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Diet choice and capture success of wild dog (*Lycaon pictus*) in Hluhluwe-Umfolozi Park, South Africa

Sonja C. Krüger[1], Michael J. Lawes[1]* and Anthony H. Maddock[2]

Department of Zoology and Entomology, University of Natal, Private Bag X01, Scottsville 3209, South Africa
KwaZulu-Natal Nature Conservation Service, P.O. Box 662, Pietermaritzburg, 3200, South Africa

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Abstract

The small population of wild dog *Lycaon pictus* ($n = 3$ to 30) in Hluhluwe-Umfolozi Park (HUP) has declined since 1992. The survival of dogs in HUP is dependent on the reintroduction of more dogs; however, wild dog reintroduction programmes are fraught with problems and many have failed. In this paper the diet and capture success of the wild dog pack in the Hluhluwe Section, and the influence of dietary considerations on the success of the future reintroduction of wild dogs in this reserve, are investigated. Diet choice was determined from scat analysis, personal observation and field staff records. Eight ungulate prey species were identified from scat analysis: nyala *Tragelaphus angasi* and impala *Aepyceros melampus* were the most abundant ungulate species in HUP and accounted for 77% of the diet. On the whole, wild dogs included prey types in the diet consistent with a rate-maximizing foraging approach, although some prey were clearly taken opportunistically. The dogs preyed mostly on small- (< 25 kg) to medium-sized (40–90 kg) prey, while the young of large (> 90 kg) prey species or scavenged carcasses supplemented the diet during the dry season. Adult nyala were taken more frequently than other age classes, but wild dog preyed on juvenile impala more than expected. Female prey were taken more frequently than males but selection did not differ from prey population sex ratios. Prey capture success was similar to that of previous studies from both open and densely wooded habitats and the wild dogs successfully caught 48% of all prey species pursued. Results suggest that wild dogs are quite capable of adapting both their diet choice and foraging technique to the dense vegetation in HUP. We conclude that prey type, prey availability and habitat constraints on prey capture success, will not affect the reintroduction of more wild dogs into HUP.

Key words: wild dog, *Lycaon pictus*, diet choice, profitability, capture success

INTRODUCTION

Wild dogs *Lycaon pictus* were once common throughout Africa south of the Sahara, but numbers have been drastically reduced and the species is currently regarded as endangered (Ginsberg & Macdonald, 1990; Woodroffe *et al*., 1997). Fewer than 5000 wild dogs occur naturally and, given the current trends of decline world-wide, the species may become extinct within 20–40 years (Fanshawe, Frame & Ginsberg, 1991; Woodroffe *et al*., 1997).

South Africa is one of six countries containing viable populations of this canid (Ginsberg & Macdonald, 1990; Fanshawe *et al*., 1991; Woodroffe *et al*., 1997) and the Hluhluwe-Umfolozi Park (HUP) population of wild dogs is one of three protected populations in South Africa. HUP is thus an important reserve for the future welfare of the species in South Africa.

The population size of wild dogs in HUP has fluctuated between three and 30 individuals since the reintroduction of 22 adult dogs in 1981. No breeding has occurred since 1993 and numbers of wild dogs have declined to between 10 and 13 individuals in 1995. The small population size makes the HUP wild dogs particularly vulnerable to predators and disease, while their isolation from other wild dogs makes losses due to emigration a cause of concern, and may result in inbreeding depression through reduced fecundity and viability (May, 1991). Some of these concerns may be addressed by introducing another pack of dogs and managing wild dogs in South Africa as artificial metapopulations (i.e. wild dogs are translocated between reserves) (S. Ellis, unpubl. data). However, a thorough understanding of the ecology of the HUP wild dog pack

*All correspondence to: M. J. Lawes, Department of Zoology and Entomology, University of Natal, Private Bag X01, Scottsville 3209, South Africa. E-mail: LAWES@zoology.unp.ac.za

