



*Lycaon pictus*

## ABSTRACT

The small population size of wild dog *Lycaon pictus* (10) in Hluhluwe-Umfolozi Park (HUP) and the decline in their numbers since 1992, has caused concern for their survival and consideration of further introductions. In the light of many failed wild dog relocation and reintroduction programmes, this study contributes towards an understanding of the ecology of the HUP wild dog pack.

Wild dog prey preference was determined from scat analysis and personal observations, and their potential impact on the primary prey species was modelled. The choice of physical habitat features by wild dog and their ranging behaviour within the Park were correlated with the distribution of their primary prey and other predators. To determine the susceptibility of prey to predation in three reserves with different predator diversities and densities, prey vigilance and prey response to playback recordings of predator calls were recorded.

The results showed that wild dog preference for females, adult nyala *Tragelaphus angasi* and juvenile impala *Aepyceros melampus*, was a function of prey abundance, profitability calculated using a diet choice model, and ease of capture. Based on the overall lack of association of wild dog and their primary prey species and predators, and the overall lack of similarity of wild dog and prey choice of physical habitat features, predator presence was the most important determinant of wild dog ranging behaviour. Prey vigilance differed significantly between reserves and was inversely correlated with predator density. Prey response to predator calls did not differ significantly between reserves but prey did, however, react sooner to those calls unfamiliar to them. Nyala were more vigilant and responded sooner to playbacks than impala suggesting that nyala may experience greater levels of


predation pressure. There was no evidence to suggest that the prey preference, habitat preference and ranging behaviour of the wild dog were influenced by the susceptibility of prey to predation. Models of prey population dynamics determined that although the introduction of an additional wild dog pack would result in a reduction of current prey population growth rates and an increase in prey population extinction probabilities, their predicted impact would be slight.

Since emigration and population viability were identified as the primary causes of the HUP wild dog population decline, the introduction of two groups of wild dog individuals into Hluhluwe was suggested to boost population numbers and stimulate breeding and dispersal within the Park. The importance of future monitoring and proactive management was stressed to ensure the survival of this valuable species in the Park.

## PREFACE

The data described in this dissertation were collected in Hluhluwe-Umfolozi Park, KwaZulu-Natal (from January 1994 - December 1994, March 1995, and June 1995) and the Kruger National Park, Transvaal (July 1995). Data analysis was carried out in the Department of Zoology and Entomology, University of Natal, under the supervision of Dr. Michael J. Lawes.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

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July, 1996

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## ACKNOWLEDGEMENTS

I acknowledge and thank the following people and organisations for their help:

My supervisor, Dr. M. Lawes, and co-supervisor and Natal Parks Board co-ordinator, Dr. A. Maddock, provided valuable advice and criticism during the field work and writing of the thesis; Mr. N. Galli, the conservator of Hluhluwe-Umfolozi Park, for his permission to work in the Park and his staff for their support; The research staff, particularly Mr. M. Robertson and Mr. O. Howison, who provided the necessary Natal Parks Board records and Ms. T. Abell for her company and enthusiastic assistance with field work; The section rangers, Mr. L. Steyn and Mr. D. Gissing and their game guards collected scats and reported sightings of wild dog and kills; Mr. I. Mngomezulu and Mr. T. Galtrey for the data they collected on the tourist night drives; The workshop staff for fixing numerous punctures; Mr. G. Andreka for discussion in the field and access to his data sets; Dr. M. Mills for interesting discussions and permission to collect comparative data in the Kruger National Park; My brother, Mr. E. Krüger, generously offered his vehicle and company for the above trip; Ms. C. Davies for a copy of her masters thesis which provided interesting comparisons; Dr. S. Piper and Dr. D. Ward for their statistical advice; Dr. H. Eeley for producing the study site graphics; Mr. L. Pero read numerous rough drafts and provided valuable criticism and encouragement during the field work and writing of the thesis; My parents, for their moral and financial support and for recording wild dog vocalisations at De Wildt Cheetah Breeding Centre; and the University Research Foundation, the Foundation for Research Development, the Green Trust and the Natal Parks Board for financial assistance.



## CHAPTER 1

### INTRODUCTION

This study is concerned with the feeding ecology and conservation of the African wild dog *Lycaon pictus* in Hluhluwe-Umfolozi Park (HUP), northern KwaZulu-Natal. The plight of the wild dog is well known (Ginsberg & Macdonald, 1990). Persecution from 1900 to the present (Hines, 1990), together with other factors (see below), has drastically reduced wild dog numbers and range (Ginsberg & Macdonald, 1990), and has resulted in its present endangered status. The wild dog is extinct in 19 of the 32 countries it once inhabited and only six countries contain viable populations (Ginsberg & Macdonald, 1990; Fanshawe, Frame & Ginsberg, 1991). Given the current trends of decline worldwide, the wild dog may go extinct within 20 to 40 years (Comely, 1992).

#### **Reasons for Wild Dog Decline**

The decline of the wild dog has been attributed to several factors namely; i) intensive hunting and poisoning for vermin control programmes (Chilvers, 1994), ii) fatal diseases including rabies, canine viral distemper and anthrax (Pienaar, 1963; Schaller, 1972; Kingdon, 1977; Chilvers 1994; Kat *et al.*, 1995), iii) habitat loss and fragmentation (Ginsberg & Cole, 1994), iv) road kills (Childes, 1988a; Fanshawe, 1989), v) interspecific competition at kills (Frame *et al.*, 1979; Malcolm, 1979), vi) loss of genetic variability (O'Brien *et al.*, 1985) and, vii) the decline in wild ungulate populations (Kingdon, 1977).

The large home range area requirements of the wild dog, the relatively small size of

protected areas and their incompatibility with livestock farming holds little hope for the expansion of wild dog populations in KwaZulu-Natal. An increase in human populations and decline in suitable habitats has resulted in protected areas offering the only refuge for this species. The wild dog population of between 10 and 13 individuals during the study period, is the only other protected population in South Africa outside of Madikwe Game Reserve, and the Kruger National Park (referred to from hereon as the Kruger) and surrounding reserves which collectively contain a stable population of some 434 individuals (Wilkinson, 1995). HUP is thus an important reserve for the future welfare of the species.

Apart from the resident pack of wild dog in Hluhluwe-Umfolozi Park, a pack of dogs (estimated at 18 individuals) is known to exist in the region of Magudu (a game farming area), north of HUP, but information regarding their ecology is lacking. Occasional reports of sightings of small groups of wild dog (maximum 3) at Phinda, Mkuzi and Itala Game Reserves have also been received (Natal Parks Board records) (Figure 1.1).

### **Wild Dog in Hluhluwe-Umfolozi Park: The Problem**

Former distribution records (1830-1890) suggest that wild dog occurred throughout KwaZulu-Natal with a concentrated distribution in Zululand (Pringle, 1977). In the early 1920's wild dog were still present around Lake St. Lucia, Hluhluwe-Umfolozi Park and near the Drakensberg mountain range (Rowe-Rowe, 1990) but were extinct in KwaZulu-Natal by 1928.

Captive breeding with subsequent reintroduction may offer a solution for re-establishment. This was attempted in KwaZulu-Natal in 1980 and 1981 when 22 adult dogs (10 females and 12 males) were reintroduced into HUP by the Natal Parks Board. The

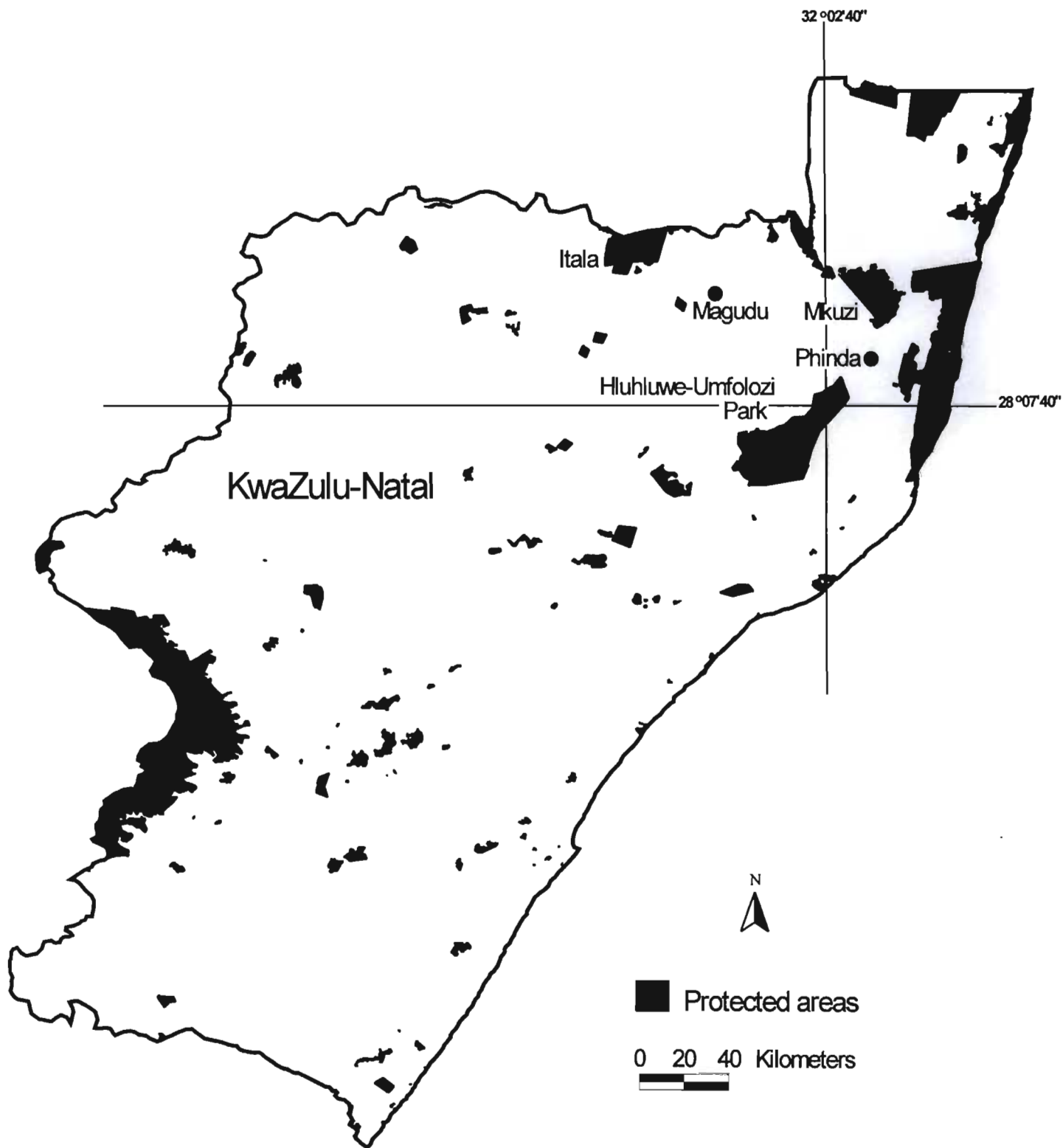


Figure 1.1. Wild dog sighting locations in northern KwaZulu-Natal.

objectives of the reintroduction were i) to re-establish an indigenous species and ii) to maintain a gene pool that may be of significance in the long term conservation of the species (Natal Parks Board records). The HUP population size has fluctuated between 3 and 30 individuals over the past 14 years (Figure 1.2). Offspring have been recorded on five occasions between 1981 and 1989, and every subsequent year from 1990. Since 1993 no breeding has occurred and wild dog numbers have declined (Natal Parks Board records).

The small number of wild dog packs and small gene pools, on average worldwide, are expected to increase the vulnerability of wild dog to the effects of disease and parasites caused by lowered levels of genetic heterozygosity (Ginsberg & Macdonald, 1990). The above, together with the low wild dog numbers within HUP and their unsuccessful breeding over two consecutive years, has led to a consideration of further introductions. In the light of many failed wild dog relocation and reintroduction attempts (Childes, 1988b; Comely, 1992; Scheepers & Venzke, 1995), a thorough understanding of the ecology of the HUP wild dog pack is required prior to contemplating further introductions.

The Natal Parks Board initiated an intensive research programme in 1992 in an attempt to formulate a management plan for the HUP wild dog population. The research programme comprised a study on i) wild dog demography revealed by a photographic survey which began in 1992 (A. Maddock\*), ii) the genetic status and ranging behaviour of the wild dog which began in 1993 (G. Andreka\*\*) and iii) the feeding ecology of the wild dog which began in 1994 (present study). These three studies form part of ongoing collaborative research throughout the wild dogs' range.

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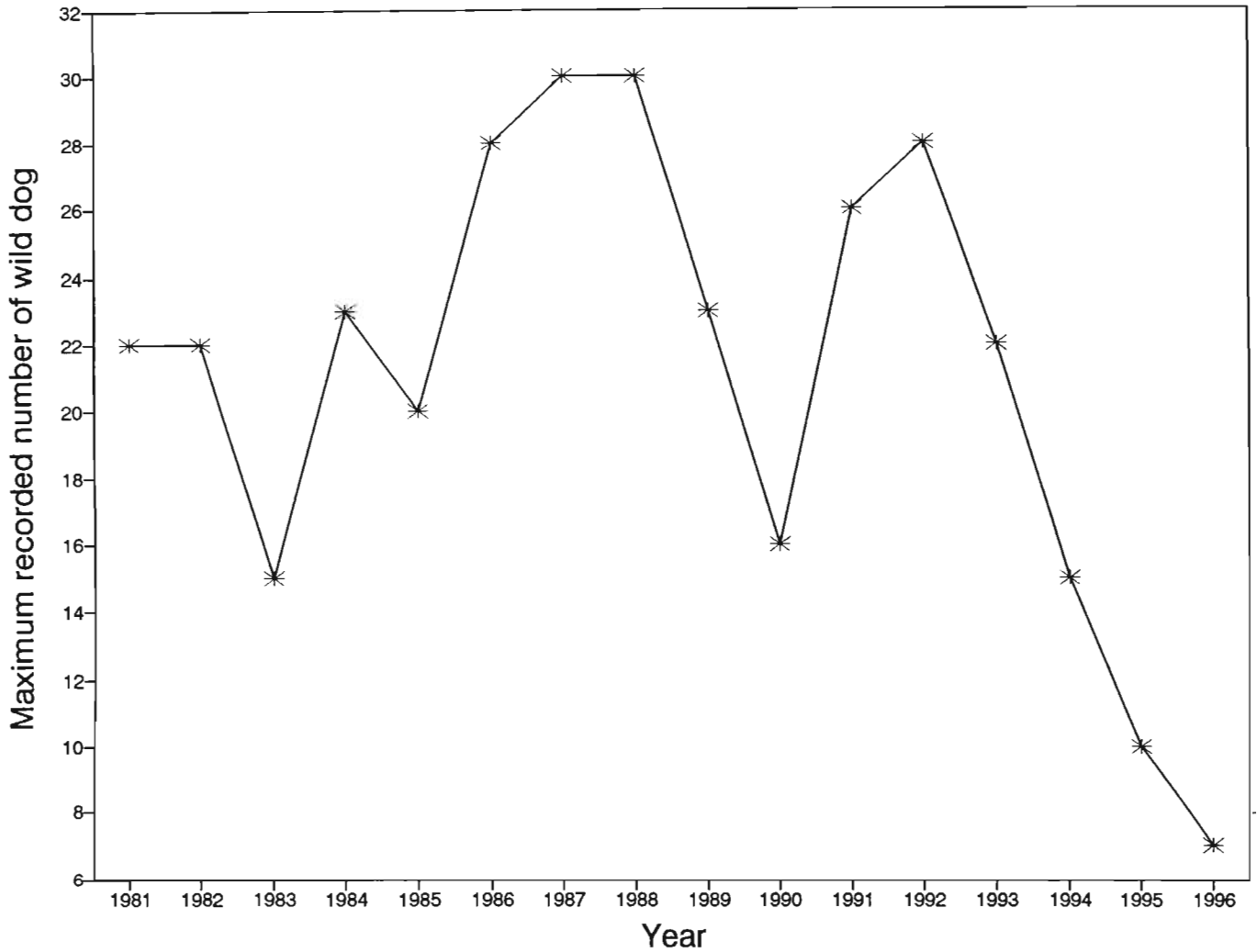


Figure 1.2. The annual maximum recorded number of wild dog in Hluhluwe-Umfolozi Park, since their reintroduction in 1981. Note the steady decline in wild dog numbers since 1992.

The broad aim of this study was to examine wild dog feeding ecology, and thus contribute towards an understanding of wild dog behaviour, ecology and population dynamics in HUP in order to develop corrective actions and solutions for the future management of wild dog in HUP. The special objectives of this study were to determine:

- i) Wild dog prey species selection and capture success (chapter 3).
- ii) Whether food availability, habitat selection and predator presence are determinants of wild dog distribution and home range area (chapter 4).
- iii) The susceptibility of prey to predation by wild dog (chapters 5 & 6)
- iv) The impact of wild dog predation on prey species numbers and population structure (chapter 7).
- v) The optimal conservation strategy for the HUP wild dog population and small wild dog populations in general (chapter 8).

### **Background to the Study Species**

The Carnivora are fundamentally adapted as predators and have diversified into a number of families, each with its own characteristics related to its particular habitat, food, method of obtaining food, and mode of life (Ewer, 1973). The seven carnivore families are classified as either cat-like (the felids) or dog-like (the canids) on the basis of a few morphological characteristics (Simpson, 1945). The latter group comprises the Ursidae, Procyonidae, Mustelidae and Canidae which includes wild dogs, wolves, jackals and foxes.

The fossil record identifies the open plains of North America as the main centre of evolution and dispersal of canids (Fox, 1975). Although the 34 canid species are distributed

worldwide, Africa and South America currently have the highest species diversity with 10 species each (Ginsberg & Macdonald, 1990). Their mobility and need for expansive geographical ranges, places the canids in direct conflict and competition with man and marks the primary reason for their decline and highlights a major difficulty with their conservation (Ginsberg & Macdonald, 1990; Ginsberg & Cole, 1994). Other factors confounding the conservation of canids include; i) limited species information, ii) the sparse and widespread distribution of species, iii) their natural low density exacerbated by the small size of protected areas and iv) the ease with which they are eradicated. Control of canids has been prompted by rabies control, fur harvest and depredation of game and domestic stock, and has led to the slaughter of thousands of foxes, wolves and wild dog. Although many foxes and wolves were able to withstand this onslaught, few wild dog remain and as a result the African wild dog has become one of the world's most endangered canids (Ginsberg & Macdonald, 1990). Almost half of the world's canids are in need of additional conservation protection (Ginsberg & Cole, 1994). Nine canid species are seriously threatened of which three (the Simean jackal *Canis simensis*, red wolf *Canis rufus* and African wild dog), are endangered (Ginsberg & Macdonald, 1990).

The name of the African wild dog *Lycaon pictus* is derived from the Greek *lykaios* 'wolfish' and latin *pictus* 'spotted' based on their coat pattern. There are several subspecies within the *Lycaon pictus* species group, the validity of which are questionable (Meester *et al.*, 1986). The southern subpopulations of wild dog are genetically distinct and slightly heavier, larger and lighter in colour than the East African populations (Ginsberg & Macdonald, 1990; Girman *et al.*, 1993).

The first published attempt to assess the status of the wild dog in Africa was made by Frame & Fanshawe in 1985. Their mail survey revealed a decline of the species

throughout much of its range (Frame & Fanshawe, 1989). The endangered status of the wild dog has focused attention on the conservation biology of this species. A metapopulation study (comprising eight other studies throughout the wild dogs' range) aimed at improving the conservation status of the wild dog and ensuring their long term survival, of which this study is a part, has been initiated. One of the most critical variables affecting long term survival is population size, hence the survival potential and ecology of the small population in HUP are of utmost concern and the focus of this study.

## **Wild Dog Sociobiology and Ecology**

### ***Social Organisation***

The wild dog is the most highly social species of all canids (Sheldon, 1992). The pack structure is fundamental to wild dog existence, strong group cohesion exists (Schaller, 1972; Rosevear, 1974; Kingdon, 1977) and packs co-operate completely in hunting, mutual defence and pup rearing (Estes & Goddard, 1967).

There is a close relationship between a predator's social behaviour and the exploitation of its food resource (Crook, 1970). Aspects of wild dog social behaviour indicate that their sociality enables them to exploit the resources they do. Wild dog frequently take prey faster and larger than themselves (Mitchell, Shenton & Uys, 1965; Estes & Goddard, 1967; Kruuk & Turner, 1967) whereas carnivores generally take prey their own size or smaller (Bourlière, 1963).

The well documented hunting behaviour and killing technique of the wild dog (see Estes & Goddard, 1967; Kruuk & Turner, 1967) necessitates the co-operation of many dogs



particularly when hunting large and fast prey, although smaller prey may be killed by individuals or pairs. Wild dog differ from other social carnivores, for example the grey wolf *Canis lupus*, in that they are exclusively social, less flexible in foraging methods and comparatively more successful in hunting (Sheldon, 1992). In East and southern Africa, pack sizes range from 2 to 40 ( $\bar{x}=10$ ,  $n=22$ ) (Pienaar, 1969; Kruuk, 1972; Frame *et al.*, 1979; Reich, 1981a; Maddock, 1989a; Maddock & Mills, 1994; Wilkinson, 1995, Creel & Creel, 1995; Natal Parks Board *unpubl. records*). By comparison, wolves have pack sizes of between 2 and 20 (Raush, 1967).

Estes and Goddard (1967) summarise the selective advantages of communal hunting as i) an increased probability of success, ii) a more efficient use of resources, iii) an increased range of available prey, iv) less disturbance of prey animals than if each dog hunted individually and v) defence against predators and reduction of interspecific competition, for example spotted hyaena *Crocuta crocuta* (referred to as hyaena).

The Canidae display several unique behavioural characteristics namely; i) long-term monogamy (Kleiman, 1977), ii) paternal investment, comparatively large litters and a long period of infant dependency (Kleiman & Eisenberg, 1973) and iii) a co-operative breeding system (Moehlman, 1986). In wild dog, alpha male and female pairs dominate breeding (Frame *et al.*, 1979) which is seasonal in southern Africa (Reich, 1981a; Mills, 1988) but is not strictly so in East Africa (Kingdon, 1977; Frame *et al.*, 1979). The birth of pups coincides with increased prey abundance in southern (Pienaar, 1969; Reich, 1981a) and East Africa (Schaller, 1972; Frame *et al.*, 1979).

Pup survival rates have been positively correlated with prey density (Frame *et al.*, 1979; Reich, 1981a; Fuller & Kat, 1990). Where prey densities are high (Masai Mara), stable (the Kruger) and scarce (the Serengeti National Park, referred to as the Serengeti), pup

survival probabilities average 0.73, 0.48 and 0.14 respectively. Adult survival probabilities are estimated between 0.75 and 0.85 in East Africa (Frame *et al.*, 1979; Fuller & Kat, 1990) and between 0.64 and 0.75 in southern Africa (Reich, 1981a).

### *Prey Selection*

The hunting behaviour and killing technique of the wild dog is adapted for, and dependant on, intraspecific co-operation (Estes & Goddard, 1967; Kruuk & Turner, 1967; Sheldon, 1992). The feeding habits of the wild dog classify it as belonging to the 'large group-hunters' together with the Indian wild dog (dhole) *Cuon alpinus* and the wolf (Sheldon, 1992). The wild dog and dhole are obligatory co-operative hunters (truly social hunters), whereas the wolf exhibits both social and solitary hunting behaviour (Mech, 1970). The wolf subsists almost entirely on larger ungulates while the wild dog, smaller than the wolf in body size, feeds on small- to medium-sized ungulates but is also capable of hunting larger species. Geographical variation in wild dog diet reflects the most abundant local prey species (Ginsberg & Macdonald, 1990) (Table 1.1). Wild dog prey species selection and age and sex class selection are investigated in chapter 3.

Foraging behaviour predictions can be based on the assumption that wild dog are rate maximisers, natural selection acting to maximise inclusive fitness (Krebs & McCleery, 1984). Most true predators have relatively broad diets and can be considered oligophagous or polyphagous. Evolution, however, usually gives rise to foraging strategies where animals consume a narrower range of food types than they are morphologically capable of consuming. It is assumed that carnivores select prey which are most valuable or profitable in terms of energy intake per unit time spent handling (Krebs & McCleery, 1984). Whether

wild dog in HUP feed on the most profitable species available to them is investigated by comparing observed and expected prey selection in chapter 3.

Table 1.1. A comparison of wild dog prey selection by species based on various studies.

<b>STUDY AREA</b>	<b>PRIMARY PREY SPECIES</b>	<b>AUTHOR</b>
Kruger National Park, South Africa	Impala, Kudu	Reich (1981a); Mills & Biggs (1993).
Hwange National Park, Zimbabwe	Impala, Kudu	Childes (1988a); Davies ( <i>unpubl. thesis</i> ).
Kafue National Park, Zambia	Grey duiker, Common reedbuck	Mitchell <i>et al.</i> (1965).
Serengeti National Park, Tanzania	Thomson's gazelle, Blue wildebeest	Schaller (1972); Frame (1986).
Tanzania	Thomson's gazelle, Blue wildebeest	Estes & Goddard (1967).
Kenya	Thomson's gazelle, Impala	Kruuk & Turner (1967); Fuller & Kat (1990).

Prey selection is adjusted to those individuals of the prey population that are easily captured (Reich, 1981a). The size and condition of prey are decisive factors determining wild dog prey species selection (Schaller, 1972). Predators such as lion *Panthera leo*, prey on healthy individuals but wild dog, through their coursing technique observed in East Africa in which they initiate a chase, survey a prey group and then select a particular individual, tend to take a relatively large number of sick, old or young individuals. This suggests that they may be prudent predators (Slobodkin & Richman, 1961; Estes & Goddard, 1967; Schaller, 1972).

Prior close-quarter visual assessment of prey condition by the wild dog is not possible in southern Africa, for example in the Kruger and Hwange National Park (referred to as

Hwange), because visibility is poor in the dense vegetation (Mills & Biggs, 1993; Ginsberg & Cole, 1994; Davies, *unpubl. thesis*) and hilly topography in HUP. In chapter 3, I test the prediction that prudent predation is unlikely to be a favoured strategy in HUP.

### ***Hunting***

Wild dog originally occurred in most habitat types, in Africa south of the Sahara, except in rain forests and certain deserts (Ginsberg & Cole, 1994). Most studies have been conducted in East African grasslands and savannas where prey selection, foraging technique and habitat selection have been well documented. The Serengeti is, however, not representative of the wild dogs' range (Frame, 1986) and information gained there may have limited application elsewhere. Extensive research in the Kruger and Hwange have identified differences in the behaviour and ecology of the southern African wild dog populations. In southern Africa the wild dog inhabits more heavily wooded areas where prey are cryptic and visibility is hampered by the dense vegetation (see above). Wild dog may therefore have to rely on surprise techniques to flush and ambush their prey.

