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Black-backed jackal diet in the Maria Moroka Nature Reserve, Free State Province: Implications for managing depredation on small stock farms

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Abstract

Feeding ecology of carnivores is integral to understanding their role in the ecosystem and the effect they have on their prey species. This study aims to better our understanding of Black-backed jackal feeding ecology in a fairly natural ecosystem, to contribute towards more informed depredation management in surrounding agri-ecosystems. Scat analysis was used to investigate the diet of Black-backed jackal inside a 5590 ha formal protected area, namely Maria Moroka Nature Reserve, which is surrounded by cattle and small stock farms. The six main prey groups identified from 334 scats were mice, springhare, antelope (*c.* 98% Springbok), hare, small carnivores and fruit. Rodents (mice mean monthly percentage occurrence 36%, springhare 31%) were utilized the most frequently, followed by antelope (Springbok 22% Occ; Blesbok 0.51%). The next most used prey group was small carnivores, present in 8% of scats. Hares and fruit, but also birds and invertebrates, were taken sporadically. No stock remains were found in the scats. Very similar results were obtained when volumetric contributions were calculated, resulting in mice (mean monthly contribution = 33% Vol; Importance Value, IV = 15.2), springhare (30% Vol; IV = 11.9) and antelope (24% Vol; IV = 10.0) being the most important prey items. Small carnivores (8% Vol) had an Importance Value of 1.2, and all other prey groups scored less than 0.4 IV. The wide variety of prey used, together with their monthly fluctuations (which for some groups could be coupled to availability) and prey switching between the three most important prey items mice, springhare and antelope, support opportunistic feeding behaviour by Black-backed jackal in the study area. The results also confirmed that Black-backed jackal does utilize Springbok as a major food source, and that this usage peaked during the two periods when Springbok lamb at Maria Moroka Nature Reserve. These periods do not only coincide with the Black-backed jackal pupping and dispersal seasons, but also with the two sheep lambing seasons in the central and southern Free State Province.

KEYWORDS: Black-backed jackal, diet, lambing season, predation impact, scat analysis, Springbok

INTRODUCTION

The Black-backed jackal *Lupulella mesomelas* is, together with Caracal *Caracal caracal*, the main predator on small stock in South Africa (Du Plessis 2013; Kerley *et al.* 2019). Renewed interest in addressing this conundrum has led to a marked increase of relevant publications since *c*. 2010. In stark contrast with the situation before, when nearly all ecological research on these two carnivores was done in nature reserves, most research has now been done on farms/rangelands (Avenant *et al*. submitted). However, valuable lessons for addressing the problem have been learned in nature reserves. This contribution investigates the Black-backed jackal's relation to prey in a central Free State nature reserve, aiming to contribute towards more sustainable predator management approaches on small stock farms in central South Africa.

The conflict between carnivores and humans arises primarily because of shared, and often limited, resources (Stadler 2006; Bothma 2012; Bergman *et al.* 2013; Seoraj-Pillai & Pillay 2017). Both mesopredators, Black-backed jackal and Caracal, cause serious economic losses by preying on livestock (see e.g. Van Niekerk 2010; Turpie & Babatopie 2018; Van der Weyde *et al*. 2020; Strauss *et al.* 2021). This concern echoes the sentiments of the agricultural industry (P. de Wet, PMF Chairman/ NWGA, presentation to the Portfolio Committee on Agriculture, Forestry and Fisheries in Parliament, 2 November 2010; Norval 2010; Van Niekerk 2010; Bezuidenhout 2008; Kerley *et al*. 2019; PMSA 2020). Accordingly, they are often hunted outside protected areas (Avenant & Du Plessis 2008; De Waal 2009; Du Plessis 2013; Avenant *et al*. 2016; Minnie *et al*. 2016; Drouilly *et al*. 2018; Nattrass & Conradie 2018). Lately, Black-backed jackal have also been hunted inside some provincial nature reserves and national parks as they are believed to have a significant negative impact on Springbok *Antidorcas marsupialis* populations (Bega 2010; Klare *et al*. 2010; SANParks 2013; DESTEA unpublished records). Simultaneously, the pressure from neighbouring farmers on nature reserves to cull Black-backed jackal numbers

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is also increasing (C. Erasmus DESTEA, pers. comm. 2016; Avenant pers. obs.).

This diet study was, together with a veterinary study on the general health and productivity of Springbok in the Maria Moroka Nature Reserve (MMNR), initiated to shed light on the Black-backed jackal's impact on the declining Springbok population. Studying a carnivore's diet and predatory behaviour are useful in understanding its role in the ecosystem, such as its position as a specialist, generalist or opportunist (Klare *et al*. 2010). In this case, this information was essential for planning and making intervention decisions concerning damage-causing species (Klare *et al*. 2010; Du Plessis 2013; Du Plessis *et al*. 2018). During this study the prey usage of Black-backed jackal and the possible detrimental impact on the Springbok population at Maria Moroka Nature Reserve, was studied by analysis of scats. Due to the secretive and nocturnal behaviour of some carnivores, this (faecal analysis) is a preferred method for gathering information on their diet (Putman 1984; Bowland & Bowland 1989; Karanth & Sunquist 1995; Kaunda & Skinner 2003; Klare *et al*. 2010, 2011; Rautenbach 2010; Van de Ven *et al*. 2013; Drouilly *et al*. 2018; and others). While the significant decrease in Springbok numbers for the period 2009-2013 at this reserve was meticulously documented (Schulze 2014), virtually no ecological research on Black-backed jackal has been conducted in any of the Free State Department of Economic, Small Business Development, Tourism and Environmental Affairs (DESTEA) reserves, and nothing to confirm that Black-backed jackal may, or may not, have a substantial impact on the observed decreases in MMNR. This information is not only vital for structuring a management plan for this species in nature reserves throughout South Africa, but is also of major importance when attempting to manage this species on adjacent agricultural properties.

