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Trophic ecology of marsupial predators in arid Australia following reshaping of predator assemblages

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The extirpation of marsupial predators and their replacement by eutherian carnivores are likely to have cascading ecological impacts on the trophic structure of arid Australia. Here, we assessed the diet and characterized the trophic role of the 3 largest remaining carnivorous marsupials (< 200 g body mass) in arid Australia: crest-tailed mulgaras (*Dasycercus cristicauda*), kowaris (*Dasyuroides byrnei*), and brush-tailed mulgaras (*Dasycercus blythi*). The species show a high level of trophic connectivity; each is highly interactive, being predator or prey of numerous species across multiple phyla. The prey base of each of the predator species was broad and included vertebrates, invertebrates, and plants. Crest-tailed mulgaras consumed the most vertebrates including prey up to the size of the southern marsupial mole (*Notoryctes typhlops*). Kowaris consumed prey up to the size of the European rabbit (*Oryctolagus cuniculus*). Although capable of capturing or scavenging vertebrates, the diet of each species was dominated by arthropods < 2 g in body mass.

Key words: arthropod, carnivore, extinction, niche, vertebrate

A dramatic mammal extinction event of global magnitude, that is ongoing, has unfolded across Australia over the past 200 years (Johnson 2006; Woinarski et al. 2015). A consequence of the extinction event has been a changeover in mammalian predators. In arid and semiarid Australia, an area that occupies 70% of the continent (Warner 2004), this process has involved the extirpation of the largest carnivorous marsupial, the western quoll (*Dasyurus geoffroii*), and a mid-range carnivorous marsupial, the red-tailed phascogale (*Phascogale calura*). As these species contracted in range, the region was colonized by 2 introduced eutherian carnivores, the red fox (*Vulpes vulpes*) and feral house cat (*Felis catus*). The top mammalian predator, the Australian dingo (*Canis dingo*), has remained in arid Australia during this period and appears to have been present for over 3,000 years (Fillios et al. 2012).

At the time of European settlement, the western quoll was the largest carnivorous marsupial (Dasyuromorphia: Dasyuridae) in arid Australia (body mass: 615–2,185 g); however, it was extirpated from the arid zone in the 1960s (Johnson and Roff 1982) and is now confined to southwestern Australia (Glen et al. 2010). The red-tailed phascogale (body mass: 38–68 g) also retracted to southwestern Australia over a similar time period (Kitchener 1981). In contrast, a suite of mid-range (body mass < 200 g) carnivorous marsupials, that are an order of magnitude smaller than the western quoll, persisted in arid Australia during this extinction event. The species are the crest-tailed mulgara (*Dasycercus cristicauda*; 65–185 g), kowari (*Dasyuroides byrnei*; 70–175 g), and brush-tailed mulgara (*Dasycercus blythi*; 60–110 g). These species occur sparsely over a broad geographic area and are the largest remaining marsupial predators in arid Australia (e.g., Morton 1982). The kowari occupies stony desert; the crest-tailed mulgara, sand ridges; whereas the brush-tailed mulgara occurs on sand plains and stony desert (Morton 1982; Van Dyck and Strahan 2008; Pavey et al. 2011). The kowari and crest-tailed mulgara are listed nationally as vulnerable under Australia's Environment Protection and Biodiversity Conservation Act of 1999.

There is limited information on the trophic ecology of mid-range carnivorous marsupials in arid Australia and it is not known whether these species overlap in diet and prey preferences. This knowledge is important to gain an understanding of their role in the functioning of arid ecosystems in Australia. It is also needed to inform management options in the likely event of the reintroduction of the western quoll. The quoll has been reintroduced to a number of temperate and semiarid locations within its former range with varying levels of success (Morris et al. 2003; Commonwealth of Australia 2015) and attention has expanded to potentially return the species to arid Australia. A sound understanding of the trophic ecology of the extant mid-range carnivorous marsupials will assist in identifying potential negative impacts from reintroductions of quolls.

Here, we quantify the diet of a population of each of the 3 mid-range carnivorous marsupials and characterize the trophic role of these predators in arid Australian ecosystems. We predict that these 3 species will have broad diets because these marsupial predators are resident with relatively stable populations in arid regions through peaks and troughs of resource availability (Masters 1998; Pavey et al. 2011; Masters and Dickman 2012; Körtner et al. 2016), whereas other arid vertebrate species exhibit marked changes in occurrence and population size (e.g., Pavey et al. 2008a, 2008b). We consider that this ability to persist is enhanced by a broad diet.