Wild dog rely on sight when hunting (Fanshawe & Fitzgibbon, 1993) and can run long distances on open plains. Wolves, on the other hand, rely on smell and short distance chases, and few of their habitats include large open plains (Mech, 1970). In southern African habitats, one might expect wild dog to adopt similar hunting techniques to the wolf, relying more on auditory and olfactory senses when hunting.

Most studies in East Africa have documented a high overall capture success rate for wild dog (between 75% and 100%) (Kühme, 1965; Estes & Goddard, 1967; Malcolm & van Lawick, 1975; Fuller & Kat, 1990; Fanshawe & Fitzgibbon, 1993). This contrasts sharply

with results from studies in southern Africa where a much lower capture success (between 20% and 30% per chase) was noted (Reich, 1981a; Ginsberg & Cole, 1994). In open habitats wild dog capture success is assumed to depend on the age of the prey and the number of dogs hunting, and not on the amount of cover, size and vigilance of prey groups or prey distance to cover (Fanshawe & Fitzgibbon, 1993), which are likely to have a much greater influence on capture success in HUP. Capture success in HUP is investigated in chapter 3.

### *Home Range Area*

The major determinants of a predator's home range area are i) its energetic requirements (Mace & Harvey, 1983), ii) food availability (Macdonald, 1983; Fuller *et al.*, 1992), iii) the habitat type (Fuller *et al.*, 1992) and iv) the presence of other predators (Reich, 1981a).

Overall, annual pack home range sizes range between 150 km<sup>2</sup> and 3800 km<sup>2</sup> (Ginsberg & Macdonald, 1990; Fuller *et al.*, 1992) with an average home range size of 1500 km<sup>2</sup> in East Africa (Schaller, 1972; Frame & Frame, 1976; Frame *et al.*, 1979) and 450 km<sup>2</sup> in southern Africa (Reich, 1978; Davies, *unpubl. thesis*). In East Africa, large home ranges may be due to scarce seasonal prey, the open habitat, low wild dog densities and the presence of no or few other packs to restrict their movement (Fanshawe, 1989). In southern Africa the smaller home ranges may be due to the fact that prey are non-migratory, prey densities fluctuate little year round and the majority of the habitat comprises thick bush (Fuller *et al.*, 1992).

Wild dog are seasonally nomadic and exhibit much smaller home range areas during the denning season (Kingdon, 1977; Reich, 1978) when they are forced to remain in a

particular area for a period of approximately three months. Denning season home range sizes decrease to between 100 km<sup>2</sup> and 200 km<sup>2</sup> in East Africa (Kühme, 1965; Schaller, 1972) and between 50 km<sup>2</sup> and 170 km<sup>2</sup> (Reich, 1981a) in southern Africa. During this period the wild dog exhibits a central place foraging strategy in contrast to the free range foraging strategy adopted for the rest of the year. Central place foragers carry prey back to a fixed, often centrally located den where they are stored, consumed and passed on to offspring (Orians & Pearson, 1979). Since the HUP wild dog did not den during the study period the effect of a central place foraging strategy on prey abundance and distribution was not determined. This concept will, however, make for interesting study in the future.

Prey availability, habitat selection and predator presence are possible determinants of wild dog home range area and distribution and are investigated in chapter 4.

#### *Prey Availability*

The 'Resource Dispersion Hypothesis' (Macdonald, 1983) states that the home range area of a particular species should correlate with prey dispersion while group size of that species should correlate with prey abundance. The Resource Dispersion Hypothesis has been successfully tested on canids such as the red fox *Vulpes vulpes* and arctic fox *Alopex lagopus* (Macdonald, 1981; Hersteinsson & Macdonald, 1982) and is tested on the wild dog in HUP in chapter 4.

#### *Habitat*

The physical features of the habitat are important in habitat selection since they affect visibility, mobility and thereby the hunting effectiveness of the wild dog. Favoured habitats of a predator could be the sites where they can hunt more successfully. Habitat variables

such as vegetation type, topographical features, the presence of permanent water and accessible movement corridors (eg. roads), will indirectly affect wild dog habitat choice by virtue of their effect on prey distribution. The correlation between wild dog and prey habitat choice will be investigated in chapter 4.

The type of habitat also influences detection by other predators and competitors. Ambushes and short chases by wild dog in dense vegetation limit the chance of detection by hyaena and lion. In chapter 4, it will be determined whether wild dog prefer dense vegetation and whether habitat type influences wild dog distribution.

### *Predator Presence*

Intimidation by predators influences habitat use, resource exploitation and species interactions. Many studies have shown that foragers shift habitats or show other behavioural changes in the presence of other predators at the cost of obtaining a lower foraging rate (Lima, Valone & Caracao, 1985; Fraser & Gilliam, 1987). These studies emphasize the effect of predators on prey populations. For example, wild dog distribution in the Kruger was a function of predator avoidance rather than prey density and the availability of suitable habitats (Reich, 1981a; Maddock, 1988).

Hyaena are assumed to limit wild dog numbers in the Serengeti (Frame & Frame, 1976; Frame *et al.*, 1979; Malcolm, 1979). Based on the work of Gorman and Mills, Barnett (1994) stated that lion limited wild dog numbers in the Kruger. In the Kruger and Hwange, hyaena were present at very few wild dog kills (10% and <10% respectively) (Mills & Biggs, 1993; Davies, *unpubl. thesis*). By comparison, East African studies have determined hyaena presence at 85% of wild dog kills (Fanshawe & Fitzgibbon, 1993). Lion have been recorded to prey on wild dog pups, and wild dog in the Kruger actively avoid

these larger predators (Reich, 1981a; Barnett, 1994).

In HUP, there is a lack of competition from other wild dog packs, and I expected wild dog home range area to be slightly larger than those exhibited in the Kruger and Hwange. Whether predator and/or competitor presence influences wild dog home range area, is examined in chapter 4.

### *The Susceptibility of Prey to Predation*

Wild dog and other predators are less likely to succeed if their prey is aware of them. Several studies provide unambiguous support for the notion that there is a link between predation risk and vigilance, and an increase in vigilance with the greater risk of predation (Lima, 1987). In addition, several studies have shown that prey species respond with defensive behaviour at the sight of a predator or the sound of alarm calls (Curio, 1976; Gyger, Marler & Pickert, 1987). The effects of vigilance and other methods of predator detection and avoidance adopted by prey are considered in chapters 5 and 6 to i) determine the susceptibility of prey to predation in reserves differing in predator density and ii) to compare the susceptibility of the primary prey species to predation. Prey reaction to predator presence is important in determining the impact of wild dog on their prey species.

### *The Impact of Wild Dog Predation on Prey Populations*

Whether wild dog in HUP are targeting specific prey species and are selecting their habitat according to the distribution of these species is investigated in chapters 3 and 4 respectively. If this proves to be the case, it is necessary to investigate the impact of predation by wild dog



on their preferred prey species. Predation, together with other factors such as the number of predator and prey species, variations in the weather patterns, and the ability of predator and prey to migrate, could have a serious impact on prey populations. The above is an important consideration in a closed management system (such as HUP), and may result in a need for the control of animal numbers. The role of predators in maintaining vigorous prey populations is therefore extremely important (Kruuk, 1972; Schaller, 1972), particularly in the consideration of wild dog numbers for further introductions. The above will be addressed in chapter 7.

## CHAPTER 2

### STUDY SITE

#### Location

Hluhluwe-Umfolozi Park (HUP) located in central Zululand (28° 00' to 28° 10' S; 31° 43' to 32° 09' E) (Figure 2.1), comprises Hluhluwe Section in the north (300 km<sup>2</sup>) and Umfolozi Section in the south (660 km<sup>2</sup>). From hereon Hluhluwe Section and Umfolozi Section are referred to as Hluhluwe and Umfolozi.

Hluhluwe and Umfolozi are separated by a main road and game-proof fencing encloses the entire area. The topography is hilly and the altitude ranges from 60 m to 540 m. HUP is surrounded by tribal KwaZulu community-owned land with high rural human population densities and extensive subsistence agriculture (predominantly maize crop, cattle and goats) (Whately & Porter, 1983).

During the study period the wild dog pack ranged primarily in Hluhluwe, only making short occasional forays into Umfolozi. Research was thus concentrated in Hluhluwe. Vegetation and prey-related data were, however, collected in Hluhluwe and Umfolozi for comparative purposes.

#### Rainfall

HUP receives an average annual rainfall of  $1014.06 \pm 77.13$  mm (525.4-1376 mm) and experiences a wet season from October to March (rainfall >60 mm per month) and a dry

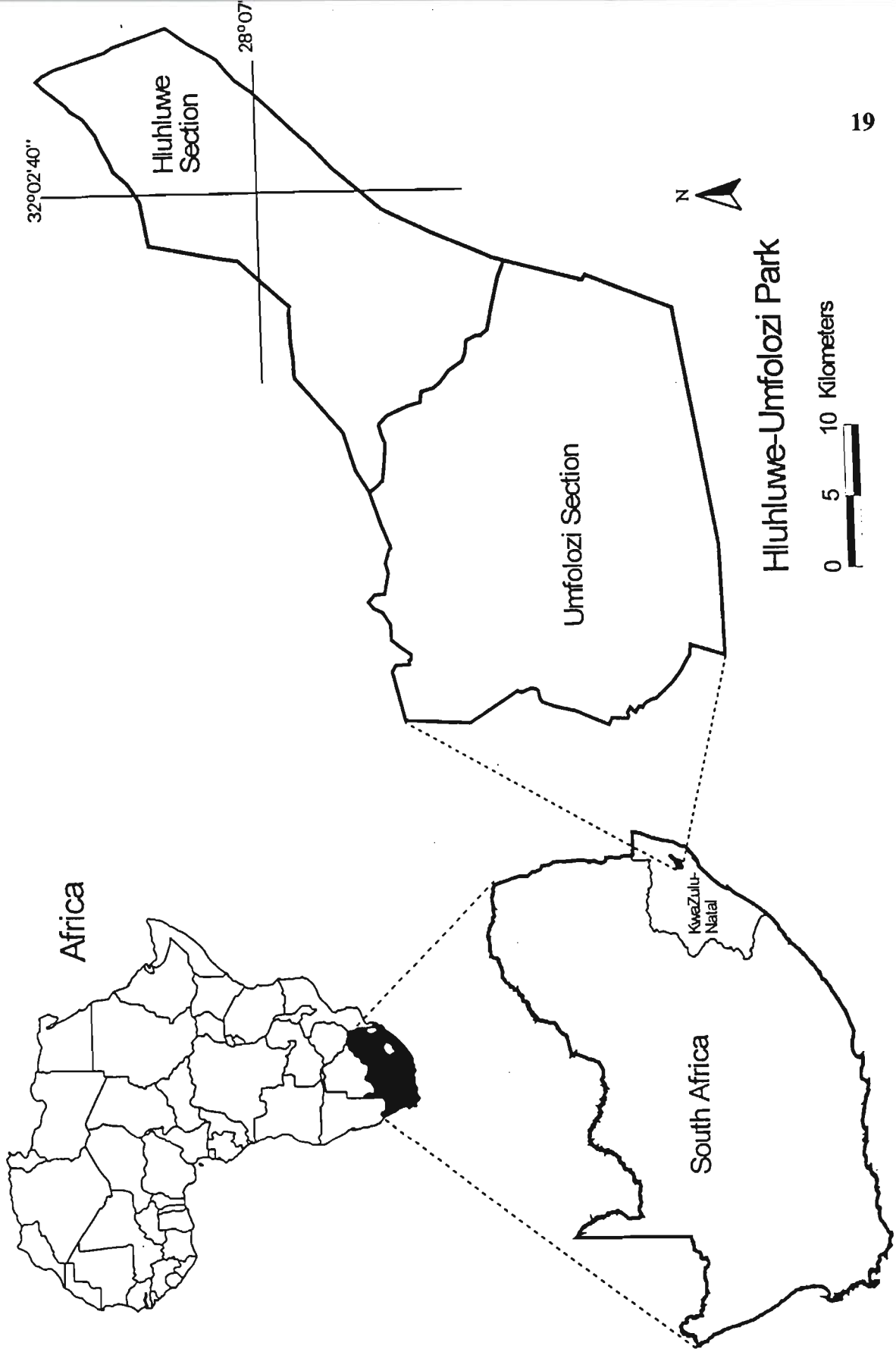


Figure 2.1. The position of Hluhluwe-Umfolozi Park in the KwaZulu-Natal province of South Africa.

season from April to September (rainfall < 60 mm per month). The seasons can be further divided into early and late wet and dry seasons. Most precipitation occurs in the summer months but it may rain in any month and there is considerable variation from one year to the next. The total annual rainfall in HUP had a normal distribution over the last 61 years. The denning period of the wild dog coincides with the late dry season, when, for three months, the dogs are concentrated in one location until the pups are old enough to join the hunt. Parturition appears to coincide with prey abundance (Fuller *et al.*, 1992). During the dry season in the Kruger, prey are concentrated along water courses (Pienaar, 1969; Reich, 1981a) and pups are old enough to join the hunt in the early wet season which coincides with the lambing/calving period of their prey.

Several dams and water courses provide water for most of the year, but many dry up during the dry season. Three permanent pools, Hidli vlei (Hluhluwe), Thiyeni hide (Hluhluwe) and Mphafa hide (Umfolozi) are supplemented by water pumped from the Manzibomvu, Hluhluwe and Mphafa rivers respectively during the dry season.

## **Flora**

HUP lies within the Zululand thornveld subcategory of coastal tropical forest types and the lowveld subcategory of tropical bush and savanna types (Acocks, 1988). Six basic vegetation physiognomies occur in HUP, each characterised by various dominant plant communities (Appendix A & B). Forests are restricted to the high rainfall hillsides or riverine belts (Brooks & MacDonald, 1983) and encroachment of large tracts of forest has taken place. Woodland communities are found in certain bottomland situations as well as on rocky and sandy hillslopes. More than half the area is covered by savanna, dominated by *Acacias*.

True grassland communities are poorly represented and are found only in areas with prolonged waterlogging. Two forest and ten woodland communities, and one thicket and one induced thicket community are recognised in HUP (Whately & Porter, 1983) (Appendix A & B). For the purposes of this study the vegetation physiognomies were grouped into four types which were distinguished by the nature of the woody plant elements of the vegetation and their density in the different height classes, namely; i) forest (forest and riverine forest), ii) woodland (open and closed woodland), iii) shrubland (thicket and induced thicket) and iv) grassland.

## **Fauna**

HUP supports a great variety of potential prey species and consequently a broad spectrum of large and small predators. Prey and predator species in HUP, and the abbreviations used in the text for these species, are listed in (Appendix C). Carnivores belonging to the same feeding guild as the wild dog include spotted hyaena, lion, leopard, *Panthera pardus* and cheetah, *Acinonyx jubatus*.

## CHAPTER 3

### Prey Selection and Capture Success

by the Wild Dog

in Hluhluwe-Umfolozi Park

#### ABSTRACT

Prey preference of the wild dog in HUP was determined from scat analysis. Eight prey species were identified. Nyala *Tragelaphus angasi* and impala *Aepyceros melampus*, the most abundant ungulate species in HUP, accounted for 78% of the diet. Wild dog predominantly preyed on small- to medium-sized prey, while large prey species supplemented the diet during the dry season. Wild dog showed a preference for adult nyala, juvenile impala and females of both species. The observed diet choice of wild dog was compared to the expected diet choice as predicted by the classical diet choice model. Wild dog diet was dominated by the most profitable prey item (nyala). Contrary to prediction, waterbuck *Kobus ellipsiprymnus* and zebra *Equus burchelli* were excluded from the diet, while bushbuck *Tragelaphus scriptus* were present in the diet more than expected from their profitability. Large body size, herding behaviour and habitat choice of these prey species are thought to account for these anomalies. Wild dog prey capture success was similar to that of previous studies in both open and densely wooded habitats. The results suggest that wild dog were able to adapt their diet choice and foraging technique and were thus not necessarily restricted by the dense vegetation in HUP. Pursuits involving nyala, juvenile nyala and impala, and female nyala were more successful than those involving impala, adult nyala and impala, and

male nyala.

## INTRODUCTION

Wild dog diet choice and capture success are constrained by the availability and abundance of their prey (Fuller *et al.*, 1992). Wild dog are size selective social predators consuming small- (<25 kg) to medium- (40-90 kg) sized ungulate prey (Reich, 1981a; Mills, 1992; Childes, 1988a). Other medium-sized social canids, such as the dingo *Canis familiaris dingo* (Newsome, Catling & Corbett, 1983) and wolf (Floyd, Mech & Jordan, 1978), also feed on small- to medium-sized prey whereas the Ethiopian wolf (Sillero-Zubiri & Gotelli, 1995) and coyote *Canis latrans* (MacCracken & Hansen, 1987) include a large proportion of small mammals (rodents and rabbits) in their diet. Although wild dog exploit a narrow size range of prey, their obligatory co-operative hunting technique enables them to take prey faster and larger than themselves (Mitchell *et al.*, 1965; Estes & Goddard, 1967; Kruuk & Turner, 1967). Wild dog differ from other social carnivores in that they are exclusively social, less flexible in foraging methods and comparatively more successful in hunting.

Geographical variation in wild dog diet reflects the most abundant local small- to medium-sized prey species (Ginsberg & Macdonald, 1990) for example, impala and kudu *Tragelaphus strepsiceros* in the Kruger (Reich, 1981a; Mills, 1992) and Hwange (Childes, 1988a) and Thomson's gazelle *Gazella thomsoni* and blue wildebeest *Connochaetes taurinus* in the Serengeti (Schaller, 1972; Frame, 1986). Similarly, dingo (Newsome *et al.*, 1983), wolf (Floyd *et al.*, 1978; Sillero-Zubiri & Gotelli, 1995) and coyote (MacCracken & Hansen, 1987) consume ungulate prey in relation to availability.

Predictions about an animal's foraging behaviour can be based on the assumption that

natural selection operates to produce an optimal behavioural pattern. Here I use a simple optimality model, the classical diet choice model (Charnov & Orians, 1973), to test predictions about wild dog diet selection. The diet choice model assumes that the forager selects prey in a way that maximises its long term mean rate of energy intake (Schoener, 1987). Optimal diet theory predicts that in order to maximise the rate of energy intake, the predator ranks prey types, including them in the diet according to their profitability (Pulliam, 1974; Stephens & Krebs, 1986), where profitability is a measure of prey energy, handling time and encounter rate. Carnivore foods contain similar 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). Accordingly, profitability can in this case be simply measured by, and positively correlated with, prey size provided encounter rate and handling time (pursuit, capture and ingestion) are included (Lendrem, 1986). Carnivores may therefore rank prey items in the diet solely on the basis of size.

Apart from prey abundance and availability, wild dog diet choice and capture success in HUP are potentially constrained by an environment where the vegetation is more dense than that found in most other wild dog studies. Since wild dog hunt primarily by sight (Fanshawe & Fitzgibbon, 1993), the visual barriers presented by the dense vegetation may hinder prior close quarter visual assessment of prey condition by wild dog, thus hindering capture success. Studies conducted in dense habitats in southern Africa and the Selous Game Reserve, Tanzania, found that wild dog successfully captured, on average, 35% (20%-44%) of the prey they selected (Reich, 1981a; Creel & Creel, 1995). This contrasts 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-Goodall, 1971; Malcolm & van Lawick, 1975; Fuller & Kat, 1990; Fanshawe & Fitzgibbon,



1993). The lower hunting success in southern Africa has been attributed to the decreased visibility in the dense vegetation (Ginsberg & Cole, 1994). The extent to which the vegetation and hilly topography in Hluhluwe may hinder wild dog visibility while hunting is explained here. Factors relating to the capture success in areas differing in visibility are important in the consideration of sites for further wild dog introductions, ie. introduction sites should be located where wild dog capture success is maximised.

## **METHODS**

### **Diet Choice**

#### *Scat analysis*

Scat analyses provide a large amount of information on prey species (Putman, 1984) and may be used to establish the degree of importance of different prey species in the diet. Scat analysis allows a continuous determination of feeding habits, relatively simple methodology and limited interference with the study animal (Putman, 1984). The hair of each prey species has a characteristic shape, length or colour (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 leaving different proportions of undigested parts in the scat (Scott, 1941; Lockie, 1959; Putman, 1984; Hiscocks & Bowland, 1989). It was assumed that the identified prey remains in each scat represented one individual. This assumption was based on the knowledge that i) differential digestion is not as pronounced for ungulate prey (Floyd *et al.*, 1978), ii) the scats of wolves, social carnivores which are similar in body size and feed on a similar size range of prey to wild dog, generally contain the remains of a single prey item

(Floyd *et al.*, 1978) and iii) scats were not collected on a regular basis from a midden, thus 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 used (Walker, 1981). On several occasions, more than one scat sample was collected at a particular site. Each site was considered a separate and single sample to avoid pseudoreplication.

Scats were macerated in water overnight and thoroughly rinsed in a 1 mm mesh sieve under running water (Maddock & Perrin, 1993). Contents were floated in water and separated into identifiable categories: hair, insects, bone fragments, hooves and vegetable matter. 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 (Appendix D) were used to identify hair cross-sections. Dr. A. Maddock confirmed the accuracy of the scat analysis by correctly identifying a representative sub-sample of hair cross-sections.

### ***Wild Dog Kills***

Data from wild dog kills (n=43), observed by G. Andreka and myself during 1994, were used. Observations provide a more accurate record of the number of smaller species (<25 kg) in the wild dog diet which would not be obtained from carcass return records (see below). The method is, however, limited by the extent to which the observer is able to

follow the dogs and the visibility in the different vegetation types.

Carcass return records from 1984 to 1994 (n=157; Natal Parks Board records) were obtained from daily game guard patrols spanning the entire reserve. These data contain several inherent biases; i) dense vegetation is inaccessible and therefore under-sampled, ii) the reserve interior is sampled to a lesser degree because more than half the patrols (65%, L. Steyn, *pers. comm.*\*) are concentrated along peripheral areas, iii) the game guards' expertise in interpreting wild dog kills has never been tested and iii) smaller species and young age classes killed are underestimated since the remains of larger species are more likely to be found than smaller species which are often totally consumed. Although carcass return records require that several assumptions are met, they provide seasonal and long term data enabling interesting comparisons with the data obtained from this study.

The relative prey percentage occurrence method (Rowe-Rowe, 1977) was used to compare prey species selection data from i) scat analysis, ii) personal observations of wild dog kills and iii) carcass return records.

Wild dog are expected to show seasonal differences in their diet choice. This is because the distribution and abundance of prey, and the susceptibility of prey to predation are expected to differ seasonally; for example a greater number of juveniles during the wet season and a decrease in prey body condition towards the end of the dry season. Wild dog diet choice was thus compared between the wet season (October to March) and the dry season (April to September).

I preferentially used scat data to describe the observed wild dog diet choice because these data contained the least biases and were obtainable in sufficient quantities. The

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observed diet choice of wild dog in HUP was compared to the expected diet choice, determined using the classical diet choice model (Charnov & Orians, 1973).

### *Expected Diet Choice*

Prey were ranked on the basis of profitability, to estimate their expected preference, using the equation;

$$E/h * \lambda$$

where  $E$  = energy,  $h$  = handling time and  $\lambda$  = encounter rate. 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 ( $h$ ) included the time (hours) taken to pursue, capture and ingest prey. Personal observations ( $n=43$ ), section rangers' reports of wild dog kills ( $n=27$ ) and the intuition of several wild dog researchers were used to estimate pursuit, capture and ingestion time of nyala and impala. Handling times for other potential prey species were extrapolated from the values obtained for nyala and impala. For this purpose handling time was considered directly proportional to body size, and prey herd structure and the presence of defence mechanisms (eg. horns) were taken into account.

Prey encounter rates ( $\lambda$ ) were obtained from road transect encounters of prey which were used as a surrogate measure of prey encounter by the dogs. Wild dog in HUP, as in many other studies, 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 wild dog coursing speed (15-20 km/h) at these times along tourist roads and management tracks covering the entire

Hluhluwe Section. Prey encounter rate was calculated as the number of times a particular prey species was encountered per hour, by dividing the total number of times a prey species was encountered by the total time taken to conduct all the transects in a particular season.

The classical diet choice model (Charnov & Orians, 1973) considers diet choice within a homogenous patch for a forager using a fixed foraging strategy (Stephens & Krebs, 1986). I assumed the habitat within Hluhluwe to be homogenous since road transects determined woodland to be the most widespread and dominant vegetation type overall within Hluhluwe (46%) and along the road (39%), the other three vegetation types each forming a small percentage of the total.

### *Prey Age and Sex Selection*

Observations of wild dog kills were used to identify prey age and sex class selection of the primary wild dog prey for comparison with the prey population abundance. The age and sex structures of the primary prey populations in Hluhluwe were obtained from a survey of individuals during road transects. The method of Child (1964) was modified to determine age classes of impala and Rowe-Rowe & Mentis's (1972) ageing method was used for nyala (Table 3.1).

Table 3.1. The criteria used to determine ages of impala and nyala in HUP. Age is expressed in months and height is expressed as a percentage of the adult female's shoulder height.

AGE CLASS	IMPALA		NYALA	
	AGE	HEIGHT	AGE	HEIGHT
Juvenile	0-18	< 91 %	0-07	50-90 %
Subadult	19-24	94 %	8-18	90 %
Adult	25+	100 %	19+	100 %

### *Prey Condition Selection*

The bone marrow fat of prey long bones was collected for condition analyses (cf. Fitzgibbon & Fanshawe, 1989). Proximal bones are the preferred bones for condition assessment (Brooks, Hanks & Ludbrook, 1977; Reich, 1981b; Gallivan, Culverwell & Girdwood, 1995). Where possible the radial and carpal bones were collected from kills and randomly culled animals. The culled animals served as controls. Between 2 g and 5 g of bone marrow were collected from the centre of the radial and carpal bones, avoiding the haemopoietic end portions of the bones (Bradley, 1977). The samples were weighed and oven dried at 100° C until a constant weight was reached. In the analysis, dry weight was expressed as a percentage of fresh weight, and the percentage of marrow fat calculated using the following equation;

$$\% \text{ marrow fat} = \% \text{ dry weight} - 7$$

where the constant (7) represents the non-fat residue in the marrow after drying (Brooks *et al.*, 1977). Two samples per bone were analysed and the average of these two values was used in the analysis. Based on these analyses, animals were estimated to be in either poor (0-30%), fair (31-60%) or good (61-100%) condition (Mitchell *et al.*, 1965; Brooks *et al.*,

1977).

