1. Introduction

Small to medium sized canids (<30 kg) are renowned for their opportunistic feeding habits, resulting in diverse and varied diets (Kok and Nel, 2004) that reflect the availability of abundant resources. In North America, coyote Canis latrans diet composition changes over time (Carrera et al., 2008; Randa et al., 2009; Young et al., 2006) and space (Morey et al., 2007) depending on the local prey availability (Young et al., 2006). Across south-eastern Europe, the middle East, northern Africa and southeast Asia, golden jackals Canis aureus are widespread and feed primarily on ungulates, livestock and small mammals, with seasonal consumption of insects and fruit being important in regions where these resources are locally abundant (Amrout et al., 2006; Lanszki et al., 2006). In eastern and southern Africa, side-striped jackals Canis adustus and black-backed jackals Canis mesomelas have opportunistic diets, with diet differences reflecting differential food availability within the respective home ranges where the two species overlap (Loveridge and Macdonald, 2003).

Across southern Africa, black-backed jackals (hereafter referred to as jackals unless otherwise stated) are widespread across both formally protected areas as well as private lands (Skinner and Chimimba, 2005). The diverse diet of jackals is one of the main reasons for their success and persistence across their range, and can be highly variable, often responding to large seasonal fluctuations in food availability (Kaunda and Skinner, 2003; Kofrel, 2007). The predominant prey items for jackals include small mammals, invertebrates, birds and reptiles (Kaunda and Skinner, 2003; Kofrel, 2007; Loveridge and Macdonald, 2003; Rowe-Rowe, 1983; Van der Merwe et al., 2009) with recent studies suggesting that ungulates are a more important resource than previously thought (Klare et al., 2010). The importance of ungulates varies, depending on the presence of large apex predators (Fourie, 2011) and on the life history pattern of the ungulates, often resulting in seasonal patterns of ungulate consumption (Klare et al., 2010).

Opportunistic predators such as bears, coyotes, red foxes and jackals have been shown to affect ungulate populations through predation on the vulnerable neonates or fawns (Kilgo et al., 2010; Kjellander and Nordström, 2003; Klare et al., 2010; Kobayashi et al., 2012). The impact on ungulate populations is expected to be greater for ungulate species that adopt the ‘hider’ maternal care strategy where vulnerability of their neonates to opportunistic predators is higher (Carl and Robbins, 1988). Selection of these specific resources by predators occurs either opportunistically (Bastille-Rousseau et al., 2010) or through active searches for these
easily obtainable food items (Kilgo et al., 2010). When ungulate juveniles are an important resource in the diet of predators, predator diets vary considerably across seasons, with ungulates peaking during the birth season (Metz et al., 2012; Schrecengost et al., 2008). Alternatively, the diet of generalist predators that scavange can be influenced by the predation patterns of apex predators with which they co-occur (Berger and Conner, 2008; Berger et al., 2008). In most cases the diet of apex predators remains fairly consistent between seasons, and thus apex predators can provide a scavenging opportunity for the meso-predator across all seasons (Pereira et al., 2013) resulting in a stable diet.

Using scats we investigated the seasonal diet of jackals on a private game reserve in the Eastern Cape, South Africa. We hypothesised that the occurrence of ungulates in the diet of jackals would be highly variable across seasons as jackals are expected to target vulnerable neonates during the birth peaks. Alternatively, if ungulates remain the predominant diet component of jackals with little seasonal variation, scavenging from co-occurring apex predators may be driving diet patterns.

2. Materials and methods

2.1. Study area description

Samara Private Game Reserve (hereafter Samara, E24° 45′; S32° 26′) is located in the Eastern Cape, South Africa, and is a private game reserve, with limited hunting primarily targeting exotic species. Samara encompasses 280 km² and covers four of the recognized biomes in South Africa, namely the thicket, savanna, grassland and Nama-Karoo biomes (Van Cauter, 2004). Samara is situated in the east of the Great Karoo and is characterized by a semi-arid climate (Van Cauter, 2004). In 2003 three cheektails Acinonyx jubatus were re-introduced, and this population has subsequently increased to sixteen in 2009 (two males and eight females with six accompanying cubs). These cheektails represent the only large predator on Samara. In addition Samara houses a wide variety of antelope species that cheetah prey on, providing scavenging opportunities for the jackal within the reserve.

2.2. Scat collection

Jackal scats were collected during two to four day sampling trips in June (winter) and October (spring) of 2008 and February (summer) and May (autumn) of 2009. Seasons selected correspond to the seasons referred to in Klare et al. (2010) where spring occurs from Sept to Nov, summer from Dec to Feb, autumn from Mar to May and winter from June to August. Scats were collected by driving the majority of the roads on Samara at ~15–20 km/h and investigating road verges. Scats were identified by their size, and most often by their placement prominently on grass, rocks or shrubs (Stuart and Stuart, 2000). A total of 240 scats equally dispersed over the four seasons were collected during the sampling period. Recent publications suggest between 30 and 50 scats are required to adequately sample seasonal variation in jackal diets (Kaunda and Skinner, 2003; Klare et al., 2010) and this formed the basis of our collection procedure.