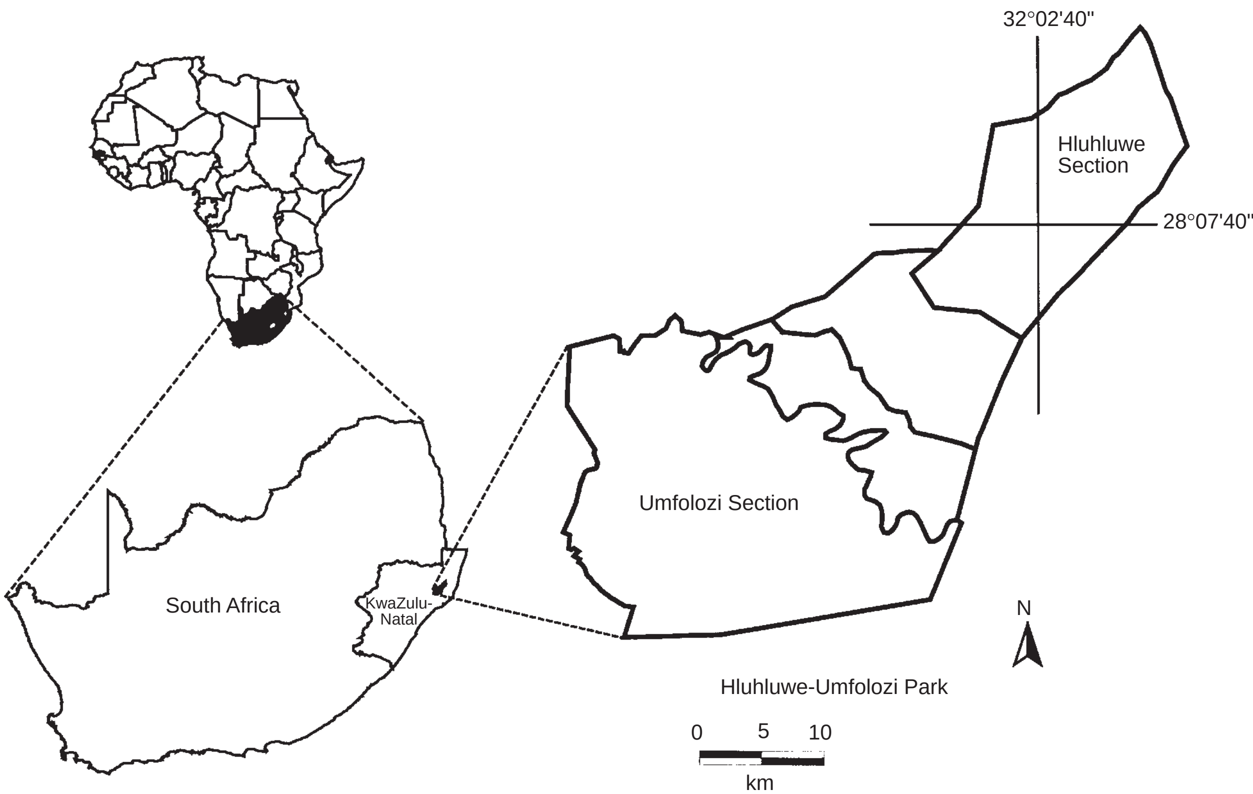

Fig. 1. The location of Hluhluwe-Umfolozi Park in the KwaZulu-Natal province, South Africa.

is required before contemplating further introductions (Fanshaw *et al.*, 1991). In this study we investigate prey selection and capture success in HUP to determine whether either have the potential to limit wild dog numbers in HUP.

Diet choice and capture success of wild dogs are constrained by the availability and abundance of their prey (Fuller *et al.*, 1992). Wild dogs are size-selective social predators consuming small- (< 25 kg) to medium-sized (40–90 kg) ungulates (Reich, 1981; Childes, 1988; Mills, 1992). Although wild dogs exploit a narrow size range of prey, their co-operative hunting technique enables them to take prey that are faster and larger than themselves (Mitchell, Shenton & Uys, 1965; Estes & Goddard, 1967; Kruuk & Turner, 1967).

A simple optimality model, the prey model (Stephens & Krebs, 1986; Bulmer, 1994), was used to test if wild dogs are rate-maximizing foragers and to explain departures from the expected diet. Since wild dogs hunt primarily by sight (Fanshawe & Fitzgibbon, 1993), the visual barriers presented by the very dense vegetation at HUP may hinder prior close-quarter visual assessment of prey and, thus capture success (Ginsberg & Cole, 1994; but see Maddock, 1989; Mills & Biggs, 1993). This may also cause the dogs to be more opportunistic in their diet and foraging behaviour than expected. The diet and diet choice of wild dogs at HUP was examined for evidence that may have led to their decline in the reserve, or may have adversely affected the planned release of more dogs to the park.

Study site

Hluhluwe-Umfolozi Park (HUP) is located in central Zululand (28°00′–28°10′S and 31°43′–32°09′E) (Fig. 1), and comprises the Hluhluwe Section in the north (300 km^2) and the Umfolozi Section in the south (660 km^2). This study was conducted in the Hluhluwe Section, the home range of the single pack. The topography is hilly and the altitude ranges from 60 m to 540 m. Hluhluwe Section receives an average annual rainfall of 1014 ± 77 mm (mean ± 1 SE; range = 525–1376 mm; 1985–1995) and has a wet season from October to March (rainfall > 60 mm per month).

