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The diet of foxes (*Vulpes vulpes*) in fragmented Wheatbelt reserves in Western Australia: implications for woylies (*Bettongia penicillata*) and other native fauna

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ABSTRACT

The diet of foxes in two fragmented Wheatbelt reserves in south-west Western Australia, Dryandra Woodland (DW) and Tutanning Nature Reserve (TNR), was investigated. Fox baiting commenced in these reserves in the early 1980s and the trap success of woylies (*Bettongia penicillata*), a threatened species, increased significantly. Woylie capture rates were sustained in TNR until 1992 and in DW until 2000 but then decreased suddenly despite ongoing fox control. The diet of foxes was investigated as part of a larger study examining the reasons for the woylie decline. The contents of 283 fox scats from DW and TNR, and 167 scats from two unbaited sites, Quinns block (QB) and Highbury block (HB), were analysed volumetrically to determine the relative importance of each dietary item. The actual consumption of each item was calculated using digestibility estimates. In baited sites the foxes' main dietary components were house mice (*Mus domesticus*, 28%), carrion (sheep, *Ovis aries* and western grey kangaroo, *Macropus fuliginosus*; 26%) and rabbits (*Oryctolagus cuniculus*, 17%). In unbaited sites the main components were carrion (predominately sheep, 60%) and some invertebrates (13%). Only one scat (from DW) contained any woylie remains. Approximately 10% of the foxes' diet in all sites consisted of brush-tail possums (*Trichosurus vulpecula*). No remains from numbats (*Myrmecobius fasciatus*), bilbies (*Macrotis lagotis*), red-tailed phascogales (*Phascogale calura*), *Antechinus* sp., *Sminthopsis* sp. or echidnas (*Tachyglossus aculeatus*) were detected. Birds (<5%) and reptiles (<2%) were of little dietary importance at all sites. There was no significant seasonal variation in the foxes' diet. The role of rabbits in the diet of foxes and the potential for the presence of this species to drive increases in fox abundance, and by deduction to increase predation on woylies and other similar prey species, is considered in relation to theoretical predator prey models and management options.

Keywords: *Bettongia*, diet, fox, predation, threatened species, woylie

INTRODUCTION

Australia has the highest rate of mammalian decline and extinction in the world (Short & Smith 1994). Many of these declines coincided with the introduction of the European fox (*Vulpes vulpes*) and its spread across most of southern Australia (Abbott 2011). Due to this, and other evidence, fox predation is now listed nationally as a Key Threatening Process in the decline of vulnerable Australian fauna (Department of Environment, Water, Heritage and the Arts 2008).

The impact of foxes on native Australian mammals is exemplified by the changing status of the woylie (*Bettongia penicillata*: Potoroidae). Woylies occupied large expanses of arid and semi-arid Australia before European settlement but their populations have declined by >99% Australia-wide. In Western Australia the decline coincided with the arrival of the fox between 1910–1930 (Abbott 2002, 2008; Short et al. 2005), and only three populations remained (de Tores & Start 2008). Fox predation on woylies in two of these populations, Dryandra Woodland (DW) and Tutanning Nature Reserve (TNR), may have been mitigated by the presence of a dense understorey of *Gastrolobium* spp. (poison peas) that provided a predation refuge (Christensen 1980; Kinnear et al. 2002). Also, secondary poisoning of foxes occurred historically as a result of 1080 (sodium fluoroacetate) baiting for rabbit control in surrounding areas, and this reduced fox abundance (Christensen 1980; Kinnear et al. 2002). Relictual populations of woylies remained in these two reserves until the early 1970s (Sampson 1971) but following the effective use of the myxoma virus during the 1970s, and the subsequent reduced use of 1080 for rabbit control, fox control through secondary poisoning decreased significantly (King et al. 1981). The trap success

