

Spatial and temporal variation in the use of supplementary food in an obligate termite specialist, the bat eared fox

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Abstract

The bat-eared fox (*Otocyon megalotis*) is considered a termite specialist. However, studies of its diet have been limited to indirect methods such as scat and stomach content analyses, resulting in intraspecific dietary variations due in part to methodological differences. Because diet plays a central role in the social dynamics of these canids, we hereby contribute further to our knowledge about their dietary habits. We present 2-year data of direct observations of foraging bouts of 19 habituated bat-eared foxes in the Kalahari Desert of South Africa, as well as data on seasonal variation in invertebrate prey communities obtained through pitfall and sweep net trapping. Despite showing a diet breadth reflective of a specialised forager across all seasons, foxes exhibited substantial seasonal variation in diet breadth with a broader range of food categories utilized in summer compared to the other seasons. Supplementary food categories appear to not have been utilized opportunistically, but it is unclear what drove the preference for some food categories over others. A literature review indicated strong effects of local conditions on the utilization of supplementary food across southern Africa. Our data support bat-eared foxes as obligate termite specialists but highlight that they appear to have the ability to show dietary flexibility based on both temporal and spatial variations in food abundance.

Keywords: Diet breadth, food availability, *Otocyon megalotis*, seasonal variation, termite specialist

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Introduction

Specialist foragers are characterised by consistently consuming their main prey to a greater extent than expected based on its abundance (Fox and Morrow 1981). This contrasts with generalist predators which typically only start to consume a particular prey type once it has reached a specific threshold in abundance (Hassel and Comins 1978). Factors contributing to specialist foraging strategies include intense resource competition (Futuyma and Moreno 1988) and resource depletion (Berumen and Pratchett 2008). Factors promoting generalist foraging strategies include avoidance of resource competition (Hanski et al. 1991; Symondson et al. 2002), minimising energy costs associated with prey search (Hughes 1979), and selecting prey to achieve a nutritionally balanced diet (Bernays and Minkenberg 1997). These contrasting dietary strategies can have profound impacts on the population dynamics of both predators and prey (Anderson and Erlinge 1977). Because specialised predators feed only on a limited set of prey and continue to feed on these prey types even at very low abundances, specialist strategies are associated with high risk of species decline due to resource depletion (Dalerum and Swanepoel 2017). Generalist predators, by comparison, can still thrive if a particular prey class declines, since they switch to supplementary prey instead. Because they stop feeding in a particular prey at low densities, they are generally regarded as having stabilizing effects on prey populations (Reid et al. 1997).

Both specialist and generalist strategies can either be obligate or facultative. In obligate specialists, predators maintain a narrow diet breadth even in the presence of supplementary prey, whereas facultative specialists have the capacity to utilize supplementary prey under certain conditions (Taylor 1984). Similarly, although generalist species typically have a broad diet breadth, some species may adapt specialist strategies either at specific points in time or in specific areas. For instance, the Arctic fox (*Vulpes lagopus*) is a small canid that exploits a vast range of food resources in coastal areas (Dalerum et al. 2012), but is highly specialised in tundra areas where there are limited resources (Elmhagen et al. 2000). The European otter (*Lutra lutra*), on the other hand, is highly specialised on fishes which constitute $\geq 80\%$ of its prey base regardless of seasonal variations (Chanin 1981). Similarly, the stoat (*Mustela erminea*) is an obligate rodent specialist (Erlinge 1983), whose sole reliance on rodents have been suggested as one of the driving causes for temporal fluctuations in rodent abundance (Anderson and Erlinge 1977).

One challenge in categorising predators along the specialist–generalist continuum lies in generating information on variation in diet breadth across time and space, both within and between populations. For instance, the diet of the arctic wolf (*Canis lupus arctos*) has been shown to vary considerably between environments with different prey availability (Dalerum et al. 2018). Across temporal scales, the raccoon dog (*Nyctereutes procyonoides*) has been shown to have a wider diet range in summer than in winter (Sutor et al. 2010), and the diet composition of the red fox (*Vulpes vulpes*) fluctuates with availability of its predominant prey, *Microtus* spp. (Dell'Arte et al. 2007). Similarly, the diet composition of black-backed jackals (*Canis mesomelas*) is markedly influenced by both geographic and seasonal variation in prey abundance, as well as in seasonal variation in the physiological needs of nursing mothers (Klare et al. 2010; Kamler et al. 2012; Van de Ven et al. 2013).

