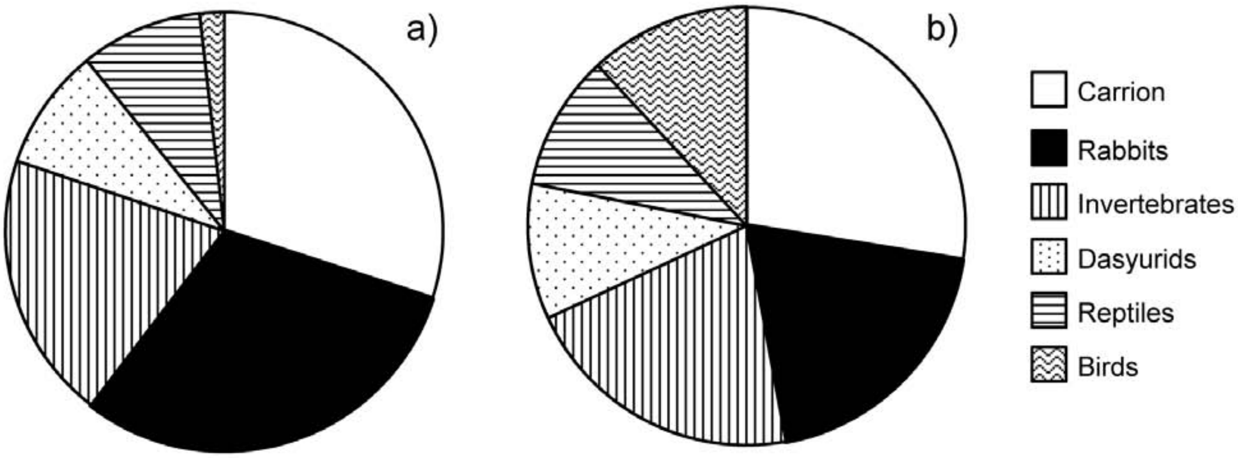

Figure 5. Composition of the diet of foxes in Site 3 (a) before (April1988, June 1988 and October 1988) and (b) after (November 1988,January 1989 and April 1989) rabbit control.

was not density dependent (Hone 1999; Short et al. 2002; Kirkwood et al. 2014). It is also consistent with the theoretical predictions made by Holt (1984), who stated that if one prey species is sufficiently productive then this would tend to increase the density of the predator and that other prey species may be driven to extinction. The predation pressure that foxes are therefore able to exert upon certain species, especially those upon which predation is inversely density-dependent, could be devastating. An example of this is described by Kruuk (1972), who anticipated that an entire gull colony could be exterminated because fox density, and therefore predation upon the colony of gulls, was not limited by the density of gulls but by a much higher rodent density. This phenomenon has been termed hyperpredation (Smith & Quin 1996) and the impact of this type of predation would be particularly detrimental if there was also surplus killing of the prey species by foxes (see Petersen 1982; Short et al. 2002). We suggest that this may have been the mechanism by which the declines in mammals across Australia occurred. Fox density may have been maintained at relatively high levels due to the availability of a wide variety of prey species, especially rabbits. When rabbit densities were reduced by drought or by epizootics of myxomatosis, foxes would have been able to switch prey preferences while maintaining their own density, at least in the short-term. They could then have sustained predation pressure upon another prey species in inverse proportion to its density until it became extinct. Similar switches in prey preference by foxes when the densities of rabbits have been reduced have been observed by Lever (1959), Englund (1965), Southern (1956), McIntosh (1963), and Sumption and Flowerdew (1985). A similar lack of change in fox density following the decline of rabbits was reported by Ratcliffe (1956) and Lever (1959).

Although there has been debate about the role of predators in the decline of mammalian species in the arid zone of Australia (Morton 1990), it is clear from studies of fox–prey interactions in other habitats (e.g. Kinnear et al. 1988, 1998; Short et al. 1992) that foxes can be the major cause of decline of prey species. Fox predation has also been recognised as a significant factor in the decline of some mammalian species that

Table 5

Results of Canonical Correlation Analysis comparing composition of fox scats collected in Site 2 for three sampling periods before (N = 76) and after rabbit (N = 61) removal in Site 3 in November 1988 (n.s. = not significant).

Root No	Percent variance	Cumulative variance (%)	Canonical correlation	*p*
1	98.89	98.89	0.57	<0.001
2	1.11	100.00	0.07	n.s.
Correlations	**Diet**	**Field**		
Rabbit	–0.11	0.23		
Bird	0.27	-0.15		
Reptile	–0.29	0.21		
Dasyurid	0.10	0.32		
Invertebrate	–0.24	-0.11		
Carrion	0.14	0.17		

previously occurred in the arid zone, such as brush-tailed bettongs (*Bettongia penicillata*; King et al. 1981), brush-tailed possums (*Trichosurus vulpecula*; Kerle et al. 1992), numbats (*Myrmecobius fasciatus*; Friend & Thomas 1995) and burrowing bettongs (*Bettongia lesueur*; Short et al. 1995). We conclude that fox predation remains a critical factor in the decline of many arid zone mammalian species.

The role of the fox in the decline of prey populations may have been greater in the arid zone than in other habitats because fox predation is exacerbated when productivity is low and where the habitat is already marginal for maintaining viable populations of metabolically expensive organisms (Pianka 1986). Any decrease in the carrying capacity of the area due to drought (or other factor) would result in more extinctions in the arid zone than in more mesic habitats (Pianka 1986). Morton (1990) also suggests that medium-sized herbivorous mammals are most vulnerable to local disappearance in arid areas due to their relatively high metabolic requirements and their inability to disperse sufficient distances to reach suitable habitat during prolonged drought. Other factors such as overgrazing and altered fire regimes would have further contributed to these declines (Morton 1990).

