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The foraging ecology of reintroduced African wild dog in small protected areas

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Restoring large predators to small confined areas (< 400 km^2) is inherently complex and therefore any data on the foraging behaviour and top–down influences hold significant value for the conservation and reintroduction planning of the species. Conservation efforts are increasingly applied to small or fragmented landscapes. However, it is unclear what the effect of these small areas have on processes such as foraging behaviour as these spatial constraints may reduce the likelihood of innate predator–prey dynamics. We investigated African wild dog *Lycaon pictus* foraging patterns on five small fenced protected areas in South Africa. We report on the diet composition, prey preferences and potential influence of pack size and fences on the diet of African wild dogs. Data from 553 kills collected by direct observations at the five sample sites were analysed. Sixteen species of prey were recorded. A narrow dietary niche breadth was determined. Impala *Aepyceros melampus* and nyala *Tragelaphus angasii* collectively, form 75% of diet, and 67% of edible biomass. However, only nyala were significantly selected for. The mean wild dog pack sizes in our sample sites were relatively smaller than those frequently encountered in larger systems. We found that larger wild dog pack sizes did not select for larger prey. Contrary to studies investigating the influence of hard boundaries on smaller protected areas, the upward bias caused by fences on prey mass selection was inconsistent across sample sites. By characterising African wild dog diet on smaller protected areas, our results are suggestive of potential top–down influences that should be investigated by future studies. The results add to a growing body of literature that aims to assist in the reintroduction planning of endangered carnivore species.

Protected areas are important conduits for the preservation of biodiversity (Le Saout et al. 2013, Watson et al. 2016). However, the ecological requirements of wide ranging species often extend beyond the periphery of the protected area (Jenkins et al. 2015), frequently leading to human–wildlife conflict within an increasingly human dominated landscape (Woodroffe and Ginsberg 1998, Balme et al. 2010). As competition for land intensifies, anthropogenic influences continue to reduce available habitat for wildlife species, and therefore conservation efforts are increasingly being applied to highly modified or small fragmented pockets of remaining habitat (Lindsey et al. 2011, Davies-Mostert et al. 2015, Miller et al. 2015).

Reintroductions are frequently used as a conservation tool to restore species to portions of their historical distribution range (Armstrong and Seddon 2008). Despite occurring throughout much of sub-Saharan Africa, the endangered African wild dog *Lycaon pictus* (wild dog hereafter) has experienced significant population size contractions on account of habitat fragmentation, conflict with human activities, and infectious diseases (Woodroffe and Sillero-Zubiri 2012). To halt population declines in South Africa, wild dog have been reintroduced into several small geographically discrete protected areas (Davies-Mostert et al. 2015), some of which are often considerably smaller than the estimated home range size (537 km^2) in a large South African system (Mills and Gorman 1997).

Wildlife-proof fencing is commonly employed as a management tool to enclose these small protected areas (Somers and Hayward 2012, Packer et al. 2013). Although useful in separating large predators from humans, these hard boundaries are a potential catalyst to a range of cascading ecological challenges (Creel et al. 2013). Large carnivores often apply significant selective forces on prey assemblages as an explicit result of predation (Hayward et al. 2006). However, when confined to small areas, natural processes that frequently characterise open intact systems are disrupted (Gadd 2012, Murphy et al. 2017, Pokorny et al. 2017). For instance, fences that enclose small areas impede the potential for prey to carry out natural migratory patterns, as

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often observed in larger open systems (Whyte and Joubert 1988, Harris et al. 2009, Løvschal et al. 2017). The sedentary nature and small population sizes of the prey base in fenced areas inflate their vulnerability to predation (Fryxell and Sinclair 1988, Power 2003). As migratory prey populations are predominantly regulated by bottom–up processes (Mduma et al. 1999), the clumping of multi-prey multi-predator assemblages in fenced protected areas can modify the trajectory of these associations (Mills and Shenk 1992, Tambling and Du Toit 2005). Predators in larger intact systems can directly and indirectly influence the diversity and stability within ecological communities (Estes et al. 2011, Ripple et al. 2014). Destabilisation can occur if the availability of refugia to escape lethal predatory encounters becomes spatially and temporally diluted, consequently increasing the influence of top–down processes (Tambling and Du Toit 2005, Robinson et al. 2010).