METHODS

Study area

The study was conducted in the MMNR (29º15'S, 26º49'E) (also the study area of Schulze 2014), approximately 42 km east of Bloemfontein, 65 km ESE of the study area of Strauss *et al*. (2021), and 150 km NNE of the Deacon (2010) and Pohl *et al*. (Submitted) study areas in the central Free State Province. This 5590 ha protected area has been managed by Free State Nature Conservation (today DESTEA) since 1985. The area has been surrounded by cattle and small stock rangeland throughout.

The MMNR area has distinct plant communities, including the Central Free State Grassland, Eastern Free State Sandy Grassland and Basotho Montane Shrubland (Mucina & Rutherford 2006). The vegetation is dominated by the grasses *Themeda triandra, Aristida diffusa, Sporobulus fimbriatus, Eragrostis curvula* and *Eragrostis chloromela* (Mucina & Rutherford 2006). Maximum and minimum temperatures range from 35.3°C (in summer) to -11.1°C (in winter) (SA Weather Service 2002). The seasonal (late-spring to late-autumn) rainfall averages *c*. 600 mm per annum. This variation in seasonal temperature and rainfall plays an important role in the availability of resources as it affects primary productivity, and therefore the reproduction season of reptiles, birds and mammals: e.g. spring (September – October) is the major birthing period for, not only common jackal prey groups Springbok, virtually all ungulates and most bird species, but also for Black-backed jackals. There is a second lambing period of Springbok in late autumn/early winter (May–June) (DESTEA unpublished records; Klare *et al*. 2010; Schulze 2014; NLA and JBM *pers. obs.*). Small rodent (mouse) densities increase exponentially from early–spring to late–autumn, and drop by *c*. 50% between late–autumn and mid–winter (see Avenant 2011). Springhare *Pedetes capensis* young are born throughout the year, but birthing peaks just after winter (*c*. August) (Skinner & Chimimba 2005).

Scat collection

Fresh (younger than *c*. 10 days; thereafter scats become less shiny, change colour and the outer layer starts to crack) Black-backed jackal scats were collected monthly from September 2011 to December 2012 (by J.B. Morwe and N.L. Avenant). Individual scats were placed in brown paper bags labelled with the relevant data [i.e. date, GPS locality, defecation site (e.g. in veld, or next to road/path, where roads/ paths meet) and substrate (on grass, shrub, soil, rock or in a road/path)]. Scats were mostly found on vegetation alongside roads/paths, often where two roads/paths meet, but also in other areas. Scats were first identified based on their size, shape, as well as where they were found, the contents, and presence of the carnivore's own hair (to separate it from Caracal scats, the only other predator in the study area with nearly similar sized scats). A second round of scat identification was conducted in the laboratory by N.L. Avenant and carnivore ecologist C. Pohl. Only positively identified scats were included for analysis; all doubtful scats were discarded.

Scat analysis

In the laboratory scats were air-dried and later teased apart with tweezers. Each individual scat was placed in a Petri dish, the different dietary components manually sorted, and their volumetric contributions determined. The typical prey remains in scats were hair, pieces of small mammal skulls, teeth and bones, invertebrate wings and carapaces, feathers and seeds. Prey items were macro and microscopically identified to species level (following Avenant & Nel 1997; Atkinson *et al.* 2002; Do Linh San *et al.* 2009; Forbes 2011), and grouped into ten categories, namely antelope, small mammals (including mice and shrews), medium-sized rodents/herbivores (springhares, hares and ground squirrels), carnivores, birds, reptiles, invertebrates, fruit, abiotic items (e.g. pieces of plastic), and unknown/unidentified items. No shrews were found in scats.

Main prey items were identified as those species contributing >40% per volume in scats (following Avenant & Nel 1997). Grass always contributed less than 2% to the volume, of a very small number of scats, and was therefore not included in further analysis here; these ingestions could happen accidentally (together with other prey, following Hawthorne 1972) or for health purposes (see Bjone *et al*. 2007; Hart 2008; Atkinson *et al*. 2002; Yoshimura *et al*. 2021). Mammalian food items were identified by hair and teeth samples. Cuticular hair imprint characteristics were employed to reach correct identification and were examined under a microscope with 10x and 40x magnifications, using the reference collection of the National Museum and the keys of Perrin & Campbell (1979) and Keogh (1983a & b). At least eight hairs per prey species were removed from each individual scat (in case the groove and/or scale patterns were damaged in some). These hair samples were placed in a petri dish, rinsed in water, later mounted on a microscope slide using the mounting medium Entellan ($C_{13}H_{22}O_4$), and removed to leave the imprint before the fixative dried.

