1.1 Natural History of African Wild Dogs.

1.1.1 Status and Distribution
The African wild dog (*Lycaon pictus*) is one of Africa’s most endangered carnivores, and is Red Listed as an endangered species by the International Union for the Conservation of Nature (IUCN 2002). The wild population of *Lycaon pictus* has been reduced dramatically over the last 50 years, and population estimates range from 2500 to 5000 animals left in Africa (Fanshawe et al. 1991; Woodroffe et al. 1997).

![Historical and current distribution of Lycaon pictus in Africa. Current distribution indicates general regions inclusive of both vagrant and resident populations. Data drawn from Woodroffe et al. (1997), Ginsberg (1993), and Fanshawe et al. (1991).](image)

Wild dogs were considered to be vermin by colonial governments who attempted to eradicate them in many areas. In Zambia alone vermin control units killed approximately 5000 wild dogs between 1945 and 1959 (Buk 1995).
It was believed that wild dogs suppressed antelope numbers and in some African countries persecution of wild dogs was official National Parks policy as late as 1979, and was carried out in some areas until the mid 1980's (Creel & Creel 1998; Woodroffe et al. 1997).

African wild dogs were historically distributed all over sub-Saharan Africa, but their range has decreased and become fragmented over recent decades (Figure 1.1). From the 34 sub-Saharan countries in which they used to exist, few countries are now thought to hold potentially viable populations. The Republic of South Africa, Namibia, Zimbabwe, Zambia, and Ethiopia are all estimated to hold populations of 400 dogs or over, while the largest extant populations reside in Botswana and Tanzania, estimated at 800 and 1800 dogs respectively. (Fanshawe et al. 1991; Woodroffe & Ginsberg 1999a; Woodroffe et al. 1997; Woodroffe et al. 2004b).

Long-term studies on wild dogs have been carried out in several African countries, which have identified the main causes of mortality for each population (Creel et al. 1997b; Creel & Creel 1996; Fuller & Kat 1990; Maddock & Mills 1994; Malcolm & Marten 1982; McNutt 1996; Van Heerdan et al. 1995; Woodroffe et al. 1997). Many of these causes were found to be linked with the encroachment of human populations into wild dog areas. The commonly cited causes of mortality observed in most study populations were road kills from fast moving traffic, illegal game snaring, shooting and poisoning, diseases from domestic dogs, and competition from other large carnivores. Each of these is discussed in greater detail in Chapter 2.

1.1.2 Description and Taxonomy
The African wild dog is a highly social group-living canid. The specific Latin name, *Lycaon pictus* (Temminck 1820), literally translates as “painted wolf-like canid”, which describes the unique tri-coloured pelage of black, white and tan. Another distinctive feature of the species is the unusually large, rounded black ears (Estes 1991). The average wild dog measures 60-75cm tall at the shoulder, and weight ranges from 18-34kg (Estes 1991; Smithers 1983; Woodroffe et al. 2004b). The species has only four toes on the foreleg and is missing the
vestigial dewclaw found in other canid species (Estes 1991).

Domestic dogs, wolves, jackals, and dingoes all belong to the genus *Canis*, however the African wild dog diverged from this group several million years ago into the genus *Lycaon* (Chen et al. 2000; Girman et al. 1993; Wozencraft 1989). The species therefore represents a unique line. Chen et al. (2000) recently used mitochondrial cytochrome b DNA sequence to classify foxes, wolves, raccoon dogs, domestic dogs and African wild dogs. The resulting molecular phylogenetic tree (Figure 1.2) suggested that African wild dogs were the earliest divergent. The genus *Canis* then diverged earlier than the raccoon dog and red and blue foxes.

![Figure 1.2 Neighbour joining phylogenetic tree of African wild dog and other Canidae species](image)

The African wild dog has evolved physiological adaptations which suit it to its specialised niche as a highly carnivorous cooperative hunter. In experiments on captive bred wild dogs, *Lycaon* maintained a higher rectal temperature than the domestic dog when running (by 1-2°C), and lost a smaller percentage of heat production through respiratory evaporation (Taylor et al. 1971). This increased
tolerance for high body temperature and low evaporation rate may increase the wild dog’s pursuit distance, and thus increase its success as a coursing predator.

Van Valkenburgh and Koepfli (1993) grouped canid species based on dental adaptations towards predation. They grouped four canid species including the African wild dog, in a group of canids which regularly take prey larger than themselves by up to a factor of ten; the other species being the grey wolf (Canis lupus), the dhole (Cuon alpinus) and the rare bush dog (Speothus venaticus). All of these species possess cranial and dental adaptations to their highly predacious diet which include: reduced grinding areas in their dentition, larger canines and incisors, larger second moments of area of the dentitary relative to its length, broader snouts, wider occiputs and increased mechanical advantage of the temporalis and masseter muscles. In comparison to predators of smaller prey, van Valkenburgh and Koepfli (1993) suggest that the wild dog group’s dental adaptations may be the result of selection for increased bite capacity. The reduced post-carnassial grinding surfaces would bring the canines closer to the jaw joint, increasing the mechanical advantage of the jaw closing muscles. Wild dogs, dholes and the bush dog all possess a modification of the first lower molar known as a trenchant heel, which is only partially developed in the grey wolf (Van Valkenburgh & Koepfli 1993). The tooth is modified so that a normally basin-like structure is converted to a blade like cusp. This lengthening of the tooth’s blade structure enhances its meat slicing capabilities and would enable the dog to consume meat more quickly. Ecologically, this adaptation would allow the African wild dog to gorge its prey quickly, before the arrival of larger competitive predators, which often attempt to steal kills (Creel & Creel 1996). Within the wild dog species Kieser and Groeneveld (1992) found that females have relatively larger postcanine tooth sizes to cope with the higher masticatory demands of lactation and pregnancy.
1.2 Purpose and Scope of the Study

1.2.1 General Objectives

This research project was aimed at the collection of strategic technical data to assess the status of Lower Zambezi National Park wild dog population, and to deliver practical conservation strategies to conserve the population and those in adjacent areas. The conservation of any species in-situ requires a site-specific assessment, to identify and prioritise the threats to the population. Most species show a degree of adaptation to prevailing environmental conditions, and wild dogs have shown themselves to be highly intelligent carnivores that adjust their behaviour to suit conditions (Fuller & Kat 1990; Kruger et al. 1999; Rasmussen 1996).