Wild dog are endangered, social, cursorial hunting carnivores (Creel and Creel 1995, Woodroffe and Sillero-Zubiri 2012). Small populations are disproportionally susceptible to demographic, environmental and genetic stochasticity (Shaffer 1981), therefore in South Africa, a managed metapopulation approach has been employed to collectively manage the species as a single population whereby dispersal and gene flow are mimicked through human intervention (Mills et al. 1998). The reintroduction of wild dog on small reserves in South Africa has become a frequent occurrence (Davies-Mostert et al. 2009), however several attempts have previously lead to unsustainable declines of prey species, subsequently leading to the removal of wild dog sub-populations from the protected area.

Understanding the foraging patterns of a predator in a small protected area (<400 km^2) is the first step in unravelling the complex ecological community networks and potential influences on the prey base (Hayward et al. 2007, Kapfer et al. 2011). Whether predatory patterns on small reserves are similar to findings elsewhere in larger areas is uncertain (Hayward et al. 2006). Insight into the feeding ecology and predatory patterns of reintroduced predators to small fenced areas is essential in guiding evidence-based conservation management actions of the protected area, but also that of the focal species.

Large carnivores generally display a degree of selectivity towards a particular prey species, mass range or demographic class (Hayward et al. 2006, Clements et al. 2014, Makin and Kerley 2016). In large African predators, prey size typically increases with predator body size (Carbone et al. 1999), however wild dogs that weigh 20–25 kg (Creel and Creel 1995) employ communal hunting strategies that enable them to catch larger prey relative to their body size (Gorman et al. 1998). Cooperative hunting is suspected to reduce chase distance, increase kill rate and allow for the capture of larger prey (Rasmussen et al. 2008). Wild dog in small protected areas are further believed to modify their hunting behaviour in the presence of electric fences, by using barriers to subdue larger prey than what would otherwise be killed (van Dyk and Slotow 2003, Rhodes and Rhodes 2004).

Here, we quantify and describe the feeding patterns of reintroduced wild dog in five small range size protected areas in South Africa. We investigate the 1) prey species and biomass contributions to wild dog diet, 2) prey species sex and age contribution, 3) prey species preference, 4) the proximity to boundary fences on wild dog prey size usage, 5) diversity and evenness of diet, and 6) the influence of pack size on prey selection. We then discuss the implications of our results for the conservation management of the species, and predator–prey related processes.

Material and methods

Study area

Wild dog have been reintroduced to several small protected areas in KwaZulu-Natal including Somkhanda Game Reserve (Somkhanda: 106 km^2), Zimanga Private Game Reserve (Zimanga: 53.3 km^2), Manyoni Game Reserve (Manyoni: 217 km^2), uMkuze Game Reserve (uMkhuze: 338 km^2) and Thanda Royal Private Game Reserve (Thanda: 68.6 km^2). The wild dog sub-population size at each protected area has fluctuated over time, however at the time of this study (May 2017), there are seven adult wild dog on Somkhanda Game Reserve, five at Manyoni Game Reserve, nine at uMkhuze Game Reserve, and 14 at Zimanga Game Reserve (Table 1, Fig. 1). Thanda currently does not host a pack of wild dog, as the 12 wild dogs were removed in 2013 due to the perceived impact on prey populations by the entire large predator guild.

The study areas are situated within the Maputaland Albany Hotspot and forms part of the African Savanna biome (Steenkamp et al. 2004, Mucina and Rutherford 2006). Two distinct seasons characterise the warm to hot, humid subtropical region; the warm dry winter from April to September and a hot humid summer from October to March (Balme et al. 2010). Eighty percent of the annual rainfall (580 mm; Mkuze Town weather station) occurs in the spring and summer months between September and March. Winters are generally cool to warm (van Rooyen and van Rooyen 2014). Frost is rare in the region, and the mean annual temperature is 21.8°C with the mean monthly temperature of 25.5°C and 16.4°C for January and July respectively (van Rooyen and van Rooyen 2014).

The protected areas support a rich diversity of ungulates and potential prey including blue wildebeest *Connochaetes taurinus*, common warthog *Phacochoerus africanus*, greater kudu *Tragelaphus strepsiceros,* impala *Aepyceros melampus*, nyala *Tragelaphus angasii*, plains zebra *Equus quagga* and waterbuck *Kobus ellipsiprymnus*. Due to the presence of potentially dangerous wildlife species, the protected areas are fully enclosed by electrified perimeter fencing (Chapman and Balme 2010).

Field sampling

Wild dog dietary data were collected from direct observations of prey killed. At least one individual in each pack was fitted with a VHF tracking device (frequency range 148–151 Mhz, from either African Wildlife Tracking (AWT cc-Pretoria, South Africa) or Sirtrack (Havelock North, New Zealand)). Wild dog were located and followed during periods that coincide with the bimodal crepuscular activity pattern (dawn and dusk) of wild dog (Creel and Creel 1996, Saleni et al. 2007, Davies-Mostert et al. 2013).

