

**Dietary niche breadth and overlap of four sympatric southern African
myrmecophagous mammal species inferred from the literature**

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Abstract

Five myrmecophagous mammal species occur sympatrically over large parts of southern Africa. Of these, the diets of four species have been studied in sufficient detail to facilitate interspecific comparisons. The diets of the armadillo *Orycteropus afer*, armadillo *Proteles cristatus*, bat-eared fox *Otocyon megalotis* and Temminck's pangolin *Smutsia temminckii* were compared based on the overall prey categories utilised and the proportion of each prey category in their diets, while Meller's mongoose *Rhynchogale melleri* had too few data to be assessed. Bat-eared fox fed on the greatest number of prey categories ($n = 116$) and had the greatest dietary niche breadth (4.71), while armadillo utilised the fewest prey categories ($n = 28$) and had the lowest dietary niche breadth (1.19) when analysing the proportion of each prey category in the diet at the genus level. Temminck's pangolin was the only species that was exclusively observed to feed on ants and termites. The diets of Temminck's pangolin and armadillo showed a moderate degree of overlap (0.49–0.57), but overlap was low between all other species pairs (0.01–0.26) when analysing the proportion of each prey item in the diet at the genus level. The results suggest that these myrmecophages have low to moderate dietary overlap, which combined with the high abundance of ants and termites and differences in their feeding ecologies likely reduces interspecific competition.

Key words: *Orycteropus afer*, *Otocyon megalotis*, *Proteles cristatus*, *Smutsia temminckii*, armadillo, armadillo, bat-eared fox, Temminck's pangolin

Introduction

Myrmecophagy (here referring to species preying on ants and/or termites) is widespread among both invertebrates and vertebrates (Redford 1987; Caldwell 1996; Pekár et al. 2013). More than 200 mammal species have been recorded feeding predominantly on ants or termites globally, *ca.* 25 of which are considered obligate myrmecophages (species whose diet consists at least 90% of ants and/or termites; Redford 1987). The prevalence of ants and termites in the diets of many species can be partly attributed to the near-circumglobal distribution of these taxa, which are a diverse and abundant constituent of biomass that have colonised nearly every terrestrial ecosystem (Hölldobler and Wilson 1994; Schoeman and Foord 2012). Although being an abundant food resource, the challenges associated with exploiting ants and termites (including dealing with their chemical defences, gaining access to their colonies and digestion constraints) has resulted in extreme specialisation and convergent evolution in many taxa that utilise them as prey (Melton 1976; Redford 1987; Abensperg-Traun and Steven 1997; Reiss 2001; Delsuc et al. 2014).

When different species rely on the same resource, use of the available resource should be partitioned spatially or temporally as the coexistence of two or more species partly hinges on these taxa utilising different environments and resources (Smith and Ganzhorn, 1996). Indeed, the competitive exclusion principle predicts that if the niches of two species overlap entirely, the weaker species will be outcompeted and excluded from the area (Gause 1934). Similarly, interference competition predicts that if there is competition between two species with regards to prey, the competitively weaker species should utilise a higher proportion of less nutritious prey as it is excluded from the more nutritious prey by its competitor (Milinski 1982).

Dietary niche breadth is defined as the diversity of prey items which a particular organism consumes and is a measure of dietary specialisation, with a catholic diet having a wider dietary niche breadth than a specialist diet (Colwell and Futuyma 1971). Similarly, dietary niche overlap is a measure of how similar two organisms' diets are (Colwell and Futuyma 1971). A high degree of overlap does not, however, necessarily mean that competition is taking place, especially if the resource is abundant (Jones and Barmuta 1998, Whitfield et al. 2013), if its use is separated in space or time (Schoener 1974; Kronfeld-Schor and Dayan 1999; Browning et al. 2014) or if there is some other mechanism separating resource use (Gause 1934) such as differences in prey handling strategies.

A generalist diet largely prevents resource competition and minimises energy spent finding food (Hanski et al. 1991; Symondson et al. 2002), while dietary specialisation can be the result of intense resource competition or resource depletion, among other factors (Futuyma and Moreno 1988; Berumen and Pratchett 2008). Dietary specialisation can be obligate or facultative, with obligate dietary specialists maintaining a narrow dietary niche breadth regardless of the abundance of their prey (Chanin 1981; Johnson et al. 1988; Gittleman 1994), while facultative dietary specialists are able to utilise additional food items outside of their usual dietary niche under certain conditions, such as when certain prey items become seasonally limited, or in certain areas (Elmhagen et al. 2000; Downs et al. 2003; Dalerum et al. 2012).