HUP lies within the Zululand thornveld subcategory of coastal tropical forest types and the lowveld subcategory of tropical bush and savanna types (Acocks, 1988). For the purpose of this study the vegetation physiognomies were grouped into five types, distinguished by the nature of the woody plant elements of the vegetation and their density in the different height classes; (1) forest, (2) open woodland, (3) closed woodland, (4) shrubland, (5) grassland. Forests are restricted to the high rainfall hillsides or riverine belts (Brooks & MacDonald, 1983). Woodland communities are found in certain bottomland situations as well as on rocky and sandy hillslopes. More than half the area of Hluhluwe Section is covered by shrubland, dominated by dense stands of *Acacias*. True grassland communities are poorly represented and are found only in areas with prolonged waterlogging.

HUP supports a great variety of potential prey species for wild dogs and consequently a broad spectrum of large and small predators. Carnivores belonging to the same feeding guild as the wild dog also occur in the park, and include spotted hyaena *Crocuta crocuta*, lion *Panthera leo*, leopard *Panthera pardus* and cheetah *Acinonyx jubatus*.

METHODS

Wild dog diet choice in HUP

Scat analysis

Scat analysis provides much information on prey species (Putman, 1984), allows a continuous determination of feeding habits, and may be used to establish the degree of importance of different prey in the diet. The hair of each prey species has a characteristic shape, length, colour, cross-section and scale pattern (Brunner & Coman, 1974) and the use of hair in determining predator feeding habits has been discussed by Keogh (1985). A factor that confounds scat analysis is the differential passage rate of ingesta through the gut (Putman, 1984). We assumed that the identified prey remains in each scat represented 1 prey individual. This assumption was based on the findings of Floyd, Mech & Jordan (1978) who showed that the differential passage rate of ungulate prey through the gut of the wolf *Canis lupus* was not pronounced. The wolf is a canid of similar body size to the wild dog and their scats generally contained the remains of a single prey item. Since scats were not collected on a regular basis from a midden, overestimation of prey items in the diet was avoided (Hiscocks & Bowland, 1989).

By radio-tracking the dogs, scats encountered along the roads could be positively identified as wild dog scats, although their characteristic shape, size and smell were also indicative (Walker, 1981). More than 1 scat sample was collected at any 1 site, but to ensure independence of samples, only 1 scat was analysed per site and 1 site was chosen per day (Woodroffe *et al.*, 1997) .

Scats were macerated in water overnight and thoroughly rinsed in a 1-mm mesh sieve under running water (Maddock, 1993). Random clumps of hair were taken as sub-samples (Bowland & Perrin, 1993), soaked in absolute alcohol and dried under a lamp. Hair cross-sections were prepared using the method of Douglas (1989) and scale impressions were used to confirm the results. Keogh's (1985) photographic reference key based on cuticular scale patterns and groove characters and a reference collection prepared from preserved specimens were used to identify hair cross-sections.

Wild dogs are expected to show seasonal differences in their diet choice, because the distribution and abundance of prey are expected to differ seasonally, e.g. there are more juveniles during the wet season. Using the scats, wild dog diet choice was compared between the wet (October–March) and the dry season (April–September).

Table 1. Relative percentage occurrence of ungulate prey species in the diet of wild dog determined from scat analysis, personal observation and carcass records

Species	Scats[a] ($n = 78$ scats)	Direct observations ($n = 37$ kills)	Carcasses[b] ($n = 157$ carcasses)
Nyala	41.7	48.8	78.4
Impala	35.7	46.6	15.9
Red duiker	8.7	2.3	1.3
Bushbuck	7	0	0
Grey duiker	3.4	0	0.6
Buffalo	1.7	0	0
Kudu	0.9	0	0.6
Blue wildebeest	0.9	2.3	0
Common reedbuck	0	0	1.9
Waterbuck	0	0	1.3

[a] Percentage values reflect the analysis of 78 scats. Since each scat contained 1.5 species on average, percentage is based on 115 prey recorded from these scats.
[b] Data are derived from the field records kept by the research staff of the KwaZulu-Natal Nature Conservation Services at Hilltop station, Hluhluwe Game Reserve, from 1984 to 1994.

Direct observations

Data from direct observations of wild dog kills ($n = 37$ kills from 103 observed hunts) provided the only reliable record of prey age and sex during this study, since KwaZulu-Natal Nature Conservation Service carcass records provided by field rangers and our own scat examinations did not discriminate between the sexes or among the age classes of prey. The numbers of observed dog kills ($n = 37$) was limited because dogs were followed by vehicle, observed from the tourist roads and were not chased off-road. Observed kills are therefore those in which the prey carcass (at which wild dogs were present) could be identified by the observers.