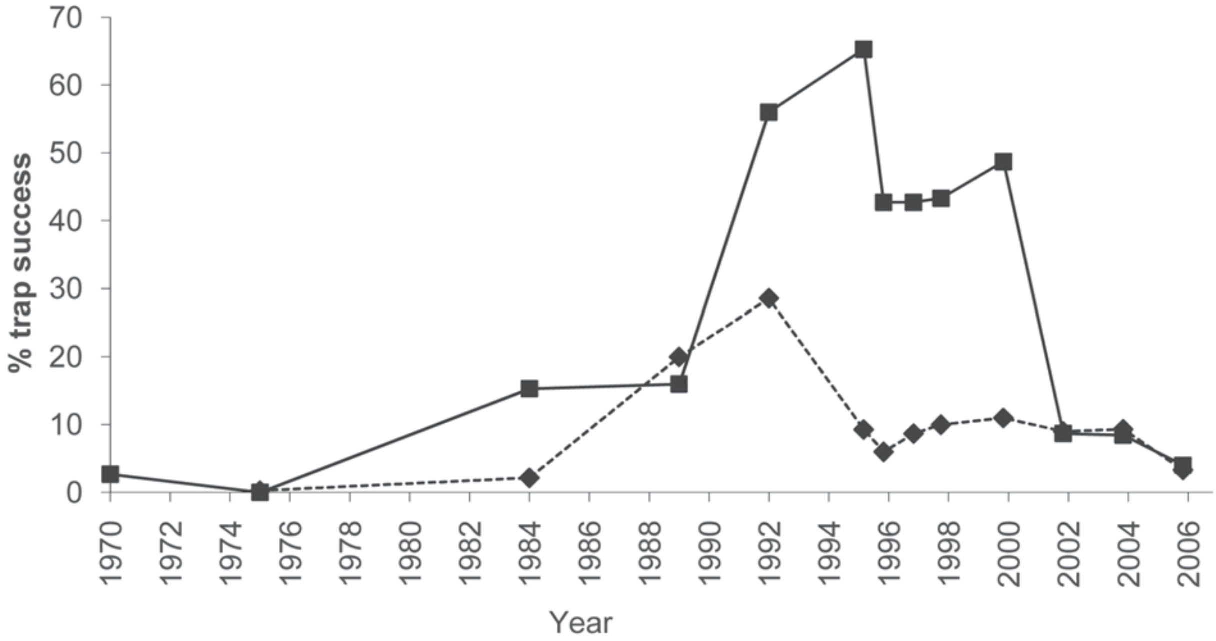

Figure 1. Woylie trap success in Dryandra Woodland (continuous line) and Tutanning Nature Reserve (dotted line) from pre-1980 to 2006 (data collected by personnel from the Department of Parks and Wildlife and earlier agencies).

of woylies in DW and TNR subsequently declined, and by the mid–late 1970s was virtually zero (Kinnear et al. 2002).

When regular fox baiting was initiated in DW and TNR in the early 1980s, the woylie populations increased once again (Kinnear et al. 2002; Fig. 1). Fox control continued and woylie trap success increased sufficiently, in these and other sites, for the species to be removed from the state, national and international threatened species lists in 1996 (Groom 2010). In that year the Western Shield Fauna Recovery Program was also initiated (Possingham et al. 2004), with fox predation being recognised as the main threat to many species of small- to medium-sized fauna (Wyre 2004). The regular delivery of fox baits containing 1080, to which fauna have a natural tolerance (King et al. 1981), was increased to 3.5 M ha. Despite maintained fox control, woylie trap-success declined in TNR after 1992 and in DW in 2000, and returned to pre-baiting levels. The reasons for these declines were unclear and were investigated in a four-year study that ran from April 2006 to November 2009 (Marlow et al. 2015a, 2015b).

The diet of foxes in DW and TNR was investigated as part of the larger study and the current consumption of woylies and other endemic fauna was determined. The foxes' diet in these baited reserves was compared with those in two unbaited sites, Quinns block (QB) and Highbury block (HB), and seasonal variations were examined. If woylies or other fauna were ingested more frequently at certain times of the year this may indicate a requirement to intensify fox control at those times if baiting was inadequate. Also, the ingestion of woylies, rabbits and brush-tail possums (*Trichosurus vulpecula*) during each season was compared with concurrent indices of their field availabilities to determine if these species were ingested in proportion to their abundance. If any of these species was being ingested disproportionally to its field abundance, this may suggest that foxes were exhibiting a preference for this species.

The diet of foxes was examined in relation to theoretical predator–prey models to obtain an explanation of how fox predation may have caused the decline of vulnerable prey species such as woylies in the past. In particular, the role of rabbits in the diet of foxes was examined because when rabbits are numerous, foxes may rely on these as their primary prey (Newsome et al. 1989). Rabbit populations can reach very high densities (Johnson 2006), and this enables fox populations to also reach high densities, with a resulting high ratio of foxes to endemic mammals (Johnson 2006). While rabbits are demographically resilient to high intensities of fox and feral cat (*Felis catus*) predation, woylies are less resilient because they are only able to produce three joeys per year (Serventy 1970). Other native species that have a higher reproductive rate than woylies may be able to better withstand fox predation but few marsupials have a reproductive output that rivals that of rabbits (Van Dyck & Strahan 2008).

METHODS

The study was undertaken at four sites: two baited sites (DW and TNR) and two unbaited sites (QB and HB). The main block of DW is a 12,000 ha bushland remnant 25 km north-west of Narrogin in the Wheatbelt of Western