Materials and Methods

Study sites.—Scats of each species were collected from individuals captured in traps from populations that were the focus of research projects undertaken from 2007 to 2010. Trapping (and all other procedures) was undertaken in accordance with the American Society of Mammalogists guidelines (Sikes et al. 2016), and was approved by the University of New England Animal Ethics Committee and Charles Darwin University Animal Ethics Committee.

The research took place during the low (or "bust") phase of small mammal population cycles in the study areas. This phase features the most typical environmental conditions that the marsupial predators experience and coincides with periods of low rainfall (e.g., Pavey and Nano 2013). The low phase can occupy up to 8.5 years of each 10-year period in our study system (Pavey et al. 2014).

We collected scats of the 2 mulgara species during a long-term monitoring project at Andado Station (25°41′S, 135°29′E), southeast Northern Territory (Pavey et al. 2014). Brush-tailed mulgara scats were collected from May 2008 to December 2010 and crest-tailed mulgara scats were collected from November 2007 to December 2010. The kowari formerly occurred in this area also; however, it has been extirpated from the western Simpson Desert. Therefore, we collected kowari scats from a population at Astrebla Downs National Park (24°10′S, 140°34′E), southwest Queensland, during a briefer time span: winter (June to August) 2007 (Körtner and Geiser 2011).

Dietary analysis.—We broadly followed the methods outlined in Pavey et al. (2009) for fecal analysis. Fifty scats were analyzed for each species except crest-tailed mulgaras (46 scats). We placed each scat in a petri dish and added 4–5 drops of 10% KOH directly to it, before teasing it apart with fine dissecting needles and covering it in 70% ethanol. We systematically searched each scat for identifiable material under a low power (6.4 to 40 magnification) binocular microscope.

Prey fragments were identified to the lowest taxonomic level possible. Material was identified by reference to collections in the Queensland Museum, Brisbane. Mammal hair was collected and sent for specialist identification (Barbara Triggs, Euroa, Victoria, Australia). The volume of each prey item in each scat was calculated by spreading all the identifiable fragments in a petri dish with graph paper underneath and estimating for each prey item the space (area) occupied by its fragments, including exoskeleton, hair, scales, and feathers. Material was assigned to a taxon only if it clearly belonged to that taxon. A single scat could contain material of a species and of the genus to which the species belonged; it was not concluded that all material in the scat belonged to a species even if some identifiable parts were present in the scat.

Percent volume was estimated to the nearest 5%. Taxa that contributed less than 2.5% were not included in percent volume estimates for a given scat.

Analysis of data.—We calculated the mean percent volume of each prey item in the diet for each species. We also calculated the frequency of occurrence (also known as percent occurrence or percent frequency of occurrence), which is the number of scats containing a specific prey taxon divided by the total number of scats analyzed. We tested for sampling completeness by generating sample-based diet component accumulation curves (1,000 randomizations) using the dietary items in Table 1 run in EstimateS version 9.1.0 (Colwell 2013). We chose the 1st-order Jackknife richness estimator for this purpose. The percentage of dietary sampling completeness was calculated for each species as $S_{obs}/S_{est} \times 100$, where S_{obs} is the number of dietary categories observed, and S_{est} is the number of dietary categories estimated.

We calculated dietary breadth for each species using the percent volume dietary data. Levins' standardized formula for niche breadth (Krebs 1999) was used to calculate diet breadth: $B_A = (1/\sum p_i^2) - 1/n - 1$, where p_i = proportion of occurrence of each prey category in the predator's diet; and n = number of prey categories in the predator's diet. B_A ranges from 0 to 1, where a value close to 0 represents a narrow niche and one close to 1, a broad niche. The percent volume data were converted to proportions for the analysis. To calculate dietary breath, we used data at an ordinal level except that termites were separated out from Blattodea and ants from Hymenoptera, and plants were a single category. This grouping resulted in 20 potential categories of food.

We calculated dietary overlap among each of the 3 species pairs of carnivorous marsupial using the percent volume dietary data. The percent volume data were converted to proportions for the analysis. We used the same 20 potential

Table 1.—The diet of 3 marsupial predators (brush-tailed mulgara, *Dasycercus blythi*; crest-tailed mulgara, *Dasycercus cristicauda*; and kowari, *Dasyuroides byrnei*) from arid Australia. A, occurrence = percentage of all scats that contained the taxon; B, volume = mean percentage volume of all identifiable material that comes from the taxon. Invertebrate volume data are given only at the level of order except for termites (Termitoidae) and ants (Formicidae) within Blattodea and Hymenoptera, respectively. Life stages of invertebrates are adult unless indicated otherwise.

