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Diets of mammalian carnivores in the deserts of north-eastern South Australia

Karl Vernes[a,*], Stephen M. Jackson[b,c,d,e], Todd F. Elliott[a], Max Tischler[f], Andrew Harper[f]

[a] Ecosystem Management, University of New England, Armidale, NSW, 2351, Australia
[b] Biosecurity NSW, NSW Department of Primary Industries, Orange, New South Wales, 2800, Australia
[c] School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, 2052, Australia
[d] Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC, 20013-7012, USA
[e] Australian Museum Research Institute, Australian Museum, 1 William St. Sydney, New South Wales, 2010, Australia
[f] Australian Desert Expeditions, 222A Barry Pde, Fortitude Valley, Queensland, 4006, Australia

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ABSTRACT

We studied diets of feral cats (*Felis catus*), dingoes (*Canis familiaris*) and red foxes (*Vulpes vulpes*) in desert environments in north-eastern South Australia by analysing prey remains in opportunistically-collected scats. Four major landscapes were sampled (Simpson Desert, Sturt Stony Desert, Strzelecki Desert – Cooper Creek and Diamantina River) which yielded 238 cat scats, 298 dingo scats and ten fox scats. There was some overlap in prey eaten by cats and dingoes, but their diets were significantly different because cats typically ate small prey such as small mammals, small lizards and birds, while dingoes ate larger prey like domestic cattle, kangaroos and large reptiles. The few fox scats collected suggested fox diets were more similar to cat than dingo diets. Scat composition also differed significantly between landscapes irrespective of predator, with landscapes differing both in diversity and relative abundances of prey consumed. We detected several species in scats that are threatened with extinction either nationally (dusky hopping mouse, *Notomys fuscus,* and crest-tailed mulgara, *Dasycercus cristicauda*) or regionally (desert mouse, *Pseudomys desertor*, and long-haired rat, *Rattus villosissimus*), adding valuable knowledge to the distribution of these mammals and demonstrating the value of predator scat analyses in mammal surveys of Australian deserts.

1. Introduction

Understanding the diets of predators provides insights into resource partitioning and competition (McDonald et al., 2018), and helps in understanding the impact predators have on community structure. This includes the role that predators have played in the decline and extinction of desert mammals (Dickman, 1996). An added benefit of studying diets of mammalian predators is the insights they provide into the distribution and relative abundance of a wide range of different prey species, including rare and threatened species (Allen et al., 2011; Claridge et al., 2010; Paltridge, 2002). Studies comparing the mammal remains occurring in carnivore scats with other forms of mammal survey typically show that carnivore scats perform favourably, often sampling a greater number of species than other methods (Brunner and Wallis, 1986; Friend, 1978), even when compared against modern survey techniques such as camera traps (Vernes et al., 2020).

Three generalist mammalian predators occur in Australian deserts. The dingo (*Canis familiaris*) is the largest of these and has enjoyed the longest occupation, having been introduced to Australia about 3500–4000 years ago (Balme et al., 2018; Dickman, 1996). More recently, two introduced predators have invaded Australia's arid interior, the feral cat (*Felis catus*) which was first recorded in central deserts in the 1880s (Abbott, 2002), and the red fox (*Vulpes vulpes*), which first colonised the region in the early 1900s (Fairfax, 2018). All three are now widespread and common mammals in Australia's arid zone (Dickman, 1996). Prior to the arrival of cats and foxes, the small predator guild was occupied by the western quoll (*Dasyurus geoffroi*) (Rowlands et al., 2020; Vernes et al., 2020) which is now extinct in central Australia. Previous studies of Australian deserts have indicated that dingoes typically take larger prey such as kangaroos, while cats and foxes prey on smaller mammals such as rodents, dasyurids, reptiles, birds and amphibians (Feit et al., 2019; Paltridge, 2002; Spencer et al., 2014, 2017). Cats and

* Corresponding author.
E-mail address: kvernes@une.edu.au (K. Vernes).

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foxes also prey upon medium-sized desert mammals (Cupples et al., 2011; Feit et al., 2019), but have either driven many of them to extinction, or greatly restricted their abundance and geographical range (Dickman, 1996; Morton, 1990; Short and Smith, 1994). Introduced species form a significant component of modern predator diets in Australia, and desert-dwelling dingoes will rely heavily on domestic cattle (*Bos taurus*) when they are present, while dingoes, cats and foxes all prey heavily on the introduced rabbit (*Oryctolagus cuniculus*) in places where it is common (Feit et al., 2019).

The deserts of north-eastern South Australia, within an area known as the Lake Eyre Basin, have not been particularly well surveyed for small mammals. Broadscale surveys of the region have been undertaken in the past (Brandle, 1998), and the small mammal community of some individual sites has been intensively studied (Lynch and Brandle, 2018), but generally this region has not received strong survey attention. Much remains to be understood of the structure and composition of mammal communities in the region, and there is a conservation need for a thorough understanding of the species of mammals that persist in these desert landscapes after 150 years of ecosystem change (Vernes et al., 2020). These changes are largely attributed to over browsing by introduced herbivores, and hyper-predation by introduced feral cats and red foxes (Morton, 1990; Morton et al., 2011) which has precipitated a sharp decline in small and medium-sized mammals (Burbidge and McKenzie, 1989; Morton, 1990). Despite these changes, some rare and threatened mammals still persist in parts of the Lake Eyre Basin of north-eastern South Australia (Vernes et al., 2020), and predator scat analysis offers a way to expand the knowledge of where these species may still occur.

Previous works on predators in the broader region have focused on sites in the north-eastern Simpson Desert of Queensland (Cupples et al., 2011; Spencer et al., 2014, 2017), the south-eastern Strzelecki Desert bordering South Australia and New South Wales (Cupples et al., 2011; Feit et al., 2019) and in arid South Australia to the south (Woinarski et al., 2018) and west (Allen and Leung, 2012) of the Lake Eyre Basin. The only detailed study of the diet of dingoes in the Lake Eyre Basin of South Australia and south-western Queensland was undertaken by Allen and Leung (2012), who found dingoes consumed a wide range of prey, but relied heavily on introduced rabbits and cattle. However, several rare, threatened or poorly sampled species were also detected by Allen and Leung (2012), including the dusky hopping mouse (*Notomys fuscus*), long-haired rat (*Rattus villosissimus*) and plains mouse (*Pseudomys australis*). The study demonstrated the strength and importance of the technique for obtaining records of animals that are hard to sample, and for which we possess an incomplete understanding of distribution (Allen et al., 2011; Allen and Leung, 2012).