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Table 1. Protected area size (km²), mean annual precipitation (mm), density of sympatric predators (estimated number of individuals/100km², u= unknown, a= absent), year of wild dog reintroduction, and focus study period in parenthesis for the five sample sites.

				Density of wild dog and sympatric predators					
Property	Size (km²)	Rainfall (mm)	Date wild dog reintroduced	Wild dog	Cheetah	Leopard	Lion	Spotted hyaena	Brown Hyaena
Somkhanda Game Reserve	106	626	2014 (2015–2016)	7.55	a	2.74	a	u	u
Thanda Royal Private Game Reserve	69	610	2004 (2010)	8.75	2.92	u	16.03	u	u
Manyoni Game Reserve	217	600	2014 (2015–2016)	2.30	8.76	4.61	7.83	3.69	0.92
Umkhuze Game Reserve	338	628	2005, 2010 (2015–2016)	7.10	3.25	6.51	5.33	7.69	a
Zimanga Private Game Reserve	53	670	2009, 2011 (2014)	26.27	3.75	2.74	a	u	u

Once the pack was located, observations recorded include the geographic coordinates (latitude and longitude) of the pack using a GPS unit (Garmin), time of day, current behaviour and observed kills. Where possible, the prey item was identified and categorised to species, sex and age (adults > 2 years; subadults 1 to 2 years; juveniles 0 to 1 year).

Direct observation as a tool to obtain kill data is considered useful to determine the diets of large predators (Mills 1992). However, due to the quick-handling time, small prey species may be underrepresented (Okuyama 2010). It has been argued that where the observation effort is high, as in our case, the bias should be low (Radloff and Du Toit 2004, Rapson and Bernard 2007).

Prey availability

To determine prey availability, we used data from a number of sources. Aerial based total wildlife censusing was done at Somkhanda, Manyoni, Zimanga and Thanda using an R44 helicopter containing a crew of the same four people; pilot, recorder and two observers. Parallel predetermined transects were flown in an east–west orientation and were systematically arranged to cover the entire protected area. Census data for uMkhuze were collected using Distance based ground sampling (Thomas et al. 2010). All prey censuses were carried out at the end of the dry season (August, September) to aid in visually detecting an animal as the foliage is reduced compared to other seasons (Bothma 2002). Potential prey abundance estimates using aerial counts may be biased towards species that are more easily detected from the air (Owen-Smith and Mills 2008). Therefore standard visibility correction factors generated for savanna ecosystems (Owen-Smith and Mills 2008) were applied to compensate for these imprecisions.

Species and species biomass contribution to diet

The contribution of each prey species from direct observations to wild dog diet has been expressed as the prey percentage composition (g) of species i, as:

$$g = \frac{ni}{N} \times 100$$

where ni represents the total prey species item and N is the total prey items of all species per protected area and year. Confidence intervals (95%) were generated by means of running 1000 bootstrap simulations around the mean relative frequency of a prey item.

To determine the overall biomass of prey killed, we estimated the mass of each kill based on the species sex and age. Adult mass for each species was obtained from Bothma (2002), and Skinner and Smithers (1990). Subadult mass was taken to be 75% of an adult female, and a juvenile as 30% (Radloff and Du Toit 2004). When the sex of an individual prey item could not be determined, the unit mass (adult female multiplied by 0.75) for the species was used (Jooste et al. 2013). To compensate for wastage, and inedible material, edible biomass (hereafter corrected mass) was determined as carcass weight > 80 kg = 67% is edible, carcass weight 40–80 kg = 75%, carcass weight 5–40 kg = 90%,

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Figure 1. The location of the wild dog metapopulation sample reserves in KwaZulu-Natal Province, South Africa; Somkhanda Game Reserve (1), Zimanga Private Game Reserve (2), Manyoni Game Reserve (3), Thanda Royal Private Game Reserve (4) and uMkhuze Game Reserve (5).

carcass weight < 5 kg = 99% (Blumenschine and Caro 1986). The mean prey mass killed, prey mass range used and bootstrap confidence intervals (95%, 1000 iterations) were determined for each sample site.

Dietary niche breadth and evenness

To determine the relative degree of diet specialisation, we determined the dietary niche breadth using Levins' index (Levins 1968) for each wild dog pack and year. We applied standardised trophic niche measures following Hurlbert (1978):

$$BA = \frac{\left(\frac{1}{\sum_{Pij}{}^{2}}\right) - 1}{n - 1}$$

where *BA* is the standardised index of niche breadth, *pij* is the proportion of diet of pack *i* on prey *j,* n is the number of possible resource states. Index values close to '0' represent specialised dietary niches, and values close to '1' represent generalist foraging patterns (Krebs 1999). The mean standardised dietary niche index value determined *(BA* ± 1 SE) from prey species composition is presented.