Higher classification (subphylum, class, order/suborder, superfamily/family)	Prey category	Brush-tailed mulgara		Crest-tailed mulgara		Kowari	
		A	B	A	B	A	B
Vertebrata	Vertebrate unidentified	22	7.3	6.5	1.7	16	1.9
Mammalia	Mammal unidentified	26	1.0	17.4	3.3	12	2.1
Dasyuromorphia							
Dasyuridae	Dasyurid unidentified	0		4.3	0.1	2	0
	Sminthopsis sp.	2	1.2	10.9	8.2	16	0.7
Notoryctemorphia	*Notoryctes typhlops*	0		6.5	3.2	0	
Rodentia							
Muridae	Rodent unidentified	8	0.9	8.7	1.0	0	
	Rattus villosissimus	0		0		14	5.8
	Notomys sp.	0		0		4	3.1
	Pseudomys sp.	0		8.7	7.1	0	
Lagomorpha	*Oryctolagus cuniculus*	0		0		8	0.2
Reptilia	Reptile unidentified	10	1.3	2.2	0.7	4	1.1
Lacertilia	Lizard unidentified	2	1.0	6.5	2.3	0	
Agamidae	Agamid lizard	2	0.9	2.2	0.1	0	
Aves	Bird unidentified	2	0.2	6.5	3.2	4	0.2
Hexapoda							
Insecta							
Blattodea	Cockroach	0		4.3	1.5	26	9.4
Termitoidae	Termite	66	32.1	39.1	17.5	16	6.0
	Drepanotermes sp.	2		6.5		0	
Orthoptera	Grasshopper/cricket	52	30.6	26.1	17.3	54	49.7
Caelifera							
Acridoidea	Short-horned grasshopper	0		0		26	
Ensifera							
Gryllidae	Cricket	0		4.3		10	
	Cricket nymph	0		0		2	
Hemiptera							
Heteroptera	True bug	10	0.9	6.5	0.2	6	0.1
Coleoptera	Beetle	24	5.9	32.6	9.1	34	8.4
	Beetle larva	2		0		0	
Curculionoidea	Weevil	0		2.2		2	
Scarabaeoidea	Scarabaeoid beetle	0		2.2		0	
Lepidoptera	Moth	12	1.2	10.9	7.6	0	
	Moth larva	2	0.7	0		0	
Hymenoptera	Wasp	6	0.4	0		0	0.4
	Wasp larvae	0		0		4	
Formicidae	Ant	8	3.1	8.7	4.6	22	5.0
	Iridomyrmex	4		8.7		0	
	Melophorus	0		4.3		0	
	Meranoplus	2		0		0	
	Monomorium	6		0		8	
	Pheidole	2		4.3		4	
	Rhytidoponera	2		0		6	
Chelicerata							
Arachnida							
Araneae	Spider	54	5.8	34.8	5.7	12	1.3
	Selenocosmia	2		0		0	
Scorpiones	Scorpion	24	5.0	6.5	2.6	4	0.4
Myriapoda							
Chilopoda	Centipede	4	0.6	8.7	3.3	2	1.8
Plant		2		2.2		12	2.4

categories of food as in the calculation of dietary breadth. We calculated dietary overlap using Pianka's modification to the MacArthur and Levin measure of niche overlap (Krebs 1999): $O_{jk} = \sum p_{ij}p_{ik}/\sqrt{(\sum p_{ij}^2 \sum p_{ik}^2)}$, where j and k are the 2 species being compared. Niche overlap ranges from 0 to 1 with 0 representing no overlap in diet and 1, complete overlap.

Differences in the diets of the 3 marsupial predators in terms of percent volume were assessed using nonmetric multidimensional scaling (NMDS) ordination run in the PRIMER 7 software package (Clarke et al. 2014). For the analysis, each scat was considered to be a sample. The data were square-root transformed prior to the construction of a Bray–Curtis similarity matrix. For our data, the successive steps of the NMDS iteration process resulted in each group collapsing to a small number of points. This produced a very clumped NMDS ordination plot. We dealt with this issue by using the "Fix Collapse" option in PRIMER 7 (Clarke and Gorley 2015). This approach mixes the stress functions of NMDS with metric MDS (MMDS) to separate points in ordination space. Specifically, it mixes 5% of MMDS stress with 95% NMDS stress to fix the relative placing of the groups (Clarke and Gorley 2015). A 1-way global analysis of similarities (ANOSIM) test examined variation in dietary composition across species (Clarke et al. 2014).