The contribution of various components in the scats was, on a monthly basis, expressed as (a) Percentage occurrence in the scats (= the number of scats containing the particular prey item, divided by total number of scats, x 100; Avenant & Nel 1997); (b) Volumetric contribution (= the sum of the percentages of the volume the prey type contribute to each scat, divided by the total number of scats; Avenant & Nel 1997); (c) Importance Value (IV, = percentage occurrence x percentage volume, divided by 100; Avenant & Nel 1997); and (d) Relative Importance Value (= Importance Value of a particular prey type, divided by the sum of the IVs all prey categories, multiplied by 100; see also Zabala & Zuberogoitia 2003; Melville *et al.* 2004). This approach, where all four steps are included, allows comparison between months/seasons/years, as well as with previous carnivore scat studies (e.g. Corbett 1989; Atkinson *et al.* 2002; Kaunda & Skinner 2003; Do Linh San *et al.* 2009). Here, the calendar year was divided into winter (June–August), spring (September–November) summer (December–February), and autumn (March–May) to assess the seasonal difference in diet (see e.g. Parker & Bernard 2005; Avenant 2011; Pohl *et al*., Submitted).

All statistical analyses and graphs were performed using the Statistica 6 for Windows program (Statsoft Inc. 1995, Tulsa, OK, USA). Tests for normality were done using the Shapiro-Wilk's W test. Relationships between specific prey consumption (as observed in the faecal samples) were analyzed using Spearman rank order correlations. In order to evaluate the importance of prey switching with temporal changes in jackal diet, we tested whether contributions of various prey items affected the contributions of others. We evaluated monthly relationships among the three most important prey items (antelopes, mice, and springhares – other items made relatively negligible contributions throughout the study period). We used simple and multiple linear regression models, including interaction terms, to test hypotheses for relationships amongst changes in the Importance Values (IV) of these prey groups, treating each item as the dependent variable in turn. For model selection we used the second-order Akaike's Information Criterion (AIC_c), which provides an index of model support while penalizing for the addition of parameters (Burnham & Anderson 2001, 2002). Models with the lowest AIC_c are considered to be best-supported by the data, focusing on models having scores that are ≤ 2 of the lowest score in the candidate set.

RESULTS

A total of 334 Black-backed jackal scats were collected (monthly mean = 20.9 ± 6.2) and analysed on a monthly basis (Table 1). The rodent groups, mice (mostly Vlei rat *Otomys auratus* 30.05%, Four-striped grass mouse *Rhabdomys dilectus* 4.11% and White-tailed rat *Mystromys albicaudatus* 2.14 %, by mean monthly percentage occurrence) and springhare were most frequently found in scats. Antelope remains were present in more than 20% of scats (Springbok 22.17% and Blesbok *Damaliscus pygargus phillipsi* 0.51% - mean monthly percentage occurrence). The other main prey item group (contributing > 40% per volume in scats) was small carnivores (Aardwolf *Proteles cristatus* 0.88% occurrence, Cape grey mongoose *Herpestes pulverulentus* 1.31%, Suricate *Suricata suricatta* 1.25% and Yellow mongoose *Cynictus penicillata* 4.49%), collectively contributing towards *c.* 8% of scats every month. Hares, birds, invertebrates and fruit also contributed varying amounts during the different months, with abiotic items (plastic, most probably part of one scavenged bout) present only in one month. On average 1.73% of scats contained some unidentified material.

The presence of each prey group varied markedly over the 16-month period (Figure 1). For antelope, for example, two clear peaks (in May and in September 2012) are obvious. Similarly there are two peaks for springhare (in August and November 2012), and relatively high occurrence of mice in the period October 2011 to March/April 2012.

Table 1. The percentage occurrence of prey groups in the scats of Black-backed jackal at Maria Moroka Nature Reserve, September 2011 to December 2012. The numbers of scats are indicated in brackets.

MONTH (n)	*Antelope	#Mice	Springhare	Carnivore	Ground squirrel	Hare	Bird	Invertebrate	Fruit	Abiotic	Unidentified
Sep11 (23)	13.04	39.13	26.09	13.04	8.70	4.35	4.35	0.00	0.00	0.00	0.00
Oct11 (22)	8.00	54.55	4.55	4.55	0.00	0.00	4.55	4.55	4.55	0.00	4.55
Nov11 (23)	30.43	30.43	39.13	0.00	0.00	0.00	4.35	0.00	4.35	0.00	0.00
Dec11 (23)	0.00	52.17	30.43	4.35	0.00	13.04	0.00	17.39	4.35	0.00	4.35
Jan12 (12)	0.00	50.00	41.67	16.67	0.00	0.00	0.00	0.00	0.00	0.00	8.33
Feb12 (12)	0.00	66.67	33.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar12 (25)	16.00	52.00	28.00	0.00	0.00	8.00	0.00	4.00	4.00	0.00	0.00
Apr12 (10)	0.00	40.00	40.00	20.00	0.00	0.00	10.00	0.00	30.00	0.00	0.00
May12 (27)	70.37	11.11	14.81	7.41	0.00	0.00	0.00	0.00	0.00	0.00	3.70
Jun12 (24)	50.00	29.17	25.00	4.17	0.00	0.00	0.00	0.00	4.17	0.00	0.00
Jul12 (26)	53.85	46.15	11.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aug12 (28)	17.86	17.86	71.43	0.00	0.00	0.00	0.00	7.14	3.57	3.57	0.00
Sep12 (23)	52.17	17.39	30.43	13.04	0.00	0.00	0.00	0.00	13.04	0.00	0.00
Oct12 (15)	40.00	20.00	20.00	20.00	0.00	13.33	6.67	0.00	26.67	0.00	6.67
Nov12 (18)	11.11	0.00	55.56	5.56	0.00	11.11	0.00	11.11	27.78	0.00	0.00
Dec12 (23)	0.00	54.55	27.27	18.18	0.00	0.00	0.00	0.00	9.09	0.00	0.00
Mean (n=20.9±6.2)	22.68	36.32	31.20	7.94	0.54	3.11	1.87	2.76	8.22	0.22	1.73