The bat-eared fox (*Otocyon megalotis*) is a small canid that feeds predominantly on termites (Berry 1981; Nel 1984, 1990; Stuart et al. 2003), with jaw musculature well adapted to its insect prey (Clark 2005; Grant and Samways 2015). Termites play a central role in the social dynamics of the bat-eared fox by promoting communal foraging and socialisation among group members (Nel 1984), which enhances group participation in anti-predatory strategies

(Clark 2005) thus enabling sustenance of this species. However, emerging studies suggest that the bat-eared fox may exhibit substantial intraspecific variation in its foraging habits, including a high consumption of wild fruits and non-invertebrate prey in some populations (Kuntzsch and Nel 1992; Klare et al. 2011; Kamler et al. 2012). We acknowledge that some of the discrepancies have likely been caused by methodological differences, where most previous diet studies have used scat or stomach content examination (Nel 1978; Berry 1981; Kok and Nel 1992; Kuntzsch and Nel 1992; Stuart et al. 2003), and others have included random or *ad hoc* direct observations (Kleiman 1967; Lamprecht 1979; Koop and Velimirov 1982; Nel 1984, 1990; Malcolm 1986; Nel and Mackie 1990; Lourens and Nel 1990). However, these findings suggest that this obligate termite specialist appear to be able to utilize locally abundant supplementary food resources in different parts of its range.

To explore if such dietary variation also exists within a single population, we implemented an alternative approach to diet assessment which involved daily animal observations on foot in the wild, for two years. To our knowledge, this is the first time that wild bat-eared foxes have been closely observed on a daily basis over a long-term period to expressly describe their foraging behaviour. We also conducted a crude assessment of prey availability for a better understanding of their diet choices. Prey abundance assessments are essential for understanding the underlying reasons for a predator's dietary strategy (Holling 1959a,b). Our explicit aim was to address the following questions: (1) What is the seasonal variation in diet breadth of this population of bat-eared foxes at the study site in the Kalahari Desert? (2) What is the seasonal variation of its alternative (non-termite) prey at the study site? (3) How do our findings correspond to the diet of other bat-eared fox populations in southern Africa?

Methods

Study area

The study was conducted at Kuruman River Reserve (KRR, 28°59'S, 21°49' E) in the Northern Cape Province of South Africa, where a wild population of bat-eared foxes had been habituated to close range observations on foot (see detailed procedure below). KRR covers an area of 33 km² with Kalahari Thornveld vegetation and sandy dunes dominated by perennial grasses (Clutton-Brock et al. 1999). This study location experiences four distinct seasons with the coldest temperatures dropping below 0°C in winter (June–August) and the hottest in summer (December–February) averaging to 40°C (Périquet and le Roux 2017). Seasons were defined as summer (December–February), autumn (March–May), winter (June–August) and spring (September–November).

Study population and foraging behaviour recordings

Pregnant or lactating females were excluded from analyses to standardize reproductive status that could influence physiological needs. Our study population consisted of eight non-lactating adult females and eleven adult males located in three sections of the reserve (Figure 1). As foraging areas overlapped between most individuals, and because social interactions did not suggest any clear boundaries between individuals, we do not associate these sections with unique social groups. Individuals were either equipped with VHF collars or had unique natural markings such as earlobe indentations that allowed for their identification in the field. The habituation process involved targeting artificial animal watering holes frequented by foxes and baiting them with raisins. An observer would sit still

a few meters from the baited area, occasionally humming and rattling a raisin packet until the animals got accustomed to their presence. This process gradually advanced to the observer slowly walking around and then following the animals, which had come to associate the hum and bag rattle to a raisin treat. To minimise foraging interference, raisin treats were limited (*ca* 10 grains) and each fox was followed once a week, with data recording only starting after the animal resumed its normal activities. Animals were followed daily for two hours between dusk and dawn, and foraging behaviour recorded on an Android Samsung tablet programmed with Cyber tracker software (www.cybertracker.org). Diet data were collected from July 2014 to April 2016, resulting in a mean observation time of 57 h per individual (SD = 29 h). Based on the close proximity of observers to study animals (2–5 m), most prey items (averaging 60%) consumed over the duration of the study were easily identifiable. Large prey items such as beetles or grasshoppers could easily be identified by the observer when the fox chased after such prey. Additionally, the fox would often spend time chewing at the head of its prey, which gave observers ample time to confirm the prey type from the rest of its body parts sticking out of the fox's mouth or lying on the ground. Smaller prey such as termites and ants that occur in clumps were also easily identifiable as animals would spend considerable time in the same location when foraging. The challenge was with small and solitary prey items hidden underneath foliage or vegetation (possibly insect larvae), which could not be identified and were thus excluded from data analyses. In such instances, the observer would confirm that the fox had successfully obtained prey from its jaw movements or chewing sounds. These unseen prey items were recorded as “unknowns” but were omitted from data analyses.

Pitfall and sweep net data

Prey availability was estimated from a total of 360 pitfall traps deployed across winter, summer and autumn, with spring season forfeited due to logistical challenges in the field. These pitfalls were deployed at eight randomly chosen sites within the demarcated areas where habituated foxes foraged (Figure 1). Pitfall layout in each site consisted of three parallel rows termed “transects” which were spaced out 10 m apart with each transect measuring 20 m in length and consisting of five pitfall traps planted 5 m apart. Therefore, each pitfall layout per site consisted of a total of 15 traps with an overall sum of 120 traps collected across all eight sites per season. The trap dimensions were 6 x 6.5 cm (diameter by height) and volume *ca* 184 ml. Traps were half-filled with 75:25 water and propylene glycol mixture, a low toxicity mixture harmless to wildlife and suitable for trapping invertebrates (Braschler et al. 2010). Pitfalls were deployed in the morning and left undisturbed for three consecutive days (*ca* 72 h) before collection on the third day.