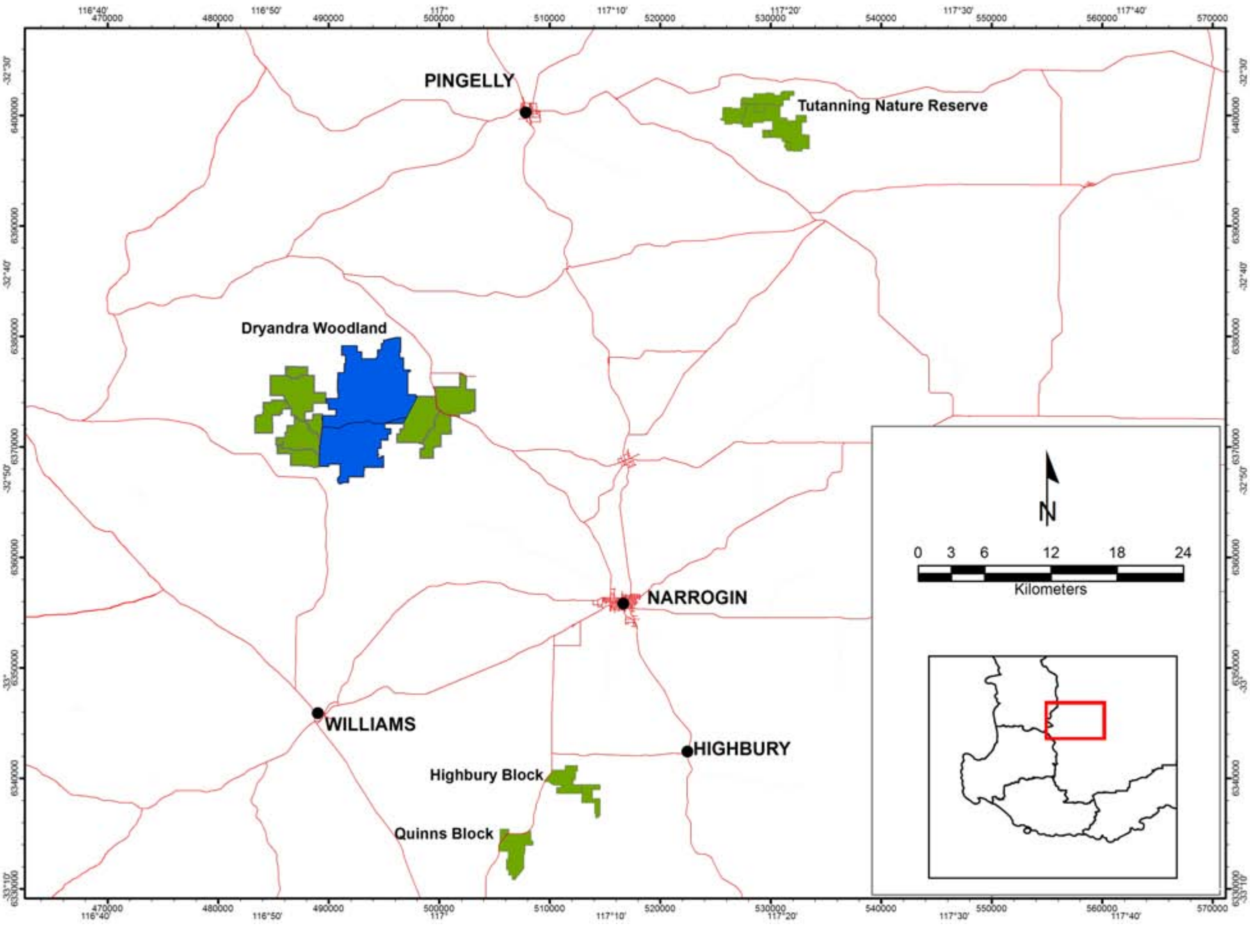

Figure 2. Map of the study sites. The blue area indicates the study site within Dryandra Woodland.

Australia. The study site was a 6800 ha area within the centre of the main block (Fig. 2). TNR is a small (2000 ha) reserve approximately 50 km to the north-east of DW. Both sites are baited monthly for fox control (12 times per year) with 3.0 mg 1080 meat baits. The nominal bait delivery rate is 5 baits km^{-2} (Thomson & Algar 2000). Dried meat baits (DMBs) sourced from the Department of Agriculture and Food, Western Australia (DAFWA) at Forrestfield were used in both sites from March 2006 to August 2008. From September 2008 to November 2009 the bait type used in DW was changed to Pro-baits, which were manufactured at the Department of Parks and Wildlife's bait factory at Harvey. In TNR, DMBs were used throughout the study.

In DW and TNR, the mammalian species present includes woylies, numbats (*Myrmecobius fasciatus*), bilbies (*Macrotis lagotis*), red-tailed phascogales (*Phascogale calura*), brush-tail possums (*Trichosurus vulpecula*), honey possums (*Tarsipes rostratus*), western pygmy-possums (*Cercartetus concinnus*), mardos (*Antechinus flavipes*), tammar wallabies (*Macropus eugenii*), brush wallabies (*M. irma*), western grey kangaroos (*M. fuliginosus*) and echidnas (*Tachyglossus aculeatus*). Quenda (southern brown bandicoots, *Isoodon obesulus*) were reintroduced into TNR between 1991 and 1995 and became naturally re-established in DW during the study. Chuditch (*Dasyurus geoffroii*) also naturally recolonised both sites during the study. Other fauna of interest due to their possible susceptibility to fox predation include the mallee fowl (*Leipoa ocellata*) and the carpet python (*Morelia spilota*). Foxes still occur in both sites, though their abundance is significantly reduced when compared with unbaited sites (Marlow et al. 2015a, 2015b). Feral cats also occur in both sites and their abundance is higher than in unbaited sites (Marlow et al. 2015a).

The two unbaited sites, QB and HB, are located approximately 25 km south-west of Narrogin and are each approximately 1000 ha in area. The fauna in these two sites was less intact with woylies, numbats, tammar wallabies and bilbies all being locally extinct. Brush-tail possums, brush wallabies, western grey kangaroos and echidnas still occur. Foxes were in higher abundance here than in the baited sites and feral cat densities were lower (Marlow et al. 2015a).

Fox scats were collected each season from March 2006 to September 2009 from predetermined 20 km transects and from sand-plots. Sand-plots were established throughout all four study sites at 500 m intervals along all tracks. They were constructed by removing 8–10 cm of the track surface and replacing the extracted material with sand. Each plot was approximately 1 m wide and extended across the track. One hundred and twenty nine sand-plots were positioned in DW, 75 in TNR, 31 in QB and 32 in HB. Sand-plots were monitored for three consecutive nights, both before and after a fox-baiting event, in each season. Foxes regularly deposited scats on freshly raked sand-plots. Two hundred and eighty-three scats were collected from DW and TNR and 167 from QB and HB.

