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Diet analysis of mammals, raptors and reptiles in a complex predator assemblage in the Blue Mountains, eastern Australia

Jack H. Pascoe[A], *Robert C. Mulley*[A,D], *Ricky Spencer*[A] *and Rosalie Chapple*[B,C]

[A]School of Science and Health, University of Western Sydney, Penrith, NSW 2751, Australia.
[B]Blue Mountains World Heritage Institute, Katoomba, NSW 2780, Australia.
[C]University of New South Wales, Kensington, NSW 2052, Australia.
[D]Corresponding author. Email: r.mulley@uws.edu.au

Abstract. South-east Australia has a complex predator assemblage which has historically been vulnerable to introduced species. This is the first Australian field study to analyse samples from members of the families Canidae, Dasyuridae, Strigidae, and Varanidae to describe the diet and diet overlap between these predators. Samples were collected opportunistically and hair and bone analysis was used to identify the content of samples. Wild dogs (*Canis lupus*) and lace monitors (*Varanus varius*) predominantly consumed large mammalian prey, which contributed to the high level of diet overlap ($O_{jk} = 0.79$) between these two species. Foxes (*Vulpes vulpes*) and spotted-tailed quolls (*Dasyurus maculatus*) also had a high level of diet overlap ($O_{jk} = 0.76$), a result of their diets containing a high proportion of medium-sized mammals. The diet of wild dogs and foxes showed moderate overlap ($O_{jk} = 0.59$), and foxes were more likely to prey on species within the critical weight range than on macropods, which made up a high proportion of the diet of wild dogs. These data confirm that significant diet overlap can occur between predators from different taxonomic classes and further investigation of potential competition will be important to ongoing management.

Additional keywords: apex predator, competition, diet analysis, mesopredator release, niche overlap.

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Introduction

The degree of niche overlap can be used as a method for predicting potential competition between species in a resource-limited system (e.g. Pianka 1974). Niche theory suggests that the greater the similarity in the niche of two species the greater the likelihood for exploitative competition. Diet niche overlap between two or more species has been used to identify potential exploitative competition for resources in numerous dietary studies (Kauhala *et al*. 1998; Fedriani *et al*. 1999; Lanszki *et al*. 1999; Ray and Sunquist 2001; Andheria *et al*. 2007; Prigioni *et al*. 2008).

In Australia many studies have measured diet overlap between two or more eutherian predators (e.g. Mitchell and Banks 2005; Glen *et al*. 2006), and between eutherian and marsupial predators (e.g. Glen and Dickman 2008). Recently, a comprehensive study by Glen *et al*. (2011) investigated diet and potential for competition between the full suite of mammalian predators – wild dog (*Canis lupus* ssp.), red fox (*Vulpes vulpes*), feral cat (*Felis catus*) and the endangered spotted-tailed quoll (*Dasyurus maculatus*) – in the Barrington Tops, eastern New South Wales.

Several field studies have described the diet of species from two classes and a number have included meta-analyses of three taxonomic classes (e.g. Bilney *et al*. 2006, 2011; Davey *et al*. 2006; Sutherland *et al*. 2011). However, despite the plethora of published Australian diet-overlap studies there are none, apart from meta-analyses, that describe the potential for food competition between predators from three taxonomic classes. Such studies have been conducted internationally (e.g. Jaksić *et al*. 1981, 1993) and these provide valuable insight into the guild structure of complex predator assemblages and would therefore be a valuable contribution to understanding a suite of interactions between Australian predators if these data were collected.

Diet studies can also provide other information apart from niche overlap. Intraguild predation from top predators can impact on populations of subordinate predators (Berger and Gese 2007). Prey populations are also affected by predation from predators. In Australia, critical weight range (CWR) mammals (mammals weighing between 35 g and 5.5 kg), have been identified as a group that has historically been at increased risk of becoming extinct due to a range of factors including predation from introduced predators (Burbidge and McKenzie 1989; McKenzie *et al*. 2007).