2.3. Identification of prey species

Following collection of samples, all scats were soaked in 5% formalin solution for >24 h to kill potential parasites. Thereafter, samples were washed in a sieve under running water, retaining all solid material. Samples were oven dried at 50 °C for 48 h. Each scat sample was examined macroscopically and the presence of vegetation, fruit, reptile, bird, invertebrate and mammal remains recorded. For mammal species identification, ten hairs were removed at random for microscopic hair scale imprint identification (Keogh, 1983, 1985; Perrin and Cambell, 1980), and soaked in 1:1 diethyl ether/ethanol solution for a minimum of 5 min. These hairs were then mounted on a slide with transparent nail varnish, and removed when dry to derive the hair scale imprint. The hair scale imprints were observed under a Motic BA400 microscope at a magnification of 400× and compared to the reference collection for mammals housed at the Centre for African Conservation Ecology, NMU. We separated jackal diets into twelve broad prey categories loosely based on previously published seasonal diet estimates (Klare et al., 2010). Categories include: 1) arthropods, 2) vegetation, 3) fruit, 4) porcupine, 5) birds, 6) carnivores (excluding jackal hairs where we could not differentiate predation from allo-grooming), 7) reptiles (including squamates and tortoises), 8) rodents (up to 150 g), 9) medium-sized mammals (mammals between 1 and 3 kg, i.e. hares, springhares and hyraxes), 10) primates 11) small ungulates (<50 kg) and 12) large ungulates (>50 kg). We were not able to differentiate juvenile from adult ungulates, therefore small and large ungulates were based on the adult female mass.

We assessed jackal diets in two ways. Firstly we calculated the frequency occurrence of prey groups in the total number of scats collected per season. Although this method is well suited to identify rare prey groups, it does not fare well when ecological questions regarding the impact on prey species are posed (Klare et al., 2011). We therefore also calculated jackal diet based on estimates of the biomass ingested of each of the prey groups. In the absence of volumetric categorisation of prey to the nearest 5% within each scat (see Loveridge and Macdonald, 2003), we corrected frequency of occurrence data by apportioning the proportion of the scat equally between the number of prey groups detected in each scat (Henschel et al., 2005). We then applied correction factors (Klare et al., 2011) to the corrected frequency of occurrence to estimate the ingested volume which was then averaged over all the scats per season. Percent biomass ingested was then calculated from the total average mass of all prey groups (Klare et al., 2011). We used correction factors from the closely related red fox (Goszczyński, 1974) rather than side-striped jackal (Loveridge and Macdonald, 2003), as correction factors developed for the latter did not consider prey items heavier than hares and would not incorporate large prey items that dominated our diet profile (Klare et al., 2010). Because ungulates comprised a large percentage of the ingested biomass we further investigated the percent biomass ingested of each ungulate for each season.

2.4. Statistical analysis

We ran non parametric G-tests to investigate potential differences in the abundance of the prey categories in the diet between seasons, accounting for the small sample sizes that characterise some of the rarer prey categories (Zar, 1999). We constructed 95% confidence limits around the means for each prey item for each season by running 1000 bootstrap simulations on both the frequency of occurrence data and biomass estimates (Reynolds and Aebischer, 1991). Spearman rank correlation tests were used to assess whether biomass ingested across all prey categories differed between seasons. For each of the large and small ungulate prey categories and each ungulate individually we tested the effect of season on biomass consumption using a Kruskal–Wallis test. All statistical tests were conducted using R software (R Development Core Team, 2008).

3. Results

Frequency of occurrence: We found 979 different prey items from the twelve described diet groups identified in the 240 scat samples.
Scats contained on average between 3.5 and 4.5 diet groups per scat depending on the season. No significant difference in the frequency of occurrence estimates were found in two of the between season differences; namely the transition between winter and spring \((G = 17.4, df = 11, p = 0.096)\) and from spring to summer \((G = 13.7, df = 11, p = 0.25)\). However, we found significant differences in the absolute frequency of occurrence of the prey groups in the diet for all the remaining transitions and seasonal comparisons \((G > 21.3, df = 11, p < 0.05)\). These significant differences were driven primarily by changes between the seasons in the presence of medium-sized mammals \((G = 16.8, df = 3, p < 0.001)\), primates \((G = 15.2, df = 3, p < 0.005)\) and fruit \((G = 10.1, df = 3, p < 0.05; \text{Table 1})\).