* 98% of all records were Springbok

Dominated by Vlei rat *Otomys auratus*, present in 30.05% of scats (mean monthly contribution)

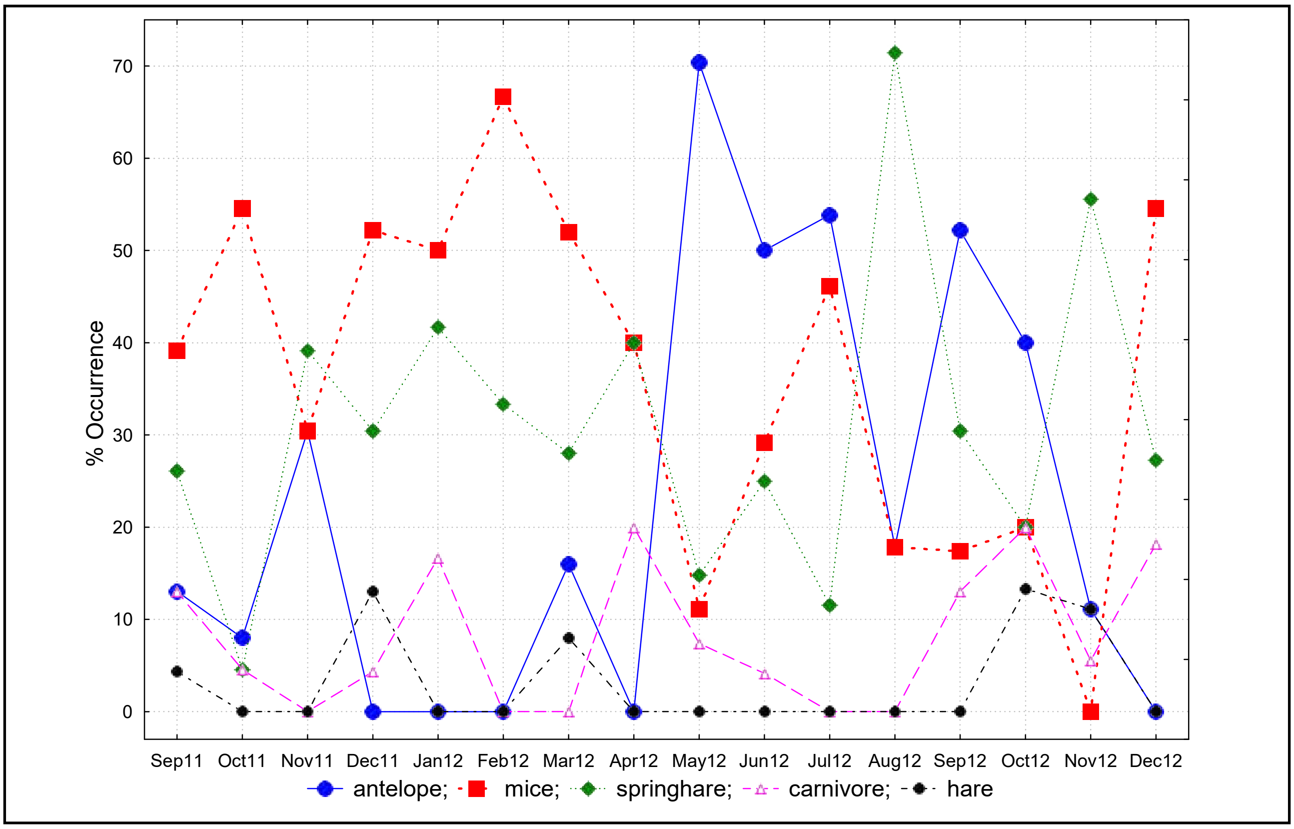

Figure 1. Monthly presence of the main prey groups in Black-backed jackal scats at *Maria Moroka* Nature Reserve, September 2011 to December 2012.

Table 2. The percentage volumetric contribution of prey groups in the scats of Black-backed jackal at Maria Moroka Nature Reserve, September 2011 to December 2012. The numbers of scats are indicated in brackets.