After collection, pitfall trap samples were immediately washed using a fine-mesh sieve to remove debris before storing content in 70% ethanol. Invertebrates were identified using Leica MZ-6 and MZ-12 stereomicroscopes and the taxonomic reference book *Insects of Southern Africa* (Scholtz and Holm 1985). Although pitfall traps are a widely utilised method for quantifying invertebrate communities (Botes et al. 2006; Braschler et al. 2010), they can bias estimates against some invertebrates such as termites (Kuntzsch and Nel 1992) and flying insects (Doxon et al. 2011). To alleviate some of these methodological biases, we added sweep net data for a broader representation of invertebrates in the study area. Data were collected along the same transects used for pitfall trapping as described above, by sweeping (42 cm diameter sweep net ring) across and above vegetation patches, using

synchronized effort of sixty pendulum sweeps for five minutes per site. Insects caught were immediately emptied into labelled containers with 70% ethanol for later identification. We collected sweep net data on the same day as pitfall data collection but only in summer and autumn seasons due to logistical challenges in the field.

Data Analysis

We expressed dietary proportions as relative percentage of occurrence (RPO), quantified as the number of identified items of a food category divided by all observed ingested diet items, multiplied by 100. Unknown prey items were excluded from analyses and we used the levels of class and order to define categories of known prey items. Prey availability proportions were derived from pooling together seasonal data per site (Figure 1) and dividing the sum of each food category (defined as above into class or order) by its corresponding seasonal data. Levins standardised index (Smith 1982) was used as a measure of diversity index, defined here as:

$$B_i = \frac{B - 1}{n - 1}$$

where B_i = standardised index of niche breadth; ranging from zero to one (highest prey diversity index), B = Levins index in un-standardised form and n = number of food categories. We calculated the un-standardised B following Levins (1968) formula as:

$$B = \frac{1}{(\sum P_i^2)}$$

where P_i = proportion of food category i per pitfall site or in an individual diet. Due to lack of dimorphism in these canids and the exclusion of pregnant or lactating females from our analyses, there was no *a priori* expectation for sex to influence diet breadth (Nel 1990). Diet data analyses were conducted on all prey types including Isoptera (Table 1). In the analysis of prey availability data, we excluded a negligible quantity (< 0.001% RPO) of Isoptera and non-prey bycatch such as Zygentoma.

Statistical analyses were performed in R (R Core Team 2018) with significance level set at 0.05. We used Linear Mixed-Effects Models (LMMs) to investigate the effect of season on Levins standardised index (B_i) calculated on diet and prey availability data. Our observation unit for diet data comprised of nineteen bat-eared foxes from which we calculated B_i values per individual fox per season. For prey communities, we based our calculations on invertebrate abundance for each season per site. We added animal identity (in the model on diet data) and pitfall location (in prey availability data) as random factors. To adjust for variance heterogeneity, we added a variance power function to the model on prey availability data and we log transformed the diet data. We evaluated the significance of season using likelihood ratio tests (LRT) and used the 'lsmeans' package (Lenth 2016) to conduct pairwise contrasts between each pair of seasons with alpha set at 0.05 using Tukey adjustment for multiple comparisons to determine significant differences between the seasons.

Literature compilation on bat-eared fox diet

To further quantify geographic variation in the dietary habits of this species, we conducted a literature survey of bat-eared fox diet studies across South Africa. We narrowed our survey

to seven articles based on their comprehensive prey lists, to better understand diet breadth in these canids. Because all studies were either conducted on scats or stomach content, we provided RPO of stomachs containing prey items (Kok and Nel 1992) or RPO of prey items in scats (Stuart et al. 2003). In studies with varied diet quantification methods such as percentage volume of prey items in faeces and percentage occurrence of prey items in faeces (e.g. Nel and Mackie 1990), we chose the latter, to keep comparisons across studies standardised. All dietary proportions per study represented here were expressed as RPO with any deviation from 100% resulting from the exclusion of rare items (e.g. feathers) from our table. We also excluded non-prey items such as grit and sand (Kok and Nel 1992), and unidentified matter such as hair and bones (Nel 1978). We used our study list of 18 food items as the template for comparison with other studies due to the shared commonality of prey items between most studies. Lastly, in the few instances where seasonal data were available, we averaged the data across seasons.

Results

Seasonal effect on diet breadth

A total of 18 different prey categories were recorded from dietary observations (Table 1). Isoptera was the most consumed prey category with an average RPO of *ca* 70% in fox diet across all seasons. Its consumption peaked in autumn (82%) and winter (76%) but declined in the warmer months of summer and spring ($\leq 65\%$). Other invertebrate prey categories consumed in relatively large amounts included Coleoptera (11%), Hymenoptera (8%) and Orthoptera – specifically grasshoppers (5%). Least prominent prey categories in fox diet ($< 0.05\%$) were Diplopoda and Amphibia.