Our observations of kills by wild dog are compared to the carcass return records ($n = 157$) obtained from daily game guard patrols spanning the entire reserve from 1984 to 1994 (see Table 1). These data contain several inherent biases: (1) dense vegetation is inaccessible and therefore under-sampled; (2) the reserve interior is sampled to a lesser degree because more than half the patrols (65%) are concentrated along the periphery; (3) the game guards' expertise in identifying wild dog kills has never been tested; (4) smaller and young age classes of prey are underestimated since the remains of larger prey are more likely to be found than smaller prey which are totally consumed. Because the reliability of carcass return records require that several assumptions are met we include these data merely for comparison and rely on our own observations and the scat data in the analyses.

The age and sex distribution of the primary prey populations in Hluhluwe were obtained from a survey of individuals during road transects and compared to the age and sex structure of prey observed being killed by wild dogs. The method of Child (1964) was modified to determine age classes of impala. Male classes I, II and III as described by Child (1964) are referred to here as juvenile, sub-adult and adult classes. The juvenile class includes calves up to 12 months. Female impala were classified into the same classes on the basis of size. Rowe-Rowe & Mentis's (1972) ageing method was used for nyala. This method relies on horn length for males and on the shoulder height relative to the average for adult females, for distinguishing male and female age classes. We grouped nyala $\leqslant 10$ months into the juvenile category, while female sub-adults were distinguished from juveniles by darker pelage coloration and size (10 months > sub-adult < ± 20 months), and adults from sub-adults by the fading of the forehead chevron and the development of a dark mane. These age categories for nyala conformed to those defined by Anderson (1980).

Capture success

Data on capture success were obtained from direct observations. Capture success was calculated as the percentage of successful pursuits by the entire pack or most of the pack (Fanshawe & Fitzgibbon, 1993). Wild dogs were subjectively considered to be hunting when alert while walking or trotting purposefully, and pursuits were identified by an increase in speed orientated towards the prey.

Visibility

To determine the effect of habitat heterogeneity on capture success, visibility at dog height (50 cm from ground) was recorded from the road for each vegetation type. Mean visibility was measured by recording the distance at which the lower half of a khaki clad assistant first disappeared from view (Bothma, 1989). Waist height was used because it was similar to nyala and impala shoulder height (approx. 95 cm). In this way the distance at which prey were visible to wild dogs was measured. This index of visibility was calculated for each vegetation type during the wet and dry seasons. Prey capture success, visibility and prey availability were compared seasonally.

The prey model and wild dog diet choice

The prey model assumes that the forager selects prey in a way that maximizes its long-term mean rate of energy intake (Schoener, 1987). Optimal diet theory predicts that to maximize the rate of energy intake the predator ranks prey types, including them in the diet according to their profitability (i.e. shows ranked preferences; Pulliam, 1974; Stephens & Krebs, 1986), where profitability (ρ) is a combined measure of prey energy (E) and handling time (h) so that ($\rho_i = E_i/h_i$ (Stephens & Krebs, 1986; Bulmer, 1994). Carnivore foods contain similar energy and nutrient returns per unit mass and the predator's nutrient requirements do not restrict the inclusion of an item in the diet if it is encountered (Stephens & Krebs, 1986). Thus, for carnivores, profitability is often positively correlated with, and can be simply measured by, prey size (Lendrem, 1986).

The observed diet choice of wild dogs in HUP was compared to the expected diet choice, determined using the prey model (Stephens & Krebs, 1986; Bulmer, 1994). The expected diet choice of wild dogs was determined by adding the prey types to the diet in order of decreasing profitability until for the first time the relationship given below was satisfied, when these first k prey types were included in the diet, and the rest were excluded (Bulmer, 1994).

$$(E/T)_{k+1} < \left(\sum_{i=1}^{k} \lambda_i E_i\right) / \left(1 + \sum_{i=1}^{k} \lambda_i h_i\right)$$

Energy (E) was taken as the edible body mass (kg) of the animal which was estimated at 60% of the animal's total body mass (Estes & Goddard, 1967; Blumenschine & Caro, 1986). Prey handling costs (h) was the sum of the time (hours) taken to pursue, capture and ingest prey. Personal observations ($n = 37$) and section rangers reports of kills by wild dogs were used to estimate pursuit, capture and ingestion time of nyala and impala. Handling times for other potential prey species were estimated by asking experienced field staff to judge the times relative to those for nyala and impala.