There is a lack of data on the Zambian African wild dog populations, from both an ecological point of view and also from a genetic perspective. Therefore this study incorporated ecological research for immediate identification and amelioration of threats, as well as the collection and analysis of genetic samples for longer term conservation measures, such as translocation and reintroduction, which may become necessary in the future.

The most extensive research on the African wild dog has come from large study populations; the Serengeti (Frame et al. 1979), Kruger National Park in South Africa (Kruger et al. 1999; Maddock & Mills 1994; Mills & Gorman 1997; Reich 1981), northern Botswana (McNutt 1996; Woodroffe et al. 1997) and the Selous in Tanzania (Creel & Creel 2002). With the exception of the Serengeti, these areas still contain viable populations of wild dogs and are generally viewed as stronghold populations for the conservation of the species (Woodroffe et al. 2004b). In contrast, the Lower Zambezi wild dog population is small and fragmented. However, because of this structure it is more representative of a large number of the remaining wild dog populations throughout Africa. Small populations are known to be more sensitive to the effects of increased mortality near reserve borders or “edge effects” (Caughley 1994; Ginsberg et al. 1995a; Woodroffe & Ginsberg 1998; Woodroffe et al. 2004b), and are more likely to require active management. Although small population dynamics have been modelled extensively, there is a lack of
empirical data on small population dynamics in wild dogs. For an endangered species where every remaining wild population is of value, it is vital that research and subsequent management of extant populations are carried out before more local extinctions occur.

In addition to its endangered status, the wild dog plays a role as an umbrella species, and is useful for identifying conservation needs for large areas of habitat. Umbrella species are those “species whose conservation confers protection to a large number of naturally co-occurring species” (Roberge & Angelstam 2004), usually through the size of the areas conserved and the amelioration of common threats. The umbrella concept is useful in the conservation of biodiversity where time and resources are limited, and is particularly relevant for the Lower Zambezi area where little ecological research has been carried out. Conserving minimum area requirements for a population of a highly mobile species such as the African wild dog would provide a protected area that benefits a range of species with smaller range requirements. Umbrella species management has also been used as an extended concept, in habitat connectivity (Roberge & Angelstam 2004; van Langevelde et al. 2000), whereby protected area networks are created by determining the area an umbrella species requires to allow for successful dispersal. By conserving the African wild dog and establishing a network of protected areas that allow for its successful dispersal, again it could be assumed that many other species would benefit. There is continued discussion on the effectiveness of the use of single species or taxa as umbrella species (Andelman & Fagan 2000; Caro 2003; Linnell et al. 2000; Roberge & Angelstam 2004; Simberloff 1998), but although further evaluation of the level of biodiversity conserved by managing areas using the African wild dog as an umbrella species may be required, in an underdeveloped country such as Zambia resultant reductions in general threats such as indiscriminate poaching by wire snare, diseases in nearby domestic animals, and habitat loss, could benefit numerous wild species, particularly large mammals. Umbrella species have been used effectively in a multi-species process for determining habitat protection, with each species selected according to sensitivity in various categories (Andelman & Fagan 2000; Lambeck 1997; Poiani et al. 2001; Watson et al. 2001). The African wild dog
alone would be appropriate for two out of four categories according to Lambeck (1997); by being area-limited in that each pack within a population requires a large home range for day to day activities, and dispersal-limited in that both sexes disperse over great distances (sometimes hundreds of kilometers) to establish new packs (Fuller et al. 1992a; McNutt 1996).

The wild dog is particularly sensitive to anthropogenic threats since its nomadic behaviour often takes it to the edge of protected areas where it encounters hazards such as illegal poaching, high speed roads, and direct persecution from livestock farmers (Woodroffe & Ginsberg 1998; Woodroffe et al. 1997; Woodroffe et al. 2004b). The species may not be representative of many other species’ level of sensitivity to poaching due to differences in population densities and range movements. However, in aiming to conserve the most sensitive species any conservation plan will err on the side of caution, particularly as snares are arguably not a natural variable to which any populations within a protected area should be subjected.

1.2.2 Scope
The African wild dog Status Survey and Action Plan (Woodroffe et al. 1997) recommended that the first priority for conservation of the African wild dog should be to conserve those populations that remain in the wild, due to the limited success of programs aimed at re-establishing populations (Fanshawe et al. 1991; Scheepers & Venzke 1995). This study was aimed at identifying the threats to the extant Lower Zambezi African wild dog population, both anthropogenic and non-anthropogenic, long and short term. Research was therefore carried out over a broad range of topics, in an effort to provide comprehensive information to maximise the accuracy of assessment and subsequent recommendations.

The scope of the project was divided into five sections:

i) Demography and pack dynamics – aimed at identifying the structure and status of the population, and the main causes of mortality.

ii) Ecology and habitat utilisation – aimed at assessing the impact of ecological factors on the population and its home range movements.

iii) Inter predator competition – aimed at assessing the effects of lions and
spotted hyaenas on the population.

iv) Genetic analysis – to assess the historic and contemporary genetic variability of the population, and to define patterns of geographic structuring and population differentiation.

v) General discussion and implications for management.

1.3 Study Area
Zambia may be able to sustain viable populations of African wild dogs due to its large conservation areas. There are several clumps of adjacent protected areas that measure over 10,000 km$^2$ each, which has been estimated as the most effective area required to sustain a viable population of large carnivores such as the African wild dog (East 1981). Few countries contain protected areas of this size.

Zambia has three basic types of wildlife conservation areas, National Parks, Game Management Areas (GMA) and Open Areas. The National Parks and GMAs makeup almost 33% of Zambia’s total land area (Fanshawe et al. 1991; Jachmann 2000; Scheepers & Venzke 1995). The National Parks are wildlife sanctuaries, under the control of the Zambia Wildlife Authority (ZAWA). Hunting takes place in some areas of the GMAs and in the Open Areas, and human settlement and agriculture are permitted in both. ZAWA’s jurisdiction is limited to the wildlife in these areas. GMAs and Open Areas are located around the National Parks, providing a buffer zone against human impacts, depending on the level and type of settlement.