Problems were experienced in collecting sufficient long bones for adequate analyses to be performed. Wild dog may consume the long bones of smaller species, and scavengers and other predators may remove/consume the remaining bones from a wild dog kill.

### **Capture Success**

Capture success data were obtained from personal observations by G. Andreka and myself during 1994. Capture success was calculated as the percentage of successful pursuits by the entire pack or the majority of the pack (Fanshawe & Fitzgibbon, 1993). Wild dog 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.

### ***Vegetation Type***

To determine the effect of habitat on hunting success, visibility at dog height (500 mm 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 (approximately 95 cm) and served to simulate at what distance prey were visible to wild dog. In this way an index of visibility was calculated, for each vegetation type in both Hluhluwe and Umfolozi during the wet and dry seasons. Prey capture success, visibility and prey availability were compared seasonally.

Vegetation type was recorded during road transect counts of prey and observations

and telemetry locations of wild dog. The vegetation preferences of the dominant prey and wild dog were calculated using a rank preference index (Johnson, 1980). This index ranks the vegetation use ( $r_i$ ) and availability ( $s_i$ ) and calculates the difference in these ranks ( $t_i$ ) as a measure of relative preference, using the equation;

$$t_i = r_i - s_i$$

The method is advantageous in that the analysis is not affected by vegetation types that are rarely used.

## RESULTS

### Diet Choice

#### *Observed Diet Choice*

The 136 positively identified wild dog scats included 78 separate samples. Each of the 78 scat samples contained on average  $1.5 \pm 0.08$  species.

Ten prey species were identified from scat analysis ( $n=78$ ), personal observations of wild dog kills ( $n=43$ ) and carcass return records ( $n=157$ ) (Figure 3.1). Nyala and impala accounted for a significantly greater proportion ( $Z=0.38$ ,  $d.f.=315$ ,  $p<0.01$ ) of prey individuals in all three methods used to determine prey species selection. These prey also fall in the medium-size prey category when graphed in order of increasing size (Figure 3.1).

For further analyses only impala and nyala were recognised at the species level. All other prey species were captured infrequently and were pooled as 'other species'.

A comparison of scat analyses and carcass return records showed a significant difference in prey selection ( $\chi^2=39.49$ ,  $d.f.=2$ ,  $p<0.01$ ). During the study period nyala were selected slightly more than impala (42% and 36% respectively) whereas long term



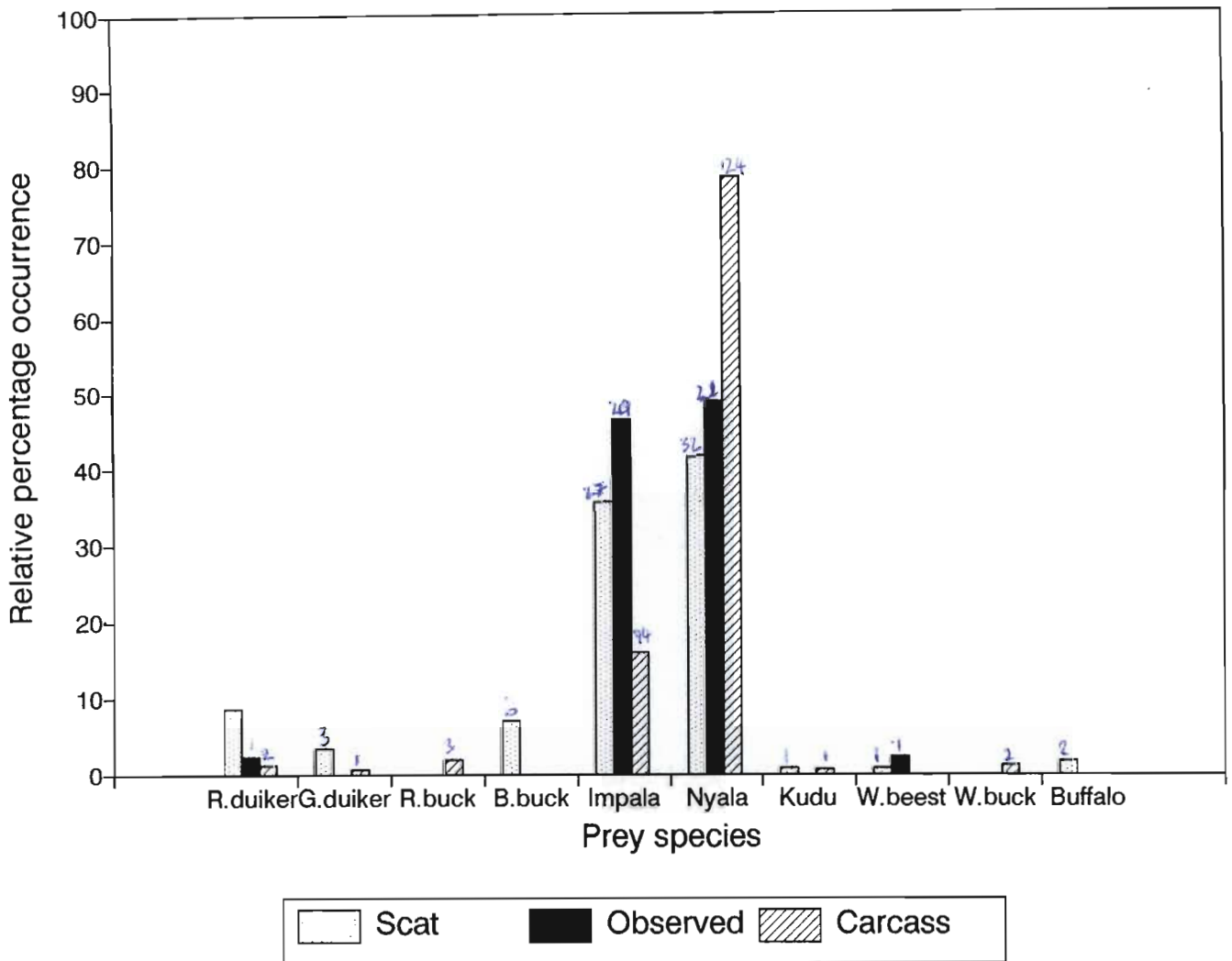


Figure 3.1. The relative percentage of occurrence of prey species in the wild dog diet determined by scat analysis (n=78), personal observations (n=43) and carcass return records (n=157). Prey species size increases from left to right along the X-axis.

records show a much greater selection for nyala (78% and 16% respectively) (Figure 3.1). The latter result could be explained by the biases associated with the use of carcass return data for diet determination (see earlier).

Significant seasonal differences in prey selection were observed ( $\chi^2=39.49$ , *d.f.* =2,  $p<0.01$ ) (Figure 3.2). Wild dog took more impala (39%,  $n=24$ ) during the wet season than nyala (28%,  $n=17$ ). In the dry season, however, wild dog took considerably more nyala (42%,  $n=26$ ) than impala (36%,  $n=22$ ) (Figure 3.2). Large prey species (kudu, buffalo *syncerus caffer* and blue wildebeest) only supplemented the diet during the dry season, each being represented once in the diet, and were therefore considered incidental. Buffalo were identified from scats collected on two consecutive days and were assumed to be from the same carcass. I assumed that the larger species were represented by calves in the diet or by incidents where wild dog had scavenged from the kills of other predators.

### *Expected Diet Choice*

Wild dog were observed (scat analysis) to take eight of 11 possible prey species in HUP. Is this the expected diet composition based on prey profitability?

The expected or optimal diet choice of wild dog depends on the relative abundance of prey types (Pulliam, 1974). A predator's only estimate of prey abundance comes from encounter frequency of prey. Road transects conducted during the early morning and late afternoon were used as a surrogate measure of prey encounter by wild dog, and were justified because i) 78% ( $n=118$ ) of telemetry observations (G. Andreka, *pers. comm.*) showed that wild dog moved and hunted within 5 m of the road and ii) hunting ( $n=103$ ) was observed between 5h30 and 9h10, and 17h15 and 19h30 during the wet season and between

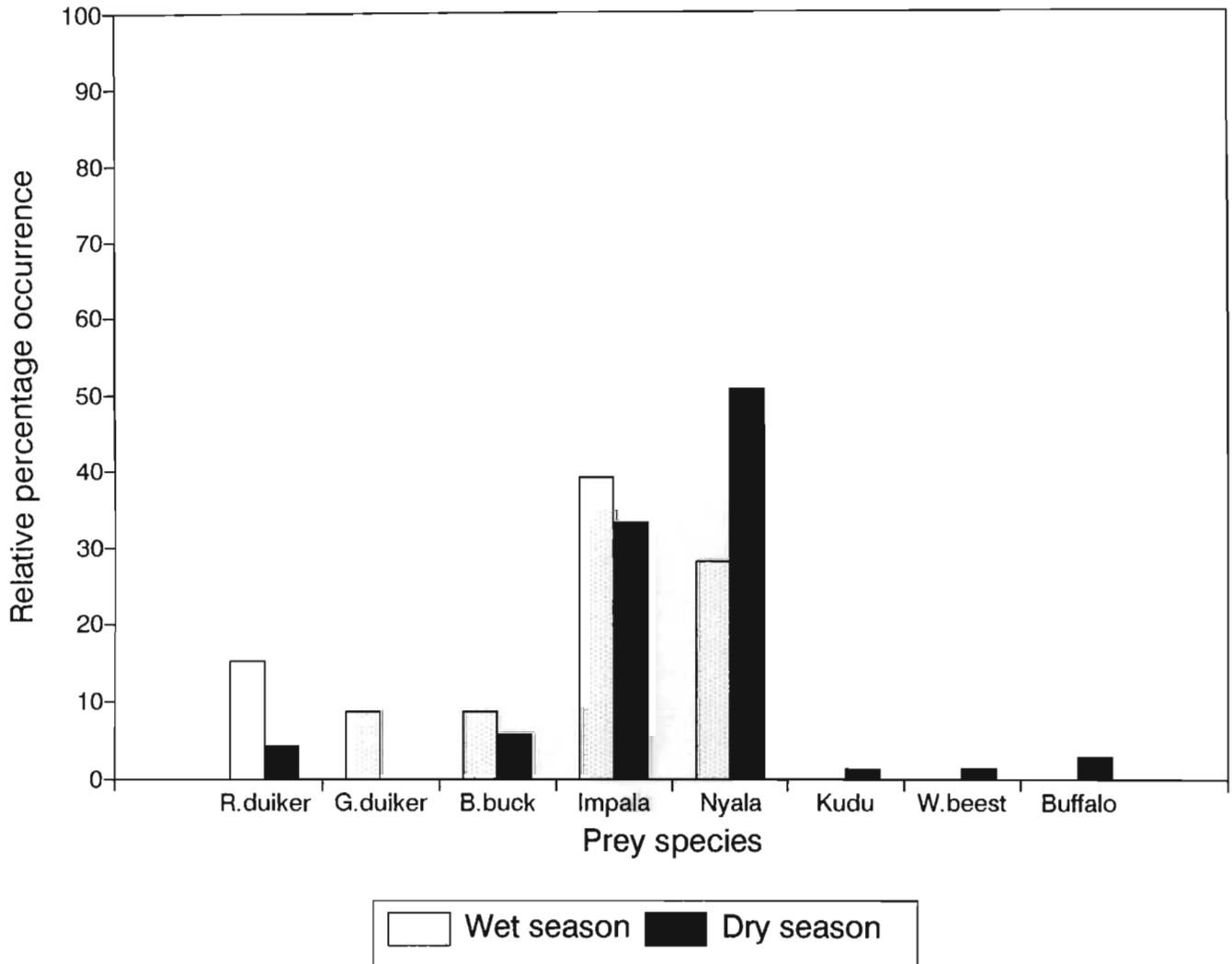


Figure 3.2. A seasonal comparison of the relative percentage occurrence of prey species in the wild dog diet, determined by scat analysis.

6h00 and 9h30, and 16h00 and 18h00 during the dry season.

All potential wild dog prey species were considered in the classical diet choice model simulation. Foraging parameters (handling, energy, encounter) of prey types are given in Table 3.2. Although identified from carcass return records (n=3), common reedbuck *Redunca arundinum* were never encountered during road transects and were thus excluded from the model.

Although the model predicts that nyala and impala should be the most profitable prey, which is in accordance with the observed diet choice, a chi-squared goodness-of-fit test determined that the observed diet choice differed significantly from expected ( $\chi^2=22.92$ ,  $d.f.=6$ ,  $p<0.05$ ) (Table 3.3). In order of profitability, zebra, blue wildebeest, buffalo, waterbuck and kudu are expected to be taken more often than observed and red duiker *Cephalophus natalensis*, grey duiker *Cephalophus grimmia* and bushbuck less often than observed (Table 3.3).

By adding species into the model based on individual species profitabilities, rate maximising foraging wild dog, are predicted to do best (ie. obtain the highest number of calories for the relationship  $E/h * \lambda$ ) by taking the seven most profitable species (nyala, impala, zebra, waterbuck, blue wildebeest and buffalo, where  $E/h * \lambda = 74.04$  cal) of the potential prey species in HUP.

The above calculations did not take wild dog age and sex selection of prey into account. With the inclusion of known wild dog age and sex preferences in the model, more accurate predictions regarding the expected wild dog diet choice may be made.

Table 3.2. The energy values ( $E$ ), handling times ( $h$ ) and encounter rates ( $\lambda$ ) of potential prey species of wild dog in HUP. Handling times (hours) were obtained by adding pursuit time, capture time and ingestion time.

SPECIES	PURSUIT	CAPTURE	INGEST	$h$	$E$	$\lambda$
Nyala	0.17	0.08	0.75	1.00	61	2.46
Impala	0.40	0.07	0.60	1.07	41	2.67
Red duiker	0.07	0.03	0.12	0.22	9	0.08
Bushbuck	0.02	0.07	0.50	0.59	38	0.01
Grey duiker	0.08	0.03	0.25	0.36	17	0.05
Kudu	0.45	0.12	1.05	1.62	152	0.20
Blue wildebeest	0.65	0.12	0.98	1.75	180	0.63
Waterbuck	0.22	0.10	0.92	1.24	200	0.19
Buffalo	0.70	0.17	2.68	3.55	513	0.19
Zebra	0.70	0.17	1.20	2.07	302	0.50

Table 3.3. A comparison between the observed and expected wild dog diet choice for the relationship  $E/h * \lambda$  cal.

SPECIES	$E/h * \lambda$	OBSERVED	EXPECTED
Nyala	150.00	1	1
Impala	102.31	2	2
Zebra	72.95	10	3
Blue wildebeest	64.80	7	4
Buffalo	43.35	9	5
Waterbuck	30.65	8	6
Kudu	18.77	6	7
Red duiker	3.27	3	8
Grey duiker	2.36	5	9
Bushbuck	0.64	4	10

### *Prey Age and Sex Selection*

Nyala prey age selection did not differ significantly from the population age structure ( $\chi^2=3.73$ ,  $d.f.=2$ ,  $p>0.05$ ). Wild dog killed more adult nyala than subadults and juveniles (Table 3.4). Impala prey age selection differed significantly from the population age structure ( $\chi^2=19.52$ ,  $d.f.=2$ ,  $p<0.01$ ) (Table 3.4). Juvenile impala were taken more than expected, and subadults and adults less than expected.

Table 3.4. A comparison of the population age structure of nyala and impala (total number of individuals in Hluhluwe obtained from transect counts) and the number of individuals killed by wild dog in each age class.

<b>SPECIES</b>	<b>DATA SOURCE</b>	<b>JUVENILE</b>	<b>SUBADULT</b>	<b>ADULT</b>
Nyala	Total	43	63	169
	Observed	3	2	15
Impala	Total	104	204	448
	Observed	8	1	6

Wild dog preyed upon more female nyala and impala than males (Table 3.5). Neither nyala ( $\chi^2=0.02$ ,  $d.f.=1$ ,  $p>0.05$ ) nor impala ( $\chi^2=0.39$ ,  $d.f.=1$ ,  $p>0.05$ ) sex selection differed significantly from the population sex ratios (Table 3.5).

Table 3.5. A comparison of the population sex structure of nyala and impala (total number of individuals in Hluhluwe obtained from transect counts) and the number of individuals killed by wild dog in each sex class.

<b>SPECIES</b>	<b>DATA SOURCE</b>	<b>MALE</b>	<b>FEMALE</b>
Nyala	Total	120	234
	Observed	7	10
Impala	Total	189	583
	Observed	0	7

Results indicate that wild dog prefer females, adult nyala and juvenile impala. With the adjustment of the foraging parameters, according to wild dog age and sex selection (Table 3.6), the overall expected diet preferences did not differ significantly from the overall observed preferences ( $\chi^2=8.16$ ,  $d.f.=6$ ,  $p>0.05$ ) (Table 3.7). Bushbuck and buffalo were present in the diet more than expected while zebra and waterbuck were avoided.

Table 3.6. The energy values ( $E$ ), handling times ( $h$ ) and encounter rates ( $\lambda$ ) of potential prey species of wild dog in HUP, adjusted according to wild dog age and sex selection. J= Juvenile.

SPECIES	PURSUIT	CAPTURE	INGEST	$h$	$E$	$\lambda$
Nyala	0.17	0.08	0.75	1.00	61	2.46
J.Impala	0.12	0.02	0.12	0.26	6	0.17
Red duiker	0.07	0.03	0.12	0.22	9	0.08
Bushbuck	0.02	0.07	0.50	0.59	38	0.01
Grey duiker	0.08	0.03	0.25	0.36	17	0.05
Kudu	0.12	0.03	0.25	0.40	16	0.03
Blue wildebeest	0.17	0.05	0.28	0.50	22	0.02
Waterbuck	0.17	0.05	0.30	0.52	26	0.02
Buffalo	0.25	0.07	0.35	0.67	34	0.01
Zebra	0.25	0.07	0.32	0.64	32	0.02

Nyala and impala are the most profitable prey and calculations suggest that wild dog rate maximise by preying solely upon nyala ( $E/h * \lambda = 43.37$  cal). The energy obtained from a diet consisting of the full spectrum of prey (the second best option) would only contain slightly less calories (0.16) than a diet containing only nyala.

Table 3.7. A comparison of the observed and expected wild dog diet choice for the relationship  $E/h * \lambda$  cal, with foraging parameters adjusted according to wild dog age and sex selection.

<b>SPECIES</b>	<b><math>E/h * \lambda</math></b>	<b>OBSERVED</b>	<b>EXPECTED</b>
Nyala	150.00	1	1
Impala	3.92	2	2
Red duiker	3.27	3	3
Grey duiker	2.36	5	4
Kudu	1.20	7	5
Waterbuck	1.00	9	6
Zebra	1.00	10	7
Blue wildebeest	0.88	8	8
Bushbuck	0.64	4	9
Buffalo	0.51	6	10

### *Observed versus Expected Diet Choice*

The differences between the observed and expected diet choice are explicable in a number of ways, namely; i) simultaneous encounter of prey, ii) predator and prey habitat choice, iii) prey social organisation and defendability, and iv) the validity of the assumption that prey are encountered randomly.

Simultaneous encounters of two species, separated by several metres, may result in the wild dog choosing prey species according to the rate maximisation rule of simultaneous encounter (Waddington & Holden, 1979) by selecting the prey of higher effective profitability. In the case of simultaneous encounters the 'take-most-profitable' rule of the diet choice model fails because smaller, less profitable prey are acceptable when close (Schoener, 1979). Distances of prey from the road were estimated during road transects



(Table 3.8). The proximity of bushbuck to the road as opposed to the larger species (kudu, blue wildebeest, waterbuck) may explain the greater observed preference for them even though they are less profitable. Wild dog therefore show opportunistic foraging behaviour.

Table 3.8. Average sighting distance of prey species measured in metres from the road during road transect counts.

SPECIES	WET SEASON		DRY SEASON	
	$\bar{X} \pm SE$	n	$\bar{X} \pm SE$	n
Bushbuck	10.67 $\pm$ 0.54	3	100.00 $\pm$ 0	1
Kudu	71.62 $\pm$ 13.51	53	102.38 $\pm$ 23.04	26
Blue wildebeest	80.00 $\pm$ 6.60	155	113.79 $\pm$ 12.57	85
Waterbuck	44.60 $\pm$ 8.05	43	48.59 $\pm$ 12.44	27
Nyala	53.08 $\pm$ 4.85	324	30.04 $\pm$ 2.09	600
Impala	47.03 $\pm$ 4.02	383	37.03 $\pm$ 2.34	593
Red duiker	11.91 $\pm$ 4.01	11	5.35 $\pm$ 1.21	20
Grey duiker	8.57 $\pm$ 2.41	7	14.83 $\pm$ 4.55	12

The rank preference index (Johnson, 1980) indicated that wild dog and nyala prefer forest, woodland, shrubland and grassland in decreasing order of preference. Wild dog choice of vegetation type is therefore similar to that of nyala (see also chapter 4). During road transects, bushbuck were only encountered in forest and closed woodland. Wild dog are more likely to encounter and capture forest-dwelling species than those which prefer open habitats where they can see the predator approaching. This would explain wild dog preference for nyala and the greater observed than expected preference for bushbuck.

The social organisation of buffalo and waterbuck herds, and defendability of these and zebra herds may explain why these species are avoided. Waterbuck occur in large groups

of up to 30 (average between 6 and 12) (Skinner & Smithers, 1990). By comparison kudu, which were included in the diet, occur in herds of only four. Fewer adult males are present in the smaller herds to defend the calves and pose less of a threat to wild dog. Buffalo in HUP occur in extremely large herds (average between 30 and 60) and their large body size and presence of adults to defend their young, makes them a formidable and unlikely prey item. Zebra are formidable prey to wild dog, which are harassed by the stallions (Malcolm & van Lawick, 1975) which have been observed chasing the dogs on several occasions at Hluhluwe.

The ranking of prey on the basis of profitability fails if the assumption that prey are encountered randomly is not met. The prey frequency of encounter data were fitted to uniform, poisson and negative binomial distributions using the Kolmogorov-Smirnov distribution fitting. The encounter of prey along the road was found to be uniform ( $D_{17,49}=0.12$ ,  $p=0.50$ ).

To account for the non-randomness of prey encounter, the scale dependency of the model was tested by comparing prey encounter for various lengths of the transects (D. Ward, *pers. comm.*\*). Overall prey encounter rates were calculated from the road transects (see above) and compared to prey encounter rates calculated from three 5 km segments, two 10 km segments and one 20 km segment selected randomly from each transect (Table 3.9). The relationship  $E/h * \lambda$  cal used in the diet choice model, was calculated (using adult prey species) for the various transect/segment lengths and prey were ranked according to profitability. Prey profitability rankings were the same regardless of segment size. Since

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segments chosen at random give equal results, the assumption that prey are encountered at random is essentially met and prey distribution therefore does not affect the predictions of the diet choice model.

Table 3.9. A comparison of the following encounter rates of adult prey; i) overall road transect encounter, ii) encounter over three random 5 km segments, iii) encounter over two random 10 km segments, and iv) encounter over one random 20 km segment.

PREY SPECIES	ENCOUNTER RATE			
	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

### *Prey Condition Selection*

Wild dog selected prey ranging greatly in condition. The percentage body fat of the primary prey of wild dog ranged from 3.65% to 85.90% (n=7). Similarly the percentage body fat of the controls ranged from 2.46% to 82.27% (n=10) (Table 3.10).

Although limited conclusions can be drawn from these data, the data suggest that wild dog sample the prey population at random without selecting prey in any particular condition.

Table 3.10. Calculated percentage fat content of bone marrow of prey killed by wild dog and control samples.

SAMPLE	SPECIES	AGE	SEX	n	% MARROW FAT
Observed	Red duiker	adult	unknown	1	37.44
Observed	Impala	subadult	female	1	3.65
		adult	female	1	85.90
	Nyala	adult	female	1	9.39
		adult	female	1	82.17
		subadult	female	1	56.10
		subadult	female	1	21.95
Control	Nyala	adult	female	1	27.77
		adult	male	9	$\bar{x} = 47.18 \pm 9.05$ range: 2.46-82.27

### Capture Success

The overall prey capture success was 41% (Table 3.11). Nyala and impala were the primary prey species pursued. There was a significant difference ( $\chi^2=6.43$ ,  $d.f. = 1$ ,  $p < 0.05$ ) in the outcome of pursuits involving these two species. Pursuits involving nyala were more successful than those involving impala. Other species (warthog *Phacochoerus aethiopicus*, blue wildebeest, kudu and buffalo) were pursued less successfully and opportunistically and formed a very small portion of the total number of chases.

Table 3.11. The capture success (expressed as a percentage of pursuits with known outcome) for various prey species pursued by the wild dog in HUP.

<b>SPECIES</b>	<b>n</b>	<b>% SUCCESS</b>
Nyala	24	67
Impala	36	33
Warthog	4	0
Blue wildebeest	2	50
Kudu	2	0
Buffalo	3	0
<b>TOTAL</b>	<b>102</b>	<b>40</b>

There was a significant difference ( $\chi^2=5.22$ ,  $d.f. = 1$ ,  $p < 0.05$ ) in the capture success between age classes of nyala and impala. The success rate of pursuits involving juvenile nyala and impala was higher than for adults (Table 3.12) even though adults were preferred (see prey age selection). Subadults were not pursued at all. Nyala females were pursued with a higher success rate (71%) than males (57%) (Table 3.12).

Table 3.12. The capture success rate (expressed as a percentage) of different age and sex classes of nyala and impala pursued by the wild dog in HUP.

<b>SPECIES</b>	<b>AGE</b>			<b>SEX</b>	
	<b>JUVENILE</b>	<b>SUBADULT</b>	<b>ADULT</b>	<b>MALE</b>	<b>FEMALE</b>
Nyala	75 (n=4)	0 (n=1)	64 (n=14)	57 (n=7)	71 (n=7)
Impala	83 (n=6)	0 (n=0)	38 (n=8)	-	-

### *Vegetation Type*

Significant seasonal variation in visibility in the four vegetation types was observed in Hluhluwe ( $F_{1,4}=54.571$ ,  $p<0.05$ ) and between Hluhluwe and Umfolozi in the wet ( $F_{1,4}=85.135$ ,  $p<0.05$ ) and dry ( $F_{1,4}=24.803$ ,  $p<0.05$ ) seasons. Overall visibility was highest in Umfolozi and in Hluhluwe during the dry season (Table 3.13).