Prey encounter rates (λ) were obtained from road transect encounters of prey which were used as a surrogate measure of prey encounter by the dogs. Road transects were conducted during the early morning and late afternoon because (1) 28.5% of observations of wild dogs were on the road and 51% of the total observations showed that wild dogs moved and hunted within 100 m of the road ($n = 1121$) (Andreka, 1996) and, (2) hunting ($n = 103$) was observed between 05:30 and 09:10, and 17:15 and 19:30 during the wet season and between 06:00 and 09:30, and 16:00 and 18:00 during the dry season. As in many other areas, wild dogs in HUP hunt predominantly in the early morning and late afternoon (Kühme, 1965; Estes & Goddard, 1967; Fuller & Kat, 1990; Creel & Creel, 1995) and frequently use roads for this purpose. Road transects were conducted at about the coursing speed of wild dogs (10–20 km/h) at these times along tourist roads and management tracks. The encounter rate of prey was calculated as the number of times a particular prey species was encountered per hour, averaged over all transects and by season, using the following equation:

$$\frac{\text{prey/h}}{\text{km/h (observer speed)}} * \text{km/h (wild dog speed)}$$

Table 2. Numbers of individuals, and their age and sex classes, of nyala and impala killed by wild dog. Data are from observations of wild dog kills ($n = 35$)

	Nyala		Impala	
Class	Observed kills	Observed abundance[a]	Observed kills	Observed abundance[a]
Juvenile	3	43	8	104
Sub-adult	2	63	1	204
Adult	15	169	6	448
Female	10	234	7	583
Male	7	120	0	189
Unknown	3		8	
Total	$n = 20$		$n = 15$	

[a] Observed abundance of individuals by class where they could be sexed or aged, and based on the road transect data.

For the purposes of calculation coursing speed was taken as 10 km/h along roads (see Creel & Creel, 1995).

The prey model considers diet choice within a homogeneous patch for a forager using a fixed foraging strategy (Stephens & Krebs, 1986). The wild dogs hunted in complex habitats, although they spent more time in woodland (39%) than other vegetation types. In using the prey model we are aware of the limitations of both our data and the simplifying assumptions of the model, and use it as a null model against which to interpret observed departures from the expected outcomes.

RESULTS

Wild dog diet in the Hluhluwe Section

The 136 positively identified wild dog scats from 78 sample sites contained on average 1.5 ± 0.1 (mean $\pm$ 1 SE, $n = 136$) species. Eight prey species were identified from the 78 scats (see Methods) included in the analyses: nyala *Tragelaphus angasi*, impala *Aepyceros melampus*, red duiker *Cephalophus natalensis*, bushbuck *Tragelaphus scriptus*, grey duiker *Sylvicapra grimmia*, buffalo *Syncerus caffer*, kudu *Tragelaphus strepsiceros* and blue wildebeest *Connochaetes taurinus* (Table 1). The medium-sized prey – nyala and impala – accounted for a significantly greater proportion (77%; $Z = 0.12$, d.f. = 77, $P < 0.01$) of prey individuals.

For seasonal comparisons of the prey species selected by wild dogs only nyala and impala were included in the analyses. All other prey species were captured infrequently by the dogs and were either pooled as ‘other species’ or excluded from the analysis. Significant seasonal differences were observed in the use of nyala and impala. Although there was no significant difference in prey choice, as measured from scats during the wet season (binomial test, $P = 0.237$; impala $n = 18$, 39%; nyala $n = 13$, 28%), there was significantly more nyala (51%, $n = 35$) than impala (33%, $n = 23$) in the scats during the dry season ($Z = -1.44$, $n = 58$, $P = 0.006$). Large prey species were incidental in the diet during the dry season, with buffalo, kudu and blue wildebeest each representing < 2% of the diet (Table 1). In all methods of recording prey items in the diet, smaller prey such as red duiker, bushbuck and grey duiker were represented slightly more frequently (~2–5%) than the very large prey. We attribute this to the fact that the dogs were observed more than expected in dense woodland, thicket and forest (Andreka, 1996), the habitat of these species, and we surmise that these species were included in the diet in an opportunistic and proportional fashion.

Direct observations showed that adult nyala were taken significantly more than other age classes ($\chi^2 = 15.7$, d.f.=2, P<0.001; Table 2). However, nyala prey age selection did not differ significantly from that expected from the population age distribution ($\chi^2 = 1.9$, d.f. = 2, $P = 0.37$). Although more juvenile impala than other age classes were taken this trend was not significant (χ^2=5.2, d.f. = 2, $P = 0.08$). But, impala prey age selection differed significantly from the population age distribution ($\chi^2 = 19.1$, d.f. = 2, P<0.001, Yates’ correction) and we conclude that juvenile impala were taken more than expected from their apparent abundance. (Table 2).

From direct observations it was apparent that both nyala and impala females were taken more frequently than males although this difference was significant for impala only (two-tailed binomial test: nyala, $n = 17$, $k = 7$, $P = 0.09$; impala, $n = 7$, $k = 0$, P<0.001) (Table 2). However, the observed use of the sexes in the diet of wild dogs did not differ significantly from the observed population sex ratios of either nyala ($\chi^2 = 0.1$, d.f.=1, $P = 0.72$) or impala ($\chi^2 = 1.1$, d.f. = 1, $P = 0.29$).