Five mammal species have converged on a myrmecophagous diet in southern Africa (here defined as the region south of the Zambezi and Kunene Rivers), viz. armadillo, *Orycteropus afer* (Pallas, 1766) (Melton and Daniels 1986; Willis et al. 1992; Taylor et al. 2002), armadillo, *Proteles cristatus* (Sparrman, 1783) (Kruuk and Sands 1972; Cooper and Skinner 1979; Richardson 1987; Anderson et al. 1992; de Vries et al. 2011), bat-eared fox, *Otocyon megalotis* (Desmarest, 1822) (Berry 1981; Nel and Mackie 1990; Kok and Nel 1992; Jumbam et al. 2019), Meller's mongoose, *Rhynchogale melleri* (Gray, 1865) (Ansell 1965; Smithers 1983) and Temminck's pangolin, *Smutsia temminckii* (Smuts, 1832) (Jacobsen et al. 1991; Richer et al. 1997; Swart et al. 1999; Pietersen et al. 2016). The armadillo, bat-eared fox and Meller's mongoose represent specialised carnivores, Temminck's pangolin is placed in the order Pholidota (together with other pangolin species), while the armadillo is placed in its own order (Hoffmann 2014; Green 2015; Taylor and Lehmann 2015; Pietersen et al. 2019). All five species are predominantly nocturnal, although all show some diurnal activity, especially during the Austral winter. The armadillo, armadillo, and bat-eared fox have broadly overlapping distribution ranges in southern Africa, while all five species occur sympatrically in the eastern and northern parts of the region (Hoffmann 2014; Green 2015; Taylor and Lehmann 2015; Pietersen et al. 2019).

Detailed dietary studies are surprisingly rare, even in the well-studied class Mammalia (Jones et al. 2009; Price et al. 2012; Davis and Pineda-Munoz 2016). Collecting dietary data from proxies such as stomach content analysis is difficult and often expensive (Kessler et al. 1981), while gathering these data from the literature comes with its own set of problems. Many published studies do not report diets quantitatively, while studies comparing the diets of

several species usually have to rely on existing datasets or published studies that often span different scales and use different methods to infer diets (Gagnon and Chew 2000; Cerling et al. 2003; Wilman et al. 2014). All these factors could impact the conclusions drawn from a study, depending on the research question being asked (Davis and Pineda-Munoz 2016).

No study has yet analysed to what extent armadillo, armadillo, bat-eared fox, Meller's mongoose and Temminck's pangolin are reliant on ants and termites as prey, and whether the diets of these five species overlap as a result. This study therefore aimed to determine the degree of dietary overlap among these five mammal species that are apparently dependent on the same prey. Although dietary overlap between species should ideally be investigated at a single site where all the species are present, across all seasons, and in combination with abundance data of the prey species, such a study would be logistically challenging. In the absence of such a study, we quantified dietary overlap among these five myrmecophagous mammal species using data from the literature. Considering that all five species occur sympatrically in at least portions of their respective ranges, combined with the morphological specialisations of each species, we hypothesise that there would be minimal overlap in the prey species selected. Furthermore, we hypothesise that the proportion of studies mentioning a prey item in the diet of a species can be used as a proxy for each prey item's abundance in that species' diet.

Methods

An initial examination of the peer-reviewed literature and subregion mammal reference guide (Skinner and Chimimba 2005) indicated that armadillo, armadillo, bat-eared fox, Meller's mongoose and Temminck's pangolin include large proportions of ants and termites in their diets (Ansell 1965; Kruuk and Sands 1972; Cooper and Skinner 1979; Berry 1981; Smithers 1983; Melton and Daniels 1986; Richardson 1987; Nel and Mackie 1990; Jacobsen et al. 1991; Anderson et al. 1992; Kok and Nel 1992; Willis et al. 1992; Richer et al. 1997; Swart et al. 1999; Taylor et al. 2002; de Vries et al. 2011; Pietersen et al. 2016; Jumbam et al. 2019). This study was restricted to southern Africa as the focal species are largely sympatric across most of this region (Hoffmann 2014; Green 2015; Taylor and Lehmann 2015; Pietersen et al. 2019), and most of the published dietary studies on these species emanate from this region. An exhaustive search was made in Google Scholar using the search terms "armadillo", "Temminck's pangolin", "Cape pangolin", "steppe pangolin", "armadillo", "bat-eared fox",

“Meller’s mongoose”, “*Manis temminckii*”, “*Smutsia temminckii*”, “*Otocyon megalotis*”, “*Rhynchogale melleri*”, “*Proteles cristatus*”, “*Proteles cristata*” and “*Orycteropus afer*”, with each search term successively combined with “diet”, “food” and “feeding”, respectively. All peer-reviewed literature and university theses were screened to verify whether they reported on the diet of at least one of the focal species in a natural environment in southern Africa. The reference list of each publication was further scrutinised for any additional appropriate studies, and any such studies were subsequently procured, examined, and if they met the above criteria, included in the analyses. Although Meller’s mongoose is reportedly a termite specialist (Ansell 1965; Smithers 1983), no studies detailing this species’ diet were found and it was therefore excluded from all analyses.