Since visibility is one of the primary factors that contributes towards capture success (Fanshawe & Fitzgibbon, 1993), one would expect an increase in capture success with an increase in visibility such as in Umfolozi and in Hluhluwe during the dry season. This was, however, not observed. On average, the observed capture success was lower in the dry season (35%,  $n=14$ ) than in the wet season (46%,  $n=26$ ). One would also expect visibility to be correlated with food availability. The encounter rates of prey (which were used as a measure of availability) did, however, not differ significantly seasonally ( $\chi^2=0.02$ ,  $d.f.=7$ ,  $p>0.05$ ).

Table 3.13. Visibility measured, in Hluhluwe (H) and Umfolozi (U), as the average distance in metres from the road to the point in the vegetation where the khaki clad assistant disappeared from view. The number of observations are given in brackets.

VEGETATION	WET SEASON		DRY SEASON	
	H (n)	U (n)	H (n)	U (n)
Forest	7.53 (49)	-	11.27 (26)	-
Open Woodland	42.44 (18)	87.20 (23)	37.47 (15)	78.70 (23)
Closed Woodland	7.07 (55)	19.00 (20)	17.38 (29)	25.75 (70)
Shrubland	7.59 (97)	27.89 (39)	28.85 (39)	16.89 (18)
Grassland	10.91 (11)	44.33 (15)	35.95 (19)	77.67 (15)

## DISCUSSION

Wild dog prey selection in HUP is size selective and dependent on prey availability. As in most other wild dog feeding studies, the HUP wild dog fed on small- to medium-sized ungulates. Juvenile classes of larger ungulates were taken during the dry season only. The large size and herding behaviour of blue wildebeest, kudu and waterbuck apparently make these species formidable prey. During the non-mating season (dry season) of potential prey, however, herd sizes are smaller with fewer males, the social structure is not as rigid (Skinner & Smithers, 1990) and calves are protected to a lesser extent. This may explain the incidences of larger prey species in the diet in the dry season only.

Wild dog are expected to adjust prey selection to ease of capture (Reich, 1981b) and therefore do not 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. Females and juveniles may be preferentially selected since they are arguably easier to capture because they are slower, smaller in size and lack horns which may pose a threat to wild dog. The greater availability and ease of capture of impala lambs during the wet season (lambing season), may explain the high incidence of impala in the diet at this time.

Although the classical diet choice model is limited by its assumptions, it does make for interesting comparisons with the observed diet choice. Wild dog are rate maximisers with respect to the primary prey species (nyala) in the diet but also consume a range of secondary species opportunistically. The diet model takes single foragers into account but wild dog are essentially group foragers. Group size and co-operative hunting, however, do not seem crucial to wild dog foraging. Indeed, single dogs are able to tackle similar sized

prey to those captured by an entire pack (Maddock, 1989b). Although larger prey may be captured with co-operative hunting, group foraging is not essential for wild dog survival. The larger prey species in this study (kudu, blue wildebeest and buffalo) were represented by only one individual in the diet, suggesting that these species and the need for group foraging are not essential for wild dog survival. Wild dog social structure seems to be related to reproductive success and is not primarily food orientated as originally thought (Malcolm & Marten, 1982; Creel & Creel, 1991).

Previous studies have documented a large range in wild dog capture success rates. However, when capture success results from East African studies were pooled, Creel & Creel (1995) found an average value 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 vastly in vegetation type suggest that the lack of visibility in dense habitats does not restrict wild dog capture success. In these habitats, olfactory and auditory senses may be more important in capture success. Wild dog appear to be opportunistic foragers which are able to adapt their foraging technique to the dense vegetation in Hluhluwe where they rely on surprise techniques to flush and ambush their prey, and chases seldom exceed 1 km. Similar results were found by Creel & Creel (1995). The above adaptation is the primary reason for wild dog foraging success in their preferred range and is an important consideration for future wild dog introductions.

Although capture success is not impaired by the dense vegetation in HUP, the coursing hunting technique of the wild dog which allows prior visual assessment of prey condition is not possible. In dense vegetation body condition may not be as important in wild dog prey selection as it is in open habitats. Wild dog in HUP have as much chance of encountering healthy individuals as the sick or weak individuals. One would, therefore,



expect a wide range in prey body condition in the wild dog diet, as found by Reich (1981b) in the Kruger where wild dog preyed on animals in very good or very poor condition. The limited data obtained from this study do not allow definite conclusions to be made.

The order of preference of species in the diet is a function of their profitabilities as predicted by the diet choice model, which species wild dog choose to hunt, and how often they succeed in making a kill. Variables other than prey availability, profitability and capture success, such as prey distribution, predator and prey habitat choice and predator detection and avoidance behaviour by prey, may influence wild dog foraging behaviour (diet choice) and are investigated in subsequent chapters.

## CHAPTER 4

### Ecological Determinants of the Distribution and Home Range Area of the Wild Dog in Hluhluwe-Umfolozi Park.

#### ABSTRACT

This chapter investigates the distribution and home range area of the wild dog in relation to its food resource dispersion, the distribution of other predators and preference for physical habitat features. Several predictions of the Resource Dispersion Hypothesis relating to wild dog home range area, prey density and wild dog pack size are tested. Road transects were used to determine prey dispersion and density, and telemetry locations were used to determine wild dog distribution. The distribution of wild dog was affected by the dispersion of their primary prey species predominately during the dry season, and was independent of predator distribution. Prey dispersion and density estimates did not vary significantly by season. Prey density did not differ significantly between road and line transects but the frequency of prey encountered along the road was higher than along the line transect which suggested that it was more advantageous for wild dog to hunt along the road. Overall, wild dog choice of physical habitat features did not correlate with that of their prey. The difference between wild dog and prey topography (slope) preference accounted for 74% of the variance in habitat choice between wild dog and their prey. Proximity to water and vegetation type preference accounted for 17% and 23% respectively of the variance between

wild dog and prey choice of habitat, with wild dog and nyala being similar in their choice of these variables.

Of the three ecological determinants measured, predator presence was the most important determinant of wild dog home range area and distribution.

## INTRODUCTION

Predator distribution and home range area have been variously attributed to i) their energy requirements (Mace, Harvey & Clutton-Brock, 1982), ii) reproductive status (Frame *et al.*, 1979; Reich, 1981a; Childes, 1988a), iii) habitat productivity or food availability (Harestad & Bunnell, 1979; Kruuk & Parish, 1982; Macdonald, 1983; Fuller *et al.*, 1992), iv) differential visibility and mobility within habitats (Fitzgibbon & Fanshawe, 1989; Creel & Creel, 1995) and v) the presence of other predators (Barnett, 1994). Food, habitat preference and predator presence, as the most important determinants of wild dog home range area and distribution, are investigated in this chapter.

Resource dispersion (the pattern of individuals in relation to one another), particularly that of food, is considered fundamental to the distribution (the arrangement of individuals in an area) of carnivores by limiting group and territory sizes (Macdonald, 1983). The distribution and home range areas of the European badger *Meles meles* (Kruuk & Parish, 1981), red fox (Macdonald, 1981) and arctic fox (Hersteinsson & Macdonald, 1982) have all been found to correlate with the dispersion of their resources. Consequently, Macdonald (1983) proposed the 'Resource Dispersion Hypothesis' which states that the dispersion of food determines territory size and richness limits group size.

The Resource Dispersion Hypothesis predicts that i) the home range area of a

particular predator species should correlate with the dispersion of its prey species, ii) there should be no correlation between home range area and prey density, iii) the group size of that predator species should correlate with prey density and iv) home range area and group size of communally living and hunting species should correlate. The hypothesis forms a good working basis for the structuring of this chapter, and since the predictions could not be tested with the data from only one pack in HUP, the HUP data were combined with that of other authors.

Physical habitat features, for example, vegetation type, water availability, topography and distance to roads affect prey distribution and are therefore expected to indirectly affect wild dog distribution. The above variables are also considered important in wild dog habitat selection as they may affect visibility and mobility in the various vegetation types, and thus the hunting efficiency of the wild dog.

Predator interactions are known to shape patterns of habitat use, resource exploitation and species interactions (Lima *et al.*, 1985; Mills & Biggs, 1993). Several studies have shown that foragers shift habitats in the presence of other predators at the cost of obtaining a low foraging rate. For example, wild dog distribution in the Kruger is a function of predator (lion) avoidance rather than prey density and the availability of suitable habitats as has been suggested above (Reich, 1981a; Maddock, 1988; Barnett, 1994).

Wild dog home range sizes vary between 1500 km<sup>2</sup> in East Africa (Schaller, 1972; Frame & Frame, 1976; Frame *et al.*, 1979) and 450 km<sup>2</sup> in southern Africa (Reich, 1981a; Fuller *et al.*, 1992; Davies, *unpubl. thesis*). By invoking the Resource Dispersion Hypothesis, the large East African home range sizes may be attributed to i) scarce seasonal prey, ii) open habitats and iii) the presence of no or few other packs to restrict their movement (Fanshawe, 1989). In southern Africa, the smaller home ranges may be attributed

to high, stable prey densities and the dense vegetation (Fuller *et al.*, 1992). Although HUP is smaller in size and the overall vegetation is denser than in other southern African reserves, one would expect wild dog home range areas to be smaller in HUP than elsewhere. This may not be the case because there is an absence of conspecifics and a low density of predators and competitors (lion, hyaena) in HUP.

The above mentioned ecological determinants are investigated in this study to determine their effect on wild dog distribution and home range area in HUP. The information gained will provide insight to the requirements of wild dog within the Park, the knowledge of which is important for their conservation. The following questions are examined: i) Do prey dispersion and density affect wild dog home range area and distribution? ii) Are the physical features of the wild dogs preferred habitat similar to those of their primary prey? and iii) Is wild dog distribution affected by that of other predators and competitors, namely lion and hyaena?

## **METHODS**

### **Prey Dispersion**

The road strip count method, a modified strip transect sampling method (Burnham, Anderson & Loake, 1980), was used to determine prey species dispersion, density and frequency of encounter during 1994. Road strip counts, referred to as road transects, are advantageous in that they are practical, have the potential to increase the chance of locating prey species in situations where visibility is restricted, and give consistent results in small- to medium-sized areas (<600 km<sup>2</sup>) where the animals are tame to vehicles (Norton-Griffiths, 1972). Road transects are disadvantageous in that the road system is unlikely to be representative of

the area and roads are usually built in good game viewing areas. Road transects were, however, considered the best method to use as a surrogate measure of wild dog hunting along the road. Because of the density of the vegetation in HUP, transect width was adjusted according to the visibility in the various habitat types.

Sampling of ungulate species in Hluhluwe covered all tourist roads (intensively sampled) and a management track (occasionally sampled) (four main routes totalling 127 km) (Figure 4.1). Road transects were conducted from April 1994 to November 1994 inclusive, during which 16 censuses for both the wet and dry seasons were completed. Routes were driven at wild dog trotting speed (approximately 15-20 km/h; Estes & Goddard, 1967) on a motorcycle by one observer only, to eliminate observer bias. The sequence and direction in which transects were conducted were rotated in order to eliminate any effect of time of day on transect data.

Transects were conducted during the early morning and the late afternoon, the primary hunting times of wild dog. Wild dog seldom hunt during midday, and only hunt at night when there is a full moon (Fuller & Kat, 1990). A limited number of transects were conducted at midday (n=10), and night transects (n=10) were undertaken in conjunction with the tourist night drives conducted in Hluhluwe.

Each prey sighting was plotted on a 500 m x 500 m grid on a 1:50 000 map of HUP. Each 500 m x 500 m grid cell was given a unique identification. Locations of wild dog when moving and hunting were similarly plotted.

To determine whether wild dog distribution was correlated with prey dispersion, I used vegetation type, of which each type was covered by the road transects, as a resource patch determinant (Macdonald, 1983; Geffen *et al.*, 1992). For this purpose the dominant vegetation type in each 500 m x 500 m grid cell was used.

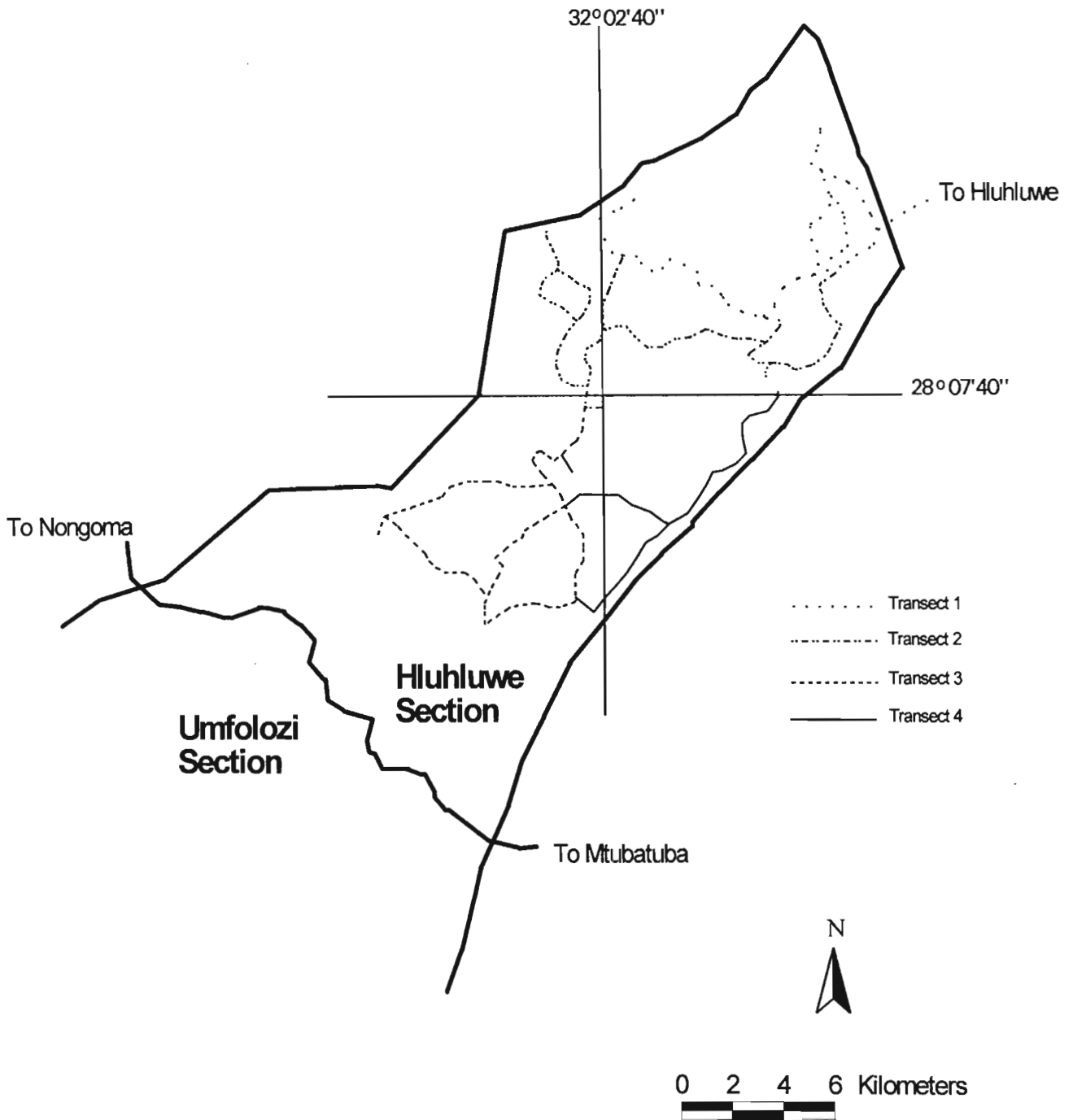


Figure 4.1. The location of the four road transects conducted in Hluhluwe-Umfolozi Park.

The chi-squared test of association of two species was used to determine i) whether wild dog and their primary prey (nyala and impala) were associated in each of the four vegetation types during the wet and dry season, ii) the degree or strength of the association between wild dog and their prey and iii) whether prey dispersion differed seasonally. Since road transects limited prey sightings to observer sighting ability in each grid cell, only those cells where potential prey and wild dog sightings were possible, were used in the analysis. Since prey distribution data were collected during road transects only, and wild dog distribution data were collected from sightings and telemetry locations, only those telemetry locations within 1 km of the road were used in the analysis to avoid bias.

If the home range area of the wild dog is such that it contains prey-rich habitats scattered in areas of barren habitats, then the use of vegetation type to define resource availability assumes that the dispersion of prey is clumped (von Schantz, 1984). To verify this assumption, the frequency of occurrence of prey species in each grid cell along the road was calculated and the distribution fitted to uniform, poisson and negative binomial distributions using the Kolmogorov-Smirnov test.

### **Prey Density**

Prey density estimates were obtained from road transect data using the programme DISTANCE (Buckland *et al.*, 1993). Data were right truncated by 15% for use in the programme. Truncation restricts the mean cluster (herd) size calculation to those calculations that are relatively unaffected by size bias. A value of 15% ensures that the bias in the estimated probability of detection is small (Buckland *et al.*, 1993). The uniform cosine model, which proved to be the best fit model from preliminary runs, was used to estimate



density and abundance.

Density estimates from road transects were compared to similarly calculated estimates from Natal Parks Board line transects. The latter were conducted in conjunction with the road transects in Hluhluwe and Umfolozi during September and October 1994. This allowed for a comparison of subjective indices of prey density.

Results from chapter 3 suggested that wild dog spent a large proportion of their time foraging along the road. Prey encounter rates obtained from road and line transects were compared (provided similar prey densities were obtained from both methods) to determine whether foraging along the road was the optimal strategy in HUP as opposed to randomly through the bush (represented by the line transect). Prey encounter rates were estimated by calculating the number of prey encountered per hour (as for chapter 3) for both the line and road transects, taking into account the kilometres per hour travelled, using the following equation:

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

Wild dog speed was estimated at 20 km/h while searching for prey along the road (see earlier) and at 10 km/h along the line transect. This is because dense vegetation hampers movement through the bush and wild dog constantly need to stand on their hind legs to improve their visibility while searching for prey.

### ***Testing the Resource Dispersion Hypothesis***

Prey density (per 1 km<sup>2</sup>), wild dog home range area (km<sup>2</sup>) and pack size (average) data were obtained for Kenya (Fuller & Kat, 1990), Tanzania (Frame & Frame, 1976; Frame *et al.*,

1979), northern Botswana (J. McNutt, *unpubl. data*), HUP (G. Andreka, *pers. comm.*), the Kruger (A. Maddock & M. Mills, *unpubl. data*) and Hwange (J. Ginsberg, *unpubl. data*), from Fuller *et al.* (1992). These values were averaged and home range area, prey density and pack size were correlated using Spearman's rank correlation coefficients.

### Physical Habitat Features

Transect entries included various physical habitat features for each prey sighting; vegetation type, distance to a permanent water source, topography and aspect. Similar variables were recorded when wild dog were located while moving or hunting.

A log-linear analysis was used to determine i) the effects of the various habitat variables on wild dog and prey habitat choice, ii) whether there was a correlation between wild dog and prey choice of habitat and iii) any interactions among the habitat variables. The analysis was limited in the number of variables, and the division within each variable, that could be used. The distance to a permanent water source (either <1 km or >1 km from water), topography (either flat slopes, <20°, or medium to steep slopes, >20°) and vegetation type were considered the most important variables determining wild dog and prey habitat choice, for use in the analysis.

The physical features of the habitat were used as the independent variables. Their individual effect on the dependent variable (wild dog and prey species) was tested by constructing a baseline model. Forward selection was used to derive a model of best fit. The fit of the model was tested using odds and maximum likelihood methods to compare observed with expected frequencies (Knoke & Burke, 1980). The larger the likelihood ratios ( $L^2$  values) relative to the available degrees of freedom, the more the expected frequencies

deviate from the actual cell entries, and the greater the power of the model's fit (accept model as best fit where  $p > 0.05$ ). To determine the degree to which each of the independent variables affected the baseline model the analogue of the coefficient of variation ( $R^2$ ), expressed as a percentage, was used;

$$R^2 = \frac{(L^2 \text{ baseline model}) - (L^2 \text{ alternative model})}{(L^2 \text{ baseline model})}$$

where the alternative model is that which tests the effect of an independent variable in each case (Knoke & Burke, 1980).

### **Predator and Competitor Distribution**

Game Guard sightings, during daily patrols, of potential predators of wild dog (lion) were recorded and plotted on the 500 m x 500 m grid. The presence of potential competitors (hyaena) was recorded at each observed wild dog kill.

## **RESULTS**

### **Prey Dispersion**

Transect 1 was conducted during the early morning (am), late afternoon (pm), at midday and at night, during the wet season. There was no significant difference in the number of prey sighted between the early morning and late afternoon ( $F_{1,29}=0.09$ ,  $p > 0.05$ ), therefore these were pooled for comparison with midday and night transects. The number of prey sighted was significantly greater ( $\chi^2=29.38$ ,  $d.f.=18$ ,  $p < 0.05$ ) during the early morning and late afternoon ( $16.18 \pm 1.61$ ) than at midday ( $8.27 \pm 0.75$ ) and at night ( $6.18 \pm 0.69$ ). This

coincides with the primary hunting times of wild dog and transects conducted at these times were used for all further analyses.

Wild dog ranged primarily in the northern part of Hluhluwe (covered by Transect 1 & 2), only making short occasional forays to the south (covered by Transect 3 & 4) (G. Andreka, *pers. comm.*). The number of prey sighted per kilometre did not differ significantly between the north and south (two-sample t-test:  $0.22 \pm 0.08$ ;  $t=2.53$ ,  $p > 0.05$ ).

The method of only considering wild dog locations within 1 km from the road when calculating the association of wild dog with their primary prey species was justified because only a small proportion (11.31%,  $n=327$ ) of wild dog locations were more than 1 km from the road, the majority of which were situated in forests (67.57%,  $n=37$ ) of which road transects only covered 6 km.

The test of association between species indicated that wild dog and nyala associated in woodland during the dry season ( $\chi^2=11.25$ ,  $d.f.=1$ ,  $p < 0.05$ ) and grassland during the wet season ( $\chi^2=7.53$ ,  $d.f.=1$ ,  $p < 0.05$ ) (Figure 4.2). Wild dog and impala associated in forest ( $\chi^2=5.63$ ,  $d.f.=1$ ,  $p < 0.05$ ), woodland ( $\chi^2=4.39$ ,  $d.f.=1$ ,  $p < 0.05$ ) and grassland ( $\chi^2=15.25$ ,  $d.f.=1$ ,  $p < 0.05$ ) during the dry season only (Figure 4.3). Wild dog and nyala were associated more often than expected in woodland during the dry season (positive association) and less often than expected in grassland during the wet season (negative association). Wild dog and impala were associated less often than expected in forest (negative association), more often than expected in woodland (positive association) and as expected in grassland.

The association of wild dog and nyala differed significantly seasonally in forest ( $\chi^2=11.13$ ,  $d.f.=3$ ,  $p < 0.05$ ) and woodland ( $\chi^2=9.97$ ,  $d.f.=3$ ,  $p < 0.05$ ) (Figure 4.2). The association of wild dog and impala differed significantly seasonally in forest ( $\chi^2=12.54$ ,

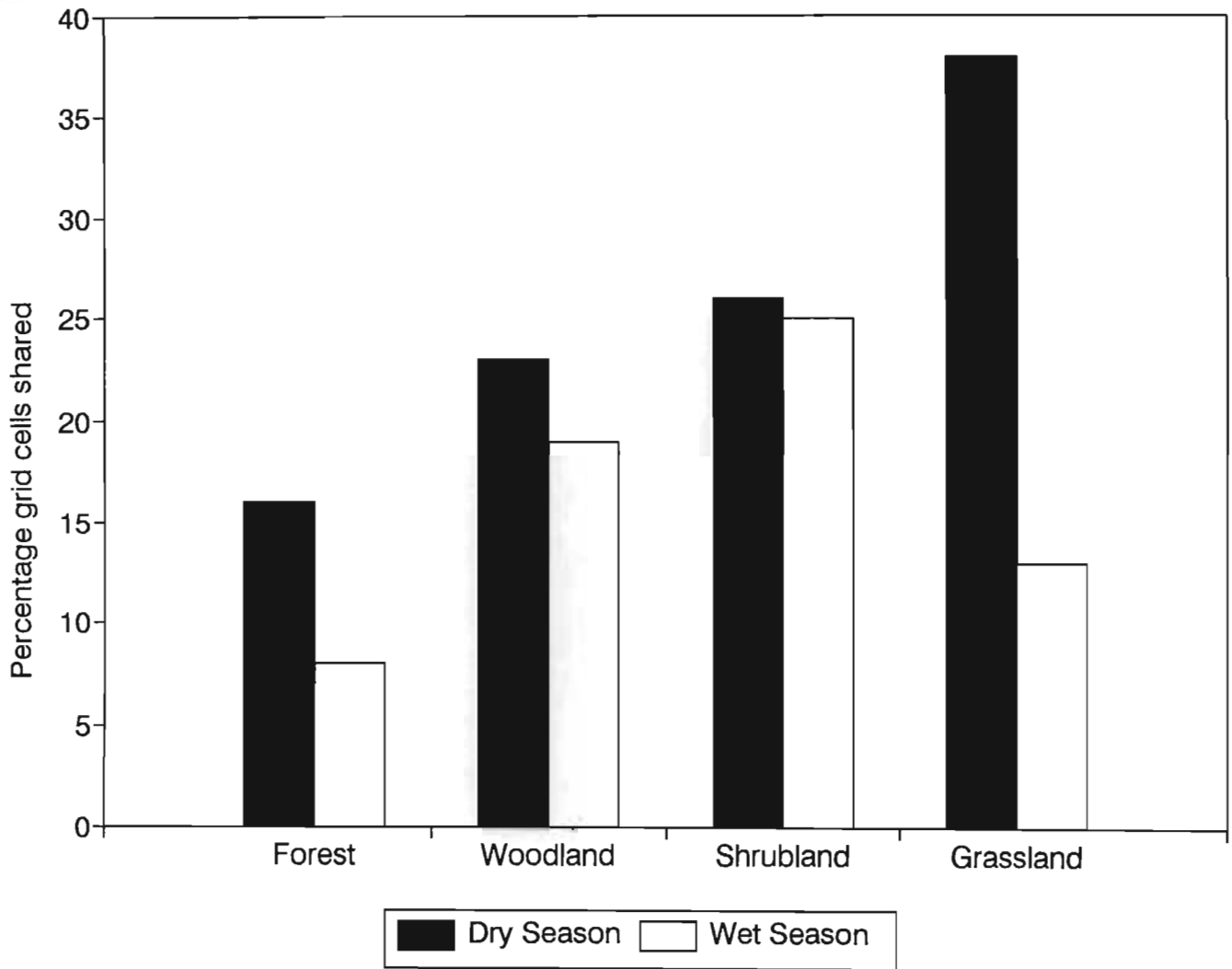


Figure 4.2. The percentage of grid cells shared by wild dog and nyala in each of the four vegetation types during the dry and wet season.