The study area overlapped two wildlife areas, the Lower Zambezi National Park (4092 km$^2$) and the adjoining Chiawa GMA (2344 km$^2$) on the south-eastern border of the country (Figure 1.3). Within the context of this thesis the study population is referred to as the Lower Zambezi population.
UTM (WGS84) coordinates for the study area were Zone 35S, between 711683.6 and 826054.8 mE, and between 8245105.8 and 814443.1 mN. The borders of the core study area and delineation of the wild dog population’s home ranges are defined in detail in Chapter 2. The valley floor between the Zambezi River to the south and the Zambian Escarpment to the north ranges between 1.9km and 19.2km wide, and the game is concentrated in this area. It is plausible to suggest that the ranges of many species are restricted by the river and the escarpment. The Zambezi River ranges from approximately 300m wide at its deepest points, to 1.5km wide in other areas, and has a fast and constant flow. The Zambian Escarpment rises steeply from the valley floor by approximately 600m, then to 900m on the plateau. Anecdotal reports on sightings and spoor frequency from Zambian Wildlife Authority patrol members suggest that game numbers appear to be low in the escarpment. Low prey numbers may reduce the everyday movement of predators, including wild dogs.
Zambia has a mild climate, with three distinct seasons; cool dry from May to August, hot dry from September to November, and warm wet from December to April. The hottest month is usually November (mean maximum temperature 39.6), July is the coldest (mean minimum temperature 10.7) and annual rainfall averages 758mm (Dunham 1994). The elevation of the area ranges between 347 -1200m.

The Lower Zambezi National Park and adjoining GMAs form part of the southern end of the East African Rift system. Soil types in the Lower Zambezi fall into the category of the Central African Rift Geomorphological region, and contain soils derived from basalts from past volcanic activity, plus fertile alluvial soils deposited by the river systems (Jachmann 2000). A preliminary report by Du Toit (1982) describes the basic geology of the area: the mountains and escarpment to the north of the river are formed from the oldest rocks in the region, from the Precambrian Basement; descending into the valley floor, ancient alluvial terraces are made up of post-Cretaceous sediments, while recently deposited alluvium from the Zambezi river appears within approximately 5-10km of the river. The flooding of the river valley has been regulated since the completion of Kariba Dam in 1958, which lies approximately 90km upstream to the southwest of the study site.

The escarpment vegetation is dominated by miombo woodland, containing Brachystegia, Julbernardia and Isoberlina species (Jachmann 2000). Gorges cutting down from the escarpment to the valley floor support richer vegetation due to seepage, and include species of Ficus, Commiphora marlothii, Afzelia quanzensis, Kirkia acuminata, Terminalia sambesiaca and Albizia zimmermannii (Bingham 1998). The alluvial terraces are further broken up by drainage lines and river channels, and support a variety of vegetation, depending on soil type and depth. The ancient alluvial terraces support a variety of mixed riverine woodland, including Kigelia Africana, Philenoptera violacea, Trichilia emetica, Combretum imberbe and Ficus zambesiaca, while the herbaceous layer is dominated by annual forbs and grasses (Dunham 1994). The lower
recent alluviums are dominated by *Acacia* woodlands, particularly *Acacia albida* and *A. tortilis*. Dispersed throughout the valley are various other vegetation types: areas of thickets near to the escarpment containing deciduous *Combretum* species; *Colophospermum mopane* scrub and woodland on the sodic soils between the thickets and alluvium (Dunham 1994); small areas of termitaria vegetation on the edges of the floodplains; open plains of short grasses and stands of *Hyphaenae* palm. Most of the available data for the region is from studies on the Mana pools side of the Zambezi River in Zimbabwe, which has a wider valley floor and some differences in dominant vegetation types. Due to a lack of published data on the study area, a preliminary vegetation survey was carried out in this study to further describe and classify habitats for wild dog and related species (see Chapter 3).
CHAPTER 2: DEMOGRAPHY AND PACK DYNAMICS

2.1 INTRODUCTION
Effective conservation of any species in-situ requires information on population demographics and knowledge of relevant life-history attributes. This chapter investigates the status of the Lower Zambezi African wild dog population by assessing survival, breeding and dispersal rates, and population structure. The following chapter (3) addresses range movements and the ecological factors affecting wild dog behaviour and population viability.

2.1.1 Density
African wild dogs are usually found in low density populations due to their wide ranging behaviour. Susceptibility to local extinction from both stochastic events and edge effects may be exacerbated in relatively small populations such as the Lower Zambezi (Caughley 1994; Ginsberg, Mace et al. 1995; Woodroffe and Ginsberg 1998).

Wild dog density is low compared to other sympatric carnivores. The highest estimate of wild dog density to date is 4 adults per 100km² in the Selous in Tanzania (Creel and Creel 1995a; Creel and Creel 2002), while more typically densities in wooded areas range between 1.5 and 3.3 adults/100km² (Fuller and Kat 1990; Maddock and Mills 1994; Creel and Creel 1996b; Woodroffe, Ginsberg et al. 1997). Densities in the east African open plains area of the Serengeti were recorded at approximately 0.5 to 1.5 adults/100km² over two decades (Frame, J.R. Malcolm et al. 1979; Woodroffe, Ginsberg et al. 1997; Creel and Creel 2002). In comparison, spotted hyaenas and lions occur at much higher densities; lion densities across a wide array of study sites ranged from 3.5 -14 adults/100km², and spotted hyaenas from 4.5 - 82 adults/ 100km² (Mills and Biggs 1993; Creel and Creel 1996b; Woodroffe, Ginsberg et al. 1997).

2.1.2 Pack Structure and Breeding
A “pack” is defined here as any group containing a potential breeding male and female, while “group” is used to refer to a single sex group of dogs. Wild dog pack or group size varies considerably, and may consist of as few as two dogs through to a pack of more than 50 dogs (including pups), which has been observed in Mana Pools.
in Zimbabwe (N. Monks personal communication). In the Zimbabwean Zambezi Valley, the Serengeti National Park Tanzania, Selous Game Reserve Tanzania, Hwange National Park Zimbabwe and Kruger National Park South Africa, average adult group sizes ranged between 8 and 11 dogs (Frame, J.R. Malcolm et al. 1979; Childes 1988; Fanshawe, Frame et al. 1991; Mills and Gorman 1997; Creel and Creel 2002). An earlier photographic survey in the Kruger National Park put mean adult pack size at a larger 13.7 dogs (Maddock and Mills 1994).