We studied the diets of cats, foxes and dingoes in north-eastern South Australia by analysing prey remains in the scats of these predators. Sampling was opportunistic but broad in geographical extent, spanning three major deserts (Simpson Desert, Sturt Stony Desert and Strzelecki Desert) in the region and the riverine floodout country of three major river systems (Diamantina, Cooper and Eyre) that flow through the study area. For much of the region sampled, these were the first predator scats collected and analysed. Our results provide insights into the diet of predators in this desert region, the variability in consumption of prey between contrasting habitat types across the Lake Eyre Basin and the distribution and relative abundance of prey that were consumed.

2. Materials and methods

2.1. Study area

The study area spans three major deserts in the Lake Eyre Basin of north-eastern South Australia and south-western Queensland: the Simpson Desert, Sturt Stony Desert and Strzelecki Desert (Fig. 1). The Lake Eyre Basin is among the largest endorheic basins on earth, and three major river systems flow through the study area, with Cooper Creek draining directly into Lake Eyre, and the Diamantina and Eyre Creek forming the confluence of the Warburton River at Goyder Lagoon (Fig. 1). Occasionally these drainages create expanses of desert that are briefly flooded, and fill wetlands and swamps, most of which are ephemeral. However, the drainage along the Diamantina River and Cooper Creek in particular has some semi-permanent and permanent waterholes. Furthermore, the sinking of bores throughout the Lake Eyre Basin for watering livestock provides surface water across much of the region, with the exception of the majority of the Simpson Desert and eastern parts of the Strzelecki Desert.

The study area has a wide variety of habitat types (for a

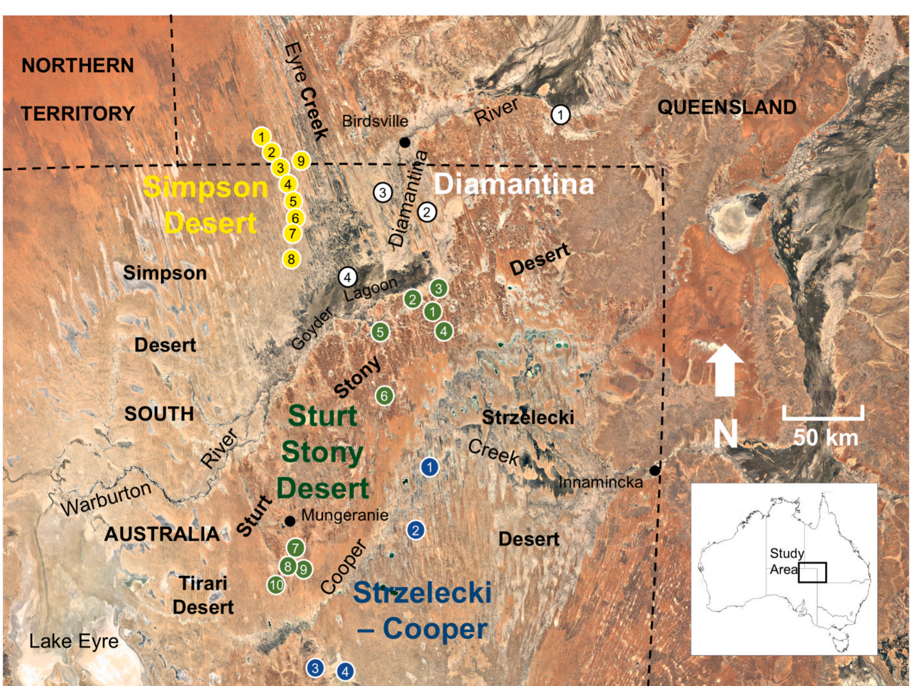

Fig. 1. Map of the study area in north-eastern South Australia, indicating major landscape where scats were collected. Collection localities within these landscapes are as follows: **Simpson Desert (yellow circles):** (1–7) represent each day of collecting during an 8-day walking trek in 2019, (8–9) collections made on two other separate walking treks in 2019; **Diamantina (white circles):** (1) Durrie, (2) Pandie Pandie, (3) Alton Downs, (4) Goyder Lagoon; **Sturt Stony Desert (green circles):** (1) Koonchera Dune, (2) Koonchera flats west, (3) Koonchera flats east (4) Singers Dam, (5) Damperannie Dam, (6) Kanowana Track, (7) Kuntha Hills, (8) Ooroowillanie, (9) Wutheroo Creek, (10) Mulka; **Strzelecki-Cooper (blue circles):** (1) Cooroomunchena, (2) Half-way Grid, (3) Etadunna (4) Lake Kopperekoppinna. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

comprehensive assessment see Brandle 1998). Sturt Stony Desert is comprised largely of stony gibber plains dominated by low open chenopod shrublands, while much of the remaining desert landscapes are dominated by parallel sand ridges ('dunes') and swales orientated approximately north-west and characterised by hummock grasslands of sandhill canegrass (*Zygochloa paradoxa*) and occasionally spinifex (*Triodia basedowii*), some low shrubs of *Grevillea stenobotrya* and wattle (*Acacia* spp.), and a wide variety of other dune species (Brandle, 1998). Open sandy plains support low shrublands dominated by nitre-bush (*Nitraria billardierei*), other herbaceous forbs (e.g. *Sclerolaena* spp. and *Gunniopsis* spp.) and saltbush (*Atriplex* spp.), while floodouts and swamps support low to medium chenopod shrublands dominated by oldman saltbush (*Atriplex nummularia*) and lignum (*Duma florulenta*) (Brandle, 1998). Rainfall in the study area declines from north , with an annual average rainfall of 165 mm at Birdsville and 132 mm at Mungeranie (data summarised from Australian Bureau of Meteorology).