The predator assemblage of the Greater Blue Mountains World Heritage Area (GBMWHA), south-eastern Australia, is complex and made up of mammalian (both eutherian and marsupial), avian and reptilian species. It is therefore an ideal study system in which to examine potential interactions between predators competing for shared food resources. This study describes the diet, and potential for diet competition, of a suite of predatory species occurring sympatrically in the GBMWHA. This research represents the first field study to investigate diet overlap between sympatric predators from all three of these taxonomic classes in Australia. The species under investigation include the introduced red fox, the endangered spotted-tailed quoll, the regionally vulnerable powerful owl (*Ninox strenua*), the lace monitor (*Varanus varius*) and the wild dog.

Materials and methods

Study system

The study was conducted within the GBMWHA, located west of Sydney (32°22′00′–34°23′00″S, 149°54′00″–151°07′00″E). This World Heritage Area is made up of over one million hectares of contiguous conservation reserves primarily managed by the New South Wales Office of Environment and Heritage for the protection of its internationally listed World Heritage values. Elevation of the GBMWHA ranges from near sea level to ~1300 m. Rainfall in the GBMWHA is variable but averages ~1000 mm per annum; diurnal temperature is also variable and dependent upon elevation; ranging from 0 to 16°C in cooler months and 10 to 29°C in warmer months. There is a diverse range of vegetation types in the GBMWHA, primarily dominated by wet and dry sclerophyll forests (the GBMWHA is home to 14% of the worlds eucalypts). Common canopy species are *Eucalyptus punctata*, *Corymbia maculata*, *E. agglomerata*, *C. eximia*, *Angophora costata* and *A. floribunda*. Macropods, including eastern grey kangaroos (*Macropus giganteus*), swamp wallabies (*Wallabia bicolor*), red-necked wallabies (*Macropus rufogriseus*) and wallaroos (*Macropus robustus*) are common prey species in the study system, as are other large mammals such as the common wombat (*Vombatus ursinus*). A range of small and medium-sized native mammals, including brush-tailed possums (*Trichosurus vulpecula*), bush rats (*Rattus fuscipes*) and yellow-bellied gliders (*Petaurus australis*), were also abundant. Exotic prey, such as European rabbits (*Oryctolagus cuniculus*) and domestic mice (*Mus musculus*), were similarly common. Patches of former pastoral farmland occur within the GBMWHA and these habitats support high densities of native and exotic grazing species.

Sample collection and content analysis

The study was conducted during 2008–11 and dietary samples, including scats and regurgitations were collected opportunistically along vehicle access trails and at sites of known predator activity such as latrines and roosts. Three isolated transects, 15 km long, located on vehicle access trails within the study system, were sampled seasonally. The entire length of the transects were walked each sampling period and more targeted searches off vehicle access trails in specific habitat were also carried out, but sampling effort was limited to one day per sampling period. Samples were matched to a predator using several indicators such as scent, diameter and shape as described by Triggs (1996). If a sample was found at a known roost or latrine of a predator, it was presumed to belong to that species. The presence of grooming hairs was also used as an identification tool. Fewer than 10 predator hairs in a sample was considered to be evidence of grooming, but more than this number was thought to indicate that the predator had eaten that prey item (G. Story, unpubl. data, 2009). Samples were broken apart to separate the sample into their components for examination.

Diet analysis

Sample components were identified using hair, bone, feather or other identifiable structures. Hair analysis was conducted using the method described by Brunner and Coman (1974). Where possible, prey species were identified to species, otherwise identification of taxa was taken as close to species level as possible. Sample size was plotted against the cumulative species richness of food items in diet samples from each predator to determine whether the curve reached asymptote, and was therefore adequate to describe the diet of each predator.

The frequency of occurrence of macropods, arboreal or semiarboreal mammals and CWR mammals (Burbidge and McKenzie 1989) in the samples of each predator were calculated to identify broad prey types.