Estimated ingested biomass: We found no difference in the composition of the estimated biomass consumed between seasons, with all seasonal biomass compositions significantly correlated to each other (Spearman’s Rank Correlation \(> 0.63, p < 0.05\) for all seasonal comparisons). The estimated biomass consumed was dominated by ungulates, with between 57% and 66% of all ingested biomass originating from the large \((9.7\text{–}31.8\%)\) and small ungulate \((31.6\text{–}47.2\%)\) categories (Fig. 1). Vegetation and invertebrates, the two diet groups most often encountered in the scats only accounted for between 1 and 3% of the ingested biomass respectively (Fig. 1).

The percentage of ingested biomass comprised of large \((\text{Kruskal–Wallis chi-squared} = 7.2, df = 3, p = 0.06731)\) and small ungulates \((\text{Kruskal–Wallis chi-squared} = 4.2, df = 3, p = 0.2376)\) remained fairly constant across season (Fig. 1). Significant differences in the seasonal abundance of individual ungulates were observed in only three of the twelve identified species in the diet (Table 2). Of the large ungulate species, eland \((Taurotragus oryx)\) was encountered in four scat samples, all in winter, and the consumption of nyala \((Tragelaphus angasii)\) in the diet increased in autumn (Table 2). Of the small ungulate species, springbok \((Antidorcas marsupialis)\) were consumed consistently \((9\text{–}15.6\%)\), whereas steenbok \((Raphicerus campestris)\) consumption declined during the winter months \((1.4\%)\) and grey duiker \((Sylvicapra grimmia)\) consumption increased during the winter months \((26.4\%, \text{Table 2})\). These three small ungulates remained consistently the most consumed prey items during the study, accounting for between a third and half of all consumed biomass across the seasons \((32.1\text{–}45.9\%)\). The remaining small ungulates; klipspringer \((Oreotragus oreotragus)\) and mountain reedbuck \((Redunca fulvorufa)\) contributed little \((3.4\text{–}5.2\%)\) to the biomass ingested across the seasons.

Table 1

<table>
<thead>
<tr>
<th>Prey Category</th>
<th>Spring (n = 60)</th>
<th>Summer (n = 60)</th>
<th>Autumn (n = 60)</th>
<th>Winter (n = 60)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ungulates</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PO</td>
<td>95% CL</td>
<td>95% CL</td>
<td>95% CL</td>
<td>95% CL</td>
</tr>
<tr>
<td>Small ungulates</td>
<td>43–55</td>
<td>37–48</td>
<td>45–70</td>
<td>35–23</td>
</tr>
<tr>
<td>Rodents (0–150 g)</td>
<td>50–63</td>
<td>38–48</td>
<td>25–48</td>
<td>50–55</td>
</tr>
<tr>
<td>Porcupine</td>
<td>0–12</td>
<td>0–6</td>
<td>2–5</td>
<td>0–0</td>
</tr>
<tr>
<td>Medium Mammals</td>
<td>32–44</td>
<td>33–45</td>
<td>38–63</td>
<td>27–15</td>
</tr>
<tr>
<td>Carnivores</td>
<td>34–47</td>
<td>30–42</td>
<td>18–42</td>
<td>27–15</td>
</tr>
<tr>
<td>Birds</td>
<td>13–22</td>
<td>12–20</td>
<td>15–20</td>
<td>7–25</td>
</tr>
<tr>
<td>Reptiles</td>
<td>10–30</td>
<td>3–8</td>
<td>7–23</td>
<td>2–5</td>
</tr>
<tr>
<td>Invertebrates</td>
<td>78–688</td>
<td>70–888</td>
<td>76–888</td>
<td>47–358</td>
</tr>
<tr>
<td>Fruit</td>
<td>23–13</td>
<td>37–15</td>
<td>12–20</td>
<td>27–15</td>
</tr>
<tr>
<td>Vegetation</td>
<td>73–62</td>
<td>60–48</td>
<td>73–57</td>
<td>59–47</td>
</tr>
</tbody>
</table>

4. Discussion

Our results show that jackal on Samara, like other jackal populations in arid environments (Klare et al., 2010) consumed a high proportion of ungulates compared to other prey items. The abundance of ungulates in the diet, accounting for a large percentage of the estimated biomass consumed, resulted in a fairly stable diet that did not differ markedly between seasons. In contrast, the frequency of occurrence varied considerably between seasons, as a result of inclusion of the smaller, more varied prey species. These observations are in accordance with suggestions that frequency of occurrence data should not be used to assess ecological questions related to jackal foraging ecology, but rather for identifying some of the rarer prey items consumed (Klare et al., 2011). Our results suggest that on Samara, sufficient resources are available through either active hunting of small ungulates or scavenging from ungulate carcasses that permits the year round stability of jackal diets.