2.2. Collection and analysis of samples

Predator scats were collected when encountered in the field, and stored in paper bags labelled with their GPS location and date of collection. We expect that scats can persist in dry desert environments for long periods; because it was not possible to determine the age of scats at the time of collection, interpretation of diet needs to consider that sampling may span a number of seasons and years. Furthermore, we could not determine how many individuals were sampled in any one location, and it is likely that on occasions, the same individual animal was sampled more than once. Any minor differences in the preference of individuals for particular prey should, however, be compensated for by the number of samples that were collected from any one location within the study region. Specific areas were targeted for collection (Fig. 1) in order to gather samples from a wide geographical area and from a variety of habitat types, but any scat encountered within the study area while undertaking field work was also collected. Fig. 1 provides a broad overview of the main collection localities grouped into four major regions: (1) Simpson Desert, (2) Sturt Stony Desert, (3) floodout country of the Diamantina River including the expansive ephemeral wetlands of Goyders Lagoon and (4) Strzelecki Desert and adjacent floodout country along Cooper Creek. For a full list of samples including their precise collection locality and dietary contents, see Supplementary Material. All scat samples were oven-dried at 100 °C for at least 10 h and sent to a professional analyst (Georgeanna Story of 'Scats About') who identified both the predator and the scat's prey contents. Predator species (cat, fox or dingo) was identified from the size and shape of the scat (Triggs, 1996), characteristic odour, the presence of grooming hairs and the pattern of prey contents, most notably fragment size and hair damage. Identification of prey remains relied on macroscopic and microscopic characteristics of hair, scale, feather, bone and exoskeletal remains within each scat. Mammal remains were identified to species where possible, or to genus when species could not be resolved. Non-mammalian prey items were categorised to a higher taxonomic level in most cases. Birds could be resolved only to 'Class Aves' (from feather and bone remains) with the exception of the emu (*Dromaius novaehollandiae*) which could be resolved to species because its feather and bone remains are easily distinguished from other birds in the study area. Frogs were resolved only to 'Order Anura', and snakes to 'Order Serpentes', however reptiles could be distinguished to family level in most cases on account of scale morphology, and the morphology of other undigested remains such as claws. One large common agamid, the central bearded dragon (*Pogona vitticeps*), was a common prey item that could be distinguished to species because of the size and morphology of its undigested remains which distinguish it from other reptiles. All other dragon species we classified only as 'Family Agamidae'. Insects were classified to class or order, while vegetation in the diet was simply noted as 'Vegetation'.

We calculated simple measures of dietary overlap between cats and dingoes using Pianka's index of dietary overlap, calculated using default settings within the package EcoSimR (Gotelli et al., 2015) within R (R Core Team, 2020). Scats from cats and dingoes were also grouped according to collections from localities within the four major landscapes (Simpson Desert, Sturt Stony Desert, Strzelecki Desert – Cooper Creek and Diamantina River and surrounding floodout country; Fig. 1) to further examine dietary differences between predators and landscapes. We constructed a matrix of percentage occurrences of prey in each group of scats of prey type x collection locality for each predator (cat or dingo) for each of the 40 prey types that were identified in predator scats. We constructed a second matrix of percentage occurrences of prey grouped by prey size classes (dasyurids, rodents, macropods, carnivores, rabbits, artiodactyls, birds, small reptiles, large reptiles and insects). We then applied non-metric multidimensional scaling (NMDS) to visualise and interpret these data. The NMDS was calculated using the function 'metaMDS' in the package vegan (Oksanen et al., 2019) within R (R Core Team, 2020) using the Bray-Curtis dissimilarity matrix with weighted averages and a maximum number of 50 random starts. The function 'envfit' was then used to fit predator species and landscape factors to the ordination using 10000 permutations, which revealed statistical significance of clusters coded by predator or landscape. Data were plotted using the function 'ordellipse' that created ellipses encompassing the standard deviation of points coded by predator type or landscape cluster, and 'ordspider' that overlaid a 'spider' diagram connecting each point to its group centroid (Oksanen et al., 2019).

3. Results

3.1. Diets of cats, foxes and dingoes

We collected 238 cat scats and 298 dingo scats from across the study area between June 2018 and August 2019 (Tables 1 and 2). More than half of all cat scats were collected from the Simpson Desert (135 scats, 57%; Table 1), and more than two thirds of all dingo scats were collected from Sturt Stony Desert (204 scats, 68%; Table 2). We also collected 10 scats from red foxes (8 from Sturt Stony Desert, 1 from Strzelecki Desert and 1 from Diamantina).

There was moderate overlap in cat and dingo diets both in terms of taxon consumed (Pianka's index of dietary overlap = 0.55), and in size class of prey (Pianka's index of dietary overlap = 0.63). The diets of these two predators were not significantly different from one another when all 40 prey species were considered in the model ($r^2 = 0.04$; $p = 0.10$; Fig. 2a). However, when the analyses were re-run using prey size classes, cat and dingo diets were significantly different from each other ($r^2 = 0.15$; $p < 0.0001$; Fig. 2b).

Cats typically ate small prey, with rodents being the most common food class, followed by insects, small lizards, rabbits, large lizards, birds and small dasyurid marsupials (Fig. 3). Of the rodents, the sandy inland mouse (*Pseudomys hermannsburgensis*) and long-haired rat were the most commonly consumed prey by cats, especially in the Simpson Desert (Table 1). Skinks were the common type of small lizard consumed by cats, and the central bearded dragon was the common large lizard consumed (Table 1). Rabbits were important prey of cats, occurring in 20% of scats (Table 1). Beetles and grasshoppers dominated the insect component of cat diet (Table 1). Overall, thirteen native and three introduced mammal species were detected in cat scats, in addition to birds and a range of reptile, amphibian and insect prey (Table 1).

Dingoes typically ate larger prey than cats, with cattle being the dominant prey item, followed by rabbits, large lizards, rodents and birds (Fig. 3). Other large prey species appeared in dingo scats more frequently than in cat scats, such as both species of large kangaroo (red kangaroo, *Osphranter rufus*, and euro, *O. robustus erebescens*), Arabian camel (*Camelus dromedarius*), emu, larger lizards such as goannas, and snakes (Table 2). Most of the reptiles could not be described beyond family level, however, the remains of some of the snakes eaten by dingoes indicated they were very large animals. Cattle were particularly

Table 1
Percentage occurrence of prey species detected in feral cat (*Felis catus*) scats collected from four desert regions in north-eastern South Australia.