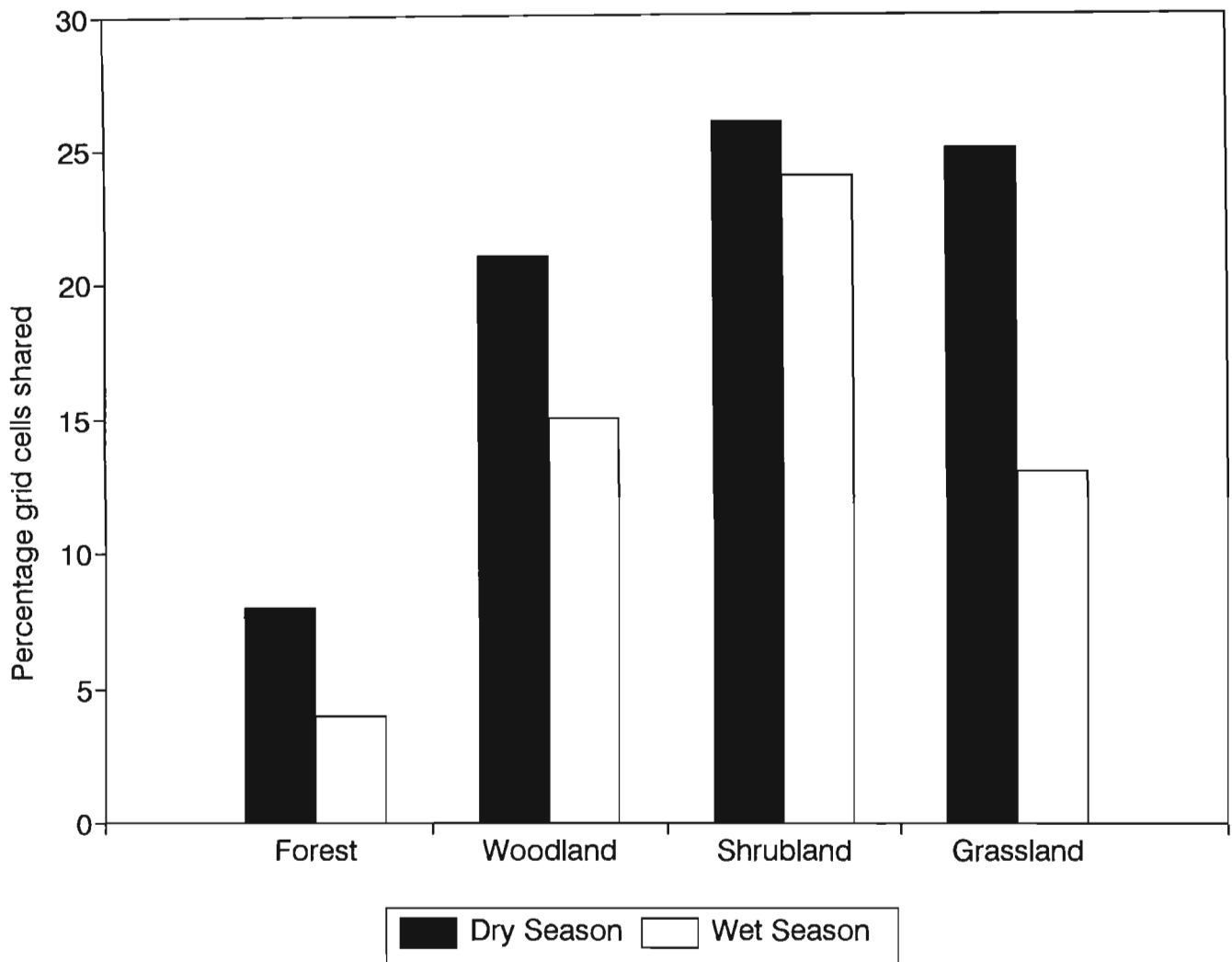


Figure 4.3. The percentage of grid cells shared by wild dog and impala in each of the four vegetation types during the dry and wet season.

$d.f. = 3, p < 0.05$ ) (Figure 4.3). The small number of grid cells occupied by grassland in HUP ( $n=8$ ) did not allow for seasonal associations in grassland to be compared or interpreted.

The use of vegetation type, as a resource patch determinant, involved making the assumption that the dispersion of prey along the road was clumped. This assumption was met since the dispersion of prey was found to be clumped during both the dry ( $D_{33,260}=0.29, p=0.09$ ) and wet ( $D_{20,256}=0.33, p=0.15$ ) seasons. This clumped dispersion is expected since the primary prey of wild dog are social. The clumps or herds of prey are dispersed uniformly along the roads (chapter 3).

### Prey Density

Prey density estimates obtained from road transects were limited by small sample sizes ( $< 30$  sightings per species per season) to those of impala ( $n=326$ ) and nyala ( $n=444$ ). There were no significant seasonal differences in the prey densities obtained from road transects (one-sample t-test:  $43.58 \pm 19.28; t=0.89, p > 0.05$ ). Similarly the number of prey species sighted did not differ significantly between seasons for all road transects ( $F_{1,79}=0.005, p > 0.05$ ).

Only density estimates of nyala, impala, blue wildebeest and waterbuck were compared between road and line transects because small sample sizes of other species resulted in high CV values. There were no significant differences between the prey density estimates obtained from road and line transects (two-sample t-test:  $0.76 \pm 0.22; t=1.01, p > 0.05$ ). Similarly no significant difference was observed between prey density estimates obtained from line transects in Hluhluwe and Umfolozi (two-sample t-test:  $0.46 \pm 0.17; t=0.53, p > 0.05$ ).

The frequency of encounter was greater along the road (1.54 prey/h,  $0.48 < p < 2.61$ ) than along the line transects (1.21 prey/h,  $1.10 < p < 1.34$ ). Wild dog are able to cover more ground at a faster pace when foraging along the roads.

***Prey Dispersion and Density and Wild Dog Home Range Area and Pack Size: Testing the Resource Dispersion Hypothesis***

Wild dog distribution was affected by prey dispersion primarily during the dry season. It was, however, not possible to correlate home range area and prey dispersion because the data were limited to that of one pack only in HUP.

Although wild dog home range area increased with prey density and pack size and pack size increased with prey density, wild dog home range area did not correlate with prey density ( $r_s=0.58$ ,  $d.f.=4$ ,  $p > 0.05$ ) or wild dog pack size ( $r_s=0.09$ ,  $d.f.=4$ ,  $p > 0.05$ ) and wild dog pack size did not correlate with prey density ( $r_s=0.54$ ,  $d.f.=4$ ,  $p > 0.05$ ). It would therefore seem that i) wild dog home range area did not correlate with pack size and ii) pack size did not correlate with prey density, in contrast to the predictions of the Resource Dispersion Hypothesis, and iii) wild dog home range area did not correlate with prey density, in accordance with the prediction of the Resource Dispersion Hypothesis.

Although prey density estimates in HUP (line transects) were similar to those obtained for the primary prey species of wild dog in other study areas in southern Africa, and predator densities were lower, wild dog home range area was constant (G. Andreka, *pers. comm.*) and much smaller in HUP than in the Kruger and Hwange (Table 4.1). The predator and prey density data in Table 4.1 were taken from Natal Parks Board records for HUP and Fuller *et al.* (1992); a paper which includes unpublished data from J. Ginsberg (Hwange), and A.



Maddock and M. Mills (Kruger). Extrapolations of home range area from the pack sizes in the Kruger and Hwange, indicate that the home range area for the population of 10 to 13 dogs in HUP could be expected to range between 305 km<sup>2</sup> and 416 km<sup>2</sup>.

Table 4.1. Home range area (HRA), predator and prey densities and wild dog pack size for three southern African wild dog populations (HUP, 1994; Hwange, 1990; the Kruger, 1990).

LOCATION	HRA (KM <sup>2</sup> )	LION/ 100 KM <sup>2</sup>	PREY/ 1 KM <sup>2</sup>	DOGS/ 1000 KM <sup>2</sup>
Kruger National Park (1990)	545	5-15	9	17 (n=4 packs)
Hwange National Park (1990)	423	5-20	10	18 (n=4 packs)
Hluhluwe-Umfolozi Park (1994)	242	6	10	13 (n=1 pack)

### Habitat Variables in relation to Wild Dog and Prey Distribution

The log-linear analysis revealed a significant difference between wild dog and prey choice of physical habitat features ( $L^2=970.37$ ,  $d.f. = 15$ ,  $p < 0.05$ ).

The best fit model describing differences between predator and prey habitat choice was a saturated model which fitted the data perfectly but used all the degrees of freedom ( $L^2=0$ ,  $d.f. = 15$ ,  $p > 0.05$ ). Alternative models considering interactions between i) topography and vegetation, ii) topography and water, and iii) vegetation and water accounted for 43.26%, 80.28% and 87.97% respectively, of the baseline model variation. Although no percentage is large enough to suggest that any one of the three alternate models accounts for the complete pattern of observed frequencies, the full set of variables accounts for 99.09% of the variance. First order interactions identify topography ( $R^2=73.92\%$ ) as the most important variable accounting for the variation in the baseline model and thereby

the differences in habitat choice between predator and prey, vegetation ( $R^2=23.07\%$ ) as the second most and water ( $R^2=16.79\%$ ) as the third most.

Wild dog spent a greater relative percentage of time on medium to steep slopes (55%) whereas nyala and impala spent a greater relative percentage of their time on flat slopes (96% and 97% respectively) which accounts for the variance in wild dog and prey choice of topography. Distance to water accounted for very little of the variance in habitat choice between wild dog and their prey ( $R^2=16.79\%$ ), suggesting that wild dog and prey distance to water was similar. Wild dog, nyala and impala spent a relatively large percentage of time (79%, 75% and 56% respectively) less than 1 km from water.

Wild dog, nyala and impala spent a relatively large percentage of time in woodland (39%, 58% and 71% respectively), which explains the positive association (see earlier) between wild dog and their prey in woodland during the dry season. Wild dog, nyala and impala spent a relatively small percentage of their time in forest (29%, 11% and 1% respectively), which explains the negative association (see earlier) between wild dog and their prey in forest during the dry season. The difference between ranked vegetation use and availability, Johnson's (1980) rank preference index, determined that wild dog choice of vegetation type correlated with the observed vegetation type choice of nyala but not impala (Table 4.2).

Table 4.2. The vegetation types in Hluhluwe ranked in order of preference for wild dog, nyala and impala using the rank preference index (Johnson, 1980).

VEGETATION	WILD DOG	NYALA	IMPALA
Forest	1	1	4
Woodland	2	2	2
Shrubland	3	3	3
Grassland	4	4	1

## Predator and Competitor presence

The overall association of wild dog and lion was independent ( $\chi^2=23.56$ ,  $d.f.=3$ ,  $p>0.05$ ) since a large proportion (64.10%) of the total lion sightings ( $n=39$ ) were in Umfolozi. Of the lion sighted in Hluhluwe, 57.14% ( $n=8$ ) were sighted in southern Hluhluwe. Hyaena were observed at less than 10% of all kills ( $n=17$ ). Where hyaena and wild dog were observed together ( $n=3$ ), wild dog were able to chase hyaena away, suggesting that this species poses little threat to wild dog in Hluhluwe.

## DISCUSSION

Road transects are arguably a reasonable measure of wild dog prey encounter rates when hunting along a road. From the results of this study, wild dog are predicted to do better when hunting along the road than through the dense vegetation. Apart from increased visibility and ease of mobility, prey were encountered at a higher rate along the road. This would explain the high percentage of wild dog observations within 5 m of the road (chapter 3). The finding, that clumps of prey were encountered in a uniform manner along the road, makes this a reliable foraging mode for the wild dog and strengthens the argument that wild dog deliberately use the road when hunting.

The results from this study did not seem to support two of the predictions tested for the Resource Dispersion Hypothesis, that wild dog home range area should correlate with pack size and pack size should correlate with prey density. Similarly, a study on the Hwange wild dog population did not support any of the predictions of the Resource Dispersion Hypothesis (Davies, *unpubl. thesis*). An alternative to the Resource Dispersion Hypothesis,

which may account for the home range area determined in this study, is the Constant Territory Size Hypothesis (von Schantz, 1984). This hypothesis proposes a constant home range area despite fluctuations in resources (von Schantz, 1984). Home range area is determined by the animals' long-term requirements and is sufficient for the worst periods. The Constant Territory Size Hypothesis can thus apply in relatively homogenous environments since it does not address the effect of the dispersion of food resources on home range area but focuses on the total abundance of food during the worst periods in contrast to the Resource Dispersion Hypothesis.

Although overall wild dog habitat choice differed from that of their prey, wild dog distance to water and vegetation type preference was similar to that of nyala. Wild dog and prey distributions resulted in their association in forest and woodland during the dry season. Wild dog distribution seemed to be affected by the clumped distribution of their prey and wild dog probably associated with their prey in forests and woodland because these are the sites of river courses and moisture and, as a result, the greater availability of suitable grazing for prey and cover for both wild dog and their prey than is available elsewhere during the dry season.

I suggest that the wild dogs' avoidance of potential predators played an important role in influencing their distribution. Although prey density in Umfolozi was similar to that in Hluhluwe, and the number of prey sighted per hour did not differ between northern and southern Hluhluwe, wild dog preferred northern Hluhluwe. I suggest that wild dog avoided Umfolozi and southern Hluhluwe primarily because of the greater presence of lion in these areas. In their preferred range, ie. northern Hluhluwe, wild dog preferred dense vegetation, particularly forest, where ambushes and short chases may limit the chance of detection by lion and hyaena. In these habitats, for example in the Kruger and Hwange, hyaena were

present at very few wild dog kills (10% and <10% respectively; Mills & Biggs, 1993, Davies, *unpubl. thesis*). By comparison, East African studies where dogs forage in the open have determined hyaena presence at 85% of the wild dog kills (Fanshawe & Fitzgibbon, 1993).

Although predators influenced wild dog distribution they did not influence wild dog home range area which was small in HUP in comparison with the Kruger and Hwange, even though predator densities were low. The hunting methods adopted by wild dog (discussed in chapter 3) result in different movement patterns since the average chase in a closed habitat lasts less than 1 km (Creel & Creel, 1995). This is particularly so in HUP where the small home range areas may be influenced by the higher percentage of, and wild dog preference for, dense vegetation. In contrast to the Kruger and Hwange, HUP is small in size (960 km<sup>2</sup>) and wild dog movement outside HUP may be restricted by the electrified boundary fence, possibly forcing them to use a smaller home range area.

Wild dog are seasonal breeders with the denning period lasting approximately three winter (dry season) months (Kühme, 1965; Schaller, 1972; Reich, 1981a). During this period, wild dog are restricted to sites near the den and their home ranges shrink considerably to approximately 10% of their normal range (the Kruger: 50-170 km<sup>2</sup>, Reich, 1981a; Hwange: 147 km<sup>2</sup>, Davies, *unpubl. thesis*.; Serengeti: 100-200 km<sup>2</sup>, Kühme, 1965; Schaller, 1972). No denning was observed during the study period and wild dog home range area remained constant. Further study could be implemented to examine seasonal changes in home range area when there is a denning period, and associated changes in prey dispersion.

## CHAPTER 5

### Vigilance Behaviour of the Primary Prey Species of Wild Dog

#### ABSTRACT

The vigilance behaviour of the primary prey species (nyala and impala) of wild dog was measured in HUP and the Kruger. Prey vigilance differed significantly between reserves and was inversely correlated with predator (wild dog and lion) density. Prey vigilance was not correlated with herd size. Only herd composition significantly influenced prey vigilance behaviour with conspecific herds exhibiting higher scan rates than heterospecific herds. The proximity of wild dog did not result in significant differences in prey vigilance. Nyala were more vigilant than impala and spent significantly more time scanning. There was no evidence to suggest that the wild dogs' habitat (dense vegetation), range (northern Hluhluwe) and prey (nyala) preference was influenced by the susceptibility of prey to predation.

#### INTRODUCTION

The primary purpose of antelope vigilance (scanning) behaviour is that of predator detection (Pulliam, 1973). Since ungulate scanning behaviour influences the probability of detecting predators, one would expect vigilance to differ between areas differing in predator densities (Lima, 1987). In HUP lion and wild dog are the primary predators of nyala (taking 27% and

22% respectively; n=84), and lion, wild dog and leopard are the primary predators of impala (taking 17%, 11% and 16% respectively; n=101) (Natal Parks Board records). Since leopard take few nyala (7%) and their densities are unknown, and hyaena take few impala and nyala (1% and 3% respectively), these predators were not considered further. The density of lion and wild dog in HUP is lower than in the Kruger. However, Hluhluwe differs from Umfolozi in that, generally, wild dog are present\* and lion are absent. Both predators are present and sympatric in the Kruger. Prey vigilance behaviour was examined in these three reserves to determine whether vigilance increases, and thus the susceptibility of prey to predation decreases, with the risk of predation.

Prey vigilance is influenced by many factors associated with the risk of predation. These include i) herd size (Elgar & Catterall, 1981; Sullivan, 1984), ii) herd composition and type (Fitzgibbon, 1990), iii) vegetation type (Underwood, 1982), iv) the proximity to cover (Barnard, 1980; Holmes, 1984), v) position within the herd (Jennings & Evans, 1980), vi) presence of predators nearby (Caracao, Martindale & Pulliam, 1980) and vii) the individual's age and sex (Holmes, 1984; Elgar, 1989). On the other hand, prey species reduce their risk of predation through increased predator detection by i) forming large, heterospecific herds, ii) foraging near the centre of the herd and close to their nearest neighbour and iii) increasing their vigilance in dense vegetation and when close to cover. The importance of several of these variables, in influencing prey vigilance behaviour in Hluhluwe, was examined.

Although prey vigilance is primarily anti-predatory, it is also influenced by several factors associated with feeding, such as forage quality or trophic level (Underwood, 1982).

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\* Wild dog were observed in Umfolozi after the study period, during 1995 and 1996.

Selectively feeding ungulates decrease their opportunity to scan for predators (Illius & Fitzgibbon, 1994). The proportion of time that nyala and impala spend feeding and vigilant may differ as a result of forage quality differences in their preferred habitats and their selectivity whilst feeding. Wild dog preyed primarily on nyala and impala in HUP (chapter 3) and their overall preference for nyala has been attributed to the nyala's abundance, and preference for dense vegetation also favoured by the wild dog. In this chapter I examine the possibility that nyala feed more selectively and therefore spend more time feeding than impala thereby reducing their vigilance levels and rendering them more susceptible to predation by wild dog.

The objectives of this study are thus i) to identify the variables that significantly influence prey vigilance in Hluhluwe, ii) to compare prey vigilance behaviour in areas of different predator densities and iii) to compare nyala and impala vigilance behaviour in Hluhluwe.

## **METHODS**

### **Prey Vigilance**

Herds of feeding and undisturbed nyala and impala were randomly selected, and observed from 50 m to 200 m from a motor vehicle. Individuals were considered part of a herd if within 50 m of another individual (Siegfried, 1980). Samples were collected when most of the individuals in the herd were visible and at least half of the individuals were feeding and/or vigilant (Alados, 1985). For all objectives, data were collected on foraging adult females because they exhibit less variation than foraging males (Berger, 1978; Reisenhofer & Bailey, 1985) and because herds usually contained only one adult male. Only one



individual was sampled per herd. Sample sessions had an average duration of five minutes. Long sampling sessions (>5 min) tended to be interrupted by the subjects moving out of sight. The time spent on any non-feeding behaviour (standing, vigilance, moving, grooming or social interaction) was recorded during the sample session. Once the individual started any major activities, such as ruminating or sleeping, the session was terminated. Samples where animals were startled by the observer or other motor vehicles, were disregarded. The number of scans per minute (scan rate) and the proportion of time spent scanning (scan duration) were recorded.

The probability of predator detection depends on the scanning rate in relation to the attack mode and duration of the attack by the predator (Lendrem, 1986). Frequent scans aid in the detection of predators, such as wild dog, whose attacks are randomly timed. Individuals with high scan rate and duration have a high probability of detecting predators. Since the probability of predator detection depends on prey scan rate, this variable was predominantly used for comparisons throughout the analyses. The proportion of time spent feeding and vigilant was compared for nyala and impala to determine whether either had a higher probability of detecting predators, thus making them less susceptible to predation.

Impala herds are frequently encountered (chapters 3 & 4), conspicuous, form discrete herds and are less excitable than nyala. This makes them ideal subjects for vigilance comparisons between and within reserves. During sampling sessions, vigilance was recorded as head up behaviour (above grass level) and overt scanning behaviour. Other recorded variables included; i) overall herd size, ii) herd type (conspecific or heterospecific), iii) herd composition (age and sex structure), iv) season, v) location (northern or southern Hluhluwe), vi) vegetation type (grassland, shrubland and woodland), vii) the position of the individual within the herd (either near the centre of the herd surrounded by other individuals or on the

periphery), viii) the distance of the entire herd to cover (either < 1 km or > 1 km to the nearest dense vegetation serving as cover) and ix) the nearest neighbour distance (measured in body lengths). The variables thought to influence vigilance most namely; location, season, vegetation type, herd type, position within the herd and distance to cover were used as factors in a Model III analysis of variance (ANOVA) with herd size as the covariate. Although the time of day was recorded during sampling sessions, the limited sample size resulted in the exclusion of these data from the analysis.

Scan rate was expected to decrease exponentially with an increase in herd size. An exponential regression equation  $y = \exp(a + bX)$  was fitted to impala scan rates from Hluhluwe, Umfolozi and the Kruger. For unavoidable reasons, data were collected in the Kruger during the dry season only, in Umfolozi during the wet season only, and in Hluhluwe during the wet and dry seasons. To avoid bias, specific herd sizes were chosen on the basis of sample size, for scan rate comparisons between Hluhluwe and the Kruger (dry season) and Hluhluwe and Umfolozi (wet season) using a Model III ANOVA (two-factor analysis).

## RESULTS

### Variables Influencing Prey Vigilance

The Model III ANOVA showed that only one of the factors originally thought to influence vigilance had any significant effect at all (Table 5.1). Heterospecific herds of impala had significantly ( $F_{1,45} = 4.09$ ,  $p < 0.05$ ) higher scan rates ( $1.27 \pm 0.13 \text{ min}^{-1}$ ) than conspecific herds ( $0.97 \pm 0.12 \text{ min}^{-1}$ ).

Table 5.1. The effect of several variables on scan rate ( $1.16 \pm 0.10$  overall) as determined by the model III ANOVA.

MODEL III ANOVA	VARIABLE	F-RATIO	P
Covariate	Group size	$F_{11,45}=2.28$	$p > 0.05$
Main Effects	Location	$F_{1,45}=3.72$	$p > 0.05$
	Vegetation	$F_{2,45}=0.83$	$p > 0.05$
	Position	$F_{1,45}=0.13$	$p > 0.05$
	Distance to Cover	$F_{1,45}=1.64$	$p > 0.05$
	Herd Type	$F_{1,45}=4.09$	$p < 0.05$

### Predator Pressure Between Reserves

There was no significant exponential fit between impala scan rate and herd size in Hluhluwe ( $F_{1,51}=0.09$ ,  $p=0.76$ ), Umfolozi ( $F_{1,67}=2.08$ ,  $p=0.15$ ) and the Kruger ( $F_{1,24}=0.28$ ,  $p=0.39$ ). Vigilance behaviour varied widely and unpredictably across herd sizes within all three reserves (eg. Figure 5.1). Since there was no apparent trend in vigilance behaviour across herd size, herd sizes of 20 and 30 individuals were chosen for comparisons between Hluhluwe and the Kruger, and herd sizes of 25 and 30 individuals were chosen for comparisons between Hluhluwe and Umfolozi. Although not ideal, the choice of large herd sizes was unavoidable (due to the small sample sizes of smaller herd sizes) and bias was assumed to be minimal because scan rates varied widely across herd sizes within reserves.

Since herd type was the only factor found to influence vigilance (see earlier), this variable was controlled for in scan rate comparisons between reserves.

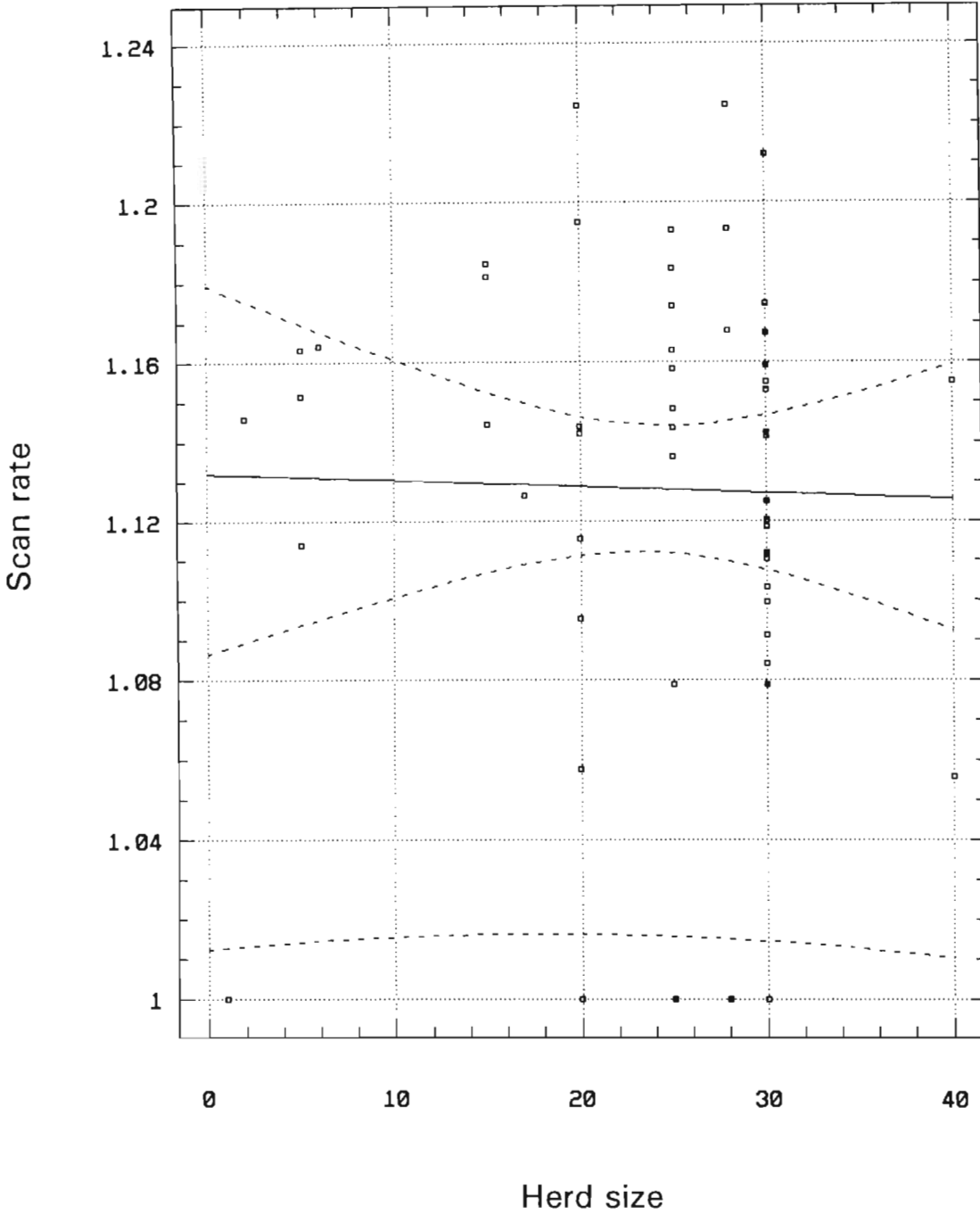


Figure 5.1. The exponential regression of impala scan rate and herd size within Hluhluwe. Similar results were obtained for both Umfolozi and the Kruger.