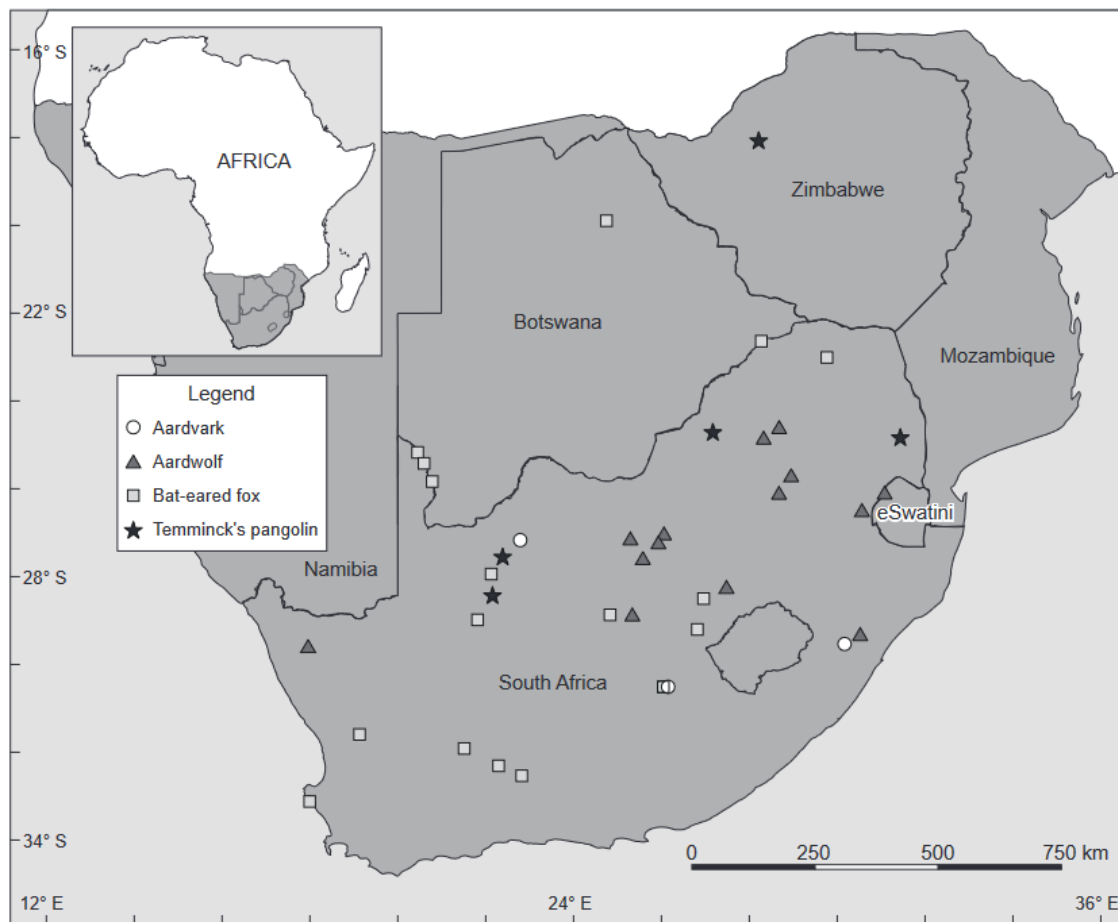


Figure 1: Location of the sites of diet studies of aardvark *Orycteropus afer*, bat-eared fox *Otocyon megalotis*, aardwolf *Proteles cristatus* and Temminck’s pangolin *Smutsia temminckii* in southern Africa. Some publications included data from more than one site; in instances where only a country was mentioned (i.e. Zimbabwe, Botswana and Namibia), these have not been plotted

Thirty-one studies reported on the diets of the four focal species (aardvark $n = 7$; aardwolf $n = 6$; bat-eared fox $n = 15$; Temminck's pangolin $n = 6$), with some studies recording the diets of more than one species (Fig. 1). These studies used different methods to record prey items in the diet, including direct observations, faecal content analyses, stomach content analyses, or combinations of these methods.

Dietary niche breadth and overlap were calculated using two approaches. First, dietary items reported in each study were recorded to the lowest reported taxonomic level, this typically being to genus but occasionally only to family or order. The number of studies mentioning each prey item in each species' diet was summed and this value expressed as a proportion of the studies on each species. This approach assumes that the main prey items for each focal species are likely to be reported in the majority of studies, while prey items that are rarely consumed should only be reported in a few studies. Although this approach is not as accurate as directly studying the proportion of each prey item in the diet, it should provide broad insights into dietary specialisation.