We further determined diet evenness by constructing Shannon (*H*) and Shannon equitability diversity (Eh) index values as:

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

Where *p* is the proportional diet contribution of prey species *i*, *ln* is the natural log transformation and *s* represents the species richness found in the respective diet. Diet evenness is derived from *H* using a Shannon equitability diversity index (Eh). *Eh* is determined as *H* / *Hmax* (here *Hmax* = *ln s*). Index values range from *Eh* = 0 (uneven) to *Eh* = 1 (complete evenness).

Selection for prey species

In order to determine the selectivity for specific prey items, a preference ratio analysis was employed by using Ivlev's electivity index (*D*) as modified by Jacobs (1974). Various selection indices have been developed to test selection, however many show bias towards rarer items and suffer from non-linearity (Jacobs 1974). The use of the Jacobs' index is expected to reduce these biases (Hayward and Kerley 2005) and in addition allows for comparison with other studies investigating large predator prey preferences (Hayward et al. 2006) as follows:

$$D = \frac{r - p}{r + p - 2rp}$$

where *r* is the proportion of kills of each species and *p* is the proportional availability of that prey species in comparison to the number of species preyed on by wild dogs during the study period. The availability of prey is based on game census data for each respective year at each study site. The *D* value of the Jacobs' index ranges from −1 to + 1, with a +1 indicating maximum preference and a −1 value indicating maximum avoidance (Jacobs 1974). Jacobs' index values $0.2 > 0 > -0.2$ are considered to be indicative of prey being used as frequently as expected (Hayward et al. 2011). Each prey species Jacobs' index was tested for significant avoidance/preference by using a t-test against a hypothetical mean on '0'. Where data did not conform to normality (Shapiro–Wilks test) we used a z-sign test. The analysis of prey preference further identifies prey species utilised proportional to their density, therefore provides an estimate of prey utilisation relative to prey abundance.

Selection for prey age and sex classes

We quantified the known sex and age (juvenile, subadult, and adult) prey composition of wild dog kills as the percentage

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of observed kills. To determine the utilisation of certain prey population classes by wild dog, we used nyala as a representative species. As nyala are non-seasonal breeders and are sexually dimorphic, the known sex ratio and age distributions from road based distance sampling were compared to observed kills. A Jacobs' selection index and a goodness-of-fit test were used by comparing the frequency of predation between male and female nyala and also for adult, subadult and juveniles. Bonferonni Z- statistics were used to generate 95% confidence intervals.

The influence of pack size on prey size

We used Kendalls tau-b correlation coefficient (τb) of independence to determine whether a monotonic relationship exists between pack size and prey mass. As wild dog subadults often contribute to hunting efforts (Vogel et al. unpubl.), we considered pack sizes as 1) adult pack size, 2) adult + subadults and 3) adult + an applied subadult weighted unit equivalent of 0.5. Wild dog are estimated to reach sexual maturity at approximately 18 months of age (Becker et al. 2012), and often disperse from natal packs at this age (Gusset et al. 2006). We therefore categorised subadult pack members as 12 to 18 months, and adults as >18 months (Malcolm and Marten 1982).

We repeated this procedure for the mean mass of prey killed for each pack size category and for the most frequently preyed upon prey item (based on prey species, sex and age) for each pack size category. Where two species equally occurred as the most frequently used prey item, the mean mass between the species was used.

The influence of fences in prey mass selection

As wild dog may alter their hunting strategies on small reserves by incorporating fences to capture larger prey items (van Dyk and Slotow 2003), we compared the mass and proportional contribution of fence impeded kills with non-fence impeded kills. If fences increase the vulnerability of larger prey to wild dog predation than what naturally would occur, the median mass of prey items (based on prey species, age and sex) will be skewed. Using wild dog kill site GPS coordinates, we binomially categorised kills by creating a 200m buffer tolerance from fences. We made the assumption that the benefit of using a fence for hunting purposes would be most rewarding at the capture (restraining and bringing down), see Bailey et al. (2013), phase of the hunt. Allowing for temporary getaways of the prey during restraining. The 200 m buffer was an estimate from observing hunts over a four year field study (Somers unpubl.). We compared the size mass of kills within the 200 m buffer to size mass of kills >200 m from fences for four protected areas (Somkhanda, Manyoni, uMkuze, Zimanga). GPS data associated with kills made by wild dog at Thanda were however not available, therefore we report on kills made with GPS coordinates at the remaining four sample sites. The upward bias caused by barriers was tested using a Mann–Whitney U-test and p-values were computed using 10 000 Monte Carlo simulations. As wild dog are generally cursorial hunting carnivores, we believe that 200 m from a boundary is sufficient to determine prey mass differences and further reduces the influence of GPS error and detection biases.