There was a significant effect of season on bat-eared fox diet breadth ($\chi^2 = 29.6$, $df = 2$, $p < 0.01$), with foxes having had a significantly wider diet breadth in summer (Figure 2) than in every other season (winter: $t_{91} = 3.00$, $p_{adj} < 0.01$; spring: $t_{81} = 2.50$, $p < 0.01$; autumn: $t_{91} = 3.75$, $p_{adj} < 0.01$). The narrowest diet breadth was in autumn, which differed significantly from all seasons except winter ($t_{95} = 1.8$, $p_{adj} = 0.07$), while spring and winter did not differ significantly from each other ($t_{81} = 1.00$, $p_{adj} = 0.33$). Levins standardised index was on average very low across all seasons ($B_i < 0.5$) denoting a narrow diet breadth in these animals.

Seasonal influence on invertebrate composition

The non-termite invertebrate community from both pitfall and sweep net data comprised of a total of 10 insect categories of which Hymenoptera and Coleoptera dominated in both sampling datasets (see Table 1). Season did not significantly influence invertebrate composition (pitfall: $\chi^2 = 3.70$, $df = 2$, $p = 0.15$; sweep net: $\chi^2 = 0.30$, $df = 2$, $p = 0.63$, Figure 3).

Invertebrate variation across South African provinces

Invertebrates dominated bat-eared fox diets across all provinces (Table 2). Isoptera was the most frequently consumed food category with an average RPO of 33% in diet across all studies. Also featuring prominently across various diet studies was Coleoptera, which was the most consumed invertebrate prey item in the Western Cape (24.2%), as well as the Free State and Northern Cape studies (21.4%). Coleoptera was the third and fourth most

consumed food item in the three remaining studies from the Northern Cape and Limpopo provinces, respectively. Completing this list of the most consumed invertebrates across the provinces is Hymenoptera, with an average of 13.1% occurrence in diet across all diet studies, consistently ranking third in all four of the Northern Cape diet studies including this study, as well as in one study from the Free State. Orthoptera and Arachnida ranked fourth and fifth in several diet studies while the least consumed food categories included Neuroptera, Lepidoptera, Hemiptera, Mantodea and Diplopoda.

Non-invertebrate diet variation across South African provinces

Plant material (seeds and wild fruits) had the highest dietary contribution ($\geq 29.3\%$) in two Northern Cape studies, and second highest in Limpopo, Free State and Northern Cape studies ($\geq 17.5\%$). Mammals were the second most abundant non-invertebrate prey in half of the fox studies (4.0% occurrence on average) but were rarely consumed in this study (0.25% occurrence), and absent in three other studies (Table 2). Ranking third in fox diet were reptiles with occurrences between 0.1–1.9% across most studies, except for the Free State, Western Cape and in one Northern Cape study with no record of reptiles in fox diet. Lastly, while Limpopo Province had the highest record of amphibians in fox diet (0.4%), this prey was the least consumed in our study (0.01%) and absent in five other studies. We therefore considered it a food category of least importance to these foxes, together with fungus (0.11%) which was only present in this study.

Discussion

Isoptera was the most consumed invertebrate food category by bat-eared foxes, which confirms the results of previous studies suggesting that these canids to a large extent depend on this prey (Berry 1981; Nel 1984, 1990; Stuart et al. 2003). However, despite this reliance on a single prey type, we found seasonal variation in bat-eared foxes' diet breadth, with the broadest variety of prey items consumed in summer. This mirrors previous studies that have examined seasonal effects on the diet of this, and other, canids, such as the raccoon dog (Sutor et al. 2010; Klare et al. 2011). The narrow diet breadth seen in this study during the colder months of autumn and winter appears to have been caused by an absence of supplementary prey during these months, such as Diplopoda, Hemiptera, Reptilia and Amphibia. Such an interpretation is supported by our observations of a significant reduction in the dietary contribution of termites during the warm and wet months of spring and summer, which coincided with an increased consumption of supplementary prey. Hence, despite their heavy reliance on Isoptera, bat-eared foxes exhibited some dietary flexibility and appear to have used supplementary non-termite prey if available. Such utilization of supplementary prey have previously been observed both in this and other facultative specialists (Waser 1980; Sutor et al. 2010; de Vries et al. 2011; Klare et al. 2011; Grant and Samways 2015). Utilization of supplementary prey may improve the energy budgets of a predator by reducing the costs associated with prey search (Hughes 1979) and could thus be an adaptive feeding strategy even for obligate specialists such as the bat-eared fox.

Our dietary observations further suggest that the utilization of supplementary prey may not have been opportunistic, but that some prey were preferred while others selected against. This selectivity among supplementary prey appears to have been most pronounced during summer. They appear to have fed on large prey if available, such as Coleoptera and Neuroptera, although they did not necessarily seem to have selected for prey based on

nutritional value. For instance, Coleoptera has higher energy (266 kcal/100g) and protein content (20.2% weight for weight; *w/w*) than some less utilized prey, such as Hymenoptera (128 kcal/100g vs 17.4% *w/w* respectively) (Bukkens 1997), but the utilization of Coleoptera appear to have been lower than what could have been expected based on their relative abundance in the traps. Similarly, Orthoptera (≤ 200 kcal/100g) (Bukkens 1997; Ramos-Elorduy 2008) and Scorpiones (331 kcal/100g) (Abulude et al. 2006) both have high energy content but appear to only have been used more than expected based on their relative occurrences in the traps during summer. However, Neuroptera, with a very high energy content (550 kcal/100g) (Robel et al. 1995), was consistently utilized more than what could be expected based on their relative occurrence in the traps, and Arachnida, with a low energetic value (≤ 5.74 kcal/100g) (Norberg 1978), was consistently utilized less. Hence, we suggest that the observed utilization of alternative prey may not have been opportunistic, but it is unclear what factors were driving the preference for certain supplementary prey over others.