Second, the proportion of each prey item in the diet of each species was recorded to the lowest reported taxonomic level, using the 20 studies which recorded this information (aardvark $n = 4$; aardwolf $n = 4$; bat-eared fox $n = 9$; Temminck's pangolin $n = 3$). When a field study separately reported the proportion of each prey item in a species' diet using both direct observation and faecal analysis ($n = 4$), or at two different study sites ($n = 1$), we treated these as two separate studies, yielding effective sample sizes of $n = 6, 4, 10$ and 4 for aardvark, aardwolf, bat-eared fox and Temminck's pangolin, respectively. When a study reported the amount of time spent feeding on a particular prey species, this was converted to a relative proportion of the diet by expressing the time spent foraging on a particular prey species as a proportion of the total foraging time. When both the number of feeding bouts and time spent feeding on each prey category were reported, the total proportion of each prey item in the diet was calculated by multiplying these two values for each prey item and calculating the overall proportion. Similarly, when both the proportion of each prey item in a scat and the proportion of scats containing that prey item were reported, the overall proportion of each food item in the diet was calculated by multiplying these two values (Viljoen and Davis 1973; Cooper and Skinner 1979). For studies spanning multiple seasons or years, the proportion of each prey item in the diet was averaged across all seasons or years. Vegetable matter (specifically grass) and sand which was not intentionally ingested was excluded from the

analyses (see also Berry 1981; MacDonald and Nel 1986; Nel and Mackie 1990; Kok and Nel 1992; Matsebula et al. 2009).

Both datasets were analysed at various taxonomic levels (order, family, genus and species) to assess what impact these resolutions have on the results. This was achieved by merging all dietary categories to the lowest reported taxonomic level, up to and including the taxonomic level of interest.

Dietary niche breadth (B) was calculated using Levins' (1968) formula while dietary overlap was calculated using Schoener's Index (Schoener 1970). Dietary niche breadth and overlap are best analysed in conjunction with prey availability (Hurlbert 1978; Petraitis 1979; Wallace 1981), where systematic surveys of prey populations are undertaken simultaneously with the diet analysis to determine how abundant, and thus how available, each prey item is to the species under study. This is not always possible, however, and Schoener's Index is considered an adequate index of dietary overlap in the absence of resource availability data (Hurlbert 1978). Levin's Index provides a measure of the uniformity of individuals across niches, or in this instance, an indication of how many individuals use each of the available resources. Dietary niche breadth ranges from 1 to n , where n is the total number of dietary items recorded for the taxon under study. Schoener's Index provides a value between zero and one, with values closer to zero indicating a lower dietary overlap and values closer to one indicating a higher degree of dietary overlap. Both analyses were calculated using the species association analysis (*spaa*) package (Gotelli 2000; Zhang 2004) implemented in the software package R v. 4.0.2 (R Core Team 2020) through the RStudio interface (RStudio Team 2020). The analyses were run separately for the order, family, genus and species datasets.

Results

The four focal species cumulatively fed on 183 prey categories across four phyla and three kingdoms (Table 1; Supplementary Table S1). Bat-eared fox fed on the greatest number of prey categories ($n = 116$), while aardwolf showed the narrowest dietary range, feeding on 28 prey categories (Table 1; Supplementary Table S1). Both carnivores consumed vertebrates and plant material in addition to invertebrates, while armadillo also consumed plant material in addition to invertebrates. Only Temminck's pangolin preyed exclusively on invertebrates, and more specifically exclusively on ants and termites (Table 1; Supplementary Table S1).

Table 1: Prey species predated by aardvark *Orycteropus afer*, bat-eared fox *Otocyon megalotis*, aardwolf *Proteles cristatus* and Temminck's pangolin *Smutsia temminckii* in southern Africa. Prey items are presented at the lowest taxonomic level reported in the literature, aggregated to genus level for ants (Formicidae) and termites (Isoptera), to order for other arthropod taxa and to class or above for non-arthropod taxa. Numbers outside parentheses are the overall proportion of each prey item in the diet of each study species as calculated from those studies specifically recording prey proportions (when this could be calculated from the literature), with the number in parentheses indicating the number of studies that recorded each prey item in the diet of the study species. Not all studies investigated the proportion of each prey item in the diet of the study species, hence not all entries have numbers outside of parentheses. Kingdoms are shaded in grey