Capture success

The overall prey capture success was 48% ($n = 37$ of 77 pursuits with known outcome). Pursuits involving nyala were significantly more successful (71%, $n = 28$) than those involving impala (38%, $n = 39$) ($\chi^2 = 5.2$, d.f. = 1, $P = 0.02$). Other species, warthog *Phacochoerus aethiopicus*, red duiker, zebra, blue wildebeest, kudu and buffalo, were pursued less successfully, and formed a smaller portion ($n = 10$) of the total number of chases of known outcome (Table 3).

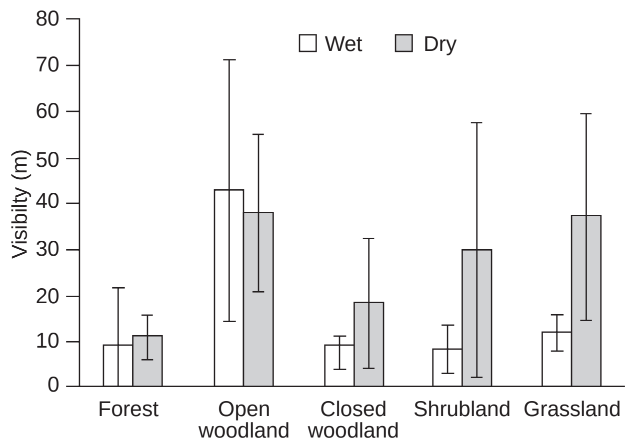

Fig. 2. Visibility measured as the average distance in metres ($\bar{x} \pm 1$ SD) from the road to the point in the vegetation where a khaki clad assistant disappeared from view.

Table 3. Capture success (expressed as a per cent of pursuits with known outcome) of various prey species pursued by wild dog in HUP

Species	Hunts	Known outcome	Observed kills	% success	Mass (kg)[a]
Nyala	38	28	20	71	46.28
Impala	51	39	15	38	26.13
Red duiker (A)	1	1	1	100	8.4
Warthog (A)	4	2	0	0	35
Wildebeest (J)	2	2	1	50	20
Kudu (J)	2	2	0	0	46
Buffalo (J)	3	3	0	0	60
Zebra (J)	2	0	0	0	32
Total	103	77	37	48	–

[a] The edible body mass of the prey species adjusted according to wild dog prey age selection. It was assumed that wild dog captured juvenile classes of the larger prey species.
A = adult; J = juvenile/sub-adult; no symbol indicates all age-classes are eaten.

There was a significant difference ($\chi^2 = 5.2$, d.f. = 1, $P = 0.02$) in the capture success of age classes of nyala ($n = 20$) and impala ($n = 15$). Juvenile nyala (75%) and impala (83%) were more successfully captured than adult nyala (64%) and impala (34%), even though adults were pursued more frequently. Sub-adults were not seen to be pursued. Nyala females were pursued with a higher success rate (71%) than males (57%) ($n = 17$).

Visibility

Significant seasonal variation in visibility in the five vegetation types was observed ($F_{1,4} = 54.6$, $P < 0.05$), and visibility was highest during the dry season when the grass died back (Fig. 2). During the wet season the grass grew tall (1–2 m) and visibility was severely restricted in grassland. As visibility is one of the primary factors that contributes towards capture success (Fanshawe & Fitzgibbon, 1993), one would expect greater capture success in a habitat with an increase in visibility (such as during the dry season), assuming that prey have equivalent spatial distributions between seasons. The encounter rates of prey (which were used as a measure of availability) did not, however, differ significantly with season ($\chi^2 = 0.02$, d.f. = 7, $P = 0.79$). In the capture success data for which we had seasonal records, capture success did not improve significantly in the dry season (dry season: 35%, $n = 14$; wet season: 46%, $n = 26$; 2×2 contingency table, $\chi^2 = 1.09$, d.f.=1, $P = 0.29$).

The prey model and wild dog diet

Observation, scat analyses and carcass records show that wild dog preyed upon 10 ungulate species in the Hluhluwe Section (Table 1). Why were two of these species (nyala and impala) used so frequently? The prey model employs a number of simplifying assumptions: one is that all prey are equally vulnerable (Boutin & Cluff, 1989). This is a complex issue and simple categorical statements as to vulnerability of prey types amount to speculation (MacCracken, 1989). However, we adjusted the model parameters for each prey type by age, size, and sex to accord with what wild dogs would be able to eat or were known to eat (e.g. where buffalo, kudu and wildebeest were included we assumed that these were calves and calculated E, h, and λ accordingly; Tables 3 & 4).