Results

Sixteen prey species (Table 2) were recorded by direct observations (n = 553) over a cumulative time period of 91 months. Impala (40% ± 3.92) followed by nyala (35% ± 6.03) formed the greatest frequency of known kills (Table 3). However, if transformed to corrected biomass, nyala forms the greatest edible biomass (8245.81 kg) followed by impala (6742.8 kg) of the total 22254.41 kg (Supplementary material Appendix Table A1).

Dietary niche breadth and evenness

Wild dog foraging patterns indicated specialised niche breadths for pooled observations ($BA = 0.17$, n = 16) and across sample sites ($BA_{mean} = 0.3 \pm 0.03$). Wild dog further showed low diversity in diet ($H = 1.68$, $H_{mean} = 1.36 \pm 0.1$), and erred (0.50 <) on uniformity (Eh = 0.61, $Eh_{mean} = 0.67 \pm 0.02$) in terms of diet evenness.

Prey preference

Jacobs' index values were calculated for sixteen species (Table 3). Wild dog within the KwaZulu-Natal cluster prefer ($D > 0.2$) to consume common duiker ($z = 0.92$, p = 0.359), and red duiker ($z = 0.97$, p = 0.333). However, only nyala ($t_7 = 6.37$, p = <0.001) are significantly preferred. Buffalo ($z = –2.79$, p = 0.005), plains zebra ($z = –8.35$, p = <0.001), warthog ($z = –4.36$, p = <0.001), waterbuck ($z = 2.46$, p = 0.014) and blue wildebeest ($t_8 = –5.01$, p = 0.002) are significantly avoided prey species. Giraffe *Giraffa giraffa* and suni *Neotragus moschatus* ($D = –1$) were completely avoided.

Table 2. Comparison between the five protected areas. n is total count of all kills observed, S is the species richness (count of prey species) in diet, mean prey (kg) and lower and upper 0.05 confidence levels (CI). Range represents the smallest and largest prey items killed.

			Mean prey				Range of prey mass	
Protected area	n	S	Body mass	SE	95% CI	95% CI	Minimum	Maximum
Manyoni	147	12	60.57	3.01	53.88	67.26	12.00	225.00
Somkhanda	177	12	57.44	2.62	52.35	62.52	12.00	215.00
Thanda	105	10	46.24	2.49	39.66	52.82	2.86	126.00
uMkhuze	56	6	55.19	2.68	45.67	64.71	12.00	215.00
Zimanga	68	6	46.91	2.12	40.15	53.66	13.50	155.00
Pooled sample sites	553	16	54.62	1.52	51.60	57.64	2.86	225.00

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Table 3. Mean annual wild dog prey species contribution (*g*) and mean prey species Jacobs' index values (D ± SE). Significant avoidance, preference or whether a species is utilised in proportion to its abundance is indicated.

		g				Preference				
Species		Mean %	SE	CI	CI	Mean	SE	t/z	p	Pattern
Syncerus caffer	buffalo	0.71	0.40	–0.16	1.59	–0.60	0.21	–2.79	0.005	avoided
Tragelaphus angasii	bushbuck	1.22	0.49	0.12	2.32	–0.43	0.36	–1.19	0.236	no pattern
Potamochoerus larvatus	bushpig	0.12	0.12	–0.15	0.39					
Thryonomys swinderianus	cane rat	0.12	0.12	–0.15	0.38					
Redunca arundinum	common duiker	2.45	0.91	0.43	4.48	0.26	0.28	0.92	0.359	no pattern
Sylvicapra grimmia	common reedbuck	1.60	0.63	0.17	3.03	–0.37	0.29	–1.26	0.264	no pattern
Giraffa giraffa	giraffe	0.00	0.00	0.00	0.00	–1.00	0.00			avoided
Aepyceros melampus	impala	39.87	3.92	31.18	48.57	0.00	0.05	–0.04	0.970	no pattern
Tragelaphus strepsiceros	kudu	4.13	1.44	0.84	7.41	–0.25	0.20	–1.24	0.255	no pattern
Redunca fulvorufula	mountain reedbuck	0.46	0.31	–0.23	1.14					
Tragelaphus angasii	nyala	35.09	6.03	21.87	48.30	0.47	0.07	6.37	0.000	preferred
Cephalophus natalensis	red duiker	2.94	1.17	0.28	5.61	0.27	0.28	0.97	0.333	no pattern
Raphicerus campestris	steenbuck	0.24	0.24	–0.27	0.75	–0.80	0.20	–4.09	< 0.0001	avoided
Neotragus moschatus	suni	0.00	0.00	0.00	0.00	–1.00	0.00			avoided
Phacochoerus africanus	warthog	6.19	4.48	–3.56	15.93	–0.69	0.16	–4.36	< 0.0001	avoided
Kobus ellipsiprymnus	waterbuck	0.63	0.44	–0.33	1.60	–0.62	0.25	–2.46	0.014	avoided
Connochaetes taurinus	wildebeest	3.94	1.19	1.32	6.56	–0.58	0.12	–5.01	0.002	avoided
Equus quagga	zebra	0.29	0.20	–0.15	0.73	–0.88	0.11	–8.35	< 0.0001	avoided