Higher taxonomy	Genus	<i>Orycteropus afer</i>	<i>Otocyon megalotis</i>	<i>Proteles cristatus</i>	<i>Smutsia temminckii</i>
ANIMALIA			1.27		
ARTHROPODA			0.34 (2)		
Class: Arachnida			0.09 (2)	(1)	
Order: Scorpiones			0.62 (7)	0.1 (1)	
Order: Solifugae			0.25 (5)	0.91 (1)	
Class: Insecta			0.32 (2)	0.02 (2)	
Order: Blattodea			0.11 (2)		
Suborder: Isoptera			(1)		0.15 (4)
Family: Hodotermitidae	<i>Hodotermes</i>	6.38 (6)	33.96 (12)	6.4 (5)	0.84 (2)
	<i>Microhodotermes</i>		(1)	0.05 (1)	
Family: Rhinotermitidae	<i>Psammotermes</i>	(1)			0.52 (1)
Family: Termitidae			21.64 (4)	0.12 (1)	(1)
	<i>Allodontotermes</i>	(1)			
	<i>Macrotermes</i>	(1)	(1)	0.02 (2)	
	<i>Odontotermes</i>	(2)	0.04 (1)	0.32 (2)	0.07 (3)
	<i>Pseudacanthotermes</i>	(1)		(1)	
	<i>Fulleritermes</i>			(1)	
	<i>Rhadinotermes</i>				0.01 (1)
	<i>Trinervitermes</i>	13.12 (7)	(2)	91.25 (7)	15.21 (5)
	<i>Amitermes</i>	(1)	0.04 (1)		
	<i>Angulitermes</i>	(1)			
	<i>Lepidotermes</i>			0.02 (1)	
Order: Coleoptera			14.24 (15)	0.02 (3)	
Order: Dermaptera			0.25 (2)		
Order: Diptera		0.02 (1)	(2)		
Order: Hemiptera			0.1 (2)		
Order: Hymenoptera			0.22 (4)		
Family: Braconidae	<i>Phanerotoma</i>		(1)		
Family: Formicidae		0.18 (3)	3.83 (7)	0.74 (4)	
	<i>Tapinoma</i>				(1)
	<i>Technomyrmex</i>				(1)
	<i>Aenictus</i>	0.32 (1)	(3)		0.01 (1)
	<i>Cerapachys</i>	(1)			
	<i>Dorylus</i>	2.27 (7)			0.01 (1)

<i>Acantholepis</i>	(1)			
<i>Anoplolepis</i>	66.29 (6)			32.66 (6)
<i>Camponotus</i>	0.29 (6)	(5)	(1)	12.67 (6)
<i>Lepisiota</i>				0.13 (3)
<i>Plagiolepis</i>	(1)			
<i>Polyrhachis</i>				0.37 (2)
<i>Tapinolepis</i>	(1)			1.82 (1)
<i>Crematogaster</i>	0.13 (6)			24.06 (4)
<i>Meranoplus</i>	(1)			
<i>Messor</i>	6.2 (4)			
<i>Monomorium</i>	3.28 (5)			0.32 (3)
<i>Myrmicaria</i>				1.19 (3)
<i>Ocymyrmex</i>	(1)			0.02 (2)
<i>Pheidole</i>	0.03 (5)			4.75 (4)
<i>Solenopsis</i>	0.06 (4)			
<i>Tetramorium</i>	(3)			4 (3)
<i>Anochetus</i>	(1)			
<i>Paltothyreus</i>				(1)
<i>Tetraponera</i>				1.2 (1)
Order: Lepidoptera		0.24 (4)	(1)	
Order: Mantodea		0.08 (2)		
Order: Neuroptera		0.21 (1)		
Order: Odonata		0.01 (1)		
Order: Orthoptera		4.64 (12)		
Subphylum: Myriapoda		0.2 (3)	0.02 (2)	
Class: Chilopoda		0.01 (3)		
Order: Scolopendromorpha		(1)		
Class: Diplopoda		0.19 (4)		
CHORDATA		1.27 (11)	(1)	
MOLLUSCA		0.11 (2)		
FUNGI		0.01 (1)		
PLANTAE	1.44 (2)	17.09 (12)		

Bat-eared fox showed the widest dietary niche breadth at the genus level for the proportion of studies dataset, while bat-eared fox and Temminck's pangolin showed nearly identical niche breadths at the genus level when analysing the diet proportions dataset (Fig. 2). Aardwolf showed the narrowest dietary niche breadth for both datasets at the genus level (Fig. 2). All four species had greater dietary niche breadths when inferred from the proportion of studies, with the dietary niche breadth of bat-eared fox being substantially broader than any of the other species (Fig. 2). Bat-eared fox showed the greatest dietary niche breadth at both the order and family levels for both datasets, while Temminck's pangolin showed the widest niche breadth at the lowest reported taxonomic level for the diet proportion dataset,

and bat-eared fox showed the broadest dietary niche breadth for the proportion of studies dataset at the lowest recorded taxonomic level. Aardwolf continuously displayed the narrowest dietary niche breadth for the diet proportion dataset regardless of the taxonomic level analysed, while Temminck's pangolin showed the narrowest dietary niche breadth for the proportion of studies dataset at the order and family levels, and aardwolf showed the narrowest dietary niche breadth at the lowest recorded taxonomic level for the proportion of studies dataset (Fig. 2).