Wild dog packs generally consist of an unrelated, dominant (or “alpha”) breeding pair, subordinate same-sex relatives, and offspring of the breeding pair (Frame, J.R. Malcolm et al. 1979; Girman, M.G.L. Mills et al. 1997). Wild dogs breed seasonally; Reich (1981) found that 90% of births in Kruger fell between May and July and proposed that this corresponded with prey gathering into higher densities around water sources, and that dens were generally located nearby, making for easier hunting and reduced travel distances for wild dogs while breeding. Other studies have since found the same pattern in southern Africa (Maddock 1993; Maddock and Mills 1994; McNutt 1996a). In the Selous in Tanzania births occurred from June to October, also peaking at the driest time of the year (Creel and Creel 2002). In other areas of east Africa wild dogs were found to den in February to June, which coincides with the wet season (Schaller 1972; Frame, J.R. Malcolm et al. 1979; Malcolm 1979). However, this is also linked to an increased density of prey which occurs during mass migrations at that time of year.

Wild dogs dig out dens, often using old hyaena dens with several entrances, or sometimes the side of river valleys in amongst rocks (Creel and Creel 2002; Malcolm unpublished report.). Pups remain in the den for the first three months of life (Malcolm and Marten 1982; Courchamp, Rasmussen et al. 2002). Litter sizes are large. In the Kruger National Park litter size in 1988/89 averaged 11.9 and ranged from 7-16 (Maddock and Mills 1994), but more recently average litter size was estimated at 9.4 pups (±SE 0.7, n=57; (Creel, McNutt et al. 2004). In the Serengeti average litter size was recorded as 10.1 (Frame et al. 1979), and the average over 38 litters in the Selous Game Reserve was 7.5 pups (±SE 0.56; Creel et al. 2004).
Pups are fully weaned at approximately eight weeks of age except in times of food scarcity, when they may nurse into the tenth or eleventh week (Malcolm and Marten 1982). Adults begin to regurgitate meat to the pups from the age of three weeks until they are ready to leave the den (Courchamp, Rasmussen et al. 2002). At nine to eleven months old pups begin killing easy prey, but they are not proficient hunters until around twelve to fourteen months old (Frame, J.R. Malcolm et al. 1979; Reich 1981).

Generally only the dominant pair in a pack will breed whilst non-breeding pack members assist to care for the pups, making the wild dog an obligate cooperative breeder (Frame, J.R. Malcolm et al. 1979; Malcolm and Marten 1982; Stephens and Sutherland 1999). Occasionally subordinate animals will breed. However, the alpha male’s hostility to other males and his behaviour of maintaining close proximity to the dominant female suggests that he would usually sire the dominant female’s pups (Malcolm and Marten 1982). Genetic data supports this observation; in the Kruger National Park subordinate reproduction occurred at similarly low levels in males (10%) and females (8%) (Girman et al. 1997). In a study in the Selous 76% of litters were produced by alpha females, and 81% of litters in the Kruger National Park (Creel, N.M. Creel et al. 1997c), while only 6-17% of subordinate females gave birth compared to 82% of dominant females. When a subordinate female does breed, often her pups will not survive to one year of age. In Kruger, at ten of twenty five dens more than one female produced pups. However, microsatellite data showed that only 8% of pups 1 year of age were produced by subordinates (Girman et al. 1997). In the Serengeti six litters of subordinate females were observed and only one litter was raised successfully (Frame et al. 1979). The successful litter was born at a different time to that of the alpha female’s litter which would have limited resource competition.

Hradecky (1985) suggested that overall suppression of marking and reproductive activity in subordinates influences their endocrine function. In a behavioural study, Hradecky (1985) found subordinate animals contributed little to territorial scent marking, and "double marking" with urine intensified between the alpha male and female in the breeding season. This behavioural pattern has been explained as a means to hide the reproductive status of the female from other males.
Creel et al. (1997c) carried out an endocrine and behavioural study in the Selous and found that during non-mating periods subordinate females had higher oestrogen levels and oestrogen/progestin ratios than dominant females, which apparently prevented ovulation. In mating periods subordinate females’ oestrogen levels dropped lower than the alpha females, and the subordinates mated less often and were less aggressive. Subordinate males also mated less often and were less aggressive, and had lower testosterone levels than dominant dogs. Beta males were similar to the alpha males in behaviour and testosterone levels, and are therefore more likely to share paternity. If this is the case then shared paternity would give beta males more incentive to remain with the pack. In contrast to the theory that reproductive suppression is caused by social stress in subordinates, Creel et al. (1997c) found basal corticosterone levels were higher in dominants.

Although the dominant role of the alpha male and female has been primarily observed in breeding, dominance in other roles has also been observed. In the Serengeti only the alpha pair regularly urine marked and they also determined most of the movements of the pack (Frame et al. 1979). Leadership of which dog leads the pack can be variable; often when the alpha female is breeding she will lead the hunts and pack movements (Courchamp and MacDonald 2001; Malcolm unpublished report). Malcolm and Marten (1982) observed that dominant dogs chased predators away from the den more often than subordinates, and the dominant male led the highest number of hunts.

2.1.3 Survivorship
Adult mortality rates in study populations across Africa have been reviewed and ranged between 57% and 20% (Creel and Creel 2002). Causes of mortality across study sites have been classified into natural and anthropogenic causes; where predation, diseases, accidents and death caused by other wild dogs were considered natural causes, and human causes include road kills, snaring, shooting and poisoning (Woodroffe, Ginsberg et al. 1997; Woodroffe, McNutt et al. 2004). The proportion of deaths caused by anthropogenic factors ranged from only 7% in the remote area of northern Botswana (n=15), to 88% in south-western Zimbabwe (n=116), an area fringed by human development and high speed roads (Woodroffe, McNutt et al.
Both adult mortality rates and their causes varied greatly, and were not strongly correlated with wild dog population density (Creel and Creel 2002). For conservation management purposes this suggests that populations need to be assessed on a case by case basis.