Prey Species	Simpson Desert	Strzelecki Desert – Cooper Ck	Sturt Stony Desert	Diamantina River floodout	% Occurrence in all scats
	N = 135	*N* = 29	*N* = 43	*N* = 31	*N* = 238
MAMMALS	**86.7**	**100.0**	**79.1**	**77.4**	**85.7**
Dasyuromorphia	7.4	6.9	7.0	16.1	**8.4**
Kultarr, *Antechinomys laniger*	0.7	–	–	–	0.4
Fat-tailed Dunnart, *Sminthopsis crassicaudata*	–	3.4	–	16.1	2.5
Stripe-faced Dunnart, *Sminthopsis macroura*	3.0	–	7.0	–	2.9
Dunnart (unspecified), *Sminthopsis* sp.	1.5	–	–	–	0.8
Planigale (unspecified), *Planigale* sp.	–	3.4	–	–	0.4
Crest-tailed Mulgara, *Dasycercus cristicauda*	1.5	–	–	–	0.8
Dasyurid (unspecified)	0.7	–	–	–	0.4
Diprotodontia	**0.7**	**–**	**2.3**	**3.2**	**1.3**
Red Kangaroo, *Osphranter rufus*	–	–	2.3	–	0.8
Euro, *Osphranter robustus erebescens*	0.7	–	–	–	0.4
Rodentia	**74.1**	**34.5**	**51.2**	**54.8**	**62.2**
Desert Short-tailed Mouse, *Leggadina forresti*	–	–	4.7	3.2	1.3
Dusky Hopping Mouse, *Notomys fuscus*	3.0	–	4.7	–	2.5
Hopping mouse (unspecified), *Notomys* sp.	0.7	3.4	–	3.2	1.3
Desert Mouse, *Pseudomys desertor*	8.9	–	–	3.2	5.5
Sandy Inland Mouse, *Pseudomys hermannsburgensis*	40.7	6.9	–	3.2	24.4
Long-haired Rat, *Rattus villosissimus*	31.1	6.9	37.2	38.7	30.3
House Mouse, *Mus musculus*	2.2	20.7	4.7	6.5	5.5
Chiroptera	**–**	**–**	**–**	**3.2**	**0.4**
Insectivorous bat (unspecified)	–	–	–	3.2	0.4
Lagomorpha	**8.1**	**72.4**	**23.3**	**6.5**	**18.5**
European Rabbit, *Oryctolagus cuniculus*	8.1	72.4	23.3	6.5	18.5
Artiodactyla	**0.7**	**3.4**	**4.7**	**0.0**	**1.7**
Domestic Cattle, *Bos taurus*	–	3.4	4.7	–	1.3
Carnivora	–	–	–	3.2	0.4
Dingo, *Canis familiaris*	–	–	–	3.2	0.4
BIRDS, REPTILES, AMPHIBIANS	**51.1**	**34.5**	**51.2**	**48.4**	**48.7**
Birds (Class Aves)	9.6	17.2	16.3	29.0	14.3
Skinks (Family Scincidae)	25.9	20.7	9.3	16.1	21.0
Central Bearded Dragon, *Pogona vitticeps*	14.1	6.9	18.6	6.5	13.0
Other Dragons (Family Agamidae)	8.9	3.4	2.3	–	5.9
Goannas (Family Varanidae)	11.1	3.4	4.7	3.2	8.0
Geckoes (Family Gekkonidae)	–	–	–	3.2	0.4
Snakes (Order Serpentes)	3.7	–	–	–	2.1
Frogs (Order Anura)	–	–	2.3	3.2	0.8
INVERTEBRATES	**37.8**	**13.8**	**16.3**	**19.4**	**28.6**
Grasshoppers (Order Orthoptera)	17.8	3.4	2.3	3.2	11.3
Beetles (Order Coleoptera)	21.5	6.9	11.6	16.1	17.2
Scorpions (Order Scorpiones)	3.7	–	–	–	2.1
Centipedes (Class Chilipoda)	5.2	3.4	2.3	3.2	4.2
Butterfly and Moth larvae (Order Lepidoptera)	1.5	0.0	0.0	0.0	0.8
VEGETATION	**3.0**	**–**	**–**	**–**	**1.7**

important food of dingoes in the Sturt Stony Desert (Table 2). Dingoes also consumed other dingoes, cats and foxes in small proportions (Table 2). Overall, 11 native and six introduced mammal species were detected in dingo scats, in addition to birds (including emu) and a range of reptile and insect prey (Table 2).

We were only able to collect ten red fox scats from across the study area. A single fox scat collected in the Diamantina floodout landscape contained the remains of the long-haired rat. Additionally, a single fox scat collected in the Strzelecki-Cooper landscape contained the remains of a goanna (*Varanus* sp.), a blind snake (*Anilios* sp.) and beetles. Eight fox scats from Sturt Stony Desert contained the remains of dusky hopping mouse (1 scat), unidentified hopping mouse (*Notomys* sp.; 1 scat), sandy inland mouse (2 scats), cattle (4 scats), central bearded dragon (4 scats), bird (3 scats), skink (4 scats), dragon (2 scats), beetle (3 scats) and spider (1 scat). We also observed a fox at Koonchera Dune in the Sturt Stony Desert carrying a freshly killed central bearded dragon.

3.2. Dietary differences between sites

Cat and dingo diets differed significantly from one another in terms of prey size (Fig. 2b), however, the strongest relationship was at the site level, with clear separation of dietary composition between sites, irrespective of predator species ($r^2 = 0.501$; $p < 0.001$; Fig. 2c). Predator diets in the Simpson Desert were characterised by high consumption of sandy inland mouse, desert mouse (*Pseudomys desertor*), long-haired rat, skinks and beetles, relatively low consumption of rabbits, and near zero consumption of cattle (Tables 1 and 2). Scats from the Simpson Desert were also the only samples that contained remains of the crest-tailed mulgara (*Dasycercus cristicauda*), which was detected in both cat and dingo scats, and the kultarr (*Antechinomys laniger*) which was detected in a cat scat (Tables 1 and 2). Scats from the Diamantina River and surrounding floodout country were characterised by relatively high abundance of long-haired rat, fat-tailed dunnart (*Sminthopsis crassicaudata*) and birds (Tables 1 and 2). Diets of predators in the Sturt Stony Desert had high occurrence of long-haired rat, rabbit and central bearded dragon, and in the case of dingo diets, high occurrence of cattle (Tables 1 and 2). Diets of predators in the Strzelecki Desert and Cooper Creek had particularly high occurrence of rabbits and relatively low occurrences of most other prey (Tables 1 and 2).

Table 2
Percentage occurrence of prey species detected in dingo (*Canis familiaris*) scats collected from four desert regions in north-eastern South Australia.