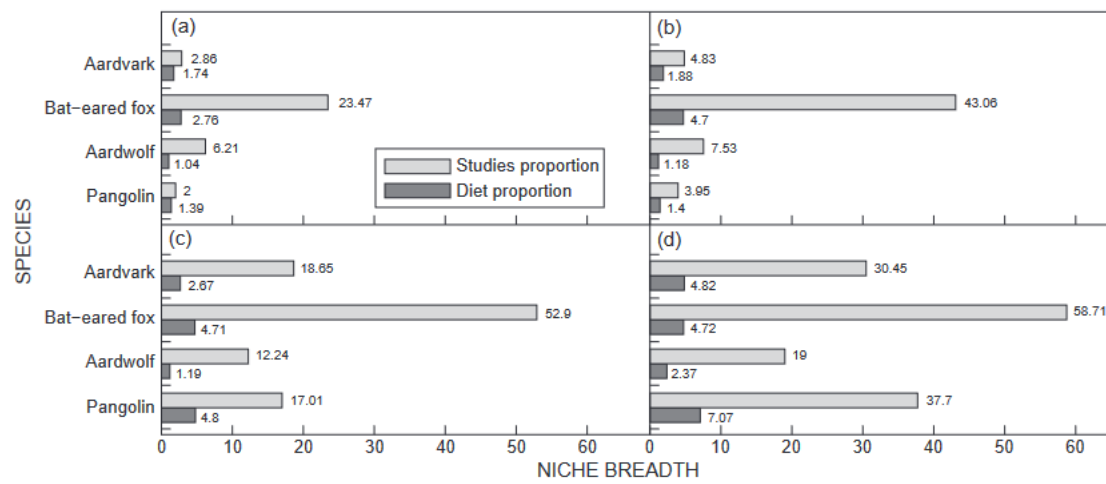


Figure 2: Levin's dietary niche breadth (B) of the aardvark *Orycteropus afer*, bat-eared fox *Otocyon megalotis*, aardwolf *Proteles cristatus* and Temminck's pangolin *Smutsia temminckii* in southern Africa. Data were compared based on the proportion of each prey item recorded in the diet of each species (dark grey bars), as well as the proportion of studies recording each prey item (light grey bars). Data were analysed at the level of (a) order, (b) family, (c) genus, and (d) species, or to the lowest reported taxonomic level up to and including the taxonomic level being analysed. Dietary niche breadth ranges from 1 to n, where n is the total number of dietary items recorded for the taxon under study

Temminck's pangolin had a high dietary overlap with aardvark (0.49) for the dietary proportions dataset when analysed at the genus level, while all other species pairs showed a low dietary overlap (0.01–0.20; Fig. 3). The proportion of studies recording each prey category indicated a similarly high dietary overlap between Temminck's pangolin and aardvark (0.57), while all other species pairs showed a relatively low dietary overlap (0.09–0.26; Fig. 3). These results were consistent across the four taxonomic levels analysed, although dietary overlap among the four species increased as the taxonomic level of the analysis increased (Fig. 3).