All scats were sent to Scats About (www.scatsabout.com) and their contents were analysed. Scats were placed in individually labelled paper bags and oven-dried at 100 °C for 12 hours to kill parasite eggs. Samples were then placed in individual fine weave nylon bags and washed in a washing machine for approximately 15 minutes (Johnson & Alred 1982). Dietary components were identified to the lowest possible taxonomic class through comparison with known reference material or from published descriptions (e.g. Triggs & Brunner 2002; Watts & Aslin 1981). Hair samples were identified using the technique described by Brunner & Coman (1974). The percent volume of each prey item within the scat was visually estimated using a grid system within the sorting tray. The actual consumption of each prey item was approximated using digestibility estimates and the methods described by Lockie (1959). The digestibilities of rabbits (34.0), small mammals (18.2), reptiles (18.0) and small birds (20.0) were obtained from, or modified from, Lockie (1959). Carrion (50.0) and invertebrate (10.0) digestibility estimates were modified from Goszczynski (1974). All remains from western grey kangaroos and sheep were assumed to have been consumed as carrion because these species are generally too large to be live prey for foxes. Some juveniles of these species may have been killed and eaten by foxes but differentiating their consumption from that of adults was beyond the scope, and was not the focus, of this study.

The field abundances of woylies, rabbits and brush-tail possums were crudely estimated by calculating the proportion of sand-plots visited by each species on each day of monitoring. This was averaged for the six monitoring days each season. No field availability estimates were made for house mice, carrion, wallabies, birds, reptiles or invertebrates. The limited value of indices in reflecting abundance accurately is acknowledged (Anderson 2003).

The seasonal variability in the diet of foxes was examined using two-way analysis of variance for baited and unbaited sites, respectively. The amount of each dietary category that was calculated to have been consumed by foxes, after digestibility estimates had been applied, was used in these analyses.

The prey preferences that foxes exhibited for rabbits and possums were investigated by regressing the amount of each species calculated to have been consumed by foxes in each season against the index of field availability of that species for that season. A high R value was assumed to indicate a strong prey preference. We acknowledge that availability and consumption were measured using different techniques, and that the indices of availability may not be directly proportional to actual abundance. These limitations precluded a multivariate analysis of the data.

RESULTS

The main components of the foxes' diet were introduced species and carrion (Fig. 3). In baited sites foxes mainly consumed house mice (28%), carrion (sheep and western grey kangaroos, 26%), and rabbits (17%). In unbaited sites, foxes mainly ate carrion (sheep, 60%) and, to a limited extent, invertebrates (13%). Approximately 10% of the foxes' diet consisted of brush-tail possums, and <5% was from birds and <2% was from reptiles. In baited sites, 4% of the foxes' diet consisted of tammar and brush wallabies. Only one scat contained any identifiable woylie remains and this was collected from DW. No remains from numbats, bilbies, red-tailed phascogales, honey possums, western pygmy-possums, mardos, quenda, chuditch, echidnas, the mallee fowl or carpet pythons were detected. Three scats from DW and one scat from TNR contained feral cat remains.

There was no significant seasonal variation in the diet of foxes in both baited ($F_{3, 35}$ = 0.14, p = 0.94) and unbaited sites ($F_{3, 35}$ = 0.13, p = 0.98; Fig. 4). A strong prey preference for rabbits was detected in both baited and unbaited sites (R^2 = 0.95 and R^2 = 0.91 respectively; Fig. 5). Foxes did not show a strong preference for brush-tailed possums (R^2 = 0.41 baited sites and R^2 = 0.30 unbaited sites; Fig. 6) but similar quantities of possum were consumed in baited (12%) and unbaited sites (9%), despite there being fewer possums available in unbaited sites. Foxes consumed considerably fewer woylies than would be expected from the estimated field availability of this species in baited sites (Fig. 7). No woylies were present in unbaited sites.

DISCUSSION

The main components of the diet of foxes in the two baited Wheatbelt reserves were house mice, carrion (sheep and western grey kangaroos) and rabbits. In the two unbaited sites, foxes mainly ate sheep carrion and a limited quantity of invertebrates. These results are consistent with those obtained from many other studies where introduced species and carrion were observed to be the main components of the foxes' diet (e.g. Croft & Hone 1978; Catling 1988; Molsher et al. 2000; Read & Bowen 2001; Saunders et al. 1995, 2004). Previous observations that foxes are opportunistic predators/scavengers with a wide range of dietary items were reconfirmed.

The main endemic mammal to be consumed by foxes was the brush-tail possum and this constituted approximately 10% of the diet in all sites. A lesser amount of tammar and brush wallabies was consumed by foxes in baited areas. The consumption of these native mammals in baited areas is consistent with the results of Kinnear et al. (1988, 1998), Paltridge (2002), Pavey et al. (2008) and Cupples et al. (2011), who all found that when foxes are controlled the proportion of endemic species in their diet increases. However, this observation contrasts with the results of Roberts et al. (2006), who did not observe increased consumption of endemic species in baited sites