Prey demographic selection

Female ungulate prey (66 ± 7.02%) occurred more frequently than male ungulates (34 ± 7.02%) in the diet of wild dog. Adult prey items were recorded more frequently (69 ± 6.92%) than subadult (21 ± 5.52%) and juvenile (9 ± 41%) age categories.

Male and female nyala were utilised disproportionally (χ^2 (1) = 6.71, p = 0.01) to their availability. Female nyala are killed more frequently by wild dog than expected, in contrast to male nyala prey items that were actively avoided (D = –0.23).

Adult and juvenile nyala are utilised as expected (Table 4), however subadults are preyed upon more frequently than their proportional availability (χ^2 (2) = 13.638, p = 0.001).

Influence of pack size on diet

In context of observed kills made by wild dog, adult pack size ranged from two to seven adults with a mean of 4.6 ± 0.08 individuals. If subadults are considered as hunting pack members, pack sizes ranged from two to 13 equivalents (6.19 ± 0.11), and two to eight if weighted as 0.5 equivalents (5.39 ± 0.07).

While pack sizes in our study were relatively small in comparison to those encountered elsewhere (Creel et al. 2004, Marnewick et al. 2014), we found no evidence to suggest that larger packs selected for larger prey. There was no significant association between mean mass of prey killed and adult pack size (τb = 0.2, p = 0.719), adult and equivalent subadult pack size (τb = –0.333, p = 0.216) or adult and weighted subadult pack size (τb = –0.200, p = 0.445). Using the most frequently preyed item, there was no significant relationship with adult pack size (τb = 0.447, p = 0.227), adult pack size including subadults as an equivalent weighting (τb = –0.511, p = 0.054) or adult and weighted subadult pack size (τb = –0.407, p = 0.099).

The influence of fences on prey mass selection

A total of 422 kills with associated GPS coordinates were observed at the four sample sites. Wild dog kills located within 200m proximity of fence lines contributed 50% of all recorded kill locations. Wild dog at each sample site used prey mass in a similar pattern (H = 5.963, p = 0.113). The median mass for prey killed within 200 m of a fence (60 kg, 60 kg, 45 kg) was not significantly larger than prey killed away from fences (45 kg, 53.25 kg, 46.5 kg) for Manyoni (U = 1988.5, p = 0.279), Somkhanda (U = 2965.5, p = 0.076) and uMkhuze (U = 131, p = 0.961) respectively. Prey killed <200 m from the fence were only significantly larger in mass at a single site, Zimanga Game Reserve (U = 238.5, p = 0.007). Prey mass difference of kills at Somkhanda were insignificant (p = 0.076), however with a less conservative alpha level (e.g. 0.10) half of our sample sites with spatial data on kill distribution would have had significantly larger prey killed within 200 m of fences.

Discussion

Our investigation into the foraging behaviour of reintroduced wild dog to five small protected areas concurs that wild dog

Table 4. Wild dog prey selection of nyala age structure, observed age utilisation (pi), expected age utilisation (pioxn) and preference (JI=Jacobs' index), Z=2,37.