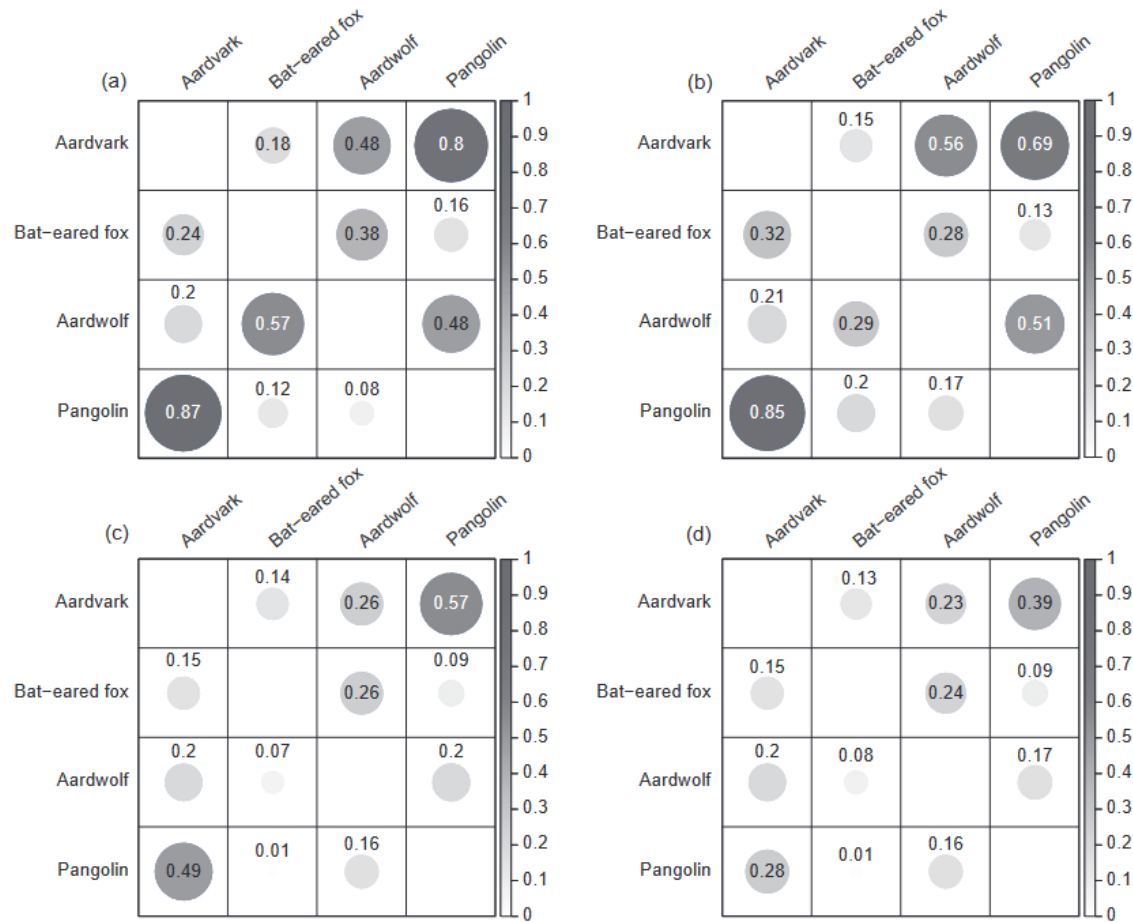


Figure 3: Dietary overlap between the aardvark *Orycteropus afer*, bat-eared fox *Otocyon megalotis*, aardwolf *Proteles cristatus* and Temminck's pangolin *Smutsia temminckii* in southern Africa, measured using Schoener's index. Prey categories were analysed at the level of (a) order, (b) family, (c), genus, and (d) species, or to the lowest reported taxonomic level up to and including the taxonomic level being analysed. Dietary overlap inferred from the proportion of each prey category in the diet is presented below the diagonal, while values above the diagonal refer to the proportion of studies recording each prey category. Values closer to 0 indicate a lower dietary overlap and values closer to 1 indicate a higher degree of dietary overlap

Discussion

The results of this study suggest that three of the four southern African myrmecophagous mammal species that were studied have low to moderately overlapping diets. Due to it feeding exclusively on ants and termites, Temminck's pangolin should be considered an obligate myrmecophage. Although both aardvark and aardwolf included additional prey items in their diets, ants and termites remained the primary prey (>90% of the diet), indicating that they too are obligate myrmecophages. A notable exception is a single aardwolf, in whose stomach *ca.* 50% of the volume consisted of *Gynanisa maja* (Saturniidae) moths, which were

erupting at the time (Smithers 1983). Despite including relatively large proportions of ants and termites in its diet (59.51%), the bat-eared fox has a very wide dietary niche breadth and a relatively low dietary overlap with the remaining three species. Considering this, the bat-eared fox should be classified as a dietary generalist, a conclusion also reached by most previous authors (Nel 1978; Kok and Nel 1992; Kuntzsch and Nel 1992; Klare et al. 2011; but see Jumbam et al. 2019).

Despite the convergent morphology and dietary overlap, the four myrmecophagous species studied here occur sympatrically across large portions of their respective ranges. One possible explanation is that although their diets overlap, ants and termites occur at sufficiently high densities and the relatively short foraging periods of each myrmecophage species because of prey dispersal and defences (Kruuk and Sands 1972; Redford 1983; Lindsey 1999; Swart et al. 1999; Taylor et al. 2002) are unlikely to result in the long-term decline of prey populations, thereby not noticeably affecting prey availability. Termites occur at an estimated density of 70–110 kg.ha⁻¹ in savannahs (Wood and Sands 1978), while ants occur at a biomass of up to 40 kg.ha⁻¹ in savannahs (Hocking 1970). This suggests that both ants and termites are an abundant resource in these ecosystems, lending credence to this hypothesis.