Prey Species	Simpson Desert	Strzelecki Desert – Cooper Ck	Sturt Stony Desert	Diamantina River floodout	% Occurrence in all scats
	N = 22	*N* = 46	*N* = 204	*N* = 26	*N* = 298
MAMMALS	**95.5**	**100.0**	**85.3**	**80.8**	**87.9**
Dasyuromorphia	4.5	–	2.5	3.8	**2.3**
Fat-tailed Dunnart, *Sminthopsis crassicaudata*	–	–	–	3.8	0.3
Stripe-faced Dunnart, *Sminthopsis macroura*	–	–	1.5	–	1.0
Dunnart (unspecified), *Sminthopsis* sp.	–	–	1.0	–	0.7
Crest-tailed Mulgara, *Dasycercus cristicauda*	4.5	–	–	–	0.3
Diprotodontia	**4.5**	**6.5**	**7.4**	**23.1**	**8.4**
Red Kangaroo, *Osphranter rufus*	4.5	–	1.5	15.4	2.7
Euro, *Osphranter robustus erebescens*	–	6.5	4.9	3.8	4.7
Wallaroo (unspecified), *Ospharanter* sp.	–	–	1.0	3.8	1.0
Rodentia	**36.4**	**6.5**	**25.5**	**19.2**	**22.8**
Desert Short-tailed Mouse, *Leggadina forresti*	–	–	0.5	–	0.3
Dusky Hopping Mouse, *Notomys fuscus*	–	–	1.5	–	1.0
Hopping mouse (unspecified), *Notomys* sp.	–	–	0.5	–	0.3
Sandy Inland Mouse, *Pseudomys hermannsburgensis*	27.3	–	2.0	3.8	3.7
Long-haired Rat, *Rattus villosissimus*	9.1	2.2	20.6	19.2	16.8
Native rodent (unspecified)	–	4.3	0.5	3.8	1.3
House Mouse, *Mus musculus*	–	–	0.5	–	0.3
Lagomorpha	**45.5**	**76.1**	**11.3**	**3.8**	**23.2**
European Rabbit, *Oryctolagus cuniculus*	45.5	76.1	11.3	3.8	23.2
Artiodactyla	**9.1**	**17.4**	**46.6**	**19.2**	**36.9**
Domestic Cattle, *Bos taurus*	–	17.4	46.6	19.2	36.2
Arabian camel, *Camelus dromedarius*	9.1	–	–	–	0.7
Carnivora	9.1	10.9	4.9	23.1	**7.7**
Dingo, *Canis familiaris*	–	8.7	3.9	7.7	4.7
Feral Cat, *Felis catus*	9.1	2.2	0.5	15.4	2.7
Red Fox, *Vulpes vulpes*	–	–	0.5	–	0.3
BIRDS, REPTILES, AMPHIBIANS	**31.8**	**17.4**	**41.7**	**34.6**	**36.6**
Birds (Class Aves)	9.1	2.2	11.3	26.9	11.1
Emu, *Dromaius novaehollandiae*	–	–	1.5	3.8	1.3
Skinks (Family Scincidae)	22.7	8.7	5.4	–	6.7
Central Bearded Dragon, *Pogona vitticeps*	9.1	4.3	25.5	–	18.8
Other Dragons (Family Agamidae)	–	2.2	3.9	–	3.0
Goannas (Family Varanidae)	4.5	8.7	2.9	–	3.7
Snakes (Order Serpentes)	–	–	3.9	11.5	3.7
Frogs (Order Anura)	–	–	0.5	–	0.3
INVERTEBRATES	**45.5**	**13.0**	**4.9**	**11.5**	**9.7**
Grasshoppers (Order Orthoptera)	9.1	4.3	1.0	3.8	2.3
Beetles (Order Coleoptera)	31.8	8.7	2.9	–	5.7
Centipedes (Class Chilipoda)	4.5	–	0.5	–	0.7
Butterfly and Moth larvae (Order Lepidoptera)	9.1	–	0.5	–	1.0
VEGETATION	**9.1**	**–**	**1.0**	**–**	**1.3**

4. Discussion

There remains an incomplete knowledge of predator diets from central Australian deserts, and this is particularly so for the deserts of north-eastern South Australia. In this region, we found dingoes, cats and foxes to predate upon a wide range of mammalian, avian and reptilian prey, in addition to a diversity of insects and other invertebrates. The results of our study suggest cats target smaller prey such as rodents, dasyurids, birds and small lizards, whereas dingoes have a wider dietary breadth in terms of prey sizes, taking the smaller mammals and lizards, but also feeding upon larger prey such as cattle, kangaroos and occasionally large snakes. Medium-sized mammals, the most dominant of which in most Australian deserts is now the introduced rabbit, are commonly eaten by both cats and dingoes. We only collected a small number of fox scats, but these were indicative of foxes also having a broad diet of small vertebrates and invertebrates, similar to what we recorded for cat diets.

We also detected considerable differences in diet across the four different landscapes that were sampled, irrespective of predator type. In particular, we recorded more native mammal species in Simpson Desert samples than we did in samples from any of the other landscapes, including species not recorded elsewhere (such as the crest-tailed mulgara, and fat-tailed dunnart, or recorded relatively less frequently (such as the desert mouse). Strzelecki–Cooper Creek samples by comparison, had the poorest native mammal richness, with native mammals recorded infrequently. Because our collecting was opportunistic, we have varying numbers of cat, fox and dingo scat from our collecting sites, and we do not know when the scats were deposited, or from how many individual animals these scats came. For these reasons we need to be cautious in drawing firm conclusions about the mechanisms behind these results. However, a few trends were apparent that may stimulate further research. Firstly, cattle are absent from the area of the Simpson Desert that we sampled, whereas cattle are common in the other landscapes. Second, in landscapes where cattle and rabbits were common elements of the diet (most notably Strzelecki–Cooper Creek), native mammal richness and relative abundance in samples was low. Cattle and rabbits are generalist browsers known to have negative impacts on desert vegetation cover, and plant biomass and diversity (Brandle 1998). Cattle also cause enduring disturbance by compacting refuges in cracking clay soils used by small rodents and dasyurids, and leave deep hoof prints in clay soils that collect soil moisture and trap seeds, thereby changing the germination patterns of some plants (Waudby and Petit, 2014). Cattle also impact other fragile habitat features such as sand mounds on gibber plains that are important landscape features for small mammals, such as kowari (*Dasycercus byrnei*) (Greenville et al., 2018).