Trophic role of the mid-range carnivorous marsupials.—We developed a simple food web diagram to indicate the trophic role of our study populations of mulgaras and kowaris. This diagram is a summary of information that has accumulated during long-term research particularly at Andado Station. The diagram shows the interactions of these mid-range carnivorous marsupials with other nocturnal animals. In cases where we did not have our own observations (e.g., diet of snakes), we relied on the scientific literature (Shine and Slip 1990). The main references on which the diagram is based are given in the figure legend.

We classify the species and higher-order categories used in the text based on the ABRS (2009). Body mass ranges for mammals used in this article are from Van Dyck and Strahan (2008). Body mass data for reptiles and invertebrates were taken from published and unpublished sources including collections of the Queensland Museum.

Results

The sampling completeness assessment across the 3 species was 70.4% for brush-tailed mulgaras, 85.6% for crest-tailed mulgaras, and 87.3% for kowaris. These results indicate that our sample sizes were sufficient to identify the major food groups consumed by each of the 3 marsupials.

Prey base.—We identified 42 food categories across the species (Table 1). The number of food categories consumed was similar across species: kowari, 27; brush-tailed mulgara, 28; crest-tailed mulgara, 29. There was extensive overlap in the prey base among the carnivorous marsupials. Each species consumed vertebrates, invertebrates (including insects, spiders, scorpions, centipedes), and plant material. Plant material consumed included leaf fragments and seeds. The insect prey base ranged from 5 to 6 orders with each predator consuming Blattodea (primarily infraorder Isoptera: termites), Coleoptera, Hemiptera, and Orthoptera. The predators predominantly consumed adult insects but both brush-tailed mulgaras and kowaris captured nonadult life stages (beetle, moth, and wasp larvae; nymphal crickets).

The species varied in niche breadth. The kowari had the narrowest value (B_A = 0.14) closely followed by the brush-tailed mulgara (B_A = 0.19). The crest-tailed mulgara, the largest of the 3 predators, had the broadest niche breadth (B_A = 0.44).

Important prey taxa.—The diet of each species was dominated by insects, in particular Orthoptera and often also termites. Insects comprised 57.8% by volume of the diet of crest-tailed mulgaras with the main prey being Orthoptera (17.3% volume) and termites (17.5% volume; Fig. 1). The dominant prey group in kowari scats was Orthoptera (49.7% volume) including both crickets (Ensifera) and grasshoppers (Caelifera). Termites contributed only 6% by volume. Other insects contributed a combined volume of 23.3% to the diet of kowaris. The diet of brush-tailed mulgaras was dominated by termites and Orthoptera (32.1% and 30.6% volume, respectively). Other insects contributed a combined volume of 12.2%.

The crest-tailed mulgara consumed the most vertebrates (30.7% volume) of the 3 predator species (Fig. 1). Mammals were the main vertebrates captured and included other carnivorous marsupials (dunnarts, *Sminthopsis* spp.), rodents (*Pseudomys* spp.), and the largely subterranean southern marsupial mole (*Notoryctes typhlops*; Table 1). Vertebrates comprised 15.1% by volume of the diet of kowaris (Fig. 1). The kowari also captured mostly mammals among vertebrate prey (Fig. 2), of which rodents was the dominant group. The brush-tailed mulgara had the lowest consumption of vertebrates (13.8% volume) of the 3 species (Fig. 1). It differed in capturing mostly reptiles, whereas rodents and carnivorous marsupials were taken occasionally (Fig. 2). A high proportion of vertebrate material in scats of this species could not be assigned to class (Table 1).

Dietary overlap.—The 3 predator species showed moderate to high levels of dietary overlap. Overlap in diet was highest between the 2 species of mulgara (0.85). The kowari had the