All diet items were sorted into the following seven food categories: large mammal (7 kg or more), medium mammal (500–6999 g), small mammal (1–499 g), arthropod, bird, reptile and vegetation. These categories were chosen to allow data comparisons with diet studies previously conducted in Australia (Glen *et al*. 2006; Glen and Dickman 2008). To compare dietary preference between predators, a matrix of similarity between species was developed using a Bray–Curtis index based on the frequency of occurrence of each food category in each predator's diet. Data were square-root-transformed and standardised, gross differences in diet categories between each predator's diet were compared by using ANOSIM (analysis of similarity), and SIMPER (similarity percentage) to determine which food categories were contributing most to the similarity between diets (Clarke and Warwick 1994; Mitchell and Banks 2005; Glen and Dickman 2008). These tests were performed using Primer ver. 5.

Levin's standardised formula was calculated to measure niche breadth using frequency occurrence of prey taxa found in all samples collected for each predator (Hurlbert 1978; Krebs 1999; Lanszki *et al*. 1999):

$$B_A = \frac{\left(\frac{1}{\Sigma(pi^2)} - 1\right)}{n - 1}$$

where pi = frequency occurrence of each prey item in the predator's diet and n = no. of food items in the diet of predators of this study. B_A is standardised to a scale of zero (low niche breadth) to 1.0 (maximum niche breadth).

Diet overlap (O_{jk}) was calculated for each pair of predators using Pianka's index (Pianka 1973; Krebs 1999):

$$O_{jk} = \frac{\left(\sum_i^n p_{ij}p_{ik}\right)}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where p_{ij} = the frequency of occurrence of prey taxon i in predator j's diet and P_{ik} = the frequency of occurrence of prey taxon *i* in predator *k*'s diet. Using this index, three categories of diet overlap can be arbitrarily distinguished as low (O_{jk} = 0–0.33), medium (O_{jk} = 0.34–0.66) and high (O_{jk} = 0.67–1.0). Similar arbitrary niche overlap values have been used in a diet study undertaken by Jaksić *et al*. (1981).

In all analysis of diet in this study, frequency of occurrence has been used as opposed to, or in conjunction with, volumetric analysis. A recent paper by Klare et al. (2011) reported that frequency of occurrence analysis alone is not as powerful as analyses that include volumetric analysis, however this review paper was published after the data for the current study were collected and therefore volumetric analysis was not possible.

Results

In total, 798 predator scats, pellets and regurgitations were collected and analysed over the 24 months of data collection (Appendix 1). In total, 451, 243 and 36 wild dog, fox and lace monitor scats were collected respectively; of these, most were located along the three sampling transects. Spotted-tailed quoll samples (n = 40) were located within two areas of ideal habitat, which were located more than 5 km from one another. Powerful owl samples were located at four separate roost sites, and these were located at a distance apart likely to include the hunting range of two or three pairs of powerful owl. Cumulative species richness of food categories reached asymptote in the diet of wild dogs and foxes ($n \approx 230$ and 160 respectively), so sample sizes were regarded as adequate (Fig. 1). This was also true for spotted-tailed quolls, lace monitors and powerful owls ($n \approx$ 13, 18 and 5 respectively) although the sample sizes were comparatively smaller (Fig. 2). In total, 51 food items were detected in dietary samples. The greatest diversity occurred in mammals, with 33 food items indentified. Mammal remains were also the most commonly occurring prey type, however birds, arthropods, reptiles and vegetation were also present in predator diets (Appendix 1). Macropods occurred in 68% and 58% of wild dog and lace monitor samples respectively. Both of these species consumed CWR mammals relatively infrequently (<12%) when compared with foxes (46%). Arboreal prey was indentified in 100% of powerful owl samples, in 27% of spotted tailed quoll samples and 18% of fox samples.

There were apparent differences in the composition of diet categories for wild dog, fox, spotted-tailed quoll, lace monitor and powerful owl (Fig. 3). On the basis of Bray–Curtis similarity indices, these differences were found to be significant (Global r = 0.383, P = 0.01). Only the comparison of occurrence of prey categories between fox and spotted tailed quoll diet showed no significant difference (P = 0.14) (Fig. 3).