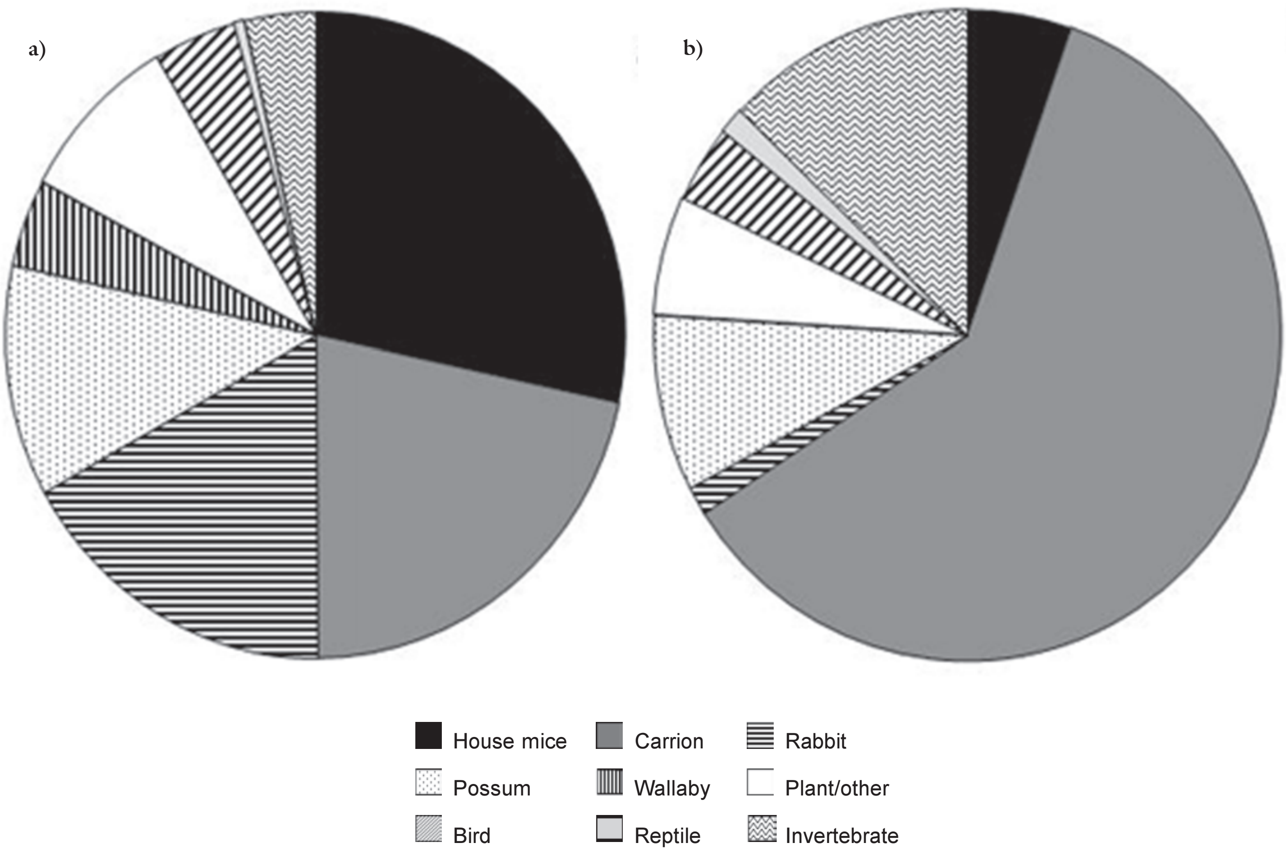

Figure 3. Overall composition of the diet of foxes in a) baited sites (N = 283) and b) unbaited sites (N = 167).

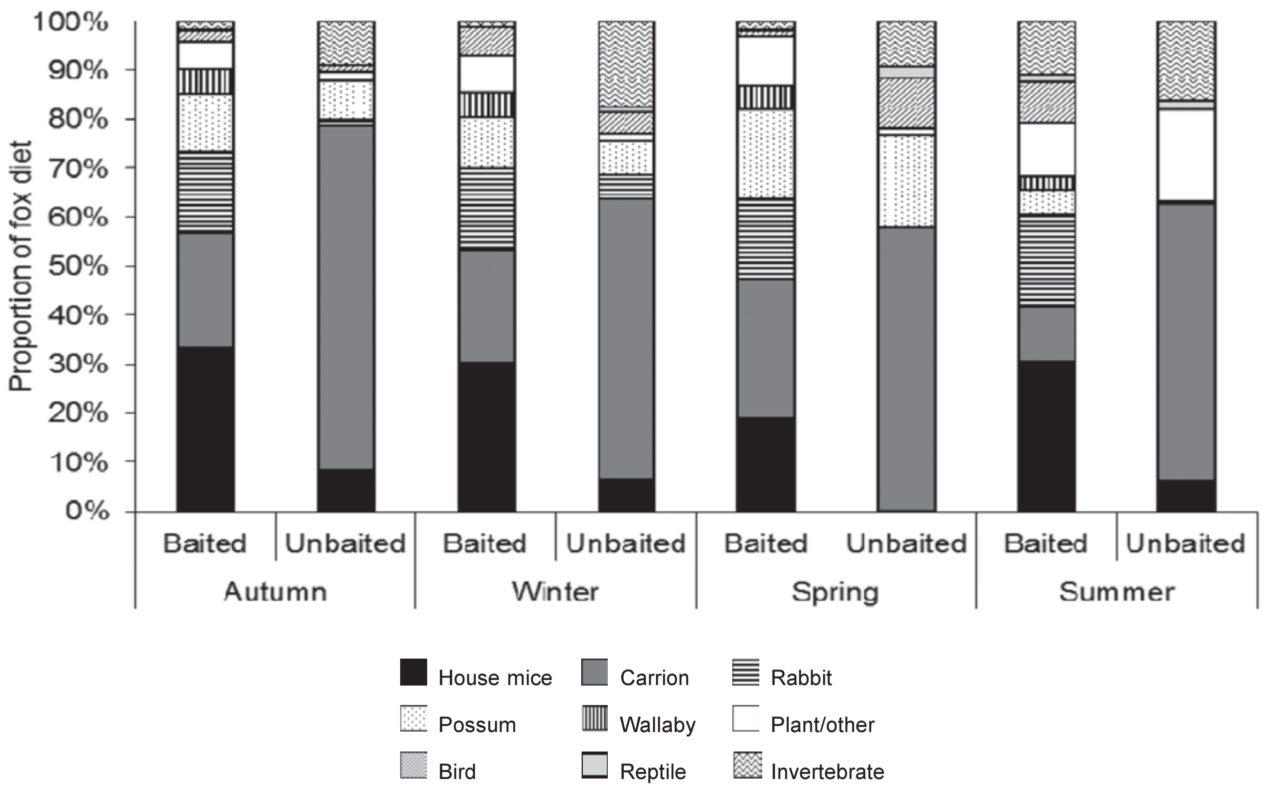

Figure 4. Seasonal composition of the diet of foxes in baited and unbaited sites.