Seasonal impact on bat-eared foxes' diet breadth

Insect development is temperature-dependent with warmer temperatures promoting larval growth (Ratte 1984). Seasonal variation in invertebrate communities have also been strongly linked to variation in rainfall, and invertebrate seasonality appears to be a consequence of interactions between temperature, water availability and the life history tactics among and within individual species (Wolda 1988, Nylin and Gotthard 1998). In most environments, these processes result in a higher abundance and diversity of invertebrates during warm and wet seasons. These results are confirmed by our study where a higher invertebrate diversity was recorded in summer. Subsequently, since foraging behaviour of the bat-eared fox is closely linked to invertebrate activity patterns (Lourens and Nel 1990), variations in rainfall and temperature appear to directly influence utilisation of alternative invertebrate prey by the bat-eared fox. We note, however, that in our study the seasonal variation in invertebrate communities was only partly reflected in bat-eared fox diet breadth. Although this finding may have been influenced by our sampling effort which was limited to two seasons, it nonetheless re-iterates our previous suggestion that alternative prey utilization by this species may not be entirely opportunistic.

Bat-eared fox diet pattern across different geographic locations in South Africa

Isoptera was one of the most utilized prey across most studies. These results generally confirm bat-eared foxes as being largely an obligate dietary specialist on termite prey. However, we note a disparity between the dietary proportions of Isoptera found in this and other studies, with more than a twofold difference in the dietary contributions. Although some of these differences could have been caused by real dietary differences, we suggest that a large part of this difference can be attributed to sampling differences. We quantified dietary contributions directly as proportion of individual diet items consumed, whereas the other studies have relied on indirect methods such as content in faeces or stomachs. Hence, our method would bias dietary contributions towards small prey that are fed on in higher frequencies.

We note a consistent occurrence of Isoptera, Coleoptera and Hymenoptera as the top three most utilized invertebrate prey categories in two of the Northern Cape studies (including this study), and in the Free State Province. These study locations share common microclimatic abiotic factors suitable for survival of these top three prey types, such as

fynbos vegetation cover (Stuart et al. 2003) and Karoo veld vegetation cover (Clutton-Brock et al. 1999; Stuart et al. 2003; Welch et al. 2017). These types of vegetation cover have been shown to increase Hymenoptera abundance, particularly of tramp species such as *Anoplolepis custodiens* which use fynbos vegetation cover for nesting and as energy source in the Cape Floristic Region (Botes et al. 2006). In addition to vegetation cover, these study sites also experience moderate annual rains of ≤ 500 mm (Stuart et al. 2003; Welch et al. 2017) which is a significant contributing factor to Hymenoptera species richness (see Botes et al. 2006).

By contrast, study sites in which these invertebrate prey categories were not utilized heavily have different vegetation structure and microclimatic conditions that appear to influence bat-eared fox diet. For instance, Nama Karoo is the prevailing vegetation structure (> 90%) in a study where plant material dominated fox diet (Klare et al. 2011). In another study with high content of plant material in fox diet, the study location is characterised by scrub savanna vegetation and heavy rainfall (Berry 1981). These microclimatic conditions differ from those of our study site with predominantly Karoo veld vegetation accompanied by dominant alternative prey such as Coleoptera and Hymenoptera, all of which highlight the influence of environment on the diet and foraging ecology of these canids.

Study limitations and way forward

While direct observations are useful in understanding the foraging behaviour of predators, we acknowledge a few shortcomings with our methodological approach. Firstly, direct observations quantified as RPO biased dietary contributions towards small and commonly used prey such as termites. We suggest that future studies include weight measurements of prey and volumetric analyses of each prey category to avoid such biases. Secondly, our sampling efforts and techniques in assessing the invertebrate community in our study site were limited. This reduced our analytical power, an in-depth understanding of the invertebrate community, and the relationship between fox diet and their prey base. We advise long-term monitoring of invertebrate communities and the use of multiple invertebrate sampling techniques that will capture the wide spectrum of invertebrates in the environment. Such a comprehensive invertebrate dataset will highlight any patterns in invertebrate abundance or decline, as well as how foxes relate to these changes. Finally, we acknowledge that differences in diet content across our literature survey may have been influenced by the diverse methodological approaches (e.g. scats, stomach contents) utilised in the different studies. Nonetheless, the literature survey provides an overall view of the variety of prey items foraged on by foxes in different locations across South Africa and it highlights the important role of their microhabitats on their prey choices. With the improved data techniques suggested above, direct observations can provide great in-depth on the foraging behaviour of these canids that would otherwise not be captured by other techniques.