Comparing the diet of wild dogs with those of all other predators in the study, large mammals contributed a major proportion of dissimilarity (>30%) (Table 1). Powerful owls preyed upon medium mammals frequently, and this explained at least 29% of dissimilarity between the diet of powerful owls and those of other predators (Table 1). Large mammals contributed significantly (>23%) to the dissimilarity between the diets of foxes and lace monitors, and spotted-tailed quolls and lace monitors (Table 1).

Intraguild predation was apparent in the apex predatory guild. Wild dogs consumed both foxes and cats, and foxes consumed feral cats (Appendix 1), although this may have been the result of scavenging. Wild dogs were also found to be cannibalistic (Appendix 1). However, intraguild predation rates were below 1% in all cases, and this could be the result of infanticide, predation or scavenging.

Wild dogs and foxes consumed a similar number of species, with 31 food items common to both. Foxes, however, had a broader dietary niche (Table 2). Wild dogs, spotted-tailed quolls and lace monitors had similar niche breadths, while the powerful owl, which consumed the least number of species, had the lowest niche breadth.

High dietary overlap occurred between foxes and spotted-tailed quolls, foxes and lace monitors and wild dogs and lace monitors (Table 2). Medium dietary overlap occurred between dogs and foxes, quolls and lace monitors, powerful owls and lace

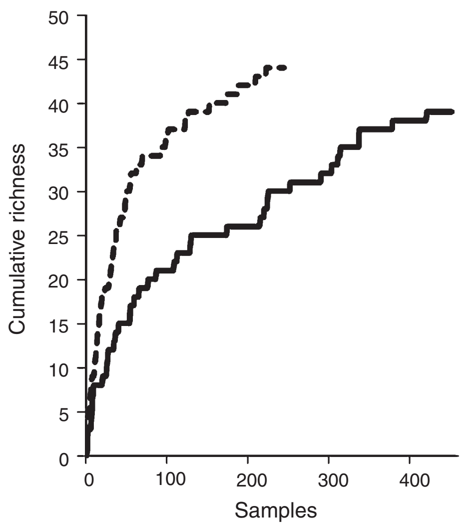

Fig. 1. Cumulative richness of species occurring in the diet of wild dogs (solid line) and foxes (dashed line).

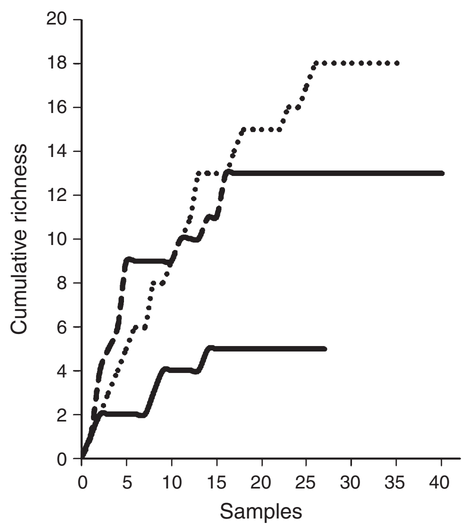

Fig. 2. Cumulative richness of species occurring in the diet of spotted-tailed quolls (dashed line), lace monitors (dotted line) and powerful owls (solid line).