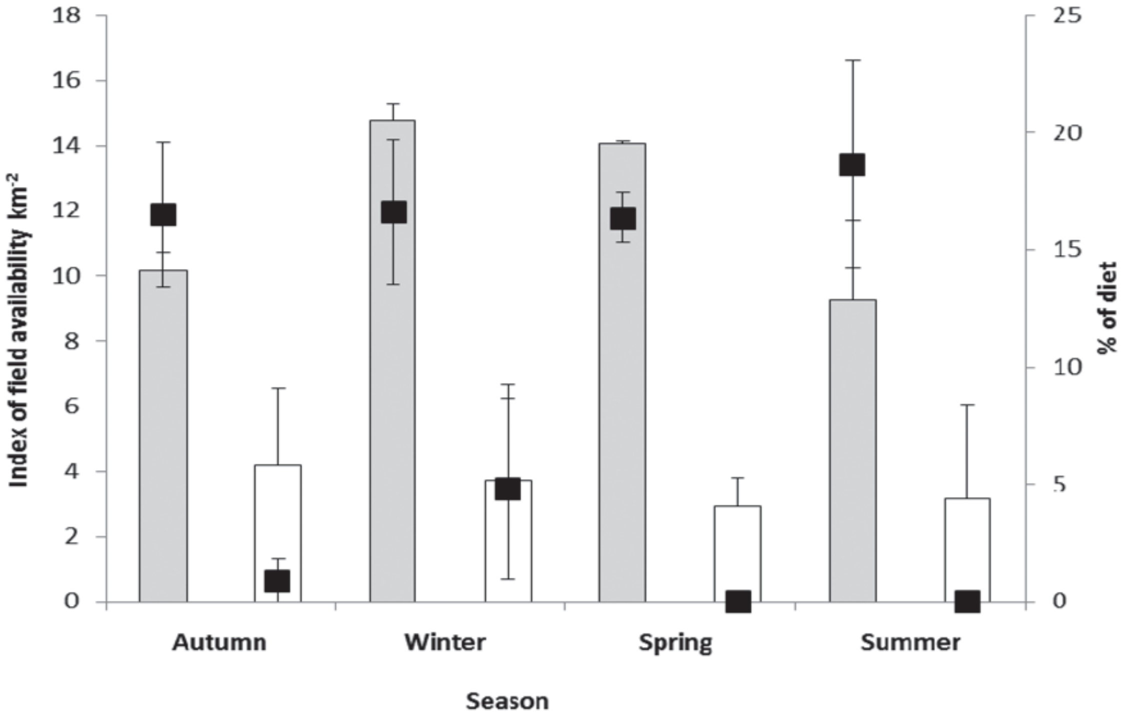

*Figure 5. Seasonal dietary occurrence and indices of field abundance of rabbits (*Oryctolagus cuniculus*) in baited and unbaited sites. Bars show indices of availability ± SE (baited sites, closed bars; unbaited sites, open bars); black squares show dietary occurrence ± SE.*