Until recently ungulates were not considered an overly important prey group (Klare et al., 2010), although numerous studies are now showing that they may be more important, especially in the Nama Karoo biome (Kamler et al., 2012). Traditionally invertebrates (De Klerk, 2005; Kok and Nel, 2004; Loveridge and Macdonald, 2003; Stuart, 1976), birds (Avery et al., 1987; Stuart, 1976), small mammals (Kaunda and Skinner, 2003; Kok and Nel, 2004; Loveridge and Macdonald, 2003; Rowe-Rowe, 1983; Van der Merwe et al., 2009) or seals (Hiscoks and Perrin, 1987) have been shown to dominate the diet. However, on Samara the dominant prey group consumed by jackals were the small ungulates, with three species in particular found in the diet on a regular basis. Jackal are more than able to actively hunt and consume these prey species with a pair of jackal being observed on Samara hunting and killing a duiker (H. Clements Pers Comm.). In addition, jackals in the Karoo have been suggested to kill and consume juveniles of hider species (Klare et al., 2010), which may account for some of the consumption by jackal on Samara. A large proportion of the consumption is likely to be the result of scavenging events as in areas without large predators, ungulates characteristically comprise less of jackal diets (Do Linh San et al., 2009). Although in another jackal diet study in the Karoo, evidence of scavenging was low and did not differ between sites irrespective of apex predator presence (Brassine and Parker, 2012).
Many of the prey species consumed by jackals on Samara fall into the preferred prey category for cheetahs (Clements, 2013; Hayward et al., 2006), and thus their presence in the diet may be a result of scavenging events from cheetah kills. If jackals are actively predating these smaller prey species, the combined impacts of cheetah and jackal predation may have resulted in the observed decline in small ungulates within the Samara section from which the jackal scats were collected when compared to areas outside of this section (Makin, 2013). A recent assessment of the cheetah diet did not reveal many small ungulates (Clements, 2013), but that may be an artefact of the method of assessing cheetah diets from which the jackal scats were collected when compared to areas outside of this section (Makin, 2013). A recent assessment of the cheetah diet did not reveal many small ungulates (Clements, 2013), but that may be an artefact of the method of assessing cheetah diets based on sporadic observations of tracked cheetah biasing against small kills, or a consequence of the low number of small ungulates currently in the predator section of Samara (Makin, 2013).

Rodents are fairly often the main prey taxa of jackal, although the traditional frequency of occurrence methods may have overestimated their importance in previous studies (Klare et al., 2011). In previous assessments where rodents have been abundant, fluctuations in their availability in the diet have led to fluctuations in the jackal diets. On Samara, rodents were equally represented across all seasons suggesting a constant availability and opportunistic predation when accessible. Although results from this study represent a measure of jackal diet across a single year, our study identified some novel dietary items that are not often reported in other jackal diet studies. Most interesting was the frequent encounter of primates in the diet in all seasons. The category ‘primates’ represents only vervet monkeys (Cercopithecus aethiops) and this prey item occurred in approximately 17% of the scats collected, although only accounting for 1–6% of the consumed biomass per season. Jackal have long been considered potential predators to vervet monkeys (Cheney and Seyfarth, 1981; Struhsaker, 1967), however no study that we are aware of has reported such a high presence of primates in jackal diets. A recent study on the vervet monkey population on Samara confirmed alarm calling behaviour directed towards jackals, thus implicating the jackals as a potential threat (Pasternak et al., 2013). However, without the benefit of direct observation it is unknown whether the jackals at Samara preyed on vervet monkeys opportunistically, or whether a strategy has been developed to hunt vervet monkeys.

Without sufficient visual confirmation of jackal foraging or knowledge on cheetah diet estimates, we have no way in knowing whether or not jackals on Samara are actively hunting small ungulate species. The estimation of cheetah kill rates and prey preference on Samara will shed light on the interaction between predators ( apex and meso) and their associated prey species. We propose that if jackal studies are conducted in areas with resident apex predators, the diet of the apex predator be assessed in association with jackal diet estimates. In this way the relative contribution of the different predators can be assessed and a better estimate of the importance of each predator for prey population dynamics can be determined. Ultimately, the relationship between apex predators and meso-predators may have severe cascading effects on ungulate populations (Berger et al., 2008), and in the light of increased large predator reintroduction programs (Hayward et al., 2007), this relationship needs to be better understood for the management of small reserves. Given the seasonally stable diet of the jackal population at Samara, we assume that the provision of scavenging opportunities by cheetahs constitutes an important facet of jackal foraging ecology. In addition, the constant proportion of ungulate biomass in the jackal diet reflects carrion ingestion rather than seasonal selection for vulnerable neonates. Our finding suggests that the presence of apex predators may have an important impact on meso-predator diets.

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