Conclusions

Our data support results from previous studies that have defined the bat-eared fox as an obligate termite specialist. Despite this specialisation, we noted substantial differences in diet breadth across seasons. Our data suggest that the utilization of alternative prey was not entirely opportunistic, but it is unclear what was driving the preference of certain alternative prey over others. Comparisons of dietary content found in studies across South

Africa revealed a strong effect of local environmental conditions on the relative dietary contributions of supplementary prey, which lends further support for the ability of this species to adapt its dietary strategies to spatial and temporal variation in food availability. However, we suggest that further studies provide direct quantification of dietary strategies using combined and, if possible, un-biased assessments of dietary contributions and abundance of the main and alternative prey classes used by this species.

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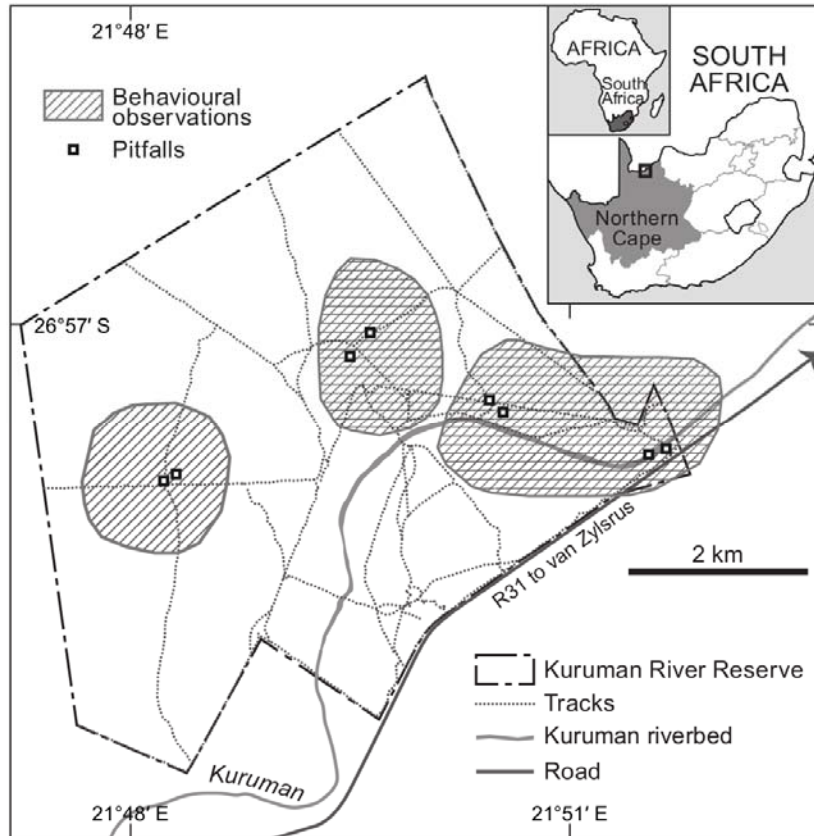


Figure 1: Study site showing pitfall trap locations (squares), unpaved roads (tracks), and home ranges (grey enclosures) where behavioural studies were conducted.