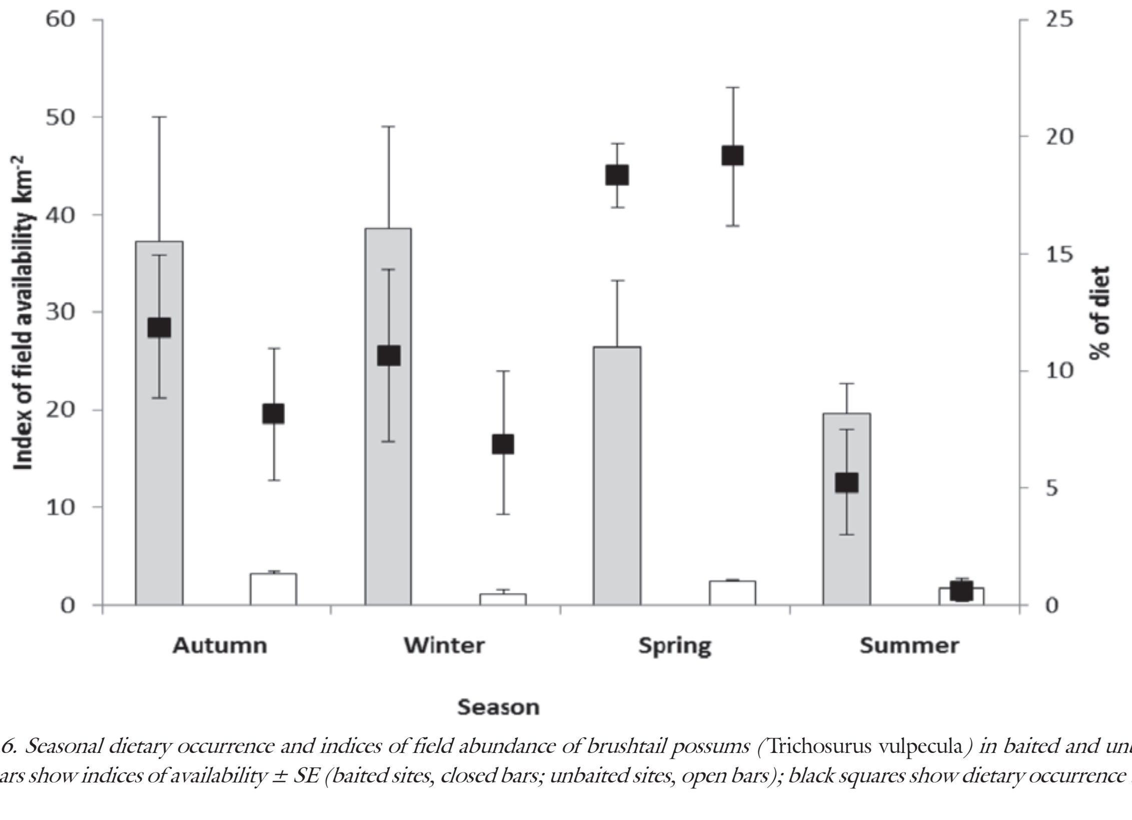

*Figure 6. Seasonal dietary occurrence and indices of field abundance of brushtail possums (*Trichosurus vulpecula*) in baited and unbaited sites. Bars show indices of availability ± SE (baited sites, closed bars; unbaited sites, open bars); black squares show dietary occurrence ± SE.*

but the results of that study are equivocal because they had no unbaited control sites.

Foxes consumed very few threatened mammals or other small vertebrates. Numbats, chuditch, red-tailed phascogales, bilbies and quenda were not detected in scats, and birds and reptiles were of little dietary importance. Virtually no woylie remains were observed and only one scat containing any woylie material was collected. Woylies were not consumed in proportion to their field availability and this observation may be explained if they eluded predators and used *Gastrolobium* thickets as predation refuges (Christensen 1980; Kinnear et al. 2002). It may

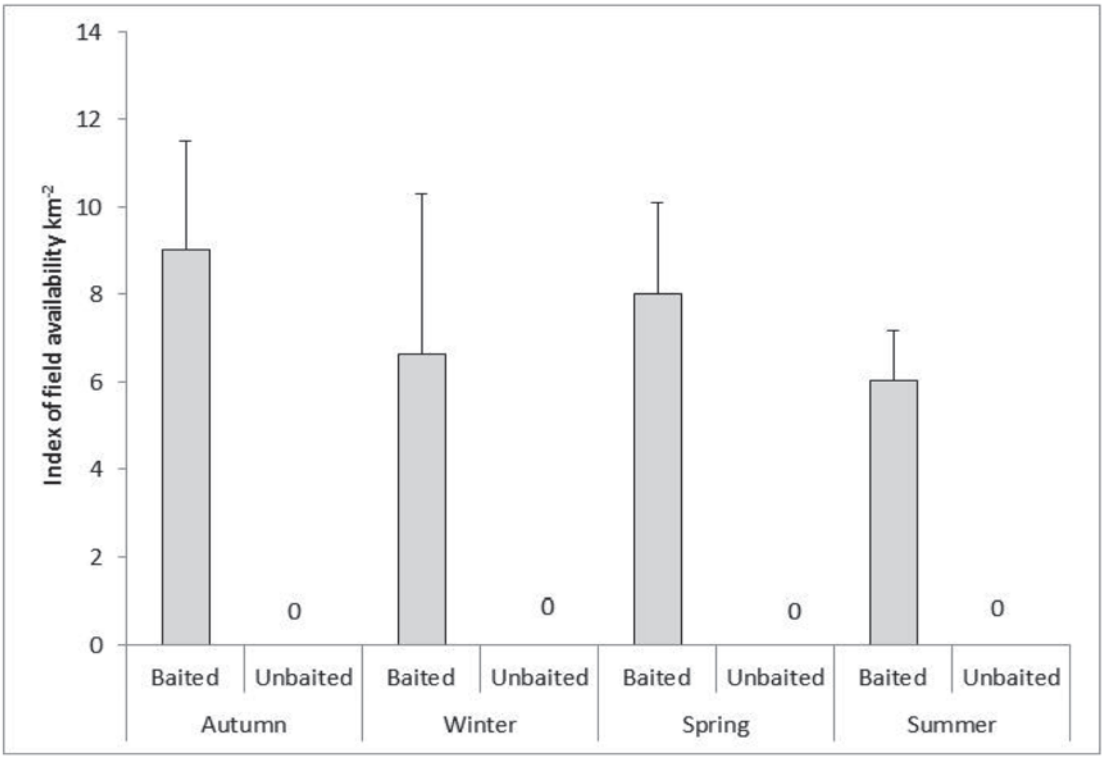

*Figure 7. Seasonal field abundance (± SE) of woylies (*Bettongia penicillata*) in baited sites. (No woylies were present in unbaited sites.)*

also be explained if the indices of field abundance were overestimates of the actual population density or if more predation occurred than was detected from scats. During a concurrent study (Marlow et al. 2015a), 21% of radio collared woylies (N = 20) were killed by foxes. However, of these, 11 were not consumed by foxes and virtually the complete carcass was recovered. The analysis of the contents of fox scats may not therefore be a useful method of detecting prey preferences for rare species, or their presence in a site, despite its use being advocated by Brunner et al. (1976).