Wild dog pup mortality is generally high, but also varies greatly. A recent study of three of the largest populations in Africa showed a range of 65% pup mortality in Kruger, to a low of only 35% in the Selous (Creel, McNutt et al. 2004). The data from Kruger and Botswana were based on approximately 15 years of field study, and the Selous on 6 years. Within populations, pup mortality was recorded to range between 70% to 36.8% in different studies in the Kruger and adjoining Transvaal area (Van Heerden et al. 1995, n=10 packs; Reich 1981, n=121 pups), and between 76% and 17% in the Serengeti (Frame, J.R. Malcolm et al. 1979; Malcolm and Marten 1982; Burrows, Hofer et al. 1994). Although juvenile survival has been identified as a key demographic variable affecting population persistence in large populations (Creel et al. 2004), it may play a more or less significant role in smaller populations and those where deterministic factors are involved in population decline, hence the need for population specific assessment.

2.1.4 Anthropogenic Causes of Mortality
Anthropogenic factors which affect wild dog populations consist of direct persecution as well as other more indirect factors. Direct persecution has most frequently involved the shooting and poisoning of dogs which enter farming areas, although this is now illegal in many African countries, including Zambia (Buk 1995; Creel and Creel 1998; Woodroffe, McNutt et al. 2004). Although wild dogs are no longer shot within National Parks their unjustified reputation as ruthless killers has remained, resulting in continued persecution of the species outside National Parks (Childes 1988). If the dogs enter farming areas, they are often still eradicated as vermin, and reports of this type of persecution were received during the course of this study. Reports of wild dogs taking goats and commercial livestock do occur, but should be considered the exception rather than the norm (Rasmussen 1999; Creel and Creel 2002; Woodroffe, McNutt et al. 2004).
Indirect anthropogenic factors include road kills and illegal poaching. Wild dogs often adapt to using open areas such as roads to travel and to hunt prey (Fanshawe, Frame et al. 1991), and are thus killed on high speed roads which border protected areas. Illegal poaching by wire snare is generally targeted at antelope species but affects many predator species. For some reason wild dogs seem to be particularly susceptible to snaring and appear to pick up snares more frequently than other predator species (Ginsberg, Mace et al. 1995; Van Heerdan, M.G.L. Mills et al. 1995; Creel and Creel 1998), possibly due to their larger home ranges. Snares have the potential to have a large edge effect on wild dog adult mortality and population persistence, since they are often placed around reserve borders which can be frequently encountered during normal wild dog range movements (Woodroffe and Ginsberg 1999a).

All of these factors combine to have an edge effect on wild dog populations. Wild dog pack home ranges have been recorded as large as 850 – 1500 km² (Frame, J.R. Malcolm et al. 1979; Gorman, M.G.L. Mills et al. 1992). Once they leave the protection of National Parks and Game Reserves mortality rates are likely to increase. Woodroffe and Ginsberg (1999a) recorded that more than 60% of adult wild dog mortality recorded in nominally protected populations was directly caused by contact with human activities on or outside reserve borders. Thus wild dogs generally have greater chances of survival in larger reserves (Ginsberg 1994).

2.1.5 The Role of Disease in Mortality

Disease exposure was included for assessment in this study since it is a potentially major cause of wild dog mortality. Diseases which have been isolated from free ranging wild dog populations include rabies, canine distemper, parvo-virus, anthrax, and canine ehrlichiosis (Fanshawe, Frame et al. 1991; Gascoyne, M.K. Laurenson et al. 1993; Van Heerdan, M.G.L. Mills et al. 1995; Creel, N.M. Creel et al. 1995a; Woodroffe and Ginsberg 1999a). African wild dogs have also been found to host several protozoal infections, including Babesia canis, Hepatozoon canis, Toxoplasma gondii, Sarcocysts and Neospora caninum (Bwangamoi and Richardson 1993; Woodroffe, Ginsberg et al. 1997). Some may cause mortality in pups (Toxoplasma and Neospora) but it is unlikely that any of these would have a substantial effect on wild dog populations (Pierce, M.K. Laurenson et al. 1995; Van Heerdan, M.G.L. 2000).
Rabies and canine distemper virus (CDV) have both caused local extinctions in wild dog populations, and many other less severe diseases carried by domestic dogs have reduced wild dog numbers (Durchfeld, W. Baumgartner et al. 1990; Fanshawe, Frame et al. 1991; Alexander, P.W Kat et al. 1996; Woodroffe and Ginsberg 1999a). Because of the wild dog’s typically low density populations, it is unlikely that wild dogs could sustain such diseases. Evidence suggests that domestic dog populations may serve as a disease reservoir for this species (Alexander, P.A Conrad et al. 1993; Gascoyne, M.K. Laurenson et al. 1993; Ginsberg, Mace et al. 1995; Woodroffe, Ginsberg et al. 1997; Woodroffe and Ginsberg 1999a) and for other carnivores (Van Heerden 1979; Roelke-Parker M.E., L. Munson et al. 1996). Disease transmission in wild dogs is likely to be rapid for both rabies and CDV, due to the dogs’ close social interactions, resulting in high mortality (Fenner, E.P.J. Gibbs et al. 1993; Kat, K.A Alexander et al. 1995; Scheepers and Venzke 1995; Hofmeyer, J. Bingham et al. 2000).