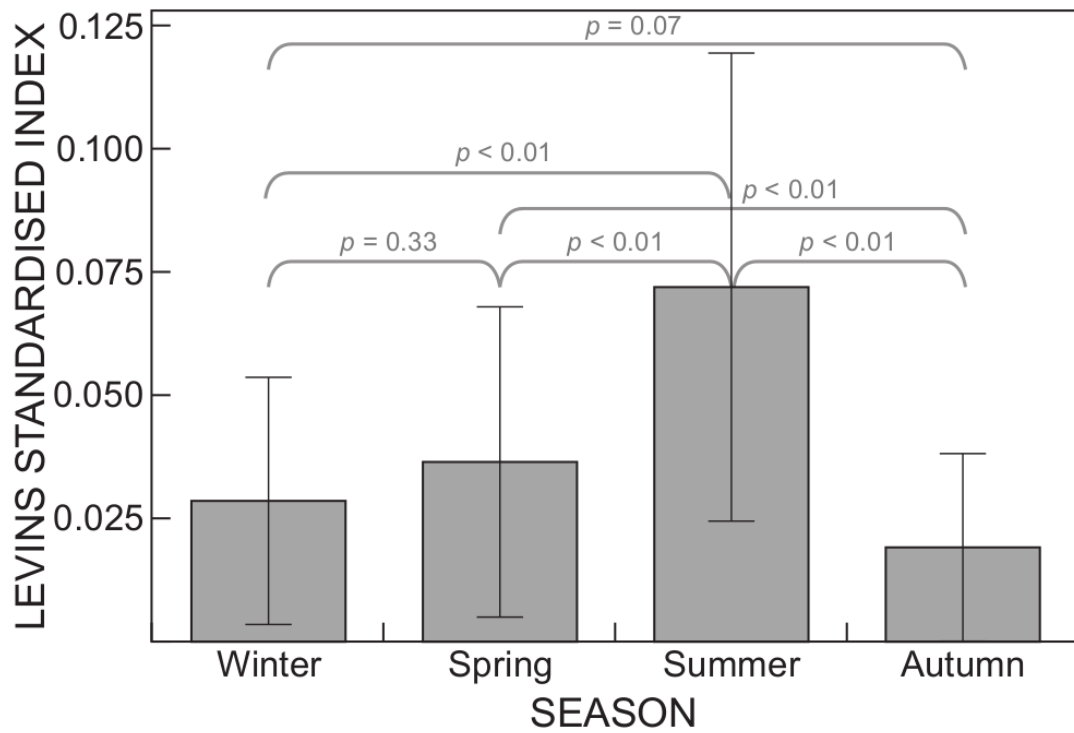


Figure 2: Bat-eared fox diet breadth, quantified as Levins' standardized index (B_i) in the Kuruman River Reserve during four seasons: summer (December–February), autumn (March–May), winter (June–August) and spring (September–November). Error bars represent ± 1 standard error from the mean. Tukey's post hoc test: $\alpha \leq 0.05$.

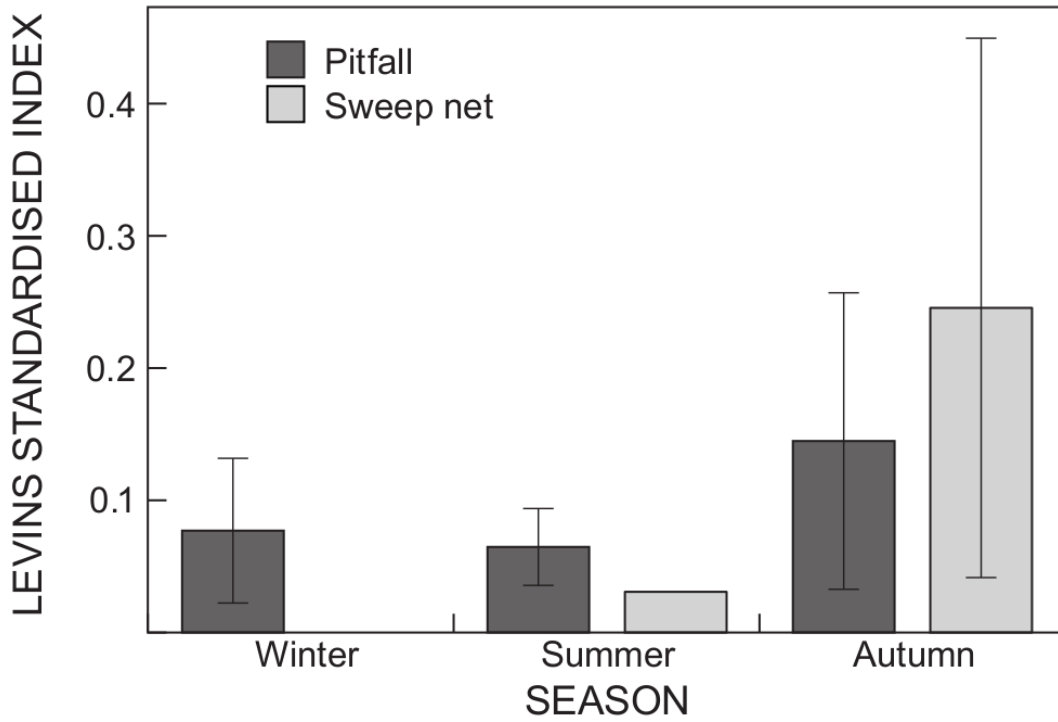


Figure 3: Invertebrate diversity quantified from pitfall and sweep net data across three seasons: summer (December–February), autumn (March–May) and winter (June–August). Sweep net data available for summer and autumn only. Error bars represent ± 1 standard error from the mean.

Table 1: Seasonal diet data from 19 bat-eared foxes and prey availability data from 360 individual pitfall traps distributed in groups of 15 traps in each home range of respective fox groups. Pitfall trapping was done in 2015 (autumn and winter) and 2016 (summer), and prey availability data from sweep net surveys, at the same sites as the pitfall trapping (sweep net data were obtained for summer and autumn only). Values are expressed as relative percentage of occurrence (RPO), i.e. number of identified items of a food category divided by all consumed or trapped diet items, multiplied by 100.