*Dry Season*

Although impala in Hluhluwe scanned at a higher rate than those in the Kruger, this difference was not significant ( $F_{1,44}=3.07$ ,  $p>0.05$ ). The time spent scanning, however, differed significantly between reserves ( $F_{1,44}=7.35$ ,  $p<0.05$ ) (Table 5.2). Impala in Hluhluwe, where the lowest overall predator densities occur, had significantly higher scan durations than impala in Kruger, where the highest predator densities occur (Table 5.3). Thus, in contrast to expectation, scan durations decreased with an increase in predator density.

Table 5.2. A comparison of scan rates (scan min<sup>-1</sup>) and scan durations (expressed as a proportion) ( $\bar{x}\pm SE$ ) from herds of 20 and 30 impala in Hluhluwe, with those in the Kruger.

<b>VIGILANCE</b>	<b>HERD SIZE</b>	<b>HLUHLUWE</b>	<b>KRUGER</b>
Scan Rate	20	0.90 ± 0.27	0.71 ± 0.15
	30	1.02 ± 0.18	0.63 ± 0.11
Scan Duration	20	0.13 ± 0.04	0.08 ± 0.02
	30	0.19 ± 0.02	0.05 ± 0.01

Table 5.3. A comparison of predator densities in Hluhluwe (Natal Parks Board records) with those in Umfolozi (Natal Parks Board records) and the Kruger (Reich, 1981a).

<b>PREDATOR SPECIES</b>	<b>HLUHLUWE</b>	<b>UMFOLOZI</b>	<b>KRUGER</b>
Wild Dog/100km <sup>2</sup>	1.4	0	2
Lion/100km <sup>2</sup>	0	6	5-15

### *Wet Season*

Impala scan rates differed significantly between Hluhluwe and Umfolozi ( $F_{1,61}=4.29$ ,  $p<0.05$ ). Impala in Hluhluwe had a higher scan rate than in Umfolozi (Table 5.4). Although impala in Hluhluwe spent more time scanning than impala in Umfolozi, this difference was not significant ( $F_{1,61}=1.40$ ,  $p>0.05$ ). Impala in Hluhluwe looked up more often than impala in Umfolozi, but spent the same amount of time scanning overall (Table 5.4).

Table 5.4. A comparison of scan rates (scan  $\text{min}^{-1}$ ) and scan durations (expressed as a proportion) ( $\bar{x}\pm\text{SE}$ ) from herds of 25 and 30 impala in Hluhluwe, with those in Umfolozi.

VIGILANCE	HERD SIZE	HLUHLUWE	UMFOLOZI
Scan Rate	25	1.32 $\pm$ 0.20	0.54 $\pm$ 0.10
	30	1.14 $\pm$ 0.15	0.98 $\pm$ 0.15
Scan Duration	25	0.12 $\pm$ 0.03	0.07 $\pm$ 0.03
	30	0.19 $\pm$ 0.04	0.15 $\pm$ 0.05

### **Predator Pressure Within Reserves**

There was no significant difference in scan duration when wild dog were in the vicinity (within 3 km) during vigilance recordings ( $0.21\pm 0.03$ ;  $D_{6,37}=0.46$ ,  $p>0.05$ ) or had been in the vicinity within the 24 hours prior to recordings of vigilance behaviour ( $0.23\pm 0.03$ ;  $D_{6,28}=0.36$ ,  $p>0.05$ ).

## Prey Vigilance Between Species

Although there was no significant difference between nyala and impala scan rates ( $D_{7,49}=0.29$ ,  $p > 0.05$ ), nyala spent significantly more time scanning than impala ( $D_{7,49}=0.57$ ,  $p < 0.05$ ) (Table 5.5). Nyala and impala did not differ significantly in the amount of time spent feeding ( $0.16 \pm 0.03$ ;  $D_{16,51}=0.26$ ,  $p > 0.05$ ).

Table 5.5. A comparison of scan rates (scan  $\text{min}^{-1}$ ) and scan durations (expressed as a proportion) between impala and nyala.

VIGILANCE	NYALA	IMPALA
Scan rate	$1.41 \pm 0.23$	$1.21 \pm 0.11$
Scan duration	$0.36 \pm 0.05$	$0.21 \pm 0.02$

## DISCUSSION

It is evident from the observed differences in vigilance behaviour in reserves differing in predator density, that prey scanning behaviour may be related to the risk of predation. While a number of studies have found that scanning increases with the risk of predation (eg. Underwood, 1982; Lendrem, 1986; Fitzgibbon, 1988), the opposite was found in this study. The lower vigilance of prey in the reserve with the highest predator densities (Kruger) can be attributed to the more open vegetation in the Kruger, where prey may be able to detect predator approach from a distance, and could thus afford to spend less time scanning.

The attack mode of the dominant predator in a reserve may result in changes in scanning behaviour (Lendrem, 1986). Although prey in Hluhluwe and Umfolozi had similar

scan durations, the higher percentage of dense vegetation (see chapter 4) and the presence of a random attacking predator (wild dog) in Hluhluwe as opposed to a stalking predator (lion) in Umfolozi, may result in prey having to scan more often to increase their chances of predator detection.

Of the various vigilance variables measured, only herd composition influenced prey vigilance behaviour as expected, ie. individuals in heterospecific herds were more vigilant than in conspecific herds. Impala in HUP seem to reduce the risk of predation by associating with other species. Similar results have been found in other studies of African ungulates, such as impala (Underwood, 1982) and Thomson's and Grant's gazelle *Gazella thomsoni* and *G. granti* (Fitzgibbon, 1990). The reduced predation risk arises from an increased herd size and increased corporate vigilance and detection of approaching predators by early warning from heterospecifics within the herd (Thompson & Thompson, 1985). Conspecifics are able to share vigilance with heterospecifics and can devote more time to feeding.

The lack of correlation between herd size and scan rate may be as a result of small sample sizes. Alternatively the data suggests that the primary effect of prey herding behaviour in HUP was not to reduce the level of individual vigilance required to maintain a given probability of predator detection. Similarly Colagross and Cockburn (1993) found that vigilance in the Eastern grey kangaroo *Macropus giganteus* was not affected by herd size. They suggested that kangaroo vigilance behaviour was influenced by the proportion of individuals on the edge of the group rather than simply the number of individuals within the group.

Vision and mobility have been assumed to contribute to predator detection (Goldsmith, 1990). In closed habitats, early detection of predators is more important than in open habitats and several African ungulate species, such as impala, common reedbuck and blue



wildebeest, increase their vigilance as vegetation cover becomes more dense (Underwood, 1982). In this study impala vigilance did not differ between vegetation types. In HUP impala did not frequent forest and their vigilance levels in this vegetation type were therefore not measured. Nyala, however, preferred dense vegetation (see chapters 3 & 4) and had significantly higher vigilance levels (scan duration) by comparison to impala which inhabited more open vegetation. The results suggest that as far as vigilance and the time spent feeding are concerned, nyala are not, as originally believed, more susceptible to wild dog predation. The discussion in chapters 3 and 4, that wild dog preference for nyala is a function of nyala abundance, profitability and preference for dense vegetation, must therefore be accepted.

If prey vigilance levels are used as a predictor of wild dog habitat preference, the non significant differences in prey vigilance behaviour between locations indicate that wild dog do not benefit from frequenting northern Hluhluwe since prey vigilance behaviour did not differ between northern and southern Hluhluwe. Since prey vigilance, prey density and the number of prey sighted did not differ significantly between northern and southern Hluhluwe (chapter 4), I favour the explanation that wild dog predator avoidance is the primary reason for wild dog frequenting northern Hluhluwe.

Prey vigilance recordings in the proximity to wild dog suggests that prey vigilance remains unchanged if the threat of predation is not imminent.

## CHAPTER 6

### Prey Response to Predator Presence as Determined from Playback Experiments

#### ABSTRACT

Field playback experiments were conducted in HUP and the Kruger to determine prey response to predator presence in reserves differing in predator diversity and density. Predator presence was simulated and prey response behaviour and vigilance levels were investigated. The time taken for prey to respond to wild dog, hyaena and lion calls and control stimuli did not differ between reserves. Prey did, however, differ in their response to the different stimuli within each reserve reacting with a stronger response (ie. sooner) to those stimuli unfamiliar to them. Prey responded with flight to more than 50% of the playback recordings of predators while fewer prey individuals responded to the control, suggesting that prey are able to recognise potential predators by their vocalisations. The comparatively slow response of prey to playback recordings of wild dog calls, suggests that the impact of wild dog presence on its preferred prey, is low. Nyala were more alert than impala to playbacks suggesting that nyala may experience greater levels of predation pressure.

## INTRODUCTION

Previous chapters have dealt with the susceptibility of prey species to wild dog predation as measured by prey profitability, abundance, choice of physical habitat features and vigilance behaviour. Here I examine the response of prey to direct predation threats through simulated predator presence by using playback experiments of predator calls.

Several previous studies, particularly those concerned with non-human primates, have shown that vocalisations (either from potential predators or alarm calls from conspecifics) are sufficient to elicit a significant response from prey species (Hauser & Wrangham, 1990; Cheney & Seyfarth, 1988). The primates gain the advantage of being alerted to the presence of a potential predator and respond with anti-predator behaviour. It seems reasonable to assume that ungulate prey may benefit in a similar way.

The above studies show that vocalisations are sufficient to elicit prey response. Since the hunting and killing techniques of wild dog are believed to affect the behaviour and distribution of their prey populations (Reich, 1981a), it follows that although prey vigilance was similar throughout HUP (chapter 5), prey may respond sooner to direct predation threats in parts of their territory where they have been most pursued. Wild dog range primarily in Hluhluwe (chapter 4) where they are among the primary predators of impala and nyala (see earlier). Is prey catchability affected by the presence of wild dog in Hluhluwe and subsequently do wild dog benefit from frequenting this section? The awareness of prey to the presence of wild dog was tested by comparing prey reaction in Hluhluwe to that in Umfolozi, which is frequented by lion and not wild dog, and the Kruger where lion and wild dog densities are higher than those in HUP. All three reserves are frequented by hyaena which occur at higher densities than the other predators (Parks Board records). The results

from prey response to playbacks of various predator calls, in reserves differing in predator diversity and density, will contribute towards determining the impact of predator presence on prey populations and its implications for choosing future introduction sites for wild dog.

Field playback experiments were used to determine i) the mode of prey response (ie. flight or increased vigilance) to examples of potential predator calls, ii) whether prey response is predator specific and iii) whether nyala response behaviour makes them more susceptible to predation by wild dog than impala, thus accounting for the higher percentage of nyala in the wild dog diet.

## **METHODS**

### **Stimuli**

The three most commonly heard wild dog calls include the contact call, the alarm bark and the twittering call. Good descriptions of these calls have been given (see Estes & Goddard, 1967). Imitations of the contact call only resulted in mild reactions from the dogs when the full pack was assembled whereas alarm barks resulted in an immediate startled reaction (Estes & Goddard, 1967). The twittering call is the most characteristic and commonly heard call, the nature of which made it suitable to examine the objectives of this study.

Wild dog vocalisations (n=10) were obtained from video recordings (G. Andreka & myself) of the Hluhluwe pack, recordings of the de Wildt captive bred wild dog pack and the 'Calls of the Bushveld' cassette. Lion and hyaena vocalisations (roaring and whooping/giggling respectively; n=15) were obtained from Natal Parks Board records, and several documentary videos. One call type of several individuals of each stimulus species was used to ensure that samples were independent, thereby avoiding pseudoreplication.

Music (range from 1-5 kHz) and a blank tape, ie. rasping noise (range from 0-1 kHz) (Kroodsma, 1989), were used as the control stimuli.

### **Experimental Design**

Calls were played from speakers attached to the roof of a vehicle using a marantz tape recorder. The speakers were hidden from the subjects' view and observations were made from within the vehicle. The speakers were placed at between 50 m and 100 m from the subject, a range within which all calls were audible.

No playbacks were made within 30 minutes of hearing natural calls of a predator or subject species or within 30 minutes of seeing the predator species. Playbacks ceased as soon as the subject species responded or after approximately one minute. The selection of predator calls was random. Only one experiment was conducted at one site on one particular day and no predator call was played more than once in six days at any location (see Hauser & Wrangham, 1990).

### **Subject Species Response**

Impala were used as subject species because they form conspicuous, distinct and frequently encountered herds. Since herd size was expected to affect the intensity of the response to playback recordings, response time across various herd sizes was measured. Prey species response time to playback recordings was expected to increase exponentially with herd size and this response was modelled using an exponential regression equation  $y = \exp(a + bX)$ .

The behaviour of the subject species was observed before, during and for 30 seconds

immediately after the start of the playback recording. The behavioural variables that were recorded for the herd as a whole were i) the time lapse (s) until the subject species responded to the stimulus (response time) and ii) whether the subject species responded with immediate alertness or flight.

Playback experiments were tested on impala herds in woodland vegetation in Hluhluwe, Umfolozi and the Kruger. These experiments aimed to determine whether prey response differed i) between reserves differing in predator density and diversity and ii) between call types (stimuli) within each reserve. The reserve type and stimulus type were used as factors in the Model III ANOVA (two-factor analysis).

For unavoidable reasons, data were collected in the Kruger during the dry season only, in Umfolozi during the wet season only, and in Hluhluwe during the wet and dry seasons. To avoid bias, a specific herd size was chosen on the basis of sample size, for comparisons of prey response time between Hluhluwe and the Kruger (dry season) and Hluhluwe and Umfolozi (wet season).

Impala vigilance was measured and compared before and after playbacks to examine the magnitude of the effect of predator presence on prey species populations. The proportion of time spent scanning (scan duration) was recorded for impala herds before and at five minute intervals after playback recordings, starting immediately after the playback. Individuals were observed for as long as possible after the playback recording, but at least for 10 minutes. Variations on one call type from one predator species were used on separate herds of approximately 25 individuals to avoid pseudoreplication and to control for herd size and stimuli effects. Vigilance recordings were conducted as described in the methods section of chapter 5.

Response times were compared for the two primary wild dog prey, nyala and impala.

## RESULTS

### Between Reserve and Between Stimuli Comparison

There was no significant exponential fit between impala response time and herd size in Hluhluwe ( $F_{1,18}=1.73$ ,  $p=0.20$ ), Umfolozi ( $F_{1,26}=0.31$ ,  $p=0.59$ ) and the Kruger ( $F_{1,5}=0.01$ ,  $p=0.92$ ). Since response to playbacks varied across herd sizes within in all three reserves, a herd size of 25 was chosen for comparisons of prey response times between reserves, and response to stimuli within reserves. Although perhaps not ideal, the choice of a large herd size was unavoidable.

There was no significant difference in the time taken by impala to respond (with immediate alertness) to music (control 1) and the blank tape (control 2) ( $\chi^2=1.03$ ,  $d.f.=1$ ,  $p>0.05$ ). The data from these two control types were, therefore, combined for further analyses.

### *Dry Season*

Prey response time to stimuli did not differ significantly between reserves ( $F_{1,69}=1.31$ ,  $p>0.05$ ) but differed significantly between stimuli ( $F_{3,69}=5.29$ ,  $p<0.01$ ) (Table 6.1).

Table 6.1. Prey response time to playbacks ( $\bar{x}\pm SE$  s) of various stimuli (predator and control) in Hluhluwe and the Kruger during the dry season.

RESERVE	WILD DOG	HYAENA	LION	CONTROL
Hluhluwe	3.44 $\pm$ 0.67	4.25 $\pm$ 0.22	1.71 $\pm$ 0.26	3.83 $\pm$ 0.80
Kruger	4.78 $\pm$ 0.75	4.10 $\pm$ 0.39	3.10 $\pm$ 0.26	2.40 $\pm$ 0.35

In Hluhluwe, prey responded sooner to unfamiliar predators (lion) than to familiar predators (wild dog). Of the familiar predators, prey responded sooner to wild dog calls than to the control stimulus and predators that posed little threat to them (hyaena). Similarly, prey in the Kruger responded sooner to an unfamiliar stimulus (control) than to familiar stimuli (predator calls). The results suggest that prey respond to novel sounds.

### *Wet Season*

Prey response time to stimuli did not differ significantly between reserves ( $F_{1,63}=0.20$ ,  $p>0.05$ ) but did differ significantly between stimuli ( $F_{3,63}=3.30$ ,  $p<0.05$ ) (Table 6.2).

In Hluhluwe, prey responded sooner to unfamiliar predators (lion) than familiar predators (wild dog). However, in contrast to the dry season, prey responded sooner to calls of predators that posed no threat to them (hyaena). In Umfolozi prey responded sooner to unfamiliar calls, represented by the wild dog and control stimuli, suggesting that their response was a response to novelty.

Table 6.2. Prey response time to playbacks ( $\bar{x}\pm SE$  s) of various stimuli (predator and control) in Hluhluwe and Umfolozi during the wet season.

RESERVE	WILD DOG	HYAENA	LION	CONTROL
Hluhluwe	3.56 $\pm$ 0.24	2.36 $\pm$ 0.23	1.70 $\pm$ 0.26	3.50 $\pm$ 0.32
Umfolozi	2.57 $\pm$ 0.40	3.20 $\pm$ 0.44	3.14 $\pm$ 0.24	3.00 $\pm$ 0.00

Overall (wet and dry season), prey in Hluhluwe responded sooner to lion calls ( $1.712\pm 0.26$  s), ie. unfamiliar predators, and hyaena calls ( $2.87\pm 0.17$  s) than they did to



wild dog calls ( $3.5 \pm 0.19$  s) and the control ( $3.63 \pm 0.39$  s).

These results beg the question: Is prey response to playbacks merely a response to novelty or are prey able to detect the calls of potential predators?

Significantly more prey responded with flight after being subjected to the predator stimuli than the control stimuli in Hluhluwe ( $\chi^2=12.79$ ,  $d.f.=1$ ,  $p<0.01$ ) and Umfolozi ( $\chi^2=5.74$ ,  $d.f.=1$ ,  $p<0.05$ ) but not in the Kruger ( $\chi^2=1.90$ ,  $d.f.=1$ ,  $p>0.05$ ) (Table 6.3). In the Kruger, prey only responded with flight to playback recordings of wild dog calls. It would seem that prey responded to unfamiliar and unusual (hyaena) sounds but were able to distinguish whether the source of the sound posed a potential threat to them.

Table 6.3. The number of samples (expressed as a percentage) where subject species reacted with flight during the playback recordings of various stimuli.

RESERVE	WILD DOG	HYAENA	LION	CONTROL
Hluhluwe	63% n=33	69% n=16	56% n=9	21% n=14
Umfolozi	64% n=11	70% n=10	56% n=9	0% n=4
Kruger	50% n=10	0% n=10	0% n=10	0% n=10

### Prey Vigilance Behaviour

Observations of impala scanning behaviour from herds of 25 individuals, where none of the subjects reacted with flight during playback recordings, were used ( $n=18$ ). After playback recordings, 50% of the subjects reacted with flight during the first 5 minutes, 28% during the first 10 minutes and 11% during the first 15 minutes. Mean pre-playback scan durations were significantly ( $D_{=17,17}=0.53$ ,  $p<0.01$ ) lower ( $0.10 \pm 0.02$ ) than mean scan durations

immediately following predator playbacks ( $0.41 \pm 0.10$ ) and mean scan durations at five, ten and fifteen minutes after playbacks ( $0.11 \pm 0.03$ ;  $0.12 \pm 0.03$ ;  $0.18 \pm 0.03$  respectively). Only four subjects were observed over three time intervals, and two over four time intervals. The vigilance of the four subjects increased immediately after the playbacks (see above), but decreased steadily over the five minute intervals following playbacks (Figure 6.1).

### **Between Species Comparisons**

Nyala, on average, responded significantly ( $D_{9,38} = 0.82$ ,  $p < 0.01$ ) sooner ( $2.00 \pm 0.00$  s) to playbacks of wild dog calls than impala ( $3.47 \pm 0.18$  s).

## **DISCUSSION**

The flight response of prey to predator calls and not to the control stimuli, suggests that prey species perceived potential threats in the form of predator presence, from their calls. Differences in prey response to the various stimuli suggest that response was predator specific. Response towards unfamiliar predators suggests that these stimuli are recognised as potential predator threats or at least as sources of danger. Similar results were obtained by Hauser & Wrangham (1990) in their study on the recognition of predator calls in non-human primates and birds. The immediate increase in vigilance directly after the playback, followed by a steady decline over time indicates that prey cannot afford to ignore the presence of a potential predator, but they relax when the predator threat is not imminent.

By frequenting Hluhluwe (chapter 4) wild dog benefit, not only for those reasons given in previous chapters (eg. low predator presence) but also from the lower levels of prey

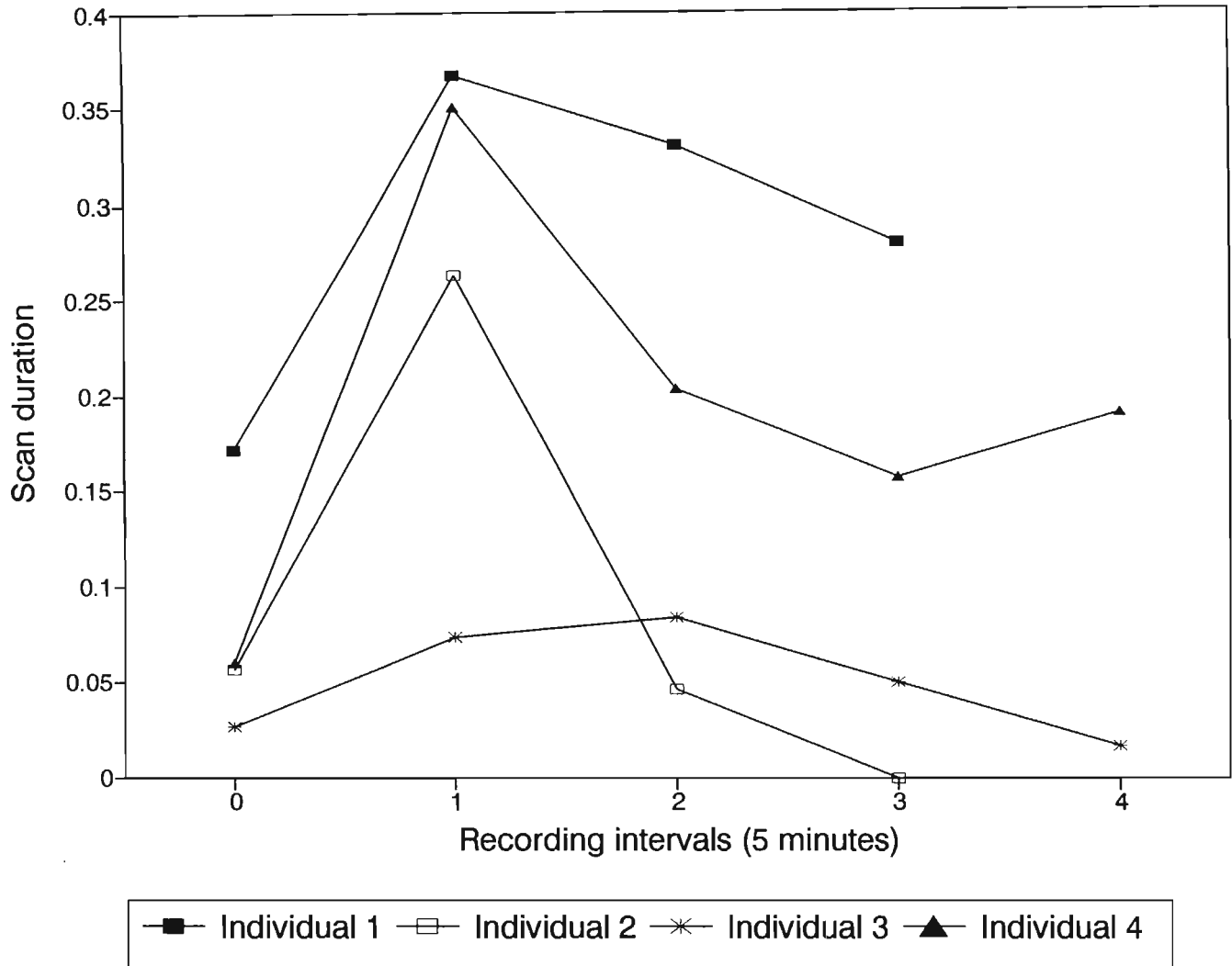


Figure 6.1. The proportion of time spent scanning (scan duration) of four prey individuals from separate herds, before (0), and at 5 min intervals after (1-4) playback recordings of predator calls.

alertness to wild dog presence by comparison to other predators. Prey catchability does not seem to be affected by the presence of wild dog which suggests prey are not notably perturbed by the presence of wild dog. Whether wild dog have a significant quantitative impact on their primary prey species will, however, be examined in the following chapter by means of mathematical models.

Nyala responded sooner to playbacks than impala. This suggests that it is their greater abundance and profitability, smaller herd sizes and choice of dense vegetation which makes them more vulnerable to attack by predators, and thus more alert to predator presence.

Features such as call type, amplitude, length and rate of delivery and the number of individual calls may be expected to provide information on how close the predator is and whether it poses an immediate threat. Further study should, therefore, concentrate on the types of response to information regarding the function of the call.