Rabies is widespread in dog populations around the world, particularly in undeveloped countries, in which dogs cause most of the human rabies infections (Fenner, E.P.J. Gibbs et al. 1993). It has been known to devastate populations of endangered wild canids, impacting populations of Ethiopian wolves and Blanford’s foxes, as well as wild dogs (Kat, K.A Alexander et al. 1995; Woodroffe, Ginsberg et al. 1997). In the Masai Mara in 1989 twenty of twenty two dogs in a single pack died of rabies (Fanshawe, Frame et al. 1991), and it has been hypothesized that rabies or distemper may have been responsible for the local extinction of the population in the Serengeti-Mara area (Woodroffe and Ginsberg 1999a; Woodroffe 2001). Rabies has also killed wild dogs in the Central African Republic (Woodroffe and Ginsberg 1999a), in Namibia (Scheepers and Venzke 1995), and was believed to be responsible for local declines in Zimbabwe (Kat, K.A Alexander et al. 1995). Wild dog populations have generally tested seronegative for rabies despite neighbouring domestic dog populations with up to 30% seroprevalence (Laurenson, J. Esterhuysen et al. 1997; Creel, N.M. Creel et al. 1997b). This suggests they would be susceptible to infection on contact.
There has been continuing debate about the role of handling (immobilisation, radio-collaring and vaccination) in the disappearance of the Serengeti wild dogs, which was discussed in detail in the IUCN Wild Dog Status Survey and Conservation Action plan (Woodroffe et al. 1997). Burrows et al. (Burrows 1992; Burrows, Hofer et al. 1994) and East (1996) hypothesised that handling and rabies vaccination may have caused high mortality in the population by compromising the dogs’ immune systems and reactivating a latent rabies infection. This debate has been continued in more recent years (Burrows 1998; Woodroffe 2001). It is likely that wild dogs carry latent rabies infections (Fekadu, Chandler et al. 1982) rather than suffering high mortality rates following infection, as has been recorded in several populations (Kat, K.A Alexander et al. 1995; Scheepers and Venzke 1995; Woodroffe, Ginsberg et al. 1997). Alexander and Appel (1994) suggested that the disappearance of wild dogs in the Serengeti in 1991 was instead due to a canine distemper outbreak, concurrent with an outbreak in the domestic dog population. The role of canine distemper in the wild dogs’ disappearance was debated by Burrows et al. (1995). Overall there has been little evidence that handling causes chronic stress in wild dogs (Creel and MacDonald 1992); in fact there is now substantial evidence to the contrary (Ginsberg, K.A. Alexander et al. 1995; Creel and Monfort 1997a).

CDV has been identified through seroprevalence in wild dog populations and has been associated with confirmed and suspected mortality (Schaller 1972; Van Heerdan, M.G.L. Mills et al. 1995; Alexander, P.W Kat et al. 1996; Woodroffe and Ginsberg 1999a) but also with low pathogenicity in other populations (Creel, N.M. Creel et al. 1997b). Similarly, anthrax has caused deaths in wild dog populations in some areas of Africa (Turnbull, R.H.V Bell et al. 1991), while resistance to the disease has been recorded in other areas (Creel, N.M. Creel et al. 1995a). *Bacillus anthracis* spores can survive in soil and tissues for many years, therefore anthrax is endemic in many areas (Turnbull 1990).

Vaccinations for several diseases have been trialed both in captivity and in free-ranging wild dog populations, and have been the subject of controversy. Wild dog pups have died following vaccination with modified-live canine distemper virus (McCormick 1983; van Heerdan, J. et al. 1989; Durchfeld, W. Baumgartner et al. 1990), and other vaccines have either failed to increase antibody levels or may have
induced immune incompetence and predisposed the animals to disease (Van Heerdan, W.H. Swart et al. 1980; Spencer 1991; Colly and Nesbit 1992). In contrast Spencer and Burroughs (1992) found positive seroconversion from a booster dose of modified-live distemper vaccine with no harmful side effects in seven captive wild dogs. Rabies vaccination in wild dogs to date has also had limited success. Vaccination failure was reported in reintroduction populations in Etosha, Namibia (Scheepers and Venzke 1995) and Madikwe, South Africa (Hofmeyer, J. Bingham et al. 2000). There was recent success with delivery of rabies oral vaccination by bait, but this was limited to a captive pack with artificial social structure (Knobel and Toit 2003). More research is required in captive populations before free-ranging wild dog vaccination programs are implemented. It may be wiser to implement rabies management programs in reservoir populations of domestic dogs and other canids living at higher densities in wild dog areas.

2.1.6 Sex Ratio and Dispersal

There is variation in overall adult sex ratios observed in different wild dog populations under study. Studies in the Kruger National Park region and the Selous Game Reserve in Tanzania found that population sex ratios were not significantly different to parity (Maddock and Mills 1994; Creel and Creel 1995a; Creel, Creel et al. 1998b), while populations in Northern Botswana and the Serengeti in Tanzania were male biased (Frame, J.R. Malcolm et al. 1979; Malcolm and Marten 1982; McNutt 1996a).

A number of explanations have been offered to explain the observed sex bias. Wild dogs disperse in single sex groups, with littermates or siblings (Frame and Frame 1976). In many mammals it is the males that are the dispersing sex, due to intra-sexual competition for mates, and as a possible mechanism for inbreeding avoidance (Tuyttens and MacDonald 2000). However, an early study of the wild dog found that dispersal was actually female biased (Frame and Frame 1976), and subsequent studies have discovered that both sexes disperse (Fuller, M.G.L. Mills et al. 1992; McNutt 1996a; Girman, M.G.L. Mills et al. 1997; Creel, Creel et al. 1998b). If female wild dogs were to emigrate more frequently and therefore suffer higher mortality this would be a feasible explanation for male sex bias in the adult age class, as was hypothesized by Creel et al. (1998b).
In Botswana McNutt (1996a) found that there was a male bias in the adult wild dog population, and that although both sexes dispersed with equal frequency, females dispersed at an earlier age, in smaller groups, and generally established ranges nearby to their natal range. Males had a much greater dispersal distance (n=57 dispersing dogs). This dispersal trend fits the mate competition hypothesis in the case of a male bias in the population, where females would be expected to emigrate more readily, in smaller groups and upon reaching reproductive age (Waser 1996). McNutt (1996a) proposed resource competition may explain dispersal in both sexes, as access to kills is reduced with increasing age for all subordinate dogs. All dogs were found to emigrate in the presence of their opposite sex parent, and inbreeding avoidance may explain why males disperse further. By waiting longer and dispersing with non-litter mates in larger groups the males may counter the associated increased mortality risks of long distance dispersal (McNutt 1996a). McNutt also re-assessed data from Frame et al.’s (1979) study in the Serengeti where an adult male bias was also found, and established that although female dispersal was observed to be more frequent in this population, females did remain close to their natal areas while males disappeared from the study area, and males who did not disperse from their natal packs had lost their probable mother and had access to unrelated females. Therefore the adult sex ratio may well have an effect on sex biases in dispersal by affecting mate competition.

In the Selous Game Reserve in Tanzania where no overall sex bias was detected in the study population, males had higher survivorship after the age of two years old resulting in a sex ratio of 0.55M: 0.45F, although this was only significant after the age of seven years (Creel and Creel 2002). Females were found to disperse significantly more frequently than males (annual probability of dispersal was 0.21 for males, 0.33 for females), the risks of which may explain the lower survivorship in females in this case (Waser 1996). Dispersal was found to have no sex bias in Kruger National Park, where the adult sex ratio was also unbiased (Maddock and Mills 1994; Girman, M.G.L. Mills et al. 1997; Creel, N.M. Creel et al. 1997c).