MONTH (n)	*Antelope	#Mice	Springhare	Carnivore	Ground squirrel	Hare	Bird	Invertebrate	Fruit	Abiotic	Unidentified
Sep11 (23)	19.96	33.03	24.57	13.04	8.70	4.35	4.35	0.00	0.00	0.00	0.00
Oct11 (22)	35.45	50.23	4.55	4.55	0.00	0.00	0.23	0.45	0.23	0.00	4.55
Nov11 (23)	30.39	30.43	39.13	0.00	0.00	0.00	0.04	0.00	0.43	0.00	0.00
Dec11 (23)	0.00	51.74	24.13	4.35	0.00	8.78	0.00	6.57	0.09	0.00	4.35
Jan12 (12)	0.00	41.67	41.25	16.67	0.00	0.00	0.00	0.00	0.00	0.00	0.42
Feb12 (12)	0.00	66.67	33.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar12 (25)	15.40	48.44	28.00	0.00	0.00	8.00	0.00	0.08	0.08	0.00	0.00
Apr12 (10)	0.00	39.50	39.00	19.9	0.00	0.00	0.10	0.00	1.50	0.00	0.00
May12 (27)	70.18	7.41	14.81	7.41	0.00	0.00	0.00	0.00	0.00	0.00	0.19
Jun12 (24)	45.96	25.63	24.17	4.17	0.00	0.00	0.00	0.00	0.08	0.00	0.00
Jul12 (26)	46.62	41.85	11.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aug12 (28)	9.50	17.61	71.36	0.00	0.00	0.00	0.00	1.32	0.18	0.04	0.00
Sep12 (23)	51.35	8.04	27.35	13.04	0.00	0.00	0.00	0.00	0.22	0.00	0.00
Oct12 (15)	40.00	13.67	12.60	19.60	0.00	13.00	0.07	0.00	0.60	0.00	0.47
Nov12 (18)	11.11	0.00	55.56	0.56	0.00	10.83	0.00	9.44	12.50	0.00	0.00
Dec 12 (23)	0.00	47.27	25.45	18.18	0.00	0.00	0.00	0.00	9.09	0.00	0.00
Mean (n=20.9±6.2)	23.50	32.70	29.80	7.59	0.54	2.81	0.30	1.12	1.56	0.003	0.62

* Dominated by Springbok *Antidorcas marsupialis*, with an average volumetric contribution of 23.03%

\# Dominated by Vlei rat *Otomys auratus*, with an average monthly volumetric contribution of 26.67%

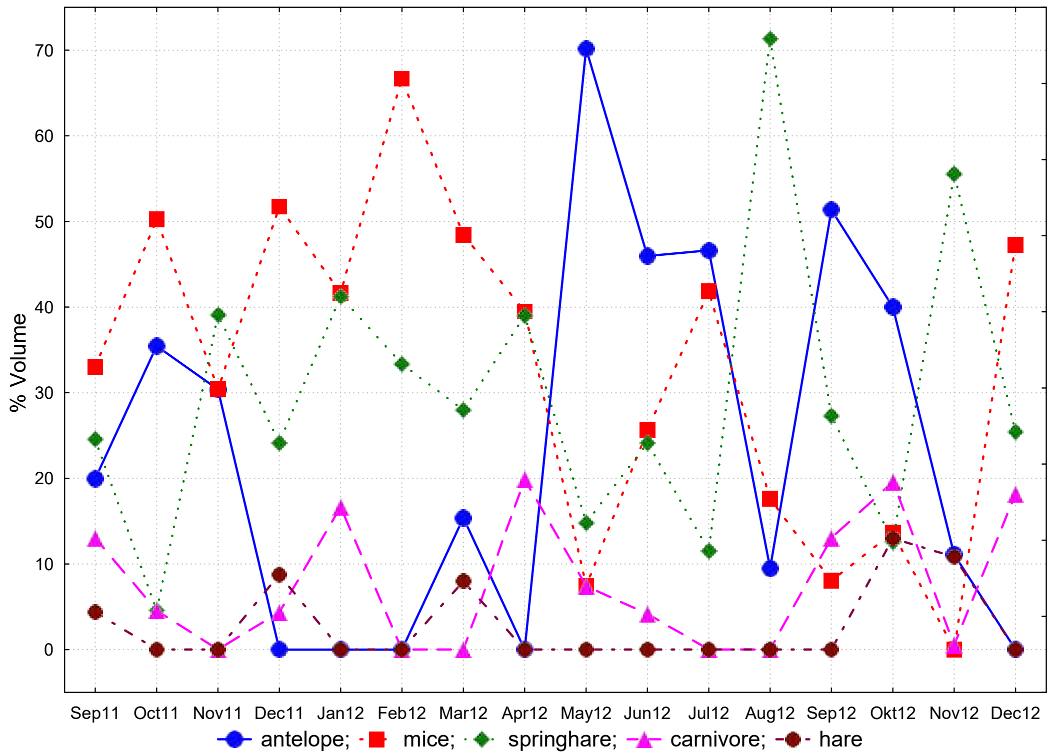

Figure 2. Monthly volumetric contribution of the main prey groups to Black-backed jackal scats at Maria Moroka Nature Reserve, September 2011 to December 2012.

Table 3. The Importance Value of prey groups in the scats of Black-backed jackal at Maria Moroka Nature Reserve, September 2011 to December 2012. The numbers of scats are indicated in brackets.