The model predicted that wild dogs should include only nyala, red duiker, bushbuck and impala in the diet, and in this order of preference (Table 4). This zero-one rule (Stephens & Krebs, 1986) or prediction, was generally followed by the dogs, and these four species were the species most frequently observed in the diet (Table 1), although impala were considerably favoured over red duiker and bushbuck. Other prey species were nevertheless included in the diet in spite of their lower profitability and we believe this partial preference is a consequence of (1) the coursing search method, (2) the encounter contingent opportunistic inclusion of these prey species and (3) the large amount of time spent by dogs in closed woodland frequented by these species. Furthermore, wild dogs appeared to rank their inclusion of prey types in the diet according to their profitability and there was no significant difference between the observed ranking of types in the diet and that predicted by the prey model on the basis of profitability alone (signs test, $z = 0.28$, $n = 10$, $P = 0.78$; Table 4). In addition the dogs did not take prey species in proportion to their encounter rate (Kolmogorov–Smirnov; $D = 55$; $P < 0.1$), and thus cannot be regarded as strictly opportunistic predators (although some prey species are taken opportunistically).

The predicted ranking of prey on the basis of profitability fails if the assumption of the model that prey are encountered randomly is not met. The frequency of encounter of each prey species was fitted to uniform, poisson and negative binomial distributions using the

Table 4. Comparison of the ranked observed (O) and expected (E) wild dog diet choice based on the profitability (*E*/*h*) of prey. Handling time (*h*) is the sum of pursuit time + capture time + ingestion time (h), subjectively estimated by the authors and other personnel (see text). Energy values (*E*) are given as kg, and encounter rates (λ, encounters per hour) of potential prey species are estimated from road transects (see text). Prey age and sex selection are taken into account in the estimates of *h*, *E* and λ. This classical prey model predicts that wild dogs should take only nyala, red duiker, bushbuck and impala, and in that order of preference (see bold text)

Species	*h*	*E*	λ	*E*/*h*	*E*/*T*	O	E
Nyala	**1**	**46.28**	**2.46**	**46.28**	**32.904**	**1**	**1**
Red duiker	**0.22**	**8.4**	**0.08**	**38.18**	**32.930**	**3**	**2**
Bushbuck	**0.59**	**21**	**0.01**	**35.59**	**32.935**	**4**	**3**
Impala	**0.77**	**26.13**	**2.67**	**33.93**	**33.306**	**2**	**4**
Grey duiker	0.36	11.2	0.05	31.11	33.299	5	5
Kudu	1.62	46	0.03	28.39	33.256	7	6
Waterbuck	1.24	26	0.02	20.96	33.203	9	7
Buffalo	3.55	60	0.01	16.90	33.101	6	8
Zebra	2.07	32	0.02	15.45	32.973	10	9
Blue wildebeest	1.75	20	0.02	11.42	32.841	8	10

Table 5. A comparison of encounter rates of adult prey derived from: overall road transect, four random 5-km segments, two random 10-km segments, and one random 20-km segment

	Encounter rate			
Prey species	Overall	5 km	10 km	20 km
Nyala	2.46	2.41	3.71	3.98
Impala	2.67	3.41	4.39	4.54
Red duiker	0.08	0.10	0.10	0.13
Bushbuck	0.01	0.03	0.03	0.03
Grey duiker	0.05	0.08	0.05	0.03
Kudu	0.20	0.30	0.25	0.28
Blue wildebeest	0.63	0.83	0.93	1.05
Buffalo	0.30	0.30	0.30	0.13

Kolmogorov–Smirnov distribution fitting statistic. The frequency of encounter of prey species along the road was found to be more randomly distributed ($D = 0.16$, $P \approx 0.14$), than uniform ($D = 0.32$, $P < 0.0001$) or clumped ($D = 0.4$, $P < 0.00001$).

To test the effect of the weak fit of the frequency of encounter data to the random model (i.e. potential non-randomness of prey encounter) on diet choice, the scale dependency of the model was tested by comparing prey encounter for various lengths of the transects. Overall prey encounter rates were calculated from the road transects (see above) and compared to prey encounter rates calculated from four 5-km segments, two 10-km segments and one 20-km segment selected randomly from each transect (Table 5). Since segments chosen at random gave equivalent results, and favoured a weak random encounter rate of prey, we assume that this prey distribution does not affect the predictions of the prey model.