Order and Class ^{††}	Summer			Autumn			Winter			Spring			All seasons		
	Diet	Pitfall	Sweep-net	Diet	Pitfall	Sweep-net	Diet	Pitfall	Diet	Diet	Pitfall	Sweep-net	Diet	Pitfall	Sweep-net
Hymenoptera (Ants)	5.73	84.56	89.00	1.85	74.89	15.00	9.62	85.89	15.45	8.16	81.78	52.00			
Neuroptera (Antlions)	6.99	0.07	-	0.74	0.03	9.00	0.00	-	0.48	2.05	0.03	5.00			
Coleoptera (Beetles)	4.26	12.08	-	12.97	18.84	24.00	11.76	11.37	13.57	10.64	14.10	12.00			
Lepidoptera (Caterpillars)	0.00	-	-	0.00	-	6.00	2.27	-	0.07	0.59	-	3.00			
Diplopoda (Millipedes)	0.01	-	-	0.00	-	-	-	-	0.10	0.03	-	-			
Hemiptera (Cicadas)	3.94	-	-	0.00	-	-	-	-	0.06	1.00	-	-			
Orthoptera (Crickets)	0.18	-	-	0.01	-	-	-	-	0.10	0.07	-	-			
Orthoptera (Grasshoppers)	14.30	0.13	-	1.57	2.88	-	0.11	-	2.90	4.72	1.00	3.00			
Mantodea (Mantises)	0.11	-	-	0.00	-	-	0.00	-	0.11	0.06	-	-			
Lepidoptera (Moths)	0.74	-	-	0.30	-	-	0.32	-	1.20	0.64	-	-			
Scorpiones (Scorpions)	0.54	0.05	-	0.04	0.13	-	0.05	-	0.33	0.24	0.06	-			
Arachnida ^{††} (Spiders)	2.16	3.11	11.00	0.08	3.24	6.00	0.00	2.74	0.69	0.73	3.03	9.00			
Isoptera (Termites)	57.33	-	-	81.51	-	-	75.73	-	64.58	69.79	-	-			
Hemiptera (Shield bugs)	-	-	-	-	-	3.00	-	-	-	-	-	2.00			
Diptera (Houseflies)	-	-	-	-	-	21.00	-	-	-	-	-	11.00			
Phasmatodea (Stick insects)	-	-	-	-	-	9.00	-	-	-	-	-	5.00			
Reptilia ^{††} (Reptiles)	0.31	-	-	0.02	-	-	-	-	0.27	0.15	-	-			
Amphibia ^{††} (Frogs)	0.01	-	-	0.01	-	-	-	-	-	0.01	-	-			
Rodentia (Rodents)	0.34	-	-	0.49	-	-	0.05	-	0.12	0.25	-	-			
Other (Plant seeds)	3.05	-	-	0.00	-	-	0.05	-	-	0.78	-	-			
Other (Fungi)	0.00	-	-	0.41	-	-	0.03	-	-	0.11	-	-			
<i>Levins standardised index</i>	0.12	na		0.038	na	na	0.054	na	0.069	0.083	na				

Table 2: Literature compilation of detailed diet lists from this study conducted in the Northern Cape province and three other provinces (Western Cape, Free State and Limpopo province) in South Africa. Diet values are expressed as relative percentage of occurrence (RPO), with individual values adjusted so that the total equals ~100% per study.

Geographic location	Northern Cape	Northern Cape	Northern Cape	Northern Cape	Western Cape	Limpopo Province	Free State	Free State and Northern Cape
Source	This study	Klare et al. 2011	Stuart et al. 2003	Nel 1978	Kuntzsch and Nel 1992	Berry 1981	Nel and Mackie 1990	Kok and Nel 1992
Study method	Forage (n = 19)	Scats (n = 177)	Scats (n = 450)	Scats (n = 382)	Scats (n = 157)	Stomach content (n = 18)	Scats (n = 180)	Stomach content (n = 103)
Hymenoptera (Ants)	8.16	20.0	15.5	13.6	13.5	-	8.04	11.7
Neuroptera (Antlions)	2.05	-	-	-	-	-	-	-
Coleoptera (Beetles)	10.6	8.41	31.7	12.6	24.2	10.8	20.9	21.4
Lepidoptera (Caterpillars)	0.59	-	-	-	-	-	-	-
Hemiptera (Cicadas)	1.00	-	-	-	-	-	-	-
Orthoptera (Crickets)	0.07	-	1.04 [†]	-	-	-	10.5 [†]	10.0 [†]
Orthoptera (Grasshoppers)	4.72	5.08	-	4.50	20.7	-	-	-
Mantodea (Mantises)	0.06	-	-	-	-	-	-	-
Lepidoptera (Moths)	0.64	-	-	2.50	-	-	-	9.95
Isoptera (Termites)	69.8	27.9	32.1	18.8	24.2	44.3	26.8	16.3
Diplopoda (Millipedes)	0.03	-	-	1.50	-	-	-	1.37
Scorpiones (Scorpions)	0.24	4.22	5.52	1.10	-	-	-	4.89
Arachnida ^{††} (Spiders)	0.73	-	1.03	4.90	-	2.50	1.07	-
Reptilia ^{††} (Reptiles)	0.15	0.52	1.03	-	-	0.10	-	1.90
Amphibia ^{††} (Frogs)	0.01	-	-	-	-	0.40	-	0.28
Mammalia ^{††}	0.25	4.52	4.14	-	-	-	2.68	4.61
Other (Plants)	0.78	29.3	8.62	36.4	17.4	33.0	5.63	17.5
Other (Fungi)	0.11	-	-	-	-	-	-	-
<i>Levins standardised index</i>	0.12	0.94	0.42	0.43	0.95	0.32	0.53	0.61

[†] = Order Orthoptera (common names not specified in cited articles) , ^{††} = Class name