Age structure	pi	pioxn	Observations	JI	lower CI	Higher Ci	Usage
Adult	0.65	0.73	116	–0.19	0.57	0.74	as expected
Subadult	0.23	0.14	21	0.31	0.15	0.31	> than expected
Juvenile	0.12	0.13	41	–0.05	0.06	0.18	as expected
			178				

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prey on the most abundant small and medium sized ungulates (Ginsberg and Macdonald 1990, Hayward et al. 2006). Nyala and impala collectively compromise 75% of the mean species preyed upon. These two-prey species featured as the most frequently observed prey item, with the exception of the smallest protected area (Zimanga), where impala and warthog were observed to be utilised far more frequently in comparison. Warthog are generally avoided by wild dog, however the preferred larger nyala occur at much lower densities at this particular site likely leading to comparatively fewer encounters with wild dog. Wild dog have disproportionally high rates of daily energetic expenditure (Gorman et al. 1998), and require high daily food consumption rates (Gorman et al. 1998, Carbone et al. 2007), but see Hubel et al. (2016) suggesting that wild dog are more energetically robust that previously thought. If wild dog optimise their foraging strategy, the more abundant warthog (corrected sow biomass 45 kg) are expected to contribute more frequently to their diet, as they would be required to concede between searching for the rarer nyala, albeit preferred (corrected ewe biomass 46.5 kg) versus selecting for the more abundant warthog in the Zimanga case, as this requires the least energy to secure through search and handling time.

Very large prey (>350 kg e.g. giraffe) were avoided across all sites. Small prey items (<5 kg) do occur in their diet, however not frequently and can be considered as rare and incidental prey items. The detectability of very small prey items using direct and opportunistic methods to quantify large predator diets have previously been questioned, as small prey items are rapidly or entirely consumed. As our times of sampling mirror that of wild dog hunting periods, these continuous observations during activity phases are likely to reliably reflect on real dietary patterns (Rasmussen et al. 2008). The viability of alternative methods such as scat analysis is further compounded particularly in context of distinguishing between prey age and sex classes (Davies-Mostert et al. 2010). In addition, wild dog in our sample sites, did scavenge on prey that had died by other means than wild dog predation and occasionally returned to kills the following days. Although we did not quantify scavenging events (feeding on prey remains known to not have been killed by wild dog) or kill return intervals (feeding on prey killed by focal pack, but defined by moving away from kill and returning at a later stage), wild dog have previously been observed to scavenge on prey remains killed by other predators (Fitzgibbon and Fanshawe 1989). Therefore using scat analysis would increase the percent occurrence and estimated percent biomass of the scavenged species (Morehouse and Boyce 2011). Returning to kills may be an artefact of limited exposure to kleptoparistism as a result of low densities of spotted hyaena *Crocuta crocuta*. Interference competition inflicted by spotted hyaena may result in considerable loss (up to 22%) of prey killed by wild dog through kleptoparistism (Fuller et al. 1995). Considering the costly expense of hunting to attain energy balances together with direct antagonistic interactions with larger carnivores, can explain the low population densities of wild dog where competition is high (Creel and Creel 1996, Gorman et al. 1998, Woodroffe and Ginsberg 1998). If the intensity of competition within the large predator guild increases within our sample sites, we envisage that the frequency of wild dog returning to kills and scavenging will decrease.

Using nyala as a frequently preyed upon proxy, it is expected that vulnerability will vary among prey sex and age classes (Pole et al. 2004). Nyala females and subadults were utilised more frequently than expected. Analogous to studies carried out in open systems (Fitzgibbon and Fanshawe 1989), the proportional partiality towards a particular prey or sex class may be a biological innate phenomenon. The avoidance of larger male nyala may be an attribute of sexual dimorphism, where males have horns that can be used for weaponry defence against potential lethal encounters with predators. The selective hunting of female and subadult prey may therefore be more profitable in terms of avoiding injury as they do not possess horns.

A narrow dietary niche, as observed with wild dog in our study, has been suggested to contribute to the inherent rarity of the species (Hayward and Kerley 2008). Dietary niche estimates are often used in the process of evaluating the potential competition amongst sympatric carnivores (Mbizah et al. 2012, Broekhuis et al. 2018). However, in our study, wild dog consistently indicated a niche specialisation across all five sample sites, despite the variability in the presence and density of competing sympatric carnivores. Wild dogs are expected to discriminate between prey items based on functional traits of prey such as defensive weaponry, size, body condition, herd structure and habitat affinity (Pole et al. 2004, Hayward et al. 2006, Clements et al. 2016). In support of this, our results from preference indices show that wild dog did not use species at random and showed a high proportional utilisation of nyala. When compared to wild dog prey preference estimates carried out elsewhere (Hayward et al. 2006), nyala was highly avoided. Nyala are nested within the preferred prey weight range of wild dog (Clements et al. 2014) Furthermore, nyala occur at greater densities and overall ungulate composition within our sample sites (16.8 ± 3.26) in comparison to other regions of wild dog distribution (6.47 ± 4.41%, Hayward et al. 2006). This confounding high variability for prey resources highlights the measure of caution when interpreting preference analysis. Values are non-independent, in that the increase in preference for species 'A' conversely influences prey species 'B' (Louw et al. 2012). Determining foraging preferences is further compounded by being primarily methodologically contingent on the known proportional prey species kills vs the species availability to the predator (Jacobs 1974). The proportional availability of a prey item is required to be known, however game census data are often subject to wide confidence intervals, particularly those for cryptic or thicket dwelling species, leading to unreliable estimates of prey species proportional availability.