Our results are consistent with other studies of mammalian predators

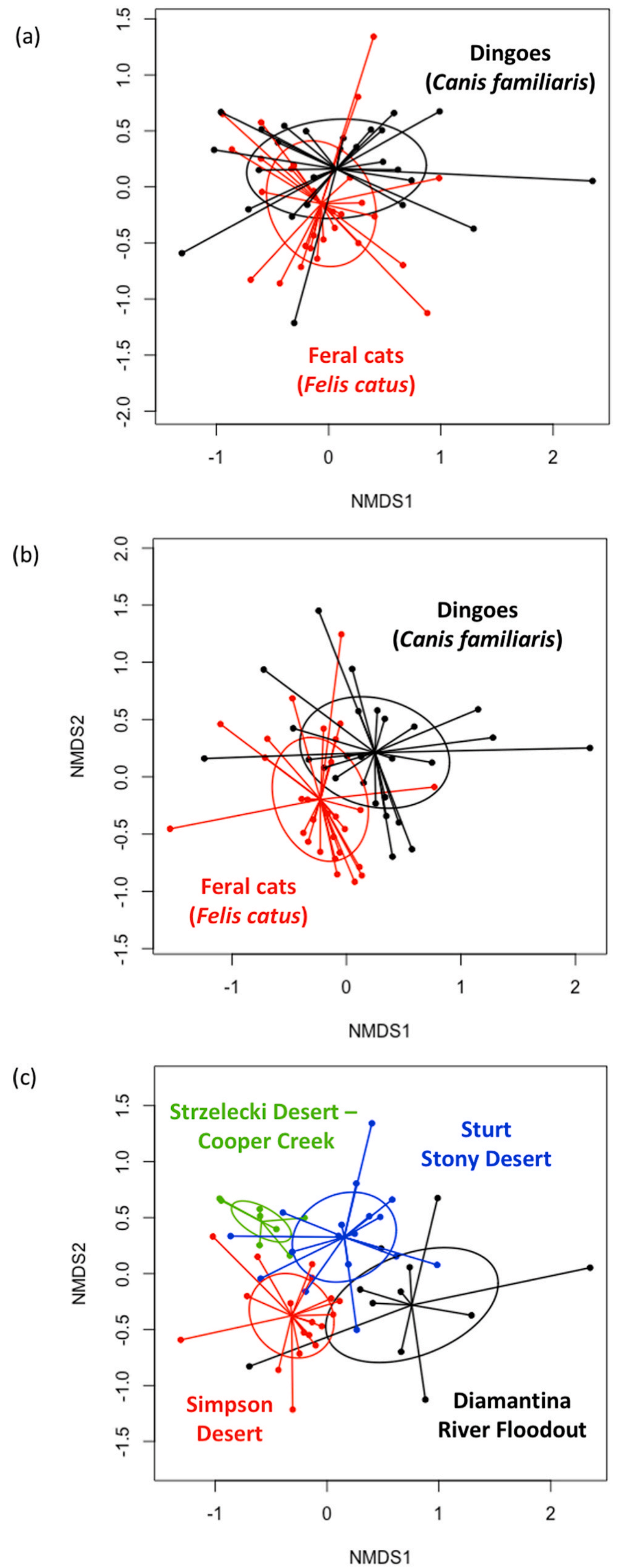

Fig. 2. Non-metric multidimensional scaling (NMDS) plot of Bray Curtis dissimilarity coefficients for each cluster of scats that represented a sampling location (see Fig. 1 for locations). Ellipses encompass the standard deviation of points coded by (a) predator type (with diets based upon prey type), (b) predator type (with diets based on prey size classes), or (c) landscape cluster, irrespective of predator type. Straight lines connect each point to its group centroid.

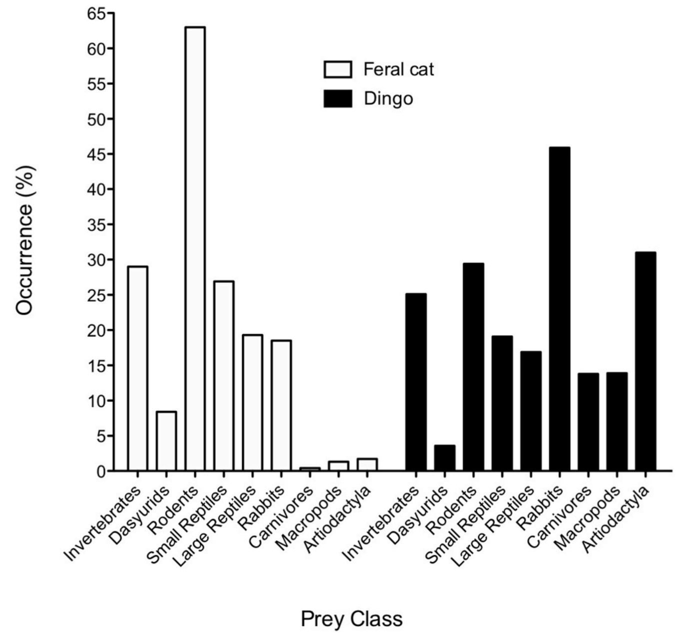

Fig. 3. Percentage occurrence of different prey classes in the diets of feral cats (*F. catus*; $N = 238$ scats) and dingoes (*C. familiaris*; $N = 298$ scats). Each prey class was only counted once in any one scat, even though multiple species within a prey class may have occurred in a single scat.

in Australian deserts, which show cats targeting smaller prey, and dingoes eating a range of prey sizes, including large prey (McDonald et al., 2018; Paltridge, 2002; Spencer et al., 2014). For example, Spencer et al. (2014) showed that cats and foxes in the Simpson Desert took mostly small prey, while dingoes took a range of prey sizes from small to large. In line with that study, our results in north-eastern South Australia showed that rodents were the most common small prey of cats, occurring in 62% of scats, with reptiles and birds, which occurred in 49% of scats, also commonly consumed. Also in similarity with other studies of cat diets in the region (Cupples et al., 2011; Spencer et al., 2014), two rodents in particular, the sandy inland mouse and the long-haired rat, dominated cat diets, although cat diets were diverse, with at least five native rodent species consumed along with a similar number of mouse-sized dasyurids. Similarly, despite only collecting a few fox scats, these contained at least three species of small mammal, as well as reptile and bird remains. In addition to larger prey, dingoes also ate a variety of small mammals, the most common of which was the long-haired rat.

Both the sandy inland mouse and the long-haired rat are widespread and common rodents throughout much of the arid zone (Van Dyck et al., 2013), and are usually among the numerically dominant species in small mammal desert communities (Pavey and Nano, 2013; Thompson and Thompson, 2008), so on the one hand, their high abundance in both cat and dingo diets, and their occurrence in the few fox scats we collected, is unsurprising. However, both species, along with many other small mammals in these deserts, undergo considerable climate-induced fluctuations in numbers (Pavey and Nano, 2013), and past predator research report variable abundances of these rodents in diets, with some reporting high occurrence of one or both of species (Cupples et al., 2011; Spencer et al., 2014), while others reported relatively low abundance (Feit et al., 2019). We collected these scats during a relatively dry period, so the occurrence of a wide range of small mammals that also included other irruptive species such as desert mouse, dusky hopping mouse, and the desert short-tailed mouse (*Leggadina forresti*) in relatively high abundance in scats is noteworthy. The last time populations of these rodents erupted in the region was following widespread rains and flooding between 2010 and 2011 (Greenville et al., 2013). It is, however, important to note that we do not know how long scats can remain intact and identifiable in this environment. In the Sonoran Desert, coyote (*Canis latrans*) scats protected from disturbance using wire cages disappeared within a few weeks (Sanchez et al., 2004). However, because so many environmental factors could influence persistence of scats, and because the question has not been adequately addressed for Australian deserts, we concede that it may be possible that our sampling covers a wide time period of perhaps several years.