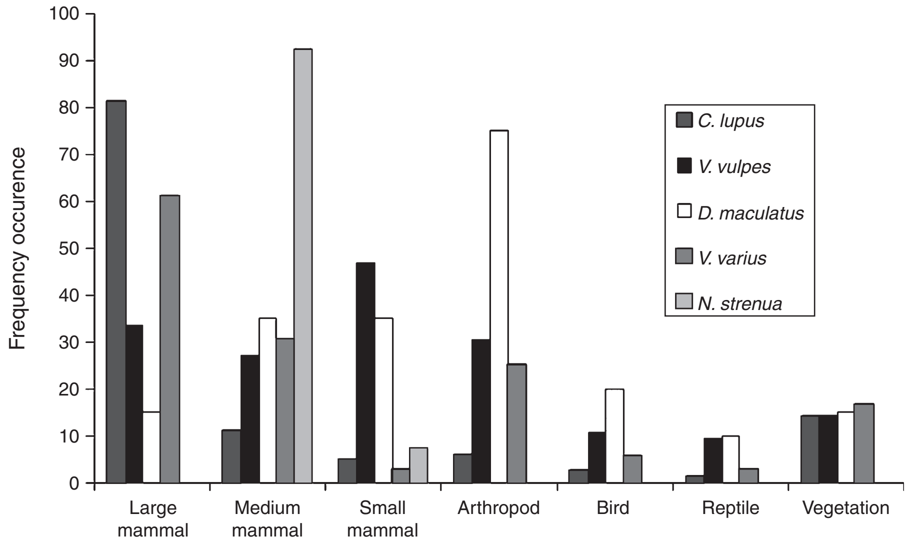

Fig. 3. Frequency of occurrence (%) of each diet category in wild dog (*C. lupus*), fox (*V. vulpes*), spotted-tailed quoll (*D. maculatus*), lace monitor (*V. varius*) and powerful owl (*N. strenua*) diets.

Table 1. Percentage contribution of dissimilarity of prey category occurrence in pairwise comparisons between predator diets
Comparisons of wild dog (D), fox (F), lace monitor (L), spotted-tailed quoll (Q) and powerful owl (P) diet based on Bray–Curtis indices (SIMPER). Values are provided only for parameters that contribute to the top 90% of dissimilarity

Prey category	Dissimilarity (% contribution)									
	D *v*. F	D *v*. Q	D *v*. L	D *v*. P	F *v*. Q	F *v*. L	F *v*. P	Q *v*. L	Q *v*. P	L *v*. P
Large mammal	30.2	29.7	31.4	41.1	16.6	24.5	17.4	23.8	9.4	33.9
Medium mammal	15.5	17.8	24.8	41.9	19.7	18.8	35.0	19.8	29.3	38.3
Small mammal	22.0	12.5			22.1	20.5	22.4	12.8	16.5	5.8
Arthropod	12.4	22.8	14.3			14.7	11.2	22.9	29.3	9.5
Bird			6.1		8.5	6.5		7.7	6.8	
Reptile										
Vegetation	10.6	8.1	16.7	5.8	8.6	10.8	6.2	9.4		8.2

Table 2. Niche breadth (B_A) of, and dietary overlap (O_{jk}) values between wild dogs (*C. lupus*), foxes (*V. vulpes*), spotted-tailed quolls (*D. maculatus*), lace monitors (*V. varius*) and powerful owls (*N. strenua*)

Species	B_A	*V. vulpes*	*D. maculatus*	*V. varius*	*N. strenua*
C. lupus	0.19	0.59	0.35	0.79	0.04
V. vulpes	0.37	–	0.76	0.63	0.11
D. maculatus	0.21	–	–	0.46	0.16
V. varius	0.24	–	–	–	0.38
N. strenua	0.05				

monitors, powerful owls and foxes, wild dogs and spotted-tailed quolls and powerful owls and spotted-tailed quolls. All other pairings showed low dietary overlap (Table 2).