Since this study was completed the interactions between foxes and rabbits at Fowlers Gap may have been influenced by the introduction of rabbit calicivirus disease. This disease spread into New South Wales in 1996 but its impact on foxes, rabbits and native species in the study area is unknown because there has been no further monitoring of the interactions of these species. However, the influence of rabbit calicivirus disease upon the densities of foxes and their prey species was examined in other sites as the disease spread across Australia (Newsome et al. 1997; Edwards et al. 2002; Holden & Mutze 2002; Saunders et al. 2004). In general, fox predation upon native species did not increase as the calicivirus disease epizootic spread through the rabbit population, although the results from the study of Holden and Mutze (2002) were confounded by concurrent fox baiting, and those of Saunders et al. (2004) by the occurrence of drought. Nevertheless, there was evidence from central Australian sites (Newsome et al. 1997) that there was a downward trend in small mammal captures. Similarly, in areas where there was an abundance of alternative prey species for foxes (e.g. waterfowl at Muncoonie Lakes) there was anecdotal evidence that suggested a corresponding decrease in the abundance of dasyurids and reptiles (Newsome et al. 1997). Thus the effect of the resulting change in rabbit numbers was influenced by the availability of alternative food items that sustained the fox population so that predation upon the rarer prey species was maintained or increased. These observations reflect the variability of fox behaviour and indicate that foxes use different survival strategies in response to differing environmental conditions (see Banks 2000; Banks et al. 2000). Further monitoring of the effects of this disease at Fowlers Gap is required.

Although the decline of small- to medium-sized mammals in arid and semi-arid areas coincided with the establishment and persistence of both foxes and rabbits (Pech et al. 1995; Caughley & Gunn 1996), declines of native species have also occurred in other biomes where rabbits are scarce (Woinarski & Braithwaite 1990; Morton 1990). Foxes are able to reside in relatively high densities in areas where there are virtually no rabbits and thus the presence of rabbits is not essential for their survival (Thomson et al. 2000; Lapidge & Henshall 2001; Paltridge 2002). It is possible that the foxes' other prey types of carrion and invertebrates were available in these areas and that the density of foxes was independent of the density of the vulnerable prey species. Thus the mechanism of decline of mammals would have been similar to that described above, although the actual prey items that maintained fox densities may have been different (see Dickman 1996, Paltridge 2002).

There are several management actions that can be undertaken to protect vulnerable prey species at low densities so that they are not driven to extinction when there is a sudden decrease in rabbit density (Sinclair et al. 1998). Firstly, during rabbit density declines simultaneous fox control should be implemented (Banks et al. 1998), especially if there is a protracted lag phase where foxes preferentially prey on rabbits despite their densities being reduced (Saunders et al. 2004). Secondly, habitat manipulation needs to be undertaken so that vulnerable species have more refugia from predators (Sinclair et al. 1998). The capacity of foxes to prey upon small populations of native species will be influenced by the prey species' ability to avoid predation, and the availability of suitable cover is therefore important in reducing or minimising fox predation upon native species (Christensen 1980; Kinnear et al. 1988; 2002; Stokes et al. 2004; Pickett et al. 2005; Strauß et al. 2008). In the arid zone, rabbits may have competed directly with native species for food and also destroyed their refugia which made them more vulnerable to fox predation (Burbidge & McKenzie 1989; Morton 1990; Dickman et al. 1993). The removal of rabbits to reduce habitat loss, the implementation of local revegetation programs, and the use of fire to overcome vegetation senescence (Burrows et al. 1987) are possible methods of increasing refugia to prevent the further extinction of relic populations and for the successful reintroduction of vulnerable species. A third management option to protect vulnerable native species is the reduction of predator densities (Sinclair et al. 1998). Many large-scale and numerous small-scale fox baiting programs are undertaken throughout southern Australia to protect native fauna and livestock from fox predation (Orell 2004; Possingham et al. 2004; Saunders & McLeod 2007; Robley et al. 2014). These programs rely on the repeated delivery of baits containing the toxin 1080 to reduce fox densities. These fox baiting programs have been very successful and if sustained they can remain effective in reducing fox densities and fox predatory impacts for at least 25 years (Marlow et al. 2015).

Despite these three management options being proposed over 15 years ago by Sinclair et al. (1998), many species of fauna that are vulnerable to fox predation are still at precariously low abundances across Australia (e. g. brush tailed bettongs and numbats, Parks and Wildlife WA, unpublished data). The control of foxes and rabbits is not routinely co-ordinated at sites where these species occur and there has been limited quantitative research on the effectiveness of refuge manipulation in reducing fox predation upon these threatened species. Also, although effective fox control has been sustained in many areas (see above), in some sites in Western Australia feral cats have increased in abundance and have replaced foxes as the dominant predator when foxes are controlled (Marlow et al. 2015). If the abundances of threatened species are to be increased, effective and co-ordinated control of both foxes and cats needs to be developed and implemented (Moseby et al. 2009; Berry et al. 2012). Predation by these introduced predators also needs to be reduced through the removal of rabbits and through habitat augmentation. The populations of endemic threatened species in arid zone sites and elsewhere may then be protected or reintroduced and this will hopefully return them to their original abundances.

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