## CHAPTER 7

### The Impact of the Hluhluwe-Umfolozi Park Wild Dog Population on their Primary Prey Species Populations.

#### ABSTRACT

The potential predatory impact of wild dog on their prey in HUP is a management concern in view of the envisaged introduction of additional wild dog individuals. A stage-structured population model was used to investigate the extent to which wild dog may limit the numbers of their primary prey species. Models of prey population dynamics determined that the introduction of an additional wild dog pack would result in the reduction of the finite rate of increase of nyala and impala populations by 1.8% and 1.4% respectively. The nyala and impala populations had maximum population extinction probabilities of 0.18 and 0.01 respectively over a 100 year period. The results indicate that if an additional wild dog pack were to be introduced into HUP, their predatory impact would be slight. Sensitivity analyses identified nyala adults and impala subadults to be the most sensitive, of all stages, to a 10% reduction in survival rate.

#### INTRODUCTION

A primary aim of the wild dog feeding ecology study was to calculate the impact of the current wild dog population on their primary prey populations, ie. nyala and impala in HUP.

By modelling prey population dynamics, the outcome of management actions can be

simulated and different scenarios can be predicted prior to their implementation. This is important for the management of predators such as wild dog, which because of their high basal metabolic rate relative to their size (Taylor *et al.*, 1971) need to kill at least once a day (Estes & Goddard, 1967; Reich, 1981a; Mills, 1988; Fuller & Kat, 1990; Fuller *et al.*, 1992), and could therefore influence prey numbers, prey sex ratios and the age distribution of prey populations within wild dog home range.

HUP is a closed management system supporting predator populations of lion, hyaena, leopard, cheetah and wild dog. Cheetah reintroductions are currently being undertaken and further wild dog introductions are planned. The potential impact of these predators on prey population numbers in HUP is an important management concern. The determination of the quantitative impacts of wild dog and other predators on their prey species is important for the overall maintenance of stable prey and predator populations within HUP.

The hypothesis that predators do not have a negative impact on their prey populations, ie. they only remove surplus individuals from the population that would have died of other natural causes, is a widely accepted one (Pienaar, 1969; Schaller, 1972; Reich, 1981a). A predator only limits a natural prey population if it eats into the breeding stock (Errington, 1956, 1967). Since wild dog selected adult female nyala and juvenile impala significantly more than expected (chapter 3), it was important to i) determine whether wild dog preference for these particular stages limited the growth and survival of the prey populations and ii) simulate the introduction of additional wild dog and their influence on prey numbers.

Modelling exercises require a knowledge of wild dog density, preferred ungulate prey species, prey population dynamics and densities, and prey age distribution and sex ratios. Using the above information obtained from previous chapters, and published data on prey population dynamics, this chapter aims to determine whether the Natal Parks Board's

intention to introduce additional wild dog individuals is feasible.

## **METHODS**

### **Modelling Prey Population Dynamics**

Stage-structured population models, which model female nyala and impala, were developed using the Ramas Stage modelling software (Ferson, 1994). Stage-structured demographic models used here are matrix models where the elements of the matrix are fixed and represent a variety of demographically significant processes such as maturation, reproduction, survival and mortality.

Nyala and impala age classes were grouped into five categories or stages, namely; calves (0-1 year), juveniles (1-2 years), subadults (2-3 years), adults (3-7 years) and senescent adults (7-9 years).

Nyala population dynamics were modelled using the average fecundity and survival rates determined by Allen-Rowlandson (1986) and Owen-Smith (1990) for bushbuck and kudu respectively. No values were available for nyala, and since bushbuck and kudu belong to the same genus as nyala, and have very similar fecundity and survival rates, the values were considered the most reliable available data. Fecundity and survival values were modelled over one year and the aseasonal breeding pattern of nyala was taken into account. Impala population dynamics were modelled using the fecundity and survival rates determined by Vincent (1979) and Fairall (1985). Vincent's (1979) data were obtained from impala populations in Mkuzi, and Fairall's (1985) data were obtained from impala in the Kruger. The above values were used because they represent the only available data for South African prey populations, they were collected in proximity to HUP and were taken from prey

populations experiencing natural predation by lion, hyaena, cheetah, leopard and wild dog.

The predatory impact of a second wild dog pack was modelled by adjusting stage-specific survival rates according to the percentage of the prey population of a particular stage that was taken by wild dog. Natal Parks Board records determined that wild dog accounted for 10% and 7% of all female nyala and impala mortalities respectively. These percentage values were substituted into the observed age selection of wild dog during the study period and subtracted from the original survival values to simulate predation by two wild dog packs.

The initial population abundances, used in the model, were determined from prey abundance values obtained from Natal Parks Board line transects (2600 female impala and 2400 female nyala). Prey age distributions and sex ratios, used in the model, were obtained from road transects (chapter 3).

Initially, an exponential density-independent growth model was run over 100 years. In order to represent a population growing under limiting conditions, logistic density-dependence was incorporated into the initial model using the following logistic equation:

$$N_{t+1} = N_t(1 + r(1 - N_t/K))$$

The future population size is expressed as a function of the present population size; where  $N$  = population size,  $t$  = time in years,  $r$  = the intrinsic population growth rate and  $K$  = equilibrium population size. While not ideal, the logistic density-dependent equation was one of the few suitable equations offered by the modelling software.

Environmental stochasticity, in the form of rainfall, was then introduced into the logistic density-dependent model. Rainfall was assumed to be a major driving factor influencing the survival of the calf, juvenile and senescent stages of the population based on the findings of several authors (Vincent, 1979; Fairall, 1985; Owen-Smith, 1993). To determine the type of rainfall distribution used in the model, the annual total rainfall in



Hluhluwe from 1933 to 1994 was tested and found to conform to a normal distribution function. Rainfall was therefore modelled as a normally distributed effect.

The rainfall-dependent logistic density-dependent model was run over 100 years and iterated 20 times per year. The probabilities of population extinction under natural mortality and predation (one wild dog pack), and predation by an additional wild dog pack, were determined for a 100 year period from the 'time to extinction' values calculated by the model.

The above models assume that i) stage distribution ratios are constant, ii) males and females both have the same probability of survival, iii) no migration or dispersal takes place, iv) wild dog population size and preference for particular stages are constant over time and v) prey species selection by a second wild dog pack is similar to that of the current pack.

### *Sensitivity Analyses*

Sensitivity analyses were used to investigate the effects of changes in survival rate of the stages on the finite rate of increase of prey populations, and the probability of extinction over time. These analyses enabled one to identify which stages of the prey population were most affected by predation and those which drive the population dynamics.

Survival rates of all prey stages experiencing predation by two wild dog packs, were reduced by 10% in separate runs of the model. The finite rate of increase and probability of population extinction at 100 years were calculated for each model. These calculations provided a scenario of the potential impact of wild dog on the respective prey stages if, following introduction, the wild dog population in HUP were to prey disproportionately more on a particular stage than at present.

## RESULTS

### Modelling Prey Population Dynamics

The female fecundity rates and stage-dependent survivorship rates, obtained for nyala (Allen-Rowlandson, 1986; Owen-Smith, 1990) and impala (Vincent, 1979; Fairall, 1985), are tabulated in Table 7.1 and Table 7.2 respectively.

Table 7.1. Nyala fecundity and survivorship rates used to model the impact of one (10 individuals) and two (20 individuals in total) wild dog packs on nyala population dynamics.

STAGE CLASS	FECUNDITY	SURVIVAL RATE	
		1 PACK	2 PACKS
Calf	0.00	0.45	0.44
Juvenile	0.05	0.84	0.83
Subadult	0.50	0.88	0.87
Adult	0.75	0.91	0.88
Senescent	0.20	0.81	0.77

Table 7.2. Impala fecundity and survivorship rates used to model the impact of one (10 individuals) and two (20 individuals in total) wild dog packs on impala population dynamics.

STAGE CLASS	FECUNDITY	SURVIVAL RATE	
		1 PACK	2 PACKS
Calf	0.00	0.70	0.68
Juvenile	0.05	0.80	0.79
Subadult	0.44	0.90	0.89
Adult	0.48	0.90	0.89
Senescent	0.10	0.60	0.58

The total rainfall measured over 61 years in Hluhluwe had a normal distribution ( $D_{17,61}=0.07$ ,  $p=0.93$ ) with a mean annual total of  $979.03 \pm 33.91$  mm.

Under conditions of current simulated predation (one wild dog pack), the density independent exponential rate of increase of both the female nyala and impala populations were 4.5%. When the impact of two wild dog packs was modelled, the annual rates of increase of the nyala and impala populations were slightly lower, 2.7% and 3.1% respectively.

With the incorporation of rainfall-dependent logistic density-dependence, the models reached equilibrium at  $2979 \pm 58.29$  nyala experiencing predation by one wild dog pack and  $1317 \pm 32.87$  nyala experiencing predation by two packs, and  $2224 \pm 39.30$  impala experiencing predation by one pack and  $1880 \pm 29.99$  impala experiencing predation by two packs.

With the addition of a second wild dog pack to HUP, the probability of nyala population extinction increased by 0.14 (from 0.04 to 0.18), and the probability of impala population extinction by 0.10 (from 0 to 0.10), over a 100 year period.

### *Sensitivity Analyses*

The relatively high population extinction probability (0.26) (Table 7.3) and the low net population rate of increase (0.4%) (Table 7.3) following an increase in predation on the adult nyala stage, suggests that additional wild dog individuals may impact negatively on this stage. The rate of population increase was least affected by a reduction in the survival rate of the senescent stage (Table 7.4), the value being most similar to the overall rate of population increase of 2.7 (see above).

Table 7.3. The probabilities of nyala population extinction at 100 years when stage dependent survival rates were reduced by 10%.

<b>STAGE</b>	<b>EXTINCTION PROBABILITY</b>
Calf	0.16
Juvenile	0.16
Subadult	0.22
Adult	0.26
Senescent	0.06

Table 7.4. The rate of increase of the nyala population (expressed as a percentage) following the reduction of individual stage dependant survival rates by 10%.

<b>CALF</b>	<b>JUVENILE</b>	<b>SUBADULT</b>	<b>ADULT</b>	<b>SENESCENT</b>
1.0	1.1	0.5	0.4	2.3

A decrease in the survival rate of subadult impala, the stage most sensitive to change, resulted in a relatively high population extinction probability (0.22) at 100 years (Table 7.5) and a relatively low rate of population increase (0.7%) (Table 7.6) in comparison to the overall rate of population increase (3.1%; see above). Less than 10% of the diet of the wild dog included subadults (chapter 3), therefore an increase in predation on this stage would not impact heavily on the rate of population increase and probability to extinction.

The comparatively low extinction probabilities (Table 7.5) and high rate of population increase (Table 7.6) following the simulated increase in predation on the calf and juvenile stages, suggests that the impact of additional wild dog on these stages would be minimal. The rate of population increase was least affected by a reduction in the survival rate of the senescent stage (Table 7.6).

Table 7.5. The probabilities of impala population extinction at 100 years when stage dependent survival rates were reduced by 10%.

<b>STAGE</b>	<b>EXTINCTION PROBABILITY</b>
Calf	0.04
Juvenile	0.04
Subadult	0.22
Adult	0.20
Senescent	0.04

Table 7.6. The rate of increase of the impala population (expressed as a percentage) following the reduction of individual stage dependant survival rates by 10%.

<b>CALF</b>	<b>JUVENILE</b>	<b>SUBADULT</b>	<b>ADULT</b>	<b>SENESCENT</b>
1.2	1.3	0.7	0.9	3

## **DISCUSSION**

The population dynamics modelling exercise has proved useful in synthesising the data collected during the study and has provided thought-provoking results for use in the management decision-making process.

The models have provided a clearer perspective of the management problem ie. that the current predation by the five large predators in HUP, as well as an increase in predation with additional wild dog individuals, do not appear to limit nyala and impala numbers in terms of population growth rates and probabilities to extinction. Similar results were obtained for the model of predator impact on impala populations in the Kruger (Mills & Biggs, 1993).

The prey age selection of wild dog (chapter 3) suggests that instead of the HUP wild

dog impacting heavily on the juvenile impala classes, they were in effect removing animals that suffer high natural mortality in relation to other stage classes and which were also targeted by other predators.

The reduction of stage-dependent prey survival rates by 10% simulated, on average, a threefold increase in wild dog predation of a particular stage. Such an increase in predation is unlikely. The results do, however, suggest that any additional harvesting of the nyala adult stage would have the potential to reduce population growth rates and increase extinction probabilities to the detriment of the population.

The annual impala population rate of increase of 4.5% obtained from the modelling exercise was within the range of growth rates obtained from impala populations in Mkuzi (3.5%; Vincent, 1979), the Kruger (6.5%; Fairall, 1985) and Hluhluwe Game Reserve and the northern Corridor (7.5%; Brooks, 1978) suggesting that the fecundity and survival rates used in this chapter were reasonable and realistic.

The logistic equation used in this chapter has been most frequently used to describe the dynamics of population growth (Pearl & Reed, 1920) but has also been criticised (Pielou, 1977). The logistic equation assumes a strictly linear density-dependence and thus population birth and death rates tend to respond instantly to changes in density, and the rate of population increase is density-dependent even at low densities. The logistic equation is a simple density-dependent model by comparison to other models, however, the limits of the modelling software made it necessary to use this equation.

The management recommendations detailed in the following chapter are based on the implications of the results obtained from modelling prey population dynamics over a 100 year period. I recommend, however, that prey population models are updated on a regular basis (at least every five years) taking into account post introduction wild dog prey age selection.

## CHAPTER 8

### Conservation and Management Recommendations for the Hluhluwe-Umfolozzi Park Wild Dog Population: Is Introduction a Viable Option?

#### INTRODUCTION

The reintroduction of wild dog into HUP in 1981 was one of the first attempts at relocating wild dog into an area where they had previously roamed (Reich, 1981a). A reintroduction is considered successful if it results in a long-term self-sustaining population (Griffith *et al.*, 1989). By this definition, the 1981 reintroduction cannot be considered successful.

The HUP wild dog population size has fluctuated since reintroduction but has declined steadily since 1992 and no breeding has occurred since 1993. At the time of writing, ie. after completion of the field work, the pack had split into a group of three males, a mixed-sex group of four and a mixed-sex group of six individuals. Of these, only the group of three males and four of the six mixed-sex individuals were still within HUP. The other individuals most likely dispersed from their natal pack to either join established packs or meet up with opposite sex groups and establish new packs. Since the single, small wild dog population in HUP precludes the possibility of individuals joining with others within the Park following dispersal, these individuals were forced to disperse beyond the Park boundaries, ie. emigrate.

The low population numbers and their isolation from other wild dog populations makes the HUP wild dog particularly vulnerable to predators, more prone to emigration and

may result in inbreeding depression through reduced fecundity and viability (May, 1991). These are causes for concern and immediate management action.

After a 12 year period of no intervention or active management of the HUP wild dog subsequent to the reintroduction, this study provides data which may aid future management decisions.

### **Reasons for the Wild Dog Decline in Hluhluwe-Umfolozi Park**

Declines or extinctions in other small wild dog populations are believed to have been caused by i) negative changes in food availability (Scheepers & Venzke, 1995; Dye, 1996), ii) the abundance of other predators (Frame *et al.*, 1979; Frame, 1986; Ginsberg, Mace & Albon, 1995a; Scheepers & Venzke, 1995), iii) the effects of disease (Creel, 1992; de Villiers *et al.*, 1995; Kat *et al.*, 1995; Macdonald *et al.*, 1992; Scheepers & Venzke, 1995), iv) human intervention by handling (Burrows, Hofer & East, 1994), v) human persecution by shooting and poisoning (Childes, 1988b) and vi) emigration (Ginsberg *et al.*, 1995a; Dye, 1996).

Prey densities in HUP are relatively high by comparison to the Kruger and Hwange (chapter 4) and wild dog in HUP are not limited by, and do not significantly limit the numbers of, their preferred prey (chapter 7). Wild dog avoid competition with, and predation by, other predators by frequenting the dense vegetation in northern Hluhluwe (chapter 4) where predator numbers are low and detection is limited. Disease may be a contributing factor in the decline since the HUP wild dog population has been exposed to a number of potentially fatal diseases (for example canine distemper) of which the domestic dog population surrounding the Park is the most likely source (G. Andreka, *pers. comm.*). Similarly, the most likely vectors and/or reservoir for disease in the Serengeti ecosystem



were the domestic dogs surrounding the Park (Alexander *et al.*, 1993). Human intervention as a possible cause of the decline in wild dog numbers since 1993 is unlikely because no causal links between handling and mortality have been found, either in captive bred wild dog (de Villiers *et al.*, 1995) or free ranging wild dog (Ginsberg *et al.*, 1995b). Of the five locations that Ginsberg *et al.* (1995b) tested, handled dogs actually had a higher survivorship rate than unhandled dogs. Although persecution by humans is not a factor within the reserve, conflict between wild dog and people can arise when wild dog prey on domestic stock or wild game beyond the boundaries of the Park.

Since none of the above-mentioned reasons can be considered responsible for the decline in the HUP wild dog population, emigration followed by persecution, and population viability must be the primary causes of the decline. Emigration of same sex siblings, which disperse from the natal pack at between one and two years, is inevitable in HUP (see earlier) and has occurred on several occasions in the past (Natal Parks Board records). Wild dog are known to disperse over large distances (Scott, 1991; Fuller *et al.*, 1992; Ginsberg *et al.*, 1995a) which brings them into contact with private landowners who shoot individuals because wild dog as predators are perceived to pose a potential economic threat.

The small HUP wild dog population is subject to genetic, environmental and demographic stochasticity which can imperil its long term persistence (Foose, 1991; Mace & Lande, 1991). Environmental conditions such as floods, droughts and epidemics are severe threats to small populations and impair survival or fertility (Foose, 1991). Demographic problems, such as biased sex ratios and unstable age distributions, can disrupt breeding and persistence. Small populations, particularly isolated populations, can lose genetic diversity necessary for fitness and adaptation to changes in the environment.

A minimum viable population size of a few hundred individuals is an accepted

standard (Soulé & Simberloff, 1986; Thomas, 1990) and similar threshold population sizes were calculated by Burrows *et al.* (1994) for the Serengeti wild dog population. Although a minimum population size below which the loss of genetic variability is likely to imperil survival must be calculated separately for the HUP wild dog population, it is initially clear that the current population is not viable.

If wild dog are to be conserved within HUP, the causes of the decline in their numbers need to be addressed to i) improve the viability of the population and ii) to ensure that dispersal from the natal pack is followed by the meeting of other individuals and the establishment of new packs within the Park.

## **Solutions**

The Natal Parks Board originally proposed the 1981 reintroduction to establish wild dog in an area where they occurred previously (Natal Parks Board records). If this policy is to be maintained, introduction followed by active management appears to be the only solution to increase wild dog numbers and reproductive success. Long term viability can only be achieved through constant proactive management and the development of a strategy aimed at the conservation of wild dog in HUP as part of a larger viable wild dog population, ie. a metapopulation. A metapopulation is a collection of disjunct subpopulations, including captive populations, the management of which should maximise the survival potential of the species (Foose, 1991). By doing so, a higher level of genetic variability is maintained (Craig, 1994) and populations are isolated from disease and catastrophes. Any subpopulation lost through chance events can be re-established from other remaining subpopulations (Craig, 1990).

Although introductions require expense and effort, wild dog have an economic and ecotourism value. Wild dog are valuable in their contribution to ecology, by virtue of their role in the control of prey species populations (Schonewald-Cox, Azari & Blume, 1991). Their economic potential is evidenced by their role as a major tourist attraction in National Parks (Bertram, 1976).

### **Reintroduction**

Reintroductions of endangered species, particularly mammals, have met with limited success (Griffith *et al.*, 1989; Kleiman, 1989). The large home range area requirements of the wild dog are considered the primary reason for the failure of several relocation attempts (Comely, 1992), while predation by lion was largely responsible for the failure of the reintroduced pack into Etosha (Scheepers & Venzke, 1995).

My data, together with that of A. Maddock and G. Andreka, provides the necessary details on wild dog population dynamics in HUP and suggests that HUP is able to support additional packs of wild dog in terms of home range area availability, habitat availability and current predator and prey densities. HUP is a comparatively large conservation area with stable populations of preferred prey and low incidences of poaching which provides an environment conducive to wild dog survival (Maddock & Mills, 1994). Further introductions of wild dog, followed by proactive management, should be successful and are in fact vital to the survival of the current individuals.

I suggest a two-part strategy to the introduction programme namely; i) the introduction of a small group of related females to supplement the current pack and ii) the introduction of a mixed group of individuals to establish another resident breeding pack and

enable dispersal and interchange of individuals within the Park. The introduction of female siblings to supplement the current pack in Hluhluwe should stimulate reproduction in the current pack. The present alpha female is maintaining her dominant position within the pack and is suppressing the breeding of conspecific females while she has not bred successfully herself since 1993. A further possibility presents itself, and this is the removal of the alpha female at the same time as the introductions thus forcing a change in the dominance structure within the pack and stimulating reproduction.

Introductions require the provision of suitable stock and adequate human and financial resources until the population is successfully established, followed by the enforcement of legal protection and corrective management actions where required.

### ***Source Population***

Southern and East African wild dog are genetically and morphologically distinct and, to prevent possible deleterious long-term genetic consequences (Ashley, Melnick & Western, 1990), mixing of these populations should be avoided (Ginsberg & Cole, 1994). Taxonomically and genetically similar wild dog to the existing HUP population are available from the Kruger (relatively disease free) and Hwange, and two captive breeding sites (de Wildt & Hoedspruit cheetah breeding stations) in South Africa, thus ensuring genetic viability.

Sufficient wild dog should be available from the source population to establish a breeding population in HUP without depleting the source population. Since translocations from the Kruger could theoretically constitute no more than a few packs at best, and practically, only a few individuals, I suggest that the Kruger is used as a source of free

ranging females. The low number of free ranging wild dog available for translocation necessitates the consideration of introductions involving captive bred wild dog populations. Captive breeding provides a temporary conservation measure to save the species (Ginsberg & Macdonald, 1990) and programmes would have little conservation value if not followed by reintroductions to supplement animal numbers in the wild (Anderson, 1986; Seal, 1986).

Presently, populations of wild dog kept in captivity are neither self-sustaining nor self-sufficient enough to form a viable population (Ginsberg & Macdonald, 1990) and reintroductions involving captive bred animals have a lesser chance of success than translocating wild caught animals (Griffith *et al.*, 1989). Several problems arose from a reintroduction of wild dog into Umtchibi in Hwange (Childes, 1988b). The pack were unable to recognise their prey species, they had reduced physical fitness levels after being kept in a holding structure (boma) too long and were too dependent on humans. An ideal solution to the above problem would be to mix free ranging same sex siblings from the Kruger with captive bred same sex siblings of the opposite sex, and hold them in a boma together near the release site. Since wild dog have extremely complex social systems this would allow the captive bred dogs to learn hunting techniques and home range area from the free ranging dogs and would enable the pack as a whole to familiarise themselves with the environment and reduce exposure to possible unfamiliar diseases, while native foods can be given to them. The social compatibility of the free ranging and captive bred wild dog is essential prior to release to ensure that the released pack is a stable unit.

### ***Release Site***

Sites for future introductions need to be carefully assessed based on the results from this study. The site of introduction should favour the existing pack, enabling contact with the introduced individuals as soon as possible. I propose northern Hluhluwe (ie. Gontshi) as an area for the release of the group of free ranging female siblings (from the Kruger). A second pack (of free ranging and captive bred wild dog) should be introduced into southern Hluhluwe (ie. Seme) where the present pack frequently ventures (G. Andreka, *pers. comm.*). Both Gontshi and Seme have existing boma structures.

Both release sites should be located in Hluhluwe because wild dog will most likely actively avoid predators and range primarily in Hluhluwe. In addition the frequency of prey encounter is similar in northern and southern Hluhluwe even though the vegetation is more dense in northern Hluhluwe, while predator densities are lower.

### ***Age and Sex Composition***

The success of an introduction is dependent on the reproductive success and survival of the population which in turn is dependent on the species' natural rate of increase, its genetic attributes and environmental conditions (Griffith *et al.*, 1989). The rate of increase is dependent on the age and sex ratios of the introduced individuals.

The introduced pack of free ranging and captive bred wild dog should constitute a stable breeding unit of which the age and sex structure should be similar to those observed in the wild. Overall wild dog sex ratios are slightly skewed towards males (Frame *et al.*, 1979; Malcolm & Marten, 1982; Fuller *et al.*, 1992; Maddock & Mills, 1994). In wild dog,

a sex bias towards males at birth suggests that adult male helpers (which predominate) usually increase pup survivorship (Malcolm & Marten, 1982). In contrast, there is a negative correlation between the number of yearlings and pup survival (Malcolm & Marten, 1982). Yearlings are less inclined to regurgitate food to the pups because they themselves need food for growth and to build energy reserves for long distance dispersal. Malcolm and Marten (1982) also found that adults took larger risks than yearlings, by tackling larger prey and chasing away predators.

It would seem that the ideal age and sex composition of the introduced individuals should be one that is skewed towards males and adults. I suggest the following age and sex compositions for the two part introduction programme mentioned earlier; i) 3-4 young adult females to supplement the existing pack and ii) three adult females and five adult males to establish another resident pack.

### ***Monitoring***

Monitoring prior to release is essential to i) obtain a photographic profile of each individual, ii) radio collar or tag as many individuals as possible and iii) to establish their social structure. Post release monitoring should i) concentrate on the age dependant reproductive success and survival of individuals and intrinsic and extrinsic factors affecting these, ii) home range use, iii) prey selection, iv) hunting success and v) intraspecific and interspecific interactions. A good understanding of the population dynamics of the introduced population is essential.

Free ranging wild dog are susceptible to diseases such as canine ehrlichiosis, canine distemper, anthrax and rabies (Schaller, 1972; Reich, 1981a; Alexander *et al.*, 1993; van

Heerden *et al.*, 1995), particularly in HUP where contact between the wild dog population within the reserve and the domestic dog population surrounding the reserve is possible and unavoidable. Introduced wild dog should be vaccinated and monitored against disease at regular intervals following their release. The domestic dog population should be subject to strict, regular disease and population control programmes (van Heerden *et al.*, 1995).

### **Public Awareness**

Throughout Africa, the wild dog has been subjected to extreme criticism and negative attitudes. Although extensive wild dog research and recent media coverage have brought about an awareness of this predator, there is continued antagonism and prejudice from the general public, game farmers and livestock owners. The quote below, taken from the 'Daily News' prior to the 1981 reintroduction of wild dog into HUP, is a typical example of the public's attitude;

'It (the wild dog) is at all times a heinous creature guilty of abominable cruelty and savagery—a loathsome wretch. Vermin fit for extermination only...let alone reintroduction.'