Another possible explanation is that the different feeding ecologies of the four species, together with differences in body size, may preclude competition. The bat-eared fox actively searches for prey, opportunistically feeding on items located on the soil surface, on low shrubs, caught from the air or by shallowly digging (Nel 1978, 1990; Koop and Velimirov 1982; Kuntzsch and Nel 1992; Jumbam et al. 2019). The aardwolf uses its broad, sticky tongue to lap up termites (and other prey) from the soil surface (Kruuk and Sands 1972; Richardson 1987; Anderson et al. 1992) and has also developed mechanisms to cope with the high terpenoid concentrations in its main termite prey (Richardson and Levitan 1994). By contrast, Temminck's pangolin and armadillo prey on ants and termites when these are inactive in their galleries, thereby presenting a clumped resource, and rely on their long, mucous-coated tongues to capture their prey (Jacobsen et al. 1991; Heath 1992; Lindsey 1999; Taylor and Skinner 2004). The armadillo is substantially larger than Temminck's pangolin (average adult mass 37.5–64.5 kg *versus* 6.0–16.1 kg; Skinner and Chimimba 2005; Supplementary Table S2) and because of their larger size and stronger claws they regularly dig through the hard exterior of epigeal termite mounds and also dig to deeper depths than Temminck's pangolin (Melton 1976; Lindsey 1999; Taylor et al. 2002; Taylor and Skinner 2003, 2004). Temminck's pangolin,

by contrast, makes shallow foraging digs to access prey galleries and open feeding ports and are unable to dig through the hard exterior of termite mounds (Jacobsen et al. 1991; Swart et al. 1999; Pietersen 2013; Pietersen et al. 2016). Although this suggests that armadillo may be preying on a different prey life stage than Temminck's pangolin, thereby representing segregation in resource use, this is not reflected in any of the studies directly examining armadillo stomach contents (Smithers 1971, 1983; Smithers and Wilson 1979) and most studies recorded predominantly adult ant and termite remains in the faeces (Taylor 1998; Lindsey 1999; Willis et al. 1992). Although soft-shelled invertebrate eggs and pupae are likely to be digested considerably faster than the keratinous exoskeletons of adults, the absence of prey life stage separation between the diets of armadillo and Temminck's pangolin in those studies that examined gut contents suggests that the apparent lack of differentiation in prey life stages being depredated is likely genuine.

The dentition of the four species is broadly congruent with their dietary niche breadths (Supplementary Table S2). Temminck's pangolin is edentate (Heath 1992; Skinner and Chimimba 2005) and is the only species to exclusively feed on ants and termites. The armadillo has reduced dentition consisting of premolars and molars (Melton 1976; Skinner and Chimimba 2005) and shows a similar prey selection to Temminck's pangolin, although also including seeds (presumably mostly inadvertently) in its diet. Even when feeding on ants, armadillo periodically masticate, presumably to chew ingested seeds (Skinner and Chimimba 2005). The armadillo has incisors, canines, premolars, and a reduced number of molars (Skinner and Chimimba 2005), in line with its broader diet. The bat-eared fox has the most advanced dentition, having 14–18 more teeth than the armadillo (Skinner and Chimimba 2005), and also has the broadest diet.

Although the current study in some instances relied on relatively small sample sizes and the methods and durations of the studies varied, these differences are unlikely to have significantly influenced the findings. We hypothesised that the proportion of studies mentioning a prey item could be used as a proxy for each prey item's abundance in the diet of the focal species. This hypothesis was largely upheld by our results, with the relationship between dietary niche breadth among the four focal species remaining fairly consistent regardless of whether the study proportions or dietary proportions dataset was analysed. The study proportions dataset did, however, consistently indicate a greater niche breadth for each focal species than did the dietary proportions dataset. This is probably because there are

fewer studies recording the proportions of each prey item in the diet of each focal species, and we believe that with increased sampling the calculated dietary niche breadths using the studies proportion and diet proportion datasets would converge. Another potentially confounding factor is the geographic location of the various studies. Although this likely influenced the prey species recorded in each study owing to their distribution and thus availability, this bias has largely been circumvented by analysing the diet at the genus level or above. It is unlikely that additional studies will greatly increase the dietary niche breadth, at least at the genus level or above, of any of the study species as many of the studies included here were in-depth and spanned multiple years.

This study is the first to compare the dietary overlap amongst these four southern African myrmecophagous mammal species. Contrary to our expectations, Temminck's pangolin and aardvark showed relatively high levels of dietary overlap, while the remaining species pairs showed fairly low levels of dietary overlap, in support of our hypothesis. The diets of all four species largely reflected their morphological adaptations and foraging ecologies, in support of our hypothesis. Much additional work remains to further study both the degree of dietary overlap among these four species, as well as the underlying mechanisms facilitating such overlap. This includes comparing the diets of the four species across their geographic ranges to assess the extent to which diets vary regionally. Another interesting avenue would be to compare the diets of the aardvark, aardwolf and Temminck's pangolin in areas where one or two of these species are absent or where they occur at different densities, to determine whether there is a dietary shift in the absence of a competitor. The ecological consequences of potentially losing one of these myrmecophagous predators should also be assessed, especially considering the high levels of exploitation of Temminck's pangolin for the illegal wildlife trade (Bräutigam et al. 1994; Baiyewu et al. 2018).

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