There was no significant seasonal variation in the diet of foxes in baited areas and therefore there is little evidence that fox baiting needs to be intensified at any specific time when endemic fauna may be more vulnerable to predation. The current fox-baiting regime in DW and TNR appears to be maintaining foxes at lower densities than in the unbaited sites and so no alteration to the baiting regime is required at present (Marlow et al. 2015b).

A high correlation between the consumption of rabbits and indices of their field availability was observed and suggests a strong prey preference for this species. A similar high incidence of rabbits in the diets of foxes in conservation areas where endemic species also occur has been observed in other studies. Seebeck (1978) observed a high occurrence of rabbits but an extremely low incidence of the long-nosed potoroo (*Potorous tridactylus*) and other native fauna remains in fox scats collected in the Ralph Illidge Sanctuary east of Warnambool, Victoria. Similarly, Lunney et al. (1990) found rabbits were a major component of the diet of foxes in a state forest and in national park areas near Bega, New South Wales, but that long-nosed potoroos, long-nosed bandicoots (*Perameles nasuta*) and brush-tail and ringtail possums (*Pseudocheirus peregrinus*) were rarely detected in fox scats.

The impact of fox predation on rabbits and endemic fauna has been theoretically modelled by Pech et al. (1992, 1995), Pech and Hood (1998) and Sinclair et al. (1998). Their models include two forms of the functional response which correspond to the differing susceptibilities of prey to fox predation at low prey densities. A Type II functional response occurs when a primary prey species such as rabbits is vulnerable to fox predation at all densities and has no refuge at low densities. In contrast, a Type III functional response is an S shaped curve which occurs when the foxes' main prey species is able to avoid predation at low densities but predation increases with density above a certain threshold (Sinclair et al. 1998; Pech & Hood 1998). Although a strong dietary preference for rabbits by foxes was observed in this study, insufficient data were collected to enable a differentiation between the presence of a Type II or a Type III functional response between foxes and rabbits. However, previous modelling of the interactions between foxes and rabbits has suggested a Type III functional response is most likely (Sinclair et al. 1998). A sub-set of these theoretical predator-prey models specifically investigates the impacts of foxes on endemic species when rabbits are the primary prey of foxes and these are reduced in density (Sinclair et al. 1998). These models predict that when a rabbit population crashes and foxes are suddenly short of food, they can inflict considerable predation pressure on endemic species and drive them to extinction (Sinclair et al. 1998). This phenomenon is termed hyperpredation (Smith & Quin 1996) and this, in conjunction with surplus killing (Short et al. 2002), may have been resulted in faunal declines in Australia.

Sinclair et al. (1998) discuss several management actions which may be undertaken to transform the functional response of foxes and rabbits so that at low densities vulnerable prey species such as woylies are not driven to extinction. These management options could be implemented in conservation estate in Western Australia and elsewhere to minimise the risks to threatened fauna from the presence of rabbits and a sudden decrease in their density. Sinclair et al. (1998) recommend undertaking habitat manipulation so that vulnerable species have more refuges from predators. The importance of suitable habitat structure in reducing the risk of fox predation to various prey species has been observed in several other studies (Stokes et al. 2004; Pickett et al. 2005; Strauß et al. 2008) and, as stated above, the presence of *Gastrolobium* thickets maybe one of the factors explaining the continued presence of woylies in DW and TNR (Christensen 1980; Kinnear et al. 2002). Burrows et al. (1987) recognised that *Gastrolobium* thickets in DW had become sparse due to senescence caused by prolonged fire suppression, and recommended the strategic burning of patches of vegetation infrequently every 20–60 years to maximise biodiversity outcomes. These goals are reflected in the current Dryandra Woodland Management Plan (Department of Environment and Conservation 2011), which attempts to increase thicket development to maximise habitat availability for fauna.

Sinclair et al. (1998) also suggest removing rabbits from the habitat of threatened species, such as the woylie, as they theorise this will reduce fox density and thus reduce predation on these species at low densities. Fox densities may decline rapidly when rabbits decline (Read & Bowen 2001; Holden & Mutze 2002) but a protracted lag phase may occur if foxes preferentially prey on rabbits despite their densities being reduced (Saunders et al. 2004). However, fox density may not always decrease even if rabbits are effectively removed (e.g. Edwards et al. 2002) due to the presence of other food items that may sustain the fox population. In some areas of conservation estate where rabbit densities are naturally low or have been reduced the main components of the foxes' diet are small- to medium-sized mammals (Triggs et al. 1984; Glen et al. 2006).

The final management option recommended by Sinclair et al. (1998) is the reduction of predator densities. Sinclair et al. (1998) recognised the effectiveness of fox baiting in the conservation of woylies and other vulnerable prey species and recommended removing predators to alter the dynamics between predators and prey and to thus increase the survival of threatened endemic species. The removal of foxes at DW and TNR appears to be occurring adequately under the current baiting regime, because fox densities are significantly lower in baited sites than in unbaited sites (Marlow et al. 2015b). However, feral cats were observed to be the main predator of woylies in DW and TNR and accounted for 65% of woylie mortalities (Marlow et al. 2015a). Feral cat control methods need to be integrated with current fox baiting programs so that effective and efficient control of both introduced predators is achieved (Moseby et al. 2009; Berry et al. 2012). If predation by introduced predators can be reduced through the removal of rabbits, by direct control and through habitat augmentation by fire, woylies and other endemic threatened species in fragmented Wheatbelt sites and elsewhere may recover to their earlier abundances.

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