Dingo diets were diverse, and were also heavily reliant upon mammalian prey. In line with other studies undertaken in the arid zone (Allen and Leung, 2012; Corbett and Newsome, 1987; Cupples et al., 2011; Doherty et al., 2019; Feit et al., 2019; Paltridge, 2002), rabbits appear to be a staple prey of dingoes in deserts, and where available, cattle are also commonly consumed, probably mostly as carrion (Corbett and Newsome, 1987). In north-eastern South Australia, as part of a large study of dingo diets at sites to the east, south and west of our study area, Allen and Leung (2012) showed dingoes had a similar diet to what we observed, with most of the same species eaten in similar ranked occurrence, and with rabbits and cattle as the two most commonly consumed foods. Dingoes also consumed other carnivores, with cat, fox and dingo (as prey) all appearing in dingo scats. Of these, cats appeared in dingo diets several times across all landscapes. Allen et al. (2014) reviewed dingo diet studies from across Australia and found only a small percentage occurrence (0.63%) of cats in dingo diets relative to our study, where cats occurred in 2.7% of scats. Although it is difficult to interpret these results without a greater understanding of prey dynamics across the study area, it is possible that dingoes had switched to cats and other prey at those sites where cattle and rabbit consumption was considerably lower than at the other landscapes sampled. Dingoes are unquestionably capable of killing wild cats and foxes (Moseby et al., 2012), but their motivation to do so for food is probably driven by reduced availability of more easily obtainable prey like rabbits or cattle carcasses. Unlike cats, foxes appeared to be at low density across the study area; although we found fox scats in the Sturt Stony Desert, Strzelecki Desert – Cooper Creek and Diamantina River regions, and saw fox tracks (but no scats) in the Simpson Desert, fox scats comprised less than 2% of all scats encountered. This is in contrast to similar research in the eastern Simpson Desert, where fox scats were the most common predator scat encountered (Spencer et al., 2014, 2017). There is evidence to suggest that dingoes may have a suppressive effect on mesopredators in Australian deserts (Cupples et al., 2011; Greenville et al., 2014; Letnic and Koch, 2010) which may trigger trophic cascades (Contos and Letnic, 2019), with a net benefit to native mammals (Gordon et al., 2015). Our results probably reflect the complex interactions occurring between predators and prey in the study area, although this was not something we tested in our study. Further work examining the complex trophic relationships between dingoes, cats and foxes is undoubtedly warranted (Allen and Fleming, 2012).

This work also improves knowledge of the current distributions of mammals in the deserts of north-eastern South Australia. Mammals in central Australia have suffered greatly from the combined impacts on vegetation structure by rabbits and cattle, and direct predation by introduced cats and foxes (Morton, 1990; Morton et al., 2011). Several species we detected are threatened with extinction either nationally (dusky hopping mouse and crest-tailed mulgara) or regionally (desert mouse and long-haired rat). Unfortunately, our understanding of the fine-scale distribution of these mammals in north-eastern South Australia is far from complete. Simpson Desert sites in particular were species rich, revealing several occurrences of crest-tailed mulgara and dusky hopping mouse, and numerous records of long-haired rats. Other notable occurrences were of dusky hopping mouse at several sites in the Sturt Stony Desert, and desert mouse in the Diamantina floodout region. Such records add to the scant distributional information for these species across the region, and present compelling evidence for these places to be more actively managed to guard against further erosion of biodiversity and mammal losses. In particular, greater effort needs to be put into managing fire and predators across the region, and more careful management of cattle grazing and trampling at sensitive sites where threatened species remain (Vernes et al., 2020).

Finally, it should also be noted that while predator scats present a sample of local mammal communities, some species known to definitely occur in the region were absent from our predator scats. For example, Koonchera Dune in the Sturt Stony Desert is a hotspot for kowari (Lynch and Brandle, 2018), yet none of the scats we collected at that same site contained identifiable kowari remains. Similarly, the fawn hopping mouse (*Notomys cervinus*) was also common at Koonchera Dune (Vernes et al., 2020), but not detected in scats. Thus, even though predator scat analysis represents an efficient way of gaining a broad understanding of mammal community composition, future surveys in the region should not rely solely on this method, but rather use it alongside other methods like camera trapping, live trapping and spotlighting, to gain the most complete picture of the mammal community.

CRediT authorship contribution statement

Karl Vernes: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Project administration, Funding acquisition. **Stephen M. Jackson:** Conceptualization, Methodology, Investigation, Writing - original draft, Funding acquisition. **Todd F. Elliott:** Conceptualization, Methodology, Investigation, Writing - original draft, Funding acquisition. **Max Tischler:** Writing - original draft, Project administration, Funding acquisition. **Andrew Harper:** Writing - original draft, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jaridenv.2020.104377.

References

Abbott, I., 2002. Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. Wildl. Res. 29, 51–74.

Allen, B., Read, J.L., Medlin, G., 2011. Additional records of small mammals in northern South Australia. Aust. Mammal. 33, 68–72.

Allen, B.L., Allen, L.R., Leung, L.K.P., 2014. Interactions between two naturalised invasive predators in Australia: are feral cats suppressed by dingoes? Biol. Invasions 17, 761–776.

Allen, B.L., Fleming, P.J.S., 2012. Reintroducing the dingo: the risk of dingo predation to threatened vertebrates of western New South Wales. Wildl. Res. 39.

Allen, B.L., Leung, L.K.-P., 2012. Assessing predation risk to threatened fauna from their prevalence in predator scats: dingoes and rodents in arid Australia. PloS One 7, e36426.

Balme, J., O'Connor, S., Fallon, S., 2018. New dates on dingo bones from Madura Cave provide oldest firm evidence for arrival of the species in Australia. Nat. Sci. Rep. 8, 9933.

Brandle, R., 1998. A Biological Survey of the Stony Deserts, South Australia. Heritage and Biodiversity Section. Department for Environment, Heritage and Aboriginal Affairs, , South Australia, Adelaide, South Australia.

Brunner, H., Wallis, L.R., 1986. Roles of predator scat analysis in Australian mammal research. Victorian Nat. 103, 79–87.

Burbidge, A.A., McKenzie, N.L., 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biol. Conserv. 50, 143–198.