MONTH (n)	Antelope	#Mice	Springhare	Carnivore	Ground squirrel	Hare	Bird	Invertebrate	Fruit	Abiotic	Unidentified
Sep 11 (23)	2.60	12.92	6.41	1.70	0.76	0.19	0.19	0.00	0.00	0.00	0.00
Oct 11 (22)	2.84	27.40	0.21	0.21	0.00	0.00	0.01	0.02	0.01	0.00	0.21
Nov 11 (23)	9.25	9.26	15.31	0.00	0.00	0.00	0.001	0.00	0.02	0.00	0.00
Dec 11 (23)	0.00	26.99	7.34	0.19	0.00	0.00	0.00	1.14	0.004	0.00	0.19
Jan 12 (12)	0.00	20.84	17.19	2.78	0.00	0.00	0.00	0.00	0.00	0.00	0.039
Feb 12 (12)	0.00	44.45	11.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 12 (25)	2.46	25.19	7.84	0.00	0.00	0.00	0.00	0.00	0.003	0.00	0.00
Apr 12 (10)	0.00	15.80	15.60	3.98	0.00	0.00	0.00	0.00	0.45	0.00	0.00
May 12 (27)	49.39	0.82	2.19	0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.008
Jun 12 (24)	22.98	7.48	6.04	0.17	0.00	0.00	0.00	0.00	0.003	0.00	0.00
Jul 12 (26)	25.10	19.31	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aug 12 (28)	1.70	3.15	50.97	0.00	0.00	0.00	0.00	0.09	0.006	0.001	0.00
Sep 12 (23)	26.79	1.40	8.32	1.70	0.00	0.00	0.00	0.00	0.029	0.00	0.00
Oct 12 (15)	16.00	2.73	2.52	3.92	0.00	1.73	0.00	0.00	0.16	0.00	0.039
Nov 12 (18)	1.23	0.00	30.87	0.03	0.00	1.20	0.00	1.05	3.47	0.00	0.00
Dec 12 (23)	0.00	25.79	6.94	3.31	0.00	0.00	0.00	0.00	0.83	0.00	0.00
Mean (n=20.9±6.2)	10.02	15.22	11.89	1.16	0.05	0.31	0.01	0.14	0.31	0.000	0.03

* Dominated by Springbok *Antidorcas marsupialis*, with an average Importance Value of 9.82
# Dominated by Vlei rat *Otomys auratus*, with an average monthly Importance Value of 8.01

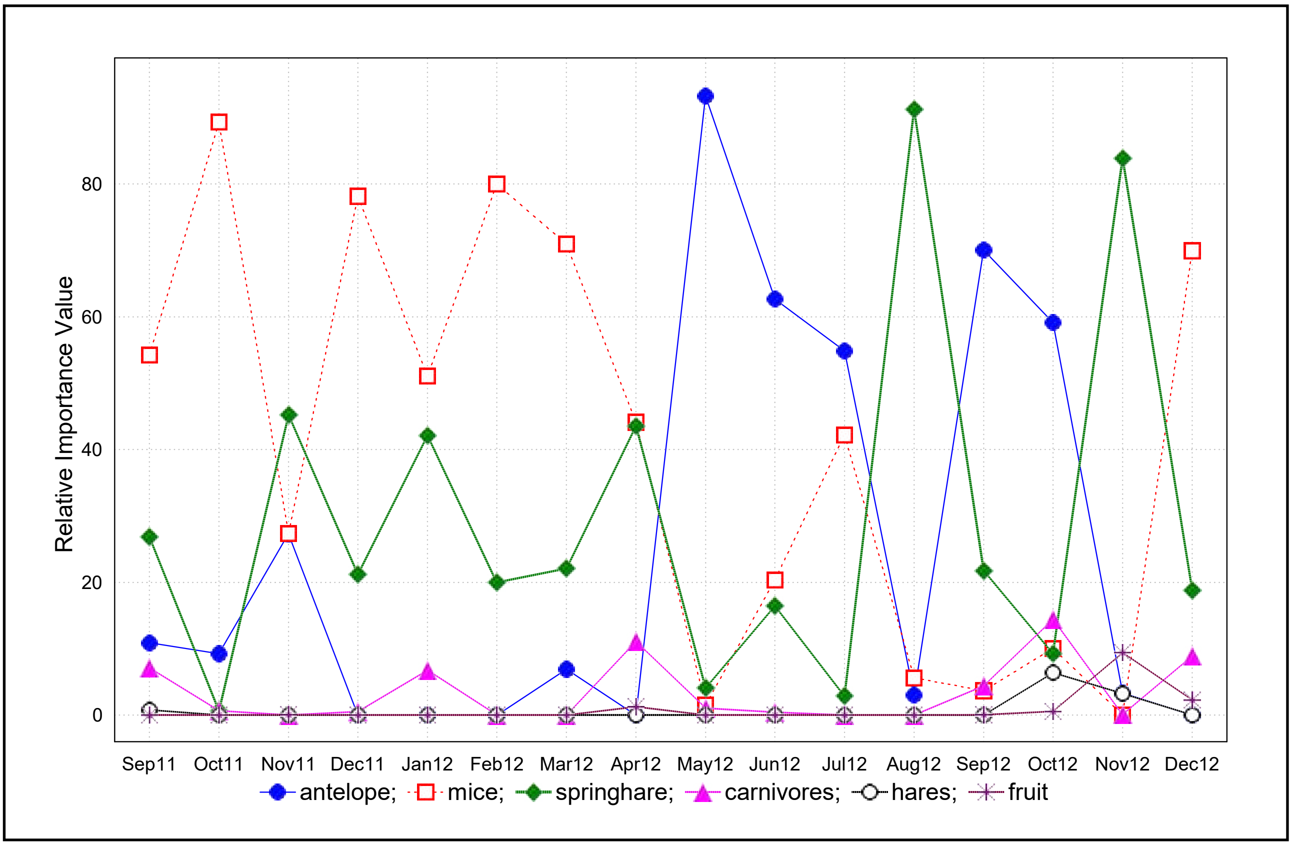

Figure 3. The relative Importance Value of the major prey groups in Black-backed jackal scats at Maria Moroka Nature Reserve, September 2011 to December 2012.