None of the hypotheses discussed above hold across all wild dog populations. Although emigration may be a source of mortality, particularly given the large dispersal distances and the threat of edge effects to wild dog populations, in the largest study populations displaying a male sex bias the females were found to stay
close to their natal ranges while the males dispersed further (McNutt 1996a, and his re-assessment of Frame et al. 1979). Therefore female emigration patterns do not seem to explain the male bias adult sex ratios, as the females are not removed from the population. Although females were observed to disperse more frequently in the Selous population, no significant male bias was observed in that population (Creel and Creel 1995a) save in age classes over 7 years old (Creel and Creel 2002).

Alternatively, adult male bias may be the cause of female emigration (due to mate competition), rather than the result of failed female emigration. However, there is limited data to support male bias in pups, and only one case in the Serengeti where male bias in pups corresponded to male bias in adults (Malcolm and Marten 1982, n=10 litters). There was no significant male bias in the adult sex ratio in the Kruger National Park or the Selous Game Reserve and no bias in the birth ratio was observed in either population (Maddock and Mills 1994; Creel and Creel 1995a; Creel, N.M. Creel et al. 1997c). Malcolm and Marten (1982) proposed that male bias observed in the pup sex ratio suggested that males contributed more to pup survival, and this has been supported by the observations above where females were found to disperse more frequently and earlier than males, and thus females helped less with communal rearing of pups. However, again, the cases of more frequent female dispersal do not necessarily correspond with the populations which exhibited male bias in sex ratios for pups and/or adults. In fact only the Serengeti population showed more frequent female emigration combined with male sex bias in pups and adults (n=10 litters, Frame et al. 1979; Malcolm and Marten 1982).

Creel et al. (1998b) investigated birth sex ratios in wild dogs and the underlying physiology, based on 18-20 litters in the Selous population. The study found that primiparous females produced litters with a significant male bias, while multiparous females produced more females. A previous study of the same population found increased oestrogen levels in subordinate female wild dogs compared to dominant females, during non-mating periods (Creel, N.M. Creel et al. 1997c). Creel et al. (1998) suggest that increased, albeit slowly decreasing, oestrogen levels in newly dominant females may be associated with male-biased sex ratios in primiparous litters. However, given the low turnover of dominant females in wild dogs (Creel and Creel 2002) one would expect at least an equal, if not higher, proportion of multiparous
litters in a stable wild dog population. Since the proportion of male pups produced by primiparous females was approximately equal to the proportion of female pups produced by multiprimous females (63% vs 64% respectively), this would be more likely to result in an equal or female biased birth ratio rather than a male biased ratio. No overall significant sex bias was observed in the 20 litters monitored in Creel et al.’s (1998) study, although of the 18 litters where the mothers parity was known, 12 were multiparous. Therefore, the information on male bias in birth ratios resulting from primiparous females would fail to explain the overall male bias observed in some wild dog populations, unless these populations had an unusually high turnover of alpha females.

Two main hypotheses have been discussed extensively in the literature to explain secondary sex ratio bias in mammals (sex ratio bias at birth); the Trivers and Willard hypothesis and the local resource competition hypothesis. The Trivers and Willard hypothesis predicts that mothers in good condition produce offspring biased towards the sex that has the highest variation in reproductive fitness, and thus increase the chances of highest future reproductive success (Trivers and Willard 1973; Maynard-Smith 1980). The second hypothesis predicts the opposite, that mothers in poor condition will produce the sex most likely to disperse, based on the principal that these offspring are less likely to compete with the parents for resources (Clark 1978). However, there are often complex interactions between environmental stochasticity and population density, which may result in inconsistent sex ratio trends and affect the fit of any proposed sex ratio models (Kruuk, Clutton-Brock et al. 1999; Post, M.C. Forchhammer et al. 1999; Bradshaw, Harcourt et al. 2003). Thus details on demographic, sociobiological and environmental factors are required for an understanding of apparent sex bias in any population.
2.2 OBJECTIVES

The objective of this section of the study was to determine the present status of the Lower Zambezi wild dog population, its structure and dynamics, and assess any causes of decline and potential threats to the population.

Specifically, the aims were to:

1) Determine population size and density in the study area

2) Determine population fecundity and rates of survivorship in adults and pups, and identify the primary causes of mortality. This included an assessment of natural and anthropogenic causes previously identified in other wild dog populations

3) Assess pack dynamics and dispersal patterns and compare these to previous studies of larger populations

4) Determine the presence or absence of secondary sex bias (sex bias at birth) or adult sex bias in the population, and test for effects of mate selection on dispersal.
2.3 METHODS

2.3.1 General Tracking Methods

Observations of the Lower Zambezi African wild dog population were carried out over a 5 year period, from May 1999 to October 2003. Field work seasons fell between April 1st and 30th November of each year. No ground tracking was carried out during the Zambian wet season (December to March) since the study area was cut off from vehicle access by high river levels and impassable areas of mud. Sporadic data were collected from December through March by occasional aerial tracking and records from staff at safari camps within the study area. An average of 208 days per year was spent in the field, a total of 1040 field days. This included days that were spent on vehicle and camp logistics, and surveying the other related species for the purposes of this study; lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*), prey counts and vegetation surveys. Wild dogs were located on a total of 388 days. Some days included sightings where more than one pack was observed; the inclusion of this data from all pack observations gave a total of 440 “pack days”.

Although largely restricted to the dry season, the field study season included the wild dog breeding and denning period plus 3 to 4 months of nomadic movements either side. The data therefore covered the period with the largest variations in wild dog home range behaviour according to previous studies (Reich 1981; Gorman, M.G.L. Mills et al. 1992; Burrows 1995). No major seasonal migrations are known to occur in the study area, possibly due to biogeographical boundaries (Figure 2.2), therefore wild dog movements during the study period were likely to be representative of pack annual movements.