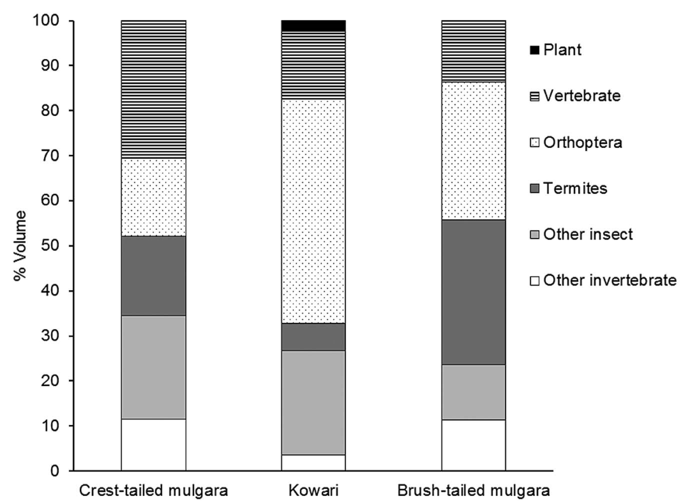

Fig. 1.—Prey composition of the diets of 3 marsupial predators (brush-tailed mulgara, *Dasycercus blythi*; crest-tailed mulgara, *Dasycercus cristicauda*; and kowari, *Dasyuroides byrnei*) in arid Australia. Data are percent volume of 6 prey categories: vertebrates, Orthoptera (grasshoppers and crickets), termites, all other insect orders combined, other invertebrates combined (spiders, scorpions, centipedes), and plants.

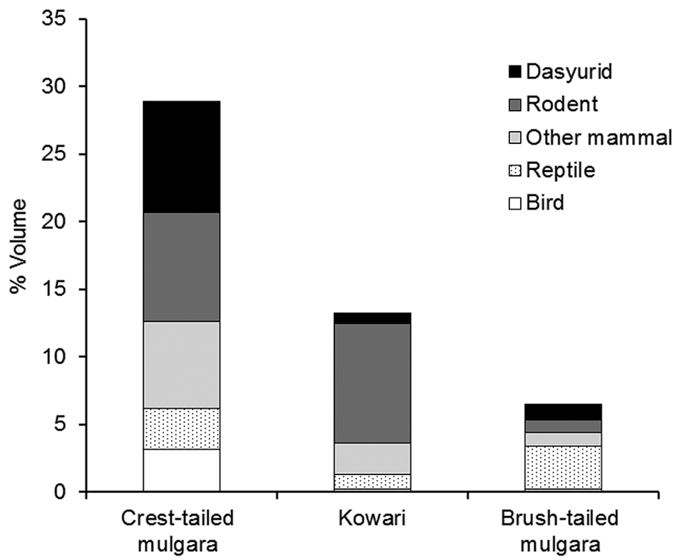

Fig. 2.—Composition of vertebrate prey in the diets of 3 marsupial predators (brush-tailed mulgara, *Dasycercus blythi*; crest-tailed mulgara, *Dasycercus cristicauda*; and kowari, *Dasyuroides byrnei*) in arid Australia. Data are percent volume of 5 vertebrate groups: birds, reptiles, rodents, dasyurid marsupials, and other mammals combined.

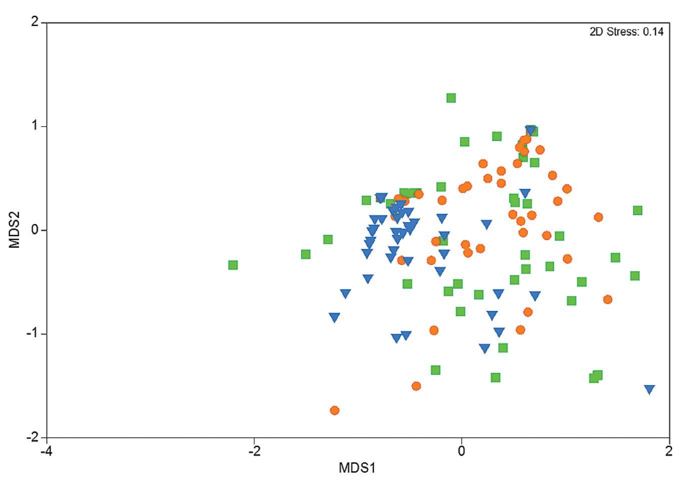

Fig. 3.—Ordination of dietary data of 3 marsupial predators (brush-tailed mulgara, *Dasycercus blythi*; crest-tailed mulgara, *Dasycercus cristicauda*; and kowari, *Dasyuroides byrnei*) using nonmetric multidimensional scaling (NMDS) with individual scats as samples. Symbols: ■ = crest-tailed mulgara; ▼ = kowari; ● = brush-tailed mulgara.

highest overlap with the brush-tailed mulgara (0.74), whereas overlap with the crest-tailed mulgara was 0.69.

Multidimensional scaling confirmed the pattern of dietary overlap between species in terms of the volume of prey items in the diet (Fig. 3). The samples from all 3 species overlapped extensively in ordination space. The samples from kowaris were the most tightly clumped in ordination space, whereas crest-tailed mulgara samples were the most dispersed (Fig. 3). Global 1-way ANOSIM revealed no significant difference in diets of the species (global $R = 0.129$, $P = 0.10$).