Discussion

This study found lace monitors and wild dogs to have the highest level of dietary overlap. Wild dogs are predators of large mammals and where carcass remains are often left after a predation event, lace monitors are likely to supplement their diet with carrion from wild dog kills. This may explain the similarity in their diets. This is consistent with a previous study of lace monitors by Guarino (2001), who found carrion to be a dominant component of their diet. During the course of this study lace monitors were regularly observed feeding on the carrion remainder of wild dog kills (J. Pascoe, unpubl. data, 2009), further indicating carrion as an important component of lace monitor diet. Spotted-tailed quolls and foxes also had a high level of dietary overlap ($O_{jk} = 0.76$). Both species consumed high proportions of small and medium-sized mammals as well as arthropods. Spotted-tailed quolls and foxes also preyed upon similar proportions of arboreal prey. These data are consistent with the findings of Glen and Dickman (2008), who showed diet overlap between foxes and spotted-tailed quolls to be $O_{jk} = 0.712$. Diet overlap and consumption of similar diet categories and diet items between foxes and spotted-tailed quolls indicates potential for resource competition which has been reported previously (Glen and Dickman 2008; Glen *et al.* 2011). Large mammal was the only mammal prey category where foxes and spotted-tailed quolls differed significantly, due to foxes consuming more macropods than spotted-tailed quolls. Presumably, a proportion of the macropod consumption was carrion, as foxes were probably taking advantage of the abundance of carrion left from wild dog predation. This would also explain the moderate level of overlap between the diets of foxes and lace monitors. A meta-analysis by Sutherland *et al*. (2011) discussed the possibility that the removal of foxes and cats would be beneficial to varanids, however in this study both foxes and varanids were in abundance, possibly as a result of the availability of carrion. In this study foxes and wild dogs had a lower niche breadth than was observed by Mitchell and Banks (2005), who reported a niche breadth of $B_A = 0.39$ for foxes and $B_A = 0.30$ for wild dogs. Wild dogs and foxes share a similar number of diet items, however foxes prey more regularly on a broader range of these items. Wild dogs and foxes in this study displayed a medium level of diet overlap ($O_{jk} = 0.59$), a lower level than that reported by Mitchell and Banks (2005) ($O_{jk} = 0.91$). Wild dogs in this study focussed their predation on large mammals, generally macropods. While foxes also consumed macropods, in general they consumed more medium and small-sized mammals. A similar result was reported by Glen *et al*. (2006) with a diet overlap ($O_{jk} = 0.697$) between wild dogs and foxes. The diet overlap reported in this study adds to the literature which indicates a potential for resource competition between wild dogs and foxes. Foxes consumed more mammals within the CWR than did wild dogs, indicating that, of the two eutherian predators in this study, foxes are more likely to place predation pressure on vulnerable species.

The powerful owl was the only species investigated in this study not to show any high or medium levels of interspecific diet overlap. This is not surprising because the powerful owl is a specialist predator of arboreal mammals (Kavanagh 2002; Cooke *et al*. 2006). In this study all pellet samples were found to contain the remains of arboreal mammals, 93% of which were medium-sized possums and gliders. This result is similar to those reported in previous studies of the diet of the powerful owl (Kavanagh 2002; Bilney *et al*. 2006; Cooke *et al*. 2006).

This is the first field study to describe the diet of sympatric species across three taxonomic classes in Australia, and their potential for competition over food resources. It raises several concerns for the ongoing maintenance of Australian native fauna. First, foxes pose a threat to the threatened spotted-tailed quoll through their potential for resource competition. Foxes also prey frequently upon CWR species, which have historically been the most likely to become extinct. This study also adds to literature which suggests that wild dogs have positive ecosystem impacts, by potentially maintaining both competition and predation pressure on foxes.

The study highlights further research avenues to address uncertainty in relation to predator assemblage and niche overlap. Several additional predators known to occur within the study system, including feral cats, sooty owls (*Tyto tenebricosa*), masked owls (*Tyto novaehollandiae*), wedge-tailed eagles (*Aquila audax*), sea eagles (*Haliaeetus leucogaster*), brown falcons (*Falco berigora*), sand monitors (*Varanus gouldii*) and diamond pythons (*Morelia spilota*), were not adequately sampled to provide comparative data that would add to the complexity of the competition for resources that this study has described.

Future management regimes will need to consider the full suite of predatory species in any approach to predator management due to the wide range in intraguild and trophic effects these actions may have. For instance, wild dog suppression effects may lead to increased competition between native predators such as spotted-tailed quolls and increased predation on CWR mammals by exotic species such as foxes. Removal of wild dogs may also impact on varanid populations, by decreasing the availability of carrion and increasing predation pressure from foxes and cats on young monitors. Management actions that are likely to influence the predator assemblage must address likely intraguild effects and how top-down trophic processes will be altered in order to maintain and re-establish balanced ecosystems in south-eastern Australia.