Wild dog are despised for their method of killing and the potential economic threat they pose to game farmers and livestock owners. Further introductions may provoke objections particularly from livestock owners and local game farmers as experienced in Zimbabwe (Townsend, 1988). The co-operation between farmers and wildlife managers is essential for wild dog conservation (Mills, 1991). If local and regional objections can be overcome then introduction is a useful tool for conserving the species.

The objections and resentment can be overcome by initiating compensation schemes and widespread education aimed at demonstrating to livestock farmers that wild dog are not



major livestock predators, and to game farmers that they can benefit from the ecotourism value of the wild dog. Legal protection must be initiated, promoted and enforced. The strict protection of wild dog populations will create an awareness of the endangered status of the wild dog. Recent and current media coverage of the wild dog serves to improve the image of the wild dog and must be continued to encourage the attitudes and perceptions of people towards a positive view of this species.

### **Future Management**

Only a few national parks are sufficiently large enough to protect viable wild dog populations (Ginsberg & Macdonald, 1990). The spatial requirements of the wild dog make it necessary to conserve them on vast areas of private land, necessitating conservation beyond national parks and administrative boundaries. This goal may be achieved by managing each population as part of a larger metapopulation. A metapopulation conservation strategy involves i) the conservation of wild dog outside protected areas which necessitates the co-operation of the local people and ii) active management such as swapping genetic material between populations on a regular basis (thereby simulating dispersal in the wild) to maintain genetic diversity and population numbers.

On a local scale, a metapopulation including HUP and nearby sites such as Magudu, Itala, Mkuzi and Phinda where wild dog were sighted during the study period, would facilitate the potential natural dispersal of individuals, provided the support of the landowners beyond park boundaries was attained. For the wild dog in HUP and surrounding areas to constitute a viable population, however, they must be managed on a regional scale as part of a metapopulation which extends to the Kruger, Madikwe Game Reserve (the site of a

recent successful wild dog reintroduction) and both captive breeding sites. Since these sites are geographically disjunct, the dispersal by wild dog necessitates human intervention.

A metapopulation strategy (of wild dog in South Africa) including HUP must be devised that will recommend the number, sizes and distribution of subpopulations and the frequency of interchange among them.

## CHAPTER 9

### CONCLUSION

This study shows that wild dog prey species preference was a function of prey profitability, abundance and intraspecific ease of capture. Contrary to expectations, wild dog in HUP did not track prey distribution throughout the year. Instead wild dog avoided other predators (lion) and this had an important role in influencing their location in Hluhluwe rather than Umfolozi. Wild dog frequented the dense vegetation in northern Hluhluwe which while it minimised their probability of detection by lion and hyaena, it offered no less likelihood of encountering suitable prey. In fact, prey species in Hluhluwe showed lower levels of alertness to wild dog in comparison to other predators.

Wild dog have adapted their hunting technique to the dense vegetation and the prey species included in the diet suggest that wild dog rely on surprise (ie. opportunistic encounters) to flush and ambush their prey. The low levels of visibility in the dense habitat did not significantly restrict wild dog capture success. Indeed, wild dog reach their highest densities in the wooded parts of Africa, for example the Selous Game Reserve (Creel & Creel, 1995). HUP is thus in many respects suitable wild dog habitat.

Although nyala were the more vigilant prey species, their abundance, size, preference for dense vegetation and their similar choice of other habitat variables to wild dog, made them the preferred prey species. Wild dog did not, however, have a significant impact on nyala population numbers.

HUP is thus a suitable environment for the continued management and conservation of wild dog. Although HUP is a suitable environment for wild dog survival, wild dog

numbers are continuing to decline. The results show that none of the factors relating to the feeding ecology of the wild dog significantly limit, or are limited by, the current wild dog pack. The decline in HUP wild dog numbers can therefore only be attributed to emigration and the viability of the population.

Further introductions are essential to achieve short term management goals, namely; to increase numbers, encourage dispersal within the Park and to stimulate breeding. In order to achieve long term management goals and contribute to the overall conservation of this endangered species, future introduction programmes must be followed by continual proactive management and research. This will ensure a viable, and economically and ecologically valuable species in HUP.

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**Appendix A.** Vegetation physiognomies in Hluhluwe Section

<b>PHYSIOGNOMY</b>	<b>PLANT COMMUNITY</b>
Forest	<i>Celtis africana</i> - <i>Harpephyllum caffrum</i> <i>Celtis africana</i> - <i>Euclea schimperi</i>
Riverine Forest	<i>Acacia robusta</i> - <i>Ficus sycamorus</i> <i>Spirostachys africana</i> - <i>Euclea schimperi</i>
Woodland	<i>Spirostachys africana</i> <i>Combretum molle</i> <i>Acacia burkei</i> <i>Acacia nilotica</i> <i>Acacia karoo</i>
Thicket	<i>Euclea divinorum</i> <i>Acacia karoo</i> <i>Acacia caffra</i> <i>Acacia davyi</i>
Induced Thicket	<i>Dichrostachys cinerea</i> - <i>Acacia karoo</i>
Grassland	<i>Panicum maximum</i> - <i>Cyperus textilis</i> <i>Themeda triandra</i>

**Appendix B. Vegetation physiognomies in Umfolozi Section**

<b>PHYSIOGNOMY</b>	<b>PLANT COMMUNITY</b>
Forest	<i>Commiphora harveyi</i>
Riverine Forest and Peed Bed	<i>Acacia robusta</i> - <i>Ficus sycamorus</i> - <i>Phragmites australis</i> <i>Spirostachys africana</i>
Closed Woodland	<i>Spirostachys africana</i> - <i>Acacia grandicornuta</i> <i>Olea africana</i> - <i>Spirostachys africana</i> <i>Acacia burkei</i> - <i>Albizia versicolour</i> - <i>Albizia adanthifolia</i> <i>Acacia nilotica</i> <i>Euclea divinorum</i>
Open Woodland	<i>Acacia tortilis</i> <i>Acacia karoo</i> <i>Acacia nilotica</i> - <i>Acacia gerrardii</i> <i>Acacia nigrescens</i> <i>Acacia burkei</i> <i>Combretum apiculatum</i> <i>Combretum molle</i>
Thicket and Wooded Grassland	<i>Acacia karoo</i> <i>Acacia caffra</i> <i>Acacia karoo</i> - <i>Dichrostachys cinerea</i>
Grassland	<i>Cyperus textilis</i> <i>Themeda triandra</i>

**Appendix C.** Predator and prey species in Hluhluwe-Umfolozi Park. Abbreviations of prey species referred to in the text are given in brackets.

<b>ANIMAL SPECIES</b>	<b>SCIENTIFIC NAME</b>
Wild dog	<i>Lycaon pictus</i>
Spotted Hyaena	<i>Crocuta crocuta</i>
Lion	<i>Panthera leo</i>
Leopard	<i>Panthera pardus</i>
Cheetah	<i>Acinonyx jubatus</i>
Impala	<i>Aepyceros melampus</i>
Nyala	<i>Tragelaphus angasi</i>
Blue Wildebeest (W.beest)	<i>Connochaetes taurinus</i>
Zebra	<i>Equus burchelli</i>
Buffalo	<i>Syncerus caffer</i>
Warthog	<i>Phacochoerus aethiopicus</i>
Giraffe	<i>Giraffa camelopardalis</i>
Red Duiker (R.duiker)	<i>Cephalophus natalensis</i>
Grey Duiker (G.duiker)	<i>Cephalophus grimmia</i>
Bushbuck (B.buck)	<i>Tragelaphus scriptus</i>
Kudu	<i>Tragelaphus strepsiceros</i>
Common Reedbuck (R.buck)	<i>Redunca arundinum</i>
Eland	<i>Taurotragus oryx</i>
Waterbuck (W.buck)	<i>Kobus ellipsiprymnus</i>
White Rhino	<i>Ceratotherium simum</i>
Black Rhino	<i>Diceros bicornis</i>
Hippopotamus	<i>Hippopotamus amphibius</i>
Elephant	<i>Loxodonta africana</i>



**Appendix D.** Photographic reference key of hair cross-sections used in the identification of ungulate species in the wild dog diet.

Figure 1. Wild dog



Figure 2. Nyala

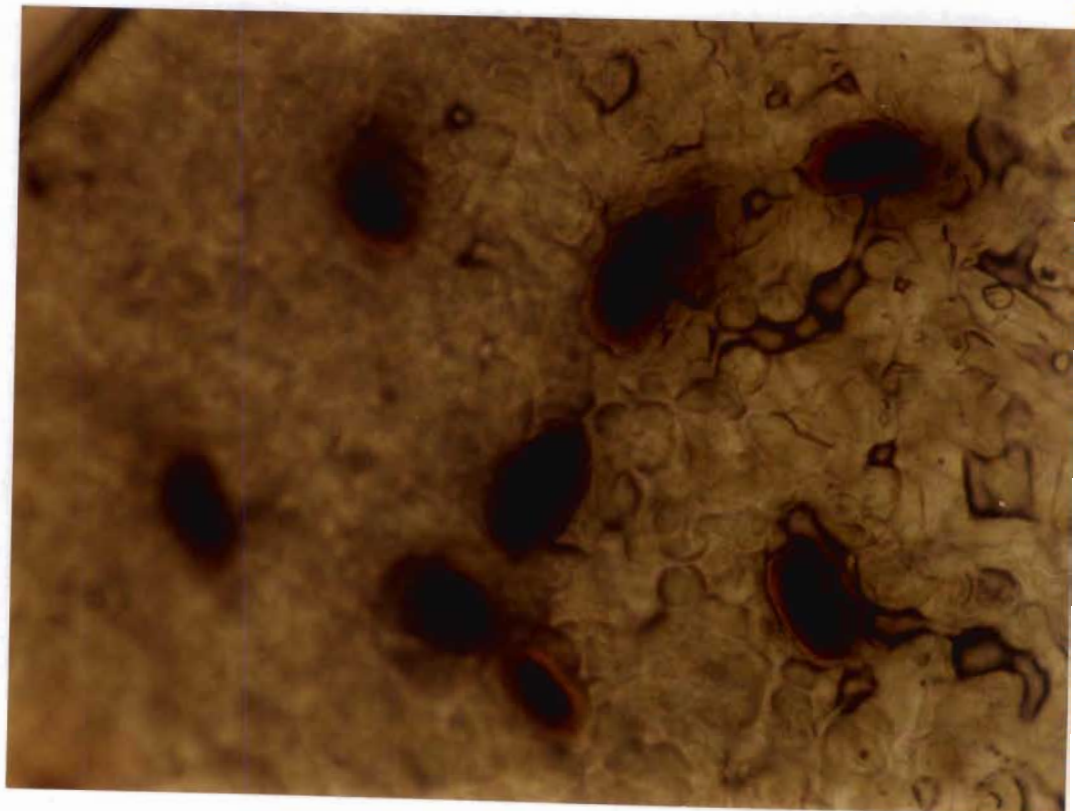


Figure 3. Impala

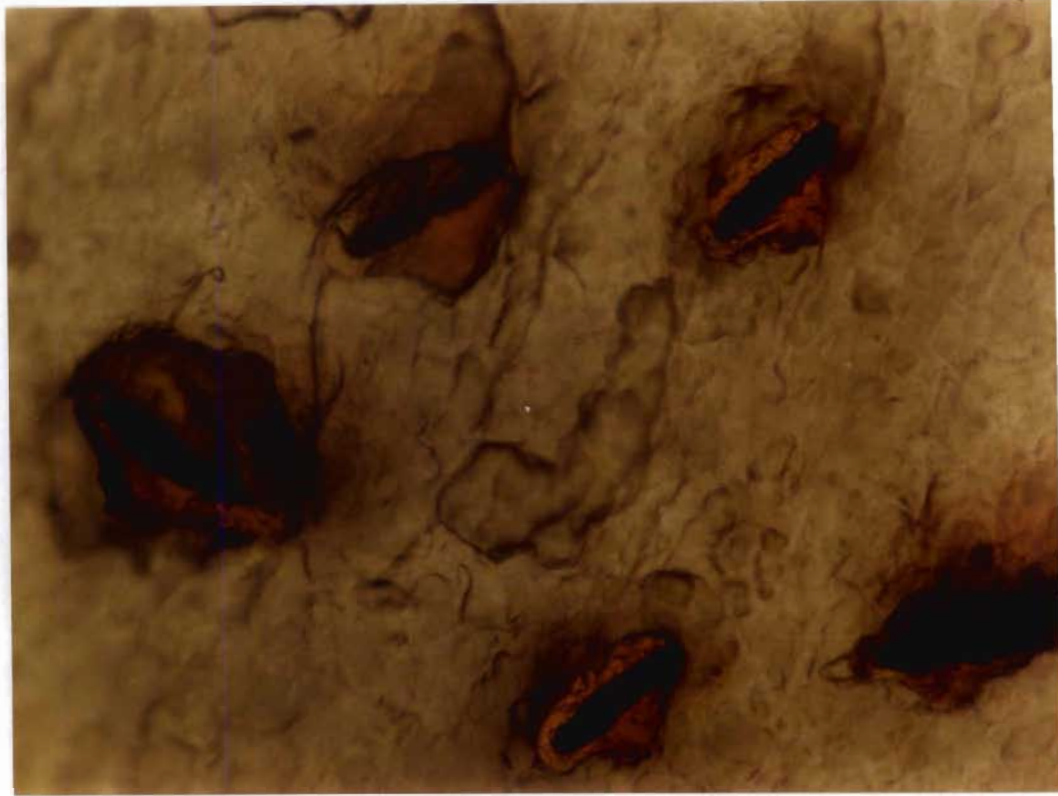


Figure 4. Kudu

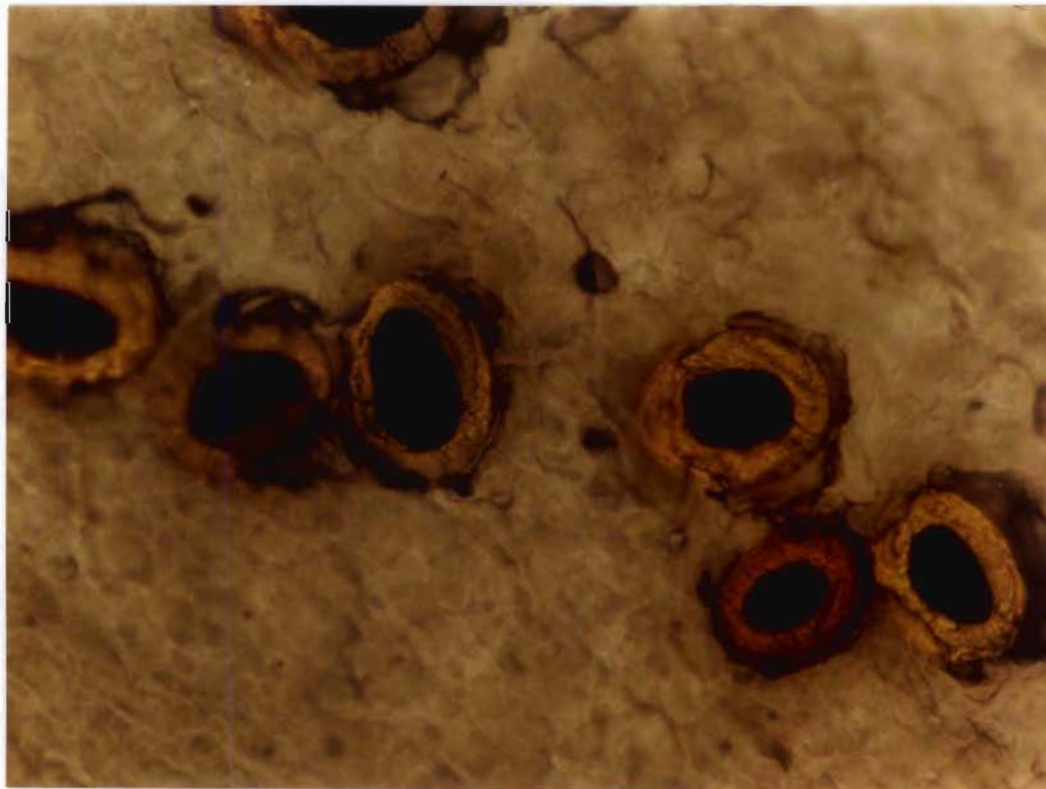


Figure 5. Red Duiker

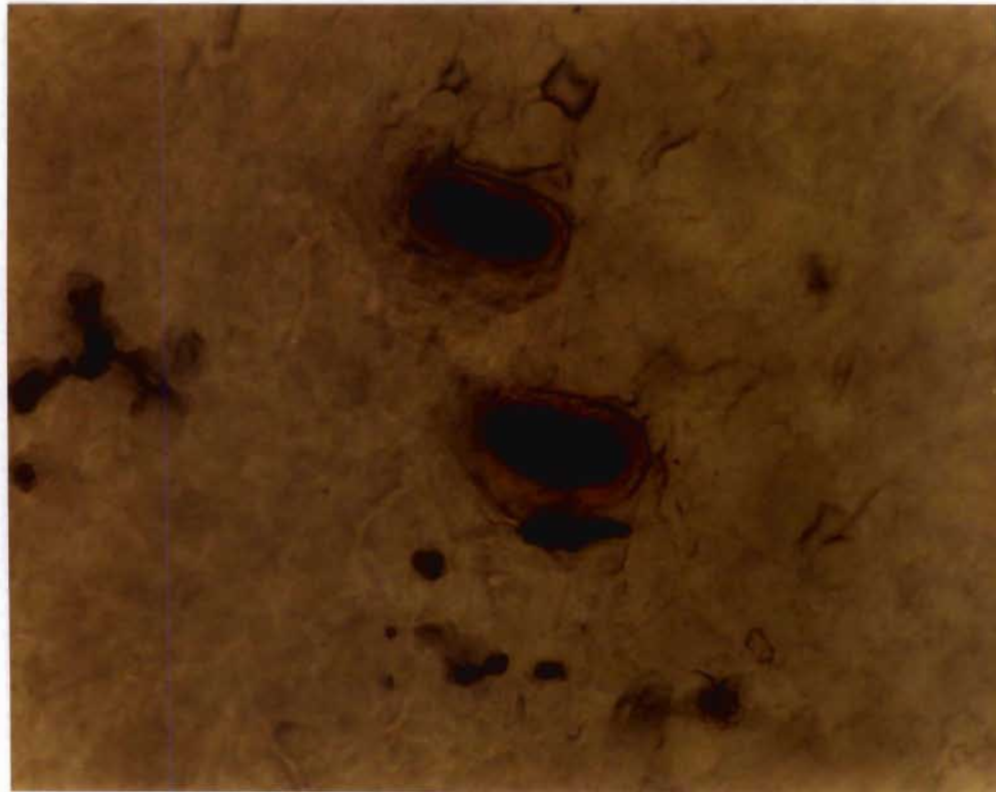


Figure 6. Grey Duiker

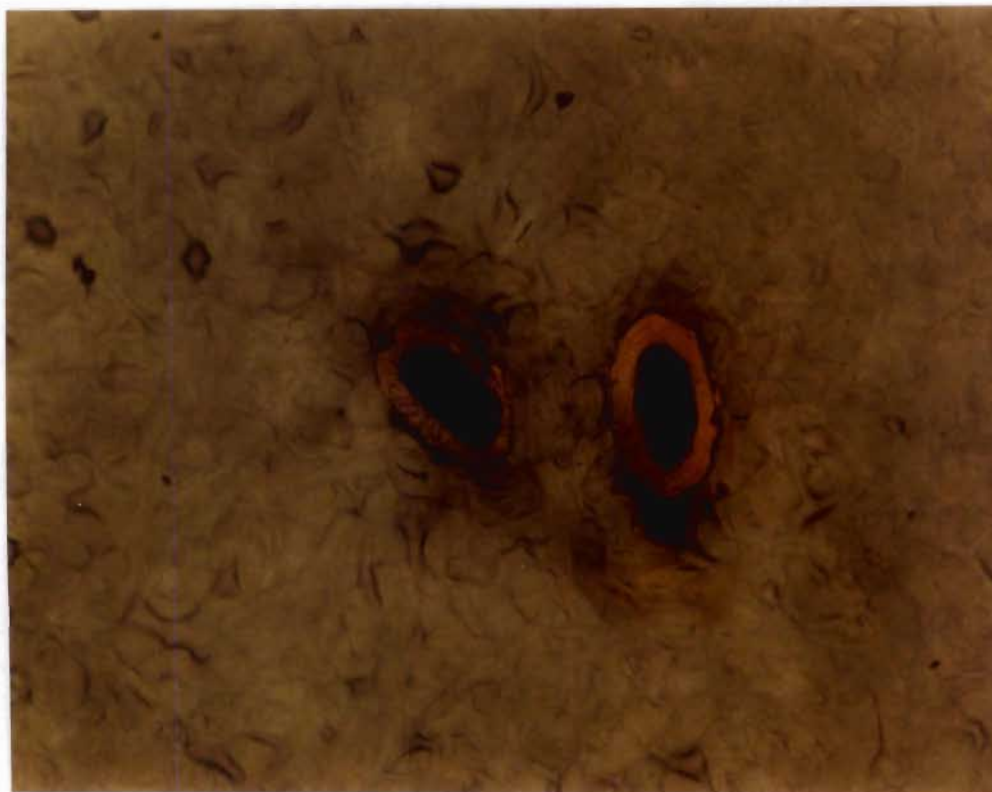


Figure 7. Bushbuck

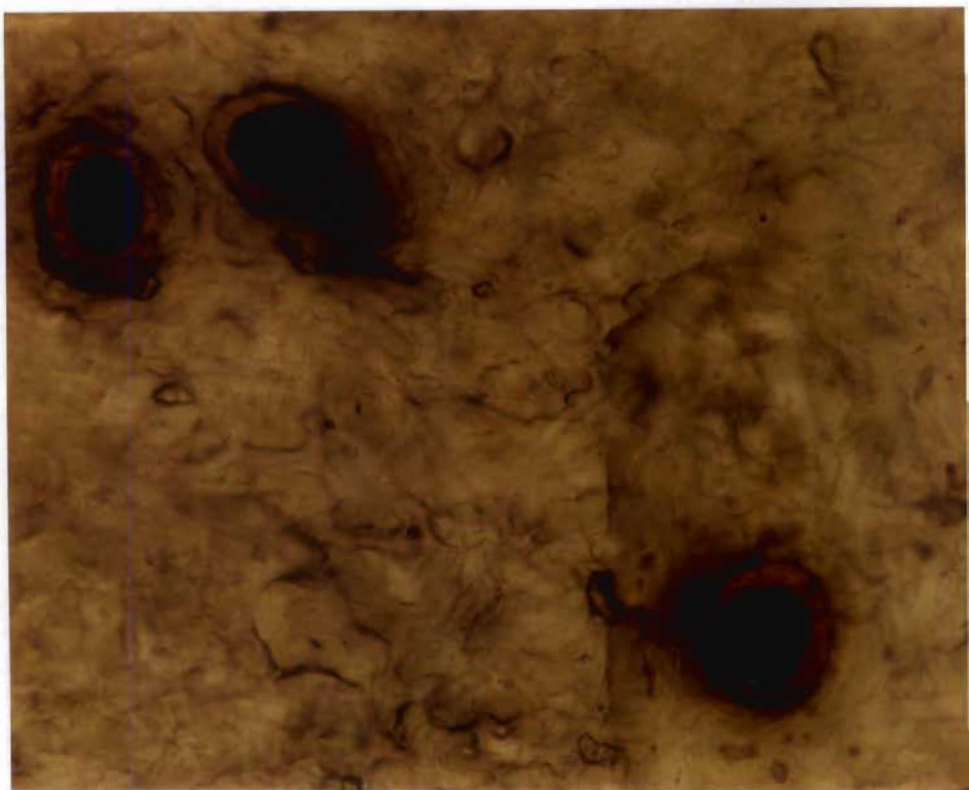


Figure 8. Blue Wildebeest

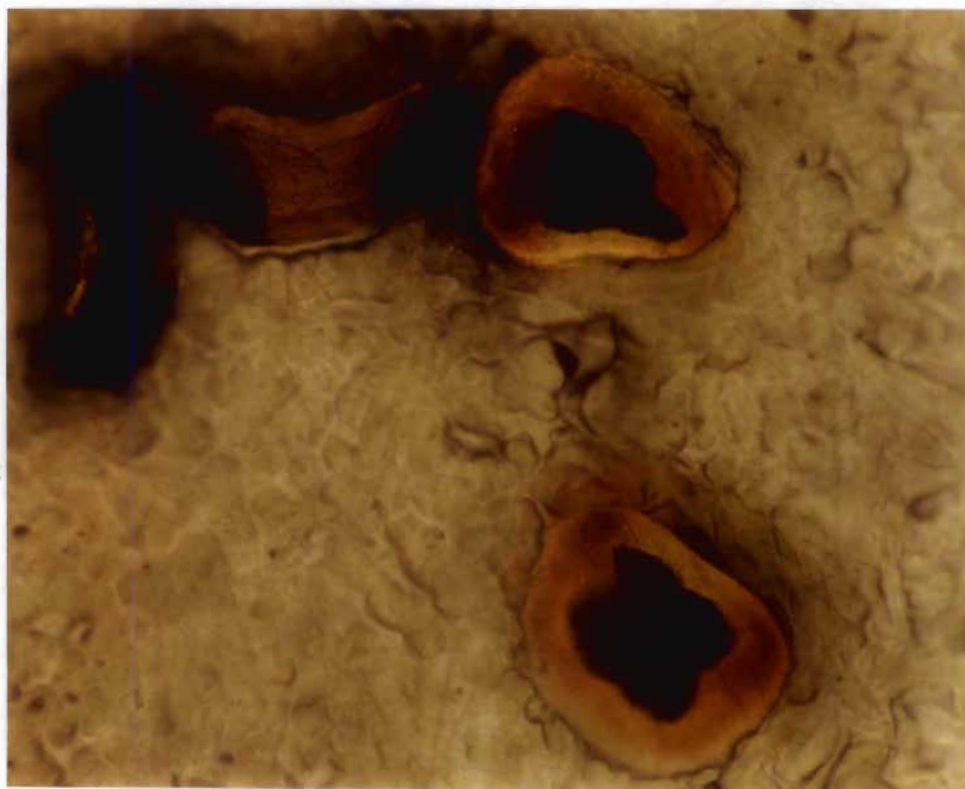


Figure 9. Waterbuck