Trophic role.—The 3 marsupial predators were highly interactive species in our study area. The simple food web diagram (Fig. 4) that we assembled shows links, as predator and prey, with all other groups of nocturnal animals in the study system. This contrasts with the specialized trophic role of the letter-winged kite (*Elanus scriptus*) and owls (*Tyto javanica*, *Ninox boobook*; Fig. 4).

Prey size.—The upper size range of prey differed among species (Table 1). Kowaris preyed on 2 species that, when adult, are much greater than them in body mass: long-haired rat (*Rattus villosissimus*; body mass: 54–280 g) and European rabbit (*Oryctolagus cuniculus*; body mass: 960–2,420 g). Both prey species may have been consumed as carrion or captured as young. Crest-tailed mulgaras preyed on species as large as the southern marsupial mole (body mass: 40–70 g). Brush-tailed mulgaras captured prey up to a mass of 20 g, including dunnarts and rodents.

The lower size range of prey was similar for the 3 predator species, consisting of a wide variety of insects that are < 2 g in mass. This prey base included groups (ants, termites, bugs) that are dominated by small species.

Animals with an estimated body mass of < 2 g, comprising mainly insects, predominated in terms of biomass (measured as percent volume) in the diets of the marsupial predators (Fig. 5). The crest-tailed mulgara was the only species to have a percent volume of more than 10% in any of the other size categories. The diet of this species included 17% in the 11–20 g size class due to predation on dunnarts and murid rodents (*Pseudomys*; Fig. 5). The kowari was the only species to capture prey in the 21–50 g size range (hopping mice, *Notomys*) as well as in the > 100 g range.

Discussion

Arid ecosystems feature complex food webs and trophic relationships that are characterized by a high density of links and long food chains (Polis 1991; van der Valk 1997; Ayal 2007; Megías et al. 2011). As a consequence, typical predators in these arid food webs show a high level of trophic connectivity. Our results demonstrate that the 3 largest extant carnivorous marsupials in arid Australia—crest-tailed mulgara, kowari, and brush-tailed mulgara—conform to this pattern. Each species is, from a trophic perspective, highly interactive, being predator or prey of many other species across multiple phyla (Fig. 4). Each of the 3 predators has a broad prey base that includes vertebrates, invertebrates, and plants.

The carnivorous marsupials are captured by the 3 species of eutherian carnivore that occur in arid Australia and (potentially) by nocturnal raptors and snakes (see Fig. 4 and references in the figure legend). Additional predation pressure from varanid lizards (not shown in the figure) will potentially occur during the day. These reptiles are a major group of predators across Australia (e.g., Sutherland et al. 2011) and are likely to dig up carnivorous marsupials and other nocturnal species from their diurnal shelters.

Our prediction that the diets of the 3 marsupial predators would be broad was supported by the data collected. This prediction was based on observations of the persistence of resident