DISCUSSION

On the whole wild dogs in HUP appear to be rate-maximizers, but they are not optimal foragers to the exclusion of opportunistic behaviour. The model predicts that the three species (nyala, red duiker and bushbuck) most closely associated with closed woodland (i.e. thick woodland, thicket and forest) are the most profitable and that, of the grassland/open woodland prey types, only impala should be taken; all other species should be ignored. In other words, the model predicts habitat-related differences in the diet of the dogs. The dogs were observed moving and hunting in closed woodland (65%) more than in open woodland (35%). The observed diet reflects this difference and follows the predictions of the model closely.

The expected profitabilities of particular prey types will fluctuate with many factors (e.g. size and vulnerability, which in turn is related to the social structure and likelihood of defence by the prey). The effect of variation in the expected profitability of particular prey was apparent in the tendencies of the dogs to prefer medium prey (impala) in small herds (nyala) or solitary (red duiker and bushbuck). Nyala and impala made up most of the diet. In most feeding studies of wild dogs the most abundant, local medium- to large-sized prey species dominate in the diet (Ginsberg & Macdonald, 1990). For example, impala and kudu in the Kruger National Park, South Africa, (Reich, 1981; Mills, 1992) and Hwange National Park, Zimbabwe, (Childes, 1988), Thomson's gazelle *Gazella thomsoni* and blue wildebeest in the Serengeti, Tanzania, (Schaller, 1972; Frame, 1986), and nyala and impala in HUP.

As pack size increases, wild dogs kill heavier prey and are more successful (Creel & Creel, 1995). Where larger prey species were observed in the diet at HUP, these were assumed to be scavenged by the dogs as the large size and herding behaviour of zebra, waterbuck, kudu, wildebeest and buffalo make these formidable prey to the small HUP wild dog pack (pers. obs.). Juvenile classes of larger ungulates (kudu, wildebeest and buffalo) were only taken during the dry season. Juveniles are easier to capture during this non-mating season, when herd sizes are smaller with fewer males, the social structure is not as rigid (Skinner & Smithers, 1990), and calves are less protected.

Wild dogs are expected to adjust prey selection in relation to ease of capture (Reich, 1981) and are unlikely to consider all members of a species of equal profitability under all circumstances. This is evident in the sex selection of the primary prey, nyala and impala, and impala age-class selection. Female and juvenile nyala and impala may be taken more frequently than other classes as females are more abundant. The greater availability and ease of capture of impala lambs during the wet season (lambing season), explains the higher incidence of impala in the diet at this time.

Previous studies have documented a large range in capture success rates by wild dogs. Studies conducted in dense habitats in southern Africa and the Selous Game Reserve, Tanzania, found that wild dogs successfully captured, on average, 35% (20–44%) of the prey they selected (Reich, 1981; Creel & Creel, 1995). This contrasts with studies conducted in more open habitats in East Africa where the average capture success was 64% (13–100%) (Kühme, 1965; Estes & Goddard, 1967; Kruuk & Turner, 1967; van Lawick, 1971; Malcolm & van Lawick, 1975; Fuller & Kat, 1990; Fanshawe & Fitzgibbon, 1993). However, Creel & Creel (1995) pooled the capture success results from East African studies and found an average capture success of 44%, similar to their findings in the Selous Game Reserve and studies done in southern Africa, including the present study. The similar results obtained in habitats differing in vegetation type suggest that the lack of visibility in dense habitats does not restrict capture success. Indeed, in Hluhluwe, wild dogs may rely on surprise techniques to flush and ambush their prey, and chases seldom exceed 1 km. Similar strategies were found by Creel & Creel (1995) for wild dogs in the dense vegetation of the Selous Game Reserve. Furthermore, Maddock (1989) and Mills & Biggs (1993) found that wild dogs avoided the more open areas of the Kruger National Park (~50% of observations were from thickets) and were able to hunt effectively in the thick bush areas.

The decline in numbers of wild dogs in HUP since their introduction in 1981 does not appear to be due to deficiencies in their foraging behaviour. This study was initiated to evaluate the status and likelihood of persistence of the wild dogs in HUP. Nothing about their diet or feeding behaviour appears to place the dogs in jeopardy. They have sufficient prey (predator–prey models are considered elsewhere), are quite capable of capturing these prey and are not limited by the poor visibility in the dense vegetation, and their foraging behaviour falls well within the normative limits described by other studies. Factors other than those related to their feeding ecology are contributing to the decline in wild dog numbers within HUP. It has been suggested that social structure, essential for survival, is more important for the reproductive benefits it confers than for the putative foraging advantages (Malcolm & Marten, 1982). We suggest emigration, inbreeding depression and disease as possible causes of the decline of wild dogs in HUP. Reintroduction of another pack of wild dogs to HUP, as part of a metapopulation management plan (*sensu* S. Ellis, unpubl. data) is essential to the survival of the present, declining wild dog population. However, careful monitoring of the reintroduced animals, particularly their demography and response to diseases, is essential if this option is taken.

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