Mice (*O. auratus* 26.67% volume, *R. dilectus* 3.92%, *M. albicaudatus* 2.08%), springhare and antelope (Springbok 22.99%, Blesbok 0.51%) also had the highest volumetric contribution (Table 2), with carnivores and hares the only other prey groups constituting more than 2% to the monthly volume. The mean monthly volumetric contribution of fruit (1.56%) was much lower than its contribution towards percentage occurrence (8.22%, Table 1). A similar pattern was observed for the volumetric contribution of abiotic items (plastic; monthly average now only 0.003%) and unidentified items (0.62%). Monthly fluctuations in volumetric contribution (Figure 2), displayed similar fluctuations to those observed in Figure 1 for the main prey groups, as most of these items contributed 100% (or close to) of the volume of those scats in which they were found.

Combining the percentage and volumetric contributions in scats is a better method to grasp the importance of specific prey items for a carnivore (Table 3). As such, rodents had the highest mean Importance Value (15.22), followed by springhare (11.89) and antelope (10.02). Small carnivores collectively had a score of slightly more than 1, hares and fruit had equal Importance Values (0.31), and invertebrates, ground squirrel, unidentified items and birds contributed very little to the overall Importance Value. Abiotic items (plastic) contributed less than 0.001 to the total Importance Value. When it comes to individual species, springhare had the highest mean monthly Importance Value (11.89), followed by Springbok (9.82) and Vlei rat (8.01).

Just taking mean monthly Importance Values into account may be misleading and can lead to erroneous conclusions. Calculating relative Importance Values is a good way of investigating the relationships in which prey items and groups are ingested relative to each other. In this case mice (mainly Vlei rat), springhare and antelope (*c.* 98% of which is Springbok) account for almost everything that was ingested (Figure 3); with the other prey groups contributing only sporadically. Fruit, for instance, had a high relative Importance Value in November 2012 (*c.* 8%) and carnivores in April, October and December 2012 (>9%). Significant negative correlations were found between antelope and mice Importance Values (Spearman R =-0.561, p=0.024), as well as between antelope and springhare (R = -0.561; p>0.1). None of the other prey groups correlated with each other (p>0.3).

Relationships between Importance Value of prey types
We predicted that the contributions (IV values) from the main prey types taken by Black-backed jackals would be related to each other, revealing the importance of prey switching throughout the study period. For all major prey types, i.e. antelope, mice, and springhares, the best-supported models (lowest AIC_c scores) included both other prey types as contributing parameters (Table 4). Thus, where relationships between IV values of two prey species were generally negatively correlated, but not always significant (*p*>0.05; see Table 4), the relative importance of each item was affected by contributions of the other two prey types. In the case of antelope, the IV of this prey type decreased significantly with increases in the contributions of mice or springhares, indicating that Black-backed jackals were switching from antelopes to either of the other two prey groups at different times of the year. Similar results were obtained for the effects of antelope and springhare on IV values for mice and for effects of antelope and mice on IV values for springhares. Thus, the data reveal a complex interaction between the three major prey types, which shows a distinct pattern through the seasonal cycle: in late spring through early autumn (October to March), Black-backed jackals focus their feeding activities on mice, but this prey source becomes less important after this period, and is largely replaced by either antelope (two peaks, between May and July, and in September) or springhares (in August and November) (Figures 1–3).

DISCUSSION

Scat analyses indicated that the Black-backed jackal utilised a wide variety of prey at Maria Moroka Nature Reserve. The two rodent groups, namely mice and springhares, were not only the most utilised prey but they also made the largest volumetric contributions to this carnivore's diet. Here the high contribution of Vlei rat stands out, most probably a consequence of the landscape being dominated by the Moutloatsi Saetlogelo Dam (which is fully enclosed by the reserve). The dam and the numerous little streams that feed it have a strong influence on the vegetation and the associated fauna. Antelope, almost exclusively Springbok, were the third most important prey group (see also Klare *et al*. 2010). Lesser prey items, such as fruit from the Bloubos *Diospyros lycioides*, were opportunistically utilised as it became available (Kamler *et al*. 2020). The presence of all prey items varied significantly over specific periods of the year, with their occurrence in scats and volumetric contribution to the Black-backed jackal's diet changing markedly and by the month over time.

A number of indicators point to the Black-backed jackal's opportunistic feeding behaviour. These include the relatively wide diversity of prey taken, some in small quantities, and the fact that some specific prey items increased in the diet when they became more available (Van de Ven *et al*. 2013, *Study area*, p. 24; both authors pers. obs.). Through this opportunistic usage of a large number of other prey items in the Reserve, they are expected to play an important role in the ecosystem (see Williams *et al*. 2017; Minnie *et al*. 2018; Tambling *et al*. 2018; Bagniewska & Kamler 2013; Pohl *et al*. Submitted).

Table 4. Regression models for relationships between IV (Importance Value) values of the three major prey types used by Black-backed jackals at Maria Moroka Nature Reserve through the study period. Best-fit models have the lowest AIC_c scores. Significant effects (p<0.05) are highlighted in bold typeface.