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Appendix 1. Frequency of occurrence (%) of prey in wild dog, fox, spotted-tailed quoll, lace monitor and powerful owl diets

Prey item	Wild dog	Fox	Spotted-tailed quoll	Lace monitor	Powerful owl
Large mammal					
Vombatus ursinus, common wombat	11	2	0	6	0
Macropus robustus, common wallaroo	2	<1	0	0	0
Macropus rufogriseus, red-necked wallaby	5	4	0	0	0
Macropus giganteus, eastern grey kangaroo	10	2	0	14	0
Wallabia bicolor, swamp wallaby	29	18	10	22	0
Petrogale penicillata, brush-tailed rock wallaby	<1	1	0	0	0
Macropodidae, unidentified macropod	20	5	5	17	0
Sus scrofa, pig	<1	<1	0	0	0
Bos taurus, cattle	1	1	0	0	0
Canis lupus wild dog or dingo	<1	0	0	0	0
Medium mammal					
Tachyglossus aculeatus, short-beaked echidna	2	1	0	0	0
Trichosurus vulpecula, common brush-tailed possum	5	14	3	3	19
Trichosurus caninus, mountain brush-tailed possum	0	2	0	0	0
Pseudocheirus peregrinus, ring-tailed possum	<1	1	5	0	0
Petauroides volans, greater glider	0	<1	0	0	33
Petaurus australis, yellow-bellied glider	0	0	0	0	41
Petaurus spp., unidentified glider	0	<1	0	0	0
Oryctolagus cuniculus, rabbit	3	7	0	22	0
Lepus capensis, brown hare	0	<1	0	6	0
Felis catus, feral cat	<1	1	0	0	0
Vulpes vulpes, red fox	<1	0	0	0	0
Pteropus poliocephalus, grey-headed flying fox	<1	0	0	0	0
Pteropus spp., unidentified flying fox	<1	0	0	0	0
Small mammal					
Petaurus breviceps, sugar glider	<1	2	15	0	7
Phascogale tapoatafa, brush-tailed phascogale	0	<1	0	0	0
Mus musculus, domestic mouse	2	14	15	0	0
Antechinus swainsonii, dusky antechinus	0	1	0	0	0
Antechinus flavipes, yellow-footed antechinus	0	<1	0	0	0
Antechinus stuartii, brown antechinus	0[1]	1	0	0	0
Antechinus spp., unidentified antechinus	0[1]	1	0	0	0
Rattus rattus, black rat	0	5	0	0	0
Rattus norvegicus, brown rat	0	1	0	0	0
Rattus lutreolus, swamp rat	0	<1	0	0	0
Rattus fuscipes, bush rat	2	18	0	0	0
Rattus spp., unidentified rat	1	4	0	0	0
Cercartetus nanus, eastern pygmy possum	<1	0	0	0	0
Pseudomys novaehollandiae, New Holland mouse	0	<1	0	0	0
Sminthopsis murina, common dunnart	<1	0	0	0	0
Reptile					
Tiliqua scincoides scincoides, eastern blue-tongued lizard	<1	0	0	0	0
Agamidae, unidentified dragon	0	0	0	0	0
Scincidae, unidentified skink	<1	7	10	3	0
Serpentes, unidentified snake	<1	1	0	0	0
Reptilia, unidentified reptile	<1	1	0	0	0
Arthropod					
Coleoptra/Blattaria spp., unidentified beetle/cockroach	2	17	30	14	0
Othoptera spp., unidentified grasshopper/cricket	1	4	15	6	0
Insecta, unidentified insect	3	11	40	6	0
Bird					
Aves spp., unidentified bird	3	11	25	6	0
Vegetation					
Grass	9	7	15	6	0
Seed	<1	2	0	6	0
Unidentified	6	4	0	6	0
Other					
Crustacean	<1	0	0	0	0
Grooming hair	6	2	15	0	0