The higher proportional contribution of larger bodied prey animals to diet profiles in other smaller protected areas has been described as a consequence of fence aided hunting (van Dyk and Slotow 2003, Rhodes and Rhodes 2004, Davies-Mostert et al. 2013). Except for the smallest protected area (53 km^2), wild dog in Kwazulu-Natal did not provide sufficient behavioural evidence to support this assumption. A hefty proportion of kills occur within 200 m of artificial

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boundaries, although the discrepancy in prey mass utilisation facilitated by fences is negligible.

The mean wild dog pack sizes in larger areas such as northern Botswana and the Selous Game Reserve are estimated at 10.4 and 8.9 individuals per pack respectively (Creel et al. 2004). Our largest pack, including subadults included up to 13 individuals with a mean of 6.19. The pack sizes in our sample sites were smaller than those encountered elsewhere. Despite the comparatively smaller pack sizes encountered, our larger wild dog packs were expected to select for larger prey items (Creel and Creel 1995). Wild dog in our core sample sites illustrated a dissociated relationship between pack size and prey mass. An increase in sample size and a greater spectrum in pack size may increase or decrease even further the strength of these relationships.

The differences in attitudes towards African wild dogs between conservation practitioners and the general public can potentially hinder conservation actions and efforts as these values and attitudes play a major role in acceptance of conservation activities (Karanth et al. 2008). Perceptions hold that wild dog deplete the availability of prey, particularly during the denning season, when wild dog are generally more sedentary. Mbizah et al. (2014) found that wild dog did not significantly reduce impala populations, and wild dog actually select for low prey density areas. Selecting for low prey density areas is likely to be an artefact of avoiding costly encounters with larger competitors (Mills and Gorman 1997). However this could potentially contribute to the misconception that wild dog deplete prey stocks (Mbizah et al. 2014). Although we did not test for the impact of wild dog predation on prey populations, we did not find sufficient evidence to suggest that wild dog adversely influenced prey populations sizes. Despite receiving below average regional rainfall for the latter period of this study, principal dietary prey species such as impala remained stable or increased at three of the five sample sites. At the remaining two sites, the uMkhuze impala population size were estimated at 10 937 individuals and dropped to 5076 individuals two years later in 2016. The estimate of 10 937 impala is the highest the population has been recorded in the last 20 years. Considering that wild dog have been present for the last 11 years (initial reintroduction in 2005), impala populations returned to population densities previously estimated. Impala population size at Zimanga Game Reserve was reduced from an estimated 1337 individuals to 482 individuals a year later in 2016. Management at this particular site removed substantial amounts of wildlife from the protected area during this period (exact head of game not given). However, in combination with prey removal by management, the influence of wild dog on prey species is therefore unknown.

The undesirable influences induced by fences as found in other studies (Davies-Mostert et al. 2013), were not as evident in our study. Our smallest reserve and to a lesser extent Somkhanda, displayed evidence of fencing significantly influencing prey mass selection. The proximity to these hard barriers largely influenced the proportional contribution of prey kills with more kills occurring within the vicinity of fences than expected. The affinity towards 'fence patrolling' may facilitate the capture of prey, however it may also be a reflection of spatial avoidance of larger competitors.

The use of fencing to enclose small protected areas in South Africa is useful to minimize negative interactions between wildlife and humans. Protected areas interested in reintroducing large carnivores such as wild dog should ensure that sufficient principal prey items are present to sustain their consumptive influence. Where fencing has adversely manipulated predator–prey interactions, mechanisms such as area expansion should be investigated to decrease perimeter fencing to area size (Davies-Mostert et al. 2013). This study provides evidence that wild dog in small protected areas can display a narrow dietary niche and can select specific prey for consumption. Given the prey and foraging requirements of wild dog, harbouring populations of large carnivores in small fenced protected areas is integrally complex and will likely continue to require intensive management approaches. Wild dog foraging behaviour in small protected areas we studied reflects that of larger open systems, and fences in our sample sites showed only marginal evidence of management induced niche shifts or evolutionary constraints imposed by fragmentation.

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