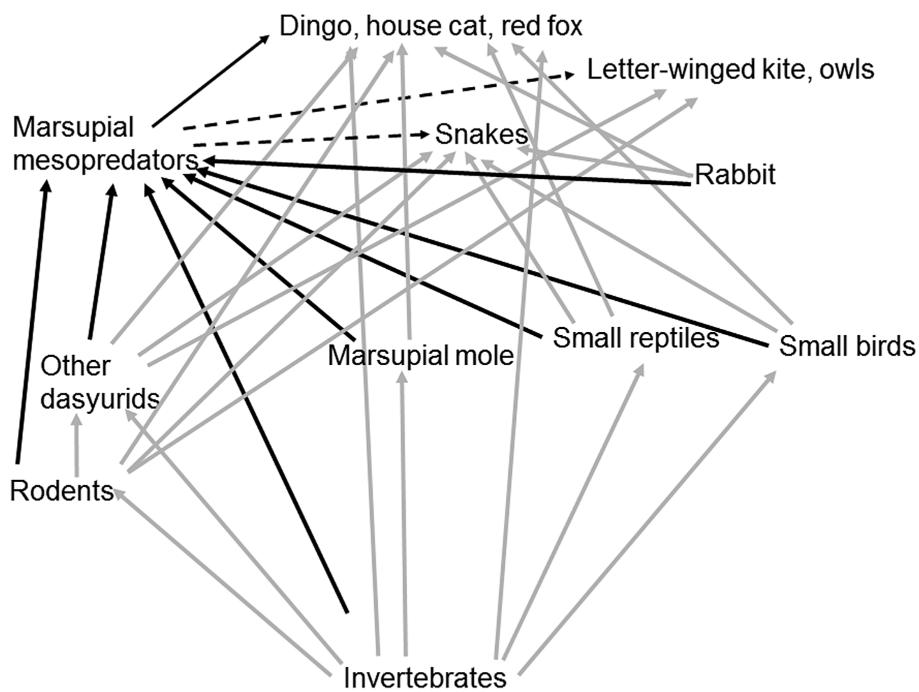

Fig. 4.—Trophic interactions involving the 3 marsupial predators (brush-tailed mulgara, *Dasycercus blythi*; crest-tailed mulgara, *Dasycercus cristicauda*; and kowari, *Dasyuroides byrnei*) and other nocturnal animals in arid Australia. Black lines indicate trophic links involving the marsupial predators; solid lines indicated observed relationships, dashed lines indicate predicted relationships. Gray solid lines indicate other predatory relationships. The "other dasyurids" category refers to all other carnivorous marsupials in the study areas. The "small reptiles" category includes herbivorous and arthropodivorous species. The "small birds" category indicates granivorous and arthropodivorous species that are diurnal and are presumably captured while roosting at night. Data sources are: this study; Shine and Slip (1990); Chen et al. (1998); Körtner et al. (2007); Pavey et al. (2008a, 2008b, 2009, 2012); McDonald and Pavey (2014).

populations of each species despite the irregular and dramatic fluctuations in resource availability that occur across their geographic ranges in arid Australia. The ability to capture a wide range of animals, including many vertebrate and invertebrate taxa, and to consume some plant material provides these species with the flexibility to take whatever food is available at a given time. This dietary breadth and the ability to conserve energy when food is limited by undergoing torpor (Körtner et al. 2008, 2016; Körtner and Geiser 2011) appear to play a key role in enabling populations to persist during periods of low resource availability. In contrast, nocturnal avian predators including owls and the letter-winged kite specialize on small mammals, especially rodents (Fig. 4). As prey populations collapse at the onset of dry periods, nocturnal avian predators disperse and do not return to an area until populations of small mammals return to high abundances (Pavey et al. 2008). Over a decade may elapse between periods of suitable prey availability.

Each of the study species, on average, captured prey that is several orders of magnitude smaller than itself in body mass. The marsupial predators captured (or gained access to carcasses of) a wide range of vertebrates including mammals, reptiles, and birds. For example, crest-tailed mulgaras in this study ate marsupial moles and kowaris consumed long-haired rats and rabbits. Although brush-tailed mulgaras in this study did not capture large prey, previous research has shown a range of birds, mammals, and reptiles in their diet, including species up to the size of long-haired rats (Chen et al. 1998; Pavey et al. 2009). Despite the capacity to capture or scavenge vertebrates, the diet of each species was dominated by arthropods < 2 g in body mass (Fig. 5). Predators were not restricted to 1 or 2 taxa of small prey, rather a wide range of prey fell in the smallest body mass category, including most insect orders.

Our dietary assessment of each species involved only a single population during the low phase of small mammal population cycles. This phase was chosen because it represents the most typical environmental conditions that the species experience. It is also a time of relatively low resource availability (e.g., Nano and Pavey 2013); therefore, we expected dietary breadth to be at its greatest. There is little published information on the diet of the kowari or the crest-tailed mulgara with which to compare our data. However, a previous study on the brush-tailed mulgara reveals that it can take a greater number of mammals, especially rodents, than indicated by our data (Chen et al. 1998). Other research has shown a greater incorporation of reptiles, birds, and mammals in the diet with a considerable amount of individual variation (Pavey et al. 2009). These differences likely reflect differences in prey availability among study areas because while our study on brush-tailed mulgaras was focused on stony desert, the previous work was carried out on populations resident in sandy environments. Previous studies were also not confined to periods of low resource availability.

The 3 mid-range carnivorous marsupials showed relatively high overlap in diet. The highest overlap among species pairs was among the crest-tailed and brush-tailed mulgaras. These