Claridge, A.W., Mills, D.J., Barry, S.C., 2010. Prevalence of threatened native species in canid scats from coastal and near-coastal landscapes in south-eastern Australia. Aust. Mammal. 32, 117–126.

Contos, P., Letnic, M., 2019. Top-down effects of a large mammalian carnivore in arid Australia extend to epigeic arthropod assemblages. J. Arid Environ. 165, 16–27.

Corbett, L.K., Newsome, A.E., 1987. The feeding ecology of the dingo. III. Dietary relationships with widely fluctuating PreyPopulations in arid Australia: an hypothesis of alternation of predation. Oecologia 74, 215–227.

Cupples, J.B., Crowther, M.S., Story, G., Letnic, M., 2011. Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? J. Mammal. 92, 590–600.

Dickman, C.R., 1996. Impact of exotic generalist predators on the native fauna of Australia. Wildl. Biol. 2, 185–195.

Doherty, T.S., Davis, N.E., Dickman, C.R., Forsyth, D.M., Letnic, M., Nimmo, D.G., Palmer, R., Ritchie, E.G., Benshemesh, J., Edwards, G., Lawrence, J., Lumsden, L., Pascoe, C., Sharp, A., Stokeld, D., Myers, C., Story, G., Story, P., Triggs, B., Venosta, M., Wysong, M., Newsome, T.M., 2019. Continental patterns in the diet of a top predator: Australia's dingo. Mamm Rev. 49, 31–44.

Fairfax, R.J., 2018. Dispersal of the introduced red fox (*Vulpes vulpes*) across Australia. Biol. Invasions 21, 1259–1268.

Feit, B., Feit, A., Letnic, M., 2019. Apex predators decouple population dynamics between mesopredators and their prey. Ecosystems 22, 1606–1617.

Friend, G.R., 1978. A Comparison of predator scat analysis with conventional techniques in a mammal survey of contrasting habitats in Gippsland, Victoria. Aust. Wildl. Res. 5, 75–83.

Gordon, C.E., Feit, A., Gruber, J., Letnic, M., 2015. Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. Proc. Biol. Sci. 282.

Gotelli, N.J., Hart, E.M., Ellison, A.M., 2015. EcoSimR: Null Model Analysis for Ecological Data. R package version 0.1.0. http://github.com/gotellilab/EcoSimR.

Greenville, A.C., Brandle, R., Canty, P., Dickman, C.R., 2018. Dynamics, habitat use and extinction risk of a carnivorous desert marsupial. J. Zool. 306, 258–267.

Greenville, A.C., Wardle, G.M., Dickman, C.R., 2013. Extreme rainfall events predict irruptions of rat plagues in central Australia. Austral Ecol. 38, 754–764.

Greenville, A.C., Wardle, G.M., Tamayo, B., Dickman, C.R., 2014. Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. Oecologia 175, 1349–1358.

Letnic, M., Koch, F., 2010. Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. Austral Ecol. 35, 167–175.

Lynch, C., Brandle, R., 2018. Kowari Monitoring in Sturt's Stony Desert, South Australia. South Australian Arid Lands Natural Resources Management Board, Port Augusta, South Australia, p. 27.

McDonald, P.J., Brim-Box, J., Nano, C.E.M., Macdonald, D.W., Dickman, C.R., 2018. Diet of dingoes and cats in central Australia: does trophic competition underpin a rare mammal refuge? J. Mammal. 99, 1120–1127.

Morton, S.R., 1990. The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. Proc. Ecol. Soc. Aust. 16, 201–213.

Morton, S.R., Stafford Smith, D.M., Dickman, C.R., Dunkerley, D.L., Friedel, M.H., McAllister, R.R.J., Reid, J.R.W., Roshier, D.A., Smith, M.A., Walsh, F.J., Wardle, G. M., Watson, I.W., Westoby, M., 2011. A fresh framework for the ecology of arid Australia. J. Arid Environ. 75, 313–329.

Moseby, K.E., Neilly, H., Read, J.L., Crisp, H.A., 2012. Interactions between a top order predator and exotic mesopredators in the Australian Rangelands. Int. J. Ecol. 2012, 1–15.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2019. vegan: community Ecology Package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan.

Paltridge, R., 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. Wildl. Res. 29, 389–403.

Pavey, C.R., Nano, C.E.M., 2013. Changes in richness and abundance of rodents and native predators in response to extreme rainfall in arid Australia. Austral Ecol. 38, 777–785.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rowlands, D., Smith, M., Macfarlane, I., Wright, D., Tischler, M., 2020. The lost oasis: archaeology of a 'forgotten' mikiri well in the Simpson Desert. Queensland Archaeol. Res. 23, 1–7.

Sanchez, D.M., Krausman, P.R., Livingston, T.R., Gipson, P.S., 2004. Persistence of carnivore scat in the Sonoran desert. Wildl. Soc. Bull. 32, 366–372.

Short, J., Smith, A., 1994. Mammal decline and Recovery in Australia. J. Mammal. 75, 288–297.

Spencer, E.E., Crowther, M.S., Dickman, C.R., 2014. Diet and prey selectivity of three species of sympatric mammalian predators in central Australia. J. Mammal. 95, 1278–1288.

Spencer, E.E., Newsome, T.M., Dickman, C.R., 2017. Prey selection and dietary flexibility of three species of mammalian predator during an irruption of non-cyclic prey. R Soc Open Sci 4, 170317.

Thompson, G.A., Thompson, S.A., 2008. Abundance and spatial distribution of five small mammals at a local scale. Aust. Mammal. 30, 65–70.

Triggs, B., 1996. Tracks, Scats, and Other Traces: a Field Guide to Australian Mammals. Oxford University Press, Melbourne.

Van Dyck, S.M., Gynther, I., Baker, A., 2013. Field Companion to the Mammals of Australia. New Holland Publishers, Sydney.

Vernes, K., Elliott, T.F., Jackson, S.M., 2020. 150 years of mammal extinction and invasion at Koonchera dune in the Lake Eyre Basin of South Australia. Biol. Invasions. https://doi.org/10.1007/s10530-020-02387-2.

Waudby, H.P., Petit, S., 2014. Disintegration of cattle hoof prints in cracking-clay soils of the arid South Australian Stony Plains region during a wet period. S. Aust. Geogr. J. 113, 5–12.

Woinarski, J.C.Z., South, S.L., Drummond, P., Johnston, G.R., Nankivell, A., 2018. The diet of the feral cat (*Felis catus*), red fox (*Vulpes vulpes*) and dog (*Canis familiaris*) over a three-year period at Witchelina Reserve, in arid South Australia. Aust. Mammal. 40, 204–213.