Prey Group	Model Effects	*K*	AIC_c	ΔAIC_c	Parameter Estimates			
					mean	se	*T*	*P*
Antelope								
Model 1	**Mouse**	4	64.31	0.00	**-0.7719**	**0.2131**	**-3.622**	**0.0031**
	Springhare				-0.6496	0.2098	-3.096	0.0085
Model 2	**Mouse**	5	65.93	1.63	**-0.9031**	**0.3821**	**-2.363**	**0.0358**
	Springhare				-0.7183	0.2715	-2.646	0.0213
	Mouse x Springhare				0.0139	0.0330	0.420	0.6818
Model 3	**Mouse**	3	78.74	14.44	**-0.5745**	**0.2583**	**-2.224**	**0.0431**
Model 4	Springhare	3	84.61	20.30	-0.4221	0.2735	-1.544	0.1450
Mice								
Model 1	**Antelope**	4	62.12	0.00	**-0.6508**	**0.1796**	**-3.622**	**0.0031**
	Springhare				-0.5694	0.1988	-2.863	0.0133
Model 2	Antelope	5	63.07	0.96	-0.4597	0.2194	-2.095	0.0580
	Springhare				-0.4458	0.2540	-1.756	0.1046
	Antelope x Springhare				-0.0565	0.0500	-1.130	0.2806
Model 3	Antelope	3	74.16	12.04	**-0.4546**	**0.2044**	**-2.224**	**0.0431**
Model 4	Springhare	3	78.37	16.26	-0.2947	0.2511	-1.174	0.2601
Springhares								
Model 1	Antelope	4	64.87	0.00	**-0.6258**	**0.2488**	**-2.515**	**0.0272**
	Mouse				-0.6637	0.2553	-2.600	0.0232
	Antelope x Mouse				-0.0059	0.0253	-0.234	0.8192
Model 2	**Antelope**	5	67.09	2.22	**-0.6533**	**0.2110**	**-3.096**	**0.0085**
	Mouse				-0.6793	0.2372	-2.863	0.0133
Model 3	Antelope	3	81.05	16.18	-0.3446	0.2232	-1.544	0.1450
Model 4	Mouse	3	72.88	8.01	-0.3040	0.2590	-1.174	0.2601

K = number of model parameters; $\Delta AIC_c = AIC_c$ score of model - lowest ΔAIC_c; se = standard error of parameter estimate.

Prey switching between mouse, springhare and antelope (Springbok) importance in Black–backed jackal scats, as well as the diversity of prey consumed, confirms the level of this carnivore's opportunistic feeding behaviour at Maria Moroka Nature Reserve. The two sudden peaks in the importance of Springbok as prey during both Springbok lambing periods, together with its gradual decline as the concentration of young lambs decrease, is testimony to the fact that Black-backed jackal opportunistically feed on Springbok (see also Klare *et al*. 2010). These periods closely follow the sheep lambing seasons and the time when most lambs are predated on in the central and southern Free State Province (Deacon 2010; Pohl *et al*. Submitted; Strauss *et al*. 2021). It also coincides with the times when Black-backed jackal has high energy-requirements due to the presence of pups and lactating females (September–October), and when a large percentage of the pups disperse/ start to fend for themselves (April–May) (Bothma 1971; Deacon 2010; Minnie *et al.* 2016; Minnie *et al.* 2018). Coincidently, these are also the high risk times for sheep farmers, when relatively high densities of "easy prey" (lambs) are available (Deacon 2010; Pohl *et al*. Submitted; Strauss *et al*. 2021; H Grobbelaar pers comm. 2014; M Le Roux pers comm. 2015).

Several important observations can be made from this nature reserve study, which should be useful when considering farm and predator management plans, and most effective when used in combination with other management strategies (see Du Plessis *et al.* 2018). (1) Black-backed jackal naturally feeds opportunistically on what is available. (2) In the central and southern Free State, and therefore in large parts of central South Africa, the most important natural prey items for jackal in the study area, apart from Sprinbok lambs, are the rodents mice and springhare (see Pohl *et al*. Submitted). (3) The availability of mice is extremely low in the period May to *c*. October/November (see Avenant 2011); this is also the time of highest energy requirements for Black-backed jackal. (4) Relatively high densities of another prey group (in this case springhare) can fill a vital gap in the prey needs of Black-backed jackal, especially when the lambs grow bigger (≈ less easy to catch). (5) Black-backed jackal have, due to their reproductive and dispersal strategies, two main periods during which Springbok (and sheep) lambs are most vulnerable to predation, viz. September–October and April–June/July. (6) Not only do these periods coincide with the Black-backed jackal's highest energy-need time (September–October), the time when their young start to disperse (April–May), and the two sheep lambing seasons, but are also associated with the low density period of their main food source, mice (Pohl *et al.* Submitted). (7) In many group-living ungulates, including Springbok, keeping the lambing season as short as possible (called "clumping") is a natural survival strategy as it improves the survival rate of lambs during this critical period (Skinner & Louw 1996); farmers should consider applying this strategy by coordinating their lambing times (≈ lambing together within the shortest period possible), in as large an area as possible, to shorten their highest risk period. (8) While it may not always be possible to move the sheep lambing seasons to earlier or later times, a four week (or even shorter) change at the right time of year, and especially when in combination with (7) above, may have a big impact on Black-backed jackal depredation. For example, mouse densities are at the highest from *c.* March to early May and farmers can potentially capitalise on this natural Black-backed jackal food source by moving the autumn lambing season to earlier. Moving the spring lambing season later may also have a beneficial impact in that other potential prey animals, such as rodents, birds and reptile species, start breeding from early spring onwards, with densities increasing towards summer, enlarging the potential prey base of Black-backed jackals.

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