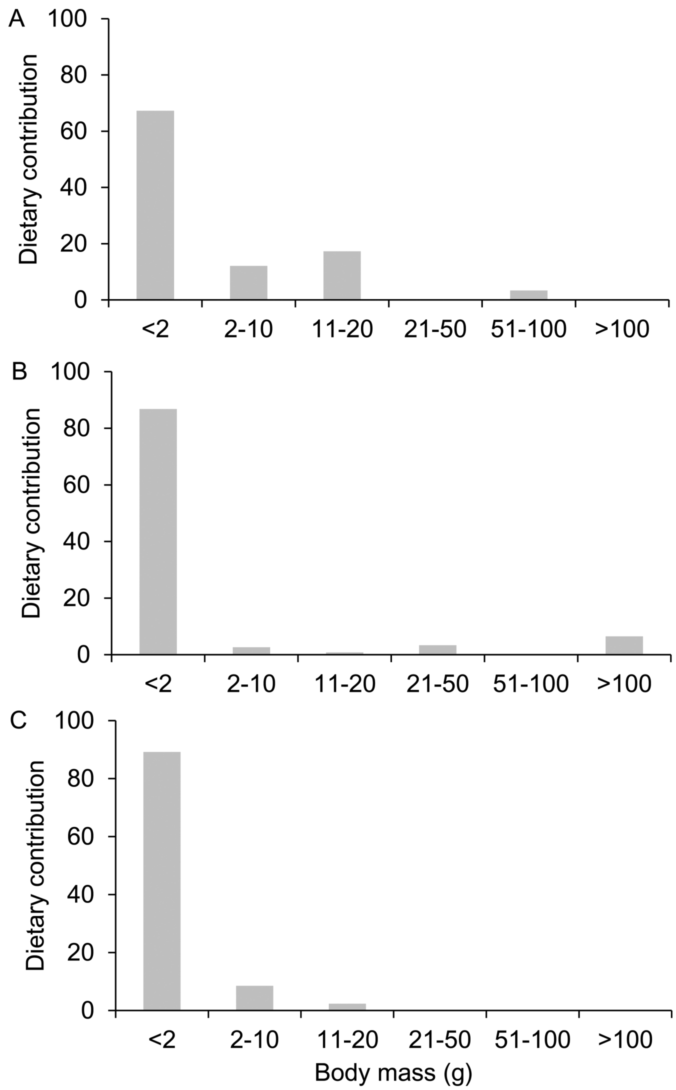

Fig. 5.—Dietary contribution (percent volume) of prey in different size classes for A) crest-tailed mulgara (*Dasycercus cristicauda*), B) kowari (*Dasyuroides byrnei*), and C) brush-tailed mulgara (*Dasycercus blythi*).

species occur in sympatry in the western Simpson Desert where the scats were collected (Pavey et al. 2011). The kowari formerly also occurred in the western Simpson Desert but it was extirpated early last century (Woolley 2005; Byrne in Mulvaney et al. 2000). The kowari had lower overlap with each of the mulgara species than the mulgaras had with each other. The kowari overlapped the most with the brush-tailed mulgara (0.74); the study populations of both species occupy stony desert. The lower overlap of the kowari with the mulgaras may have partly been a consequence of sampling for this species being confined to winter. The range of vertebrates and invertebrates available to capture may be reduced in winter, due to lower temperatures, than at other times of the year.

The dietary overlap (range of 0.69–0.85) that we quantified for the 3 carnivorous marsupials is within the range of overlap shown by assemblages of much larger carnivorous mammals in Africa and India (Hayward 2006; du Preez et al. 2017). For example, a study in Bandipur Tiger Reserve, India, showed overlap of 0.84 between tigers (*Panthera tigris*) and leopards (*P. pardus*), 0.75 between tigers and dholes (*Cuon alpinus*), and 0.93 between leopards and dholes (Andheria et al. 2007). The highest overlap within our study species was between the brush-tailed and crest-tailed mulgaras (0.85). Although these species occur in sympatry, they occupy discrete habitats. Specifically, the crest-tailed mulgara is confined to sand ridges, whereas the brush-tailed mulgara occupies stony desert (including gibber plain and cracking clay plain) and sand plain (Pavey et al. 2011). Individuals of the 2 species would rarely, if ever, encounter each other.

In summary, our study has revealed that the extant mid-range marsupial predators in arid Australia have a discrete trophic role as resident predators that capture a wide range of prey but take mostly arthropods. The reshaping of predator assemblages over the past century is likely to have resulted in the kowari and mulgara species experiencing increased predation pressure from the introduced carnivores, feral house cats and red foxes (e.g., Körtner et al. 2007). Given the dominance of small prey items in the diet of the marsupial predators, it is unlikely that the trophic niche of these species changed to include the larger prey items consumed by the western quoll. Dietary data indicate that the quoll in arid Australia functioned as a "scaled-up" version of the mid-range marsupial predators taking a wide range of invertebrates and smaller mammals but differing in consuming medium-sized and larger mammals greater than its own body size (Johnson and Roff 1982; Rayner et al. 2012).

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