Due to their large home ranges and nomadic habits the dogs were collared and tracked using radio telemetry. At least one wild dog per pack was fitted with a radio-collar wherever logistically possible. Wild dogs rarely separate from their pack for more than a few hours during hunting (McNutt 1996a; McCreery and Robbins 2001), therefore radio-collaring one dog allowed for accurate tracking of the entire pack. Telemetry was used to aid direct observations; no remote tracking data were collected.

Dogs were individually identified using their unique pelage patterns. Left and right side photographs were taken of each dog using a Digital Hi-8 Video Camera Recorder
(Sony® Australia Ltd, Sydney) and entered into a computer database file. Figure (2.1) below provides an example of the distinct patterning of black, gold and white typical of the species. Each dog was given an identification number, beginning with the pack number for the area (P2), followed by the month and year that the pack was first identified (1099) and the sex and number of the individual dog (F3). The Universal Transverse Mercator (UTM) quarter degree squared coordinate (QDS) was also recorded for the area in which each pack was discovered (1529D1).

Once dogs were sighted the location coordinates were recorded using a Global Positioning System (GPS); either a Garmin 12XL or later a Garmin Etrex model (Garmin International Inc, Olathe, KS, USA). Coordinates were imported into the Geographical Information System software package ArcGIS 8.1 (1999-2001, ESRI™ Inc., USA) for spatial analysis.

Permission was granted by the Zambia Wildlife Authority to drive off road within the National Park for research purposes. The existing vehicle roads and tracks provided a linear network of 255.4km for tracking. Given a signal range of approximately 3km, this network covered 83% of the valley floor within the study area. Radio telemetry signal range is restricted by vegetation and other line-of-sight barriers and therefore the remaining areas were covered by using high points in the foothills of the escarpment which gave increased signal range. These were accessed by vehicle or on foot. When no signal was obtained via ground telemetry aerial telemetry was used. Once the dogs were located via aerial telemetry the vehicle was driven to within sighting distance, usually 20-100m. Binoculars (8x30) were used for identification and behavioural observations.
The central study area was defined by the home range movements of the monitored packs and biogeographical boundaries. Ground tracking covered approximately 790km². Aerial tracking was generally carried out in the escarpment area and limited to linear transects within 10-15km north of the valley floor, increasing the total search area to over 1500km².

Figure 2.2 illustrates the core study area. Remote areas of the escarpment outside the study area boundary were accessible by aerial tracking but were rarely surveyed. Records of wild dog GPS locations are clustered in the valley floor area and indicate that the study area gave good coverage of wild dog home range movements. Village settlements begin immediately to the west of the study area boundary; these areas were easily accessible but rarely entered by wild dogs and therefore did not form part of the core study area. The Zambezi River formed the southern boundary of the study site, and the Zambezi Escarpment can be seen on the satellite image as a pale green area occupying a large portion of the northern section of the study area.
2.3.1.1 Immobilisation

A Zambian-registered veterinarian was called in to assist with immobilisation, as stipulated by the requirements of the Zambia Wildlife Authority. Non-veterinarians holding a recognized qualification in Wildlife Chemical Immobilisation were permitted to dart and immobilize animals to remove snares with the permission of the Lower Zambezi Area Warden. Due to the logistical difficulties and costs of locating and transporting an available veterinarian to the study area, in the case where a wild dog was immobilized for snare removal authorisation was given for a collar to be fitted if the dog was of suitable age and fitness and from an uncollared pack. Male dogs were preferentially darted due to their larger body size and strength.

Each animal was darted using a combination of approximately 6.6mg/kg of ketamine hydrochloride (Ketaject, 100mg/mL, Dopharma B.V., Zalmweg 24, 4941 VX Raamsdonksveer, Netherlands) and 1mg/kg xylazine hydrochloride (Rompun, Bayer
Laboratories, RSA), depending on the dog’s condition, age and if it had recently eaten (based on belly size). Dosages ranged from 150mg to 200mg ketamine hydrochloride and 30mg to 40mg xylazine hydrochloride per animal.

Dogs were darted in the shoulder muscle mass whilst standing, or preferably resting in a sternally recumbent position if the dogs were not habituated to the vehicle. Standing dogs often heard the dart rifle when it was fired and evaded the dart. The shoulder was chosen over the muscle mass of the hind leg because it was easier to obtain a perpendicular angle for darting in the shoulder when the dog was seated, generally with its hind legs lying to one side. The target muscle mass was roughly the same size in shoulder and upper hind leg. Darting was carried out from a distance of 24m or less, using a plastic 1.5 mL dart and 20mm needle, projected from a Dan-inject 7-JMSPEC-16 dart rifle (Dan-Inject™, Denmark), with pressure calibrated to distance (to a maximum of 6 bar for 24m).

Anaesthesia induced sternal recumbency was achieved between 3 to 20 minutes after darting. Occasionally a top-up dose was required by dart rifle or hand syringe if the dart dosage had not fully discharged intra-muscularly, or if the initial dose did not allow sufficient time to fit the collar and take biological measurements and samples. The dog was treated with a 2mL dose of long-acting penicillin (Megapen) by intramuscular injection after dart removal. The dog’s eyes were covered and cotton wool placed in the ears. Pulse, respiration rate and temperature were monitored regularly throughout the procedure. Where time permitted, standard body measurements were taken including height from longest toe to shoulder; length from nose to tail; girth around the widest part of the rib-cage; and weight.

Two 10mL blood samples were drawn from the saphenous vein, or if blood pressure was depressed by the sedative effects of xylazine hydrochloride, from the jugular vein. 10ml aliquots were stored in vacutubes containing EDTA and Heparin as preservatives, then frozen for storage until analysis. A further 5mL to 10mL of blood was drawn and allowed to stand for 6-12 hours, then the serum was drawn off by syringe and frozen in cryotubes. The blood serum samples were sent to the University of Pretoria, either within 48hrs stored cold, or frozen then transported in liquid nitrogen and stored at -75°C until analysed for antibodies to a range of pathogens.
Tissue samples were taken as a 2x4mm ear-notch which was halved, and then one sub-sample was frozen while the other sub-sample was preserved in 80% ethanol as a backup. The frozen tissue samples were transported to the University of Pretoria in liquid nitrogen and stored at -75°C until DNA extraction (see Chapter 4).

The dogs were monitored until fully recovered and reunited with their pack, which occurred between 55 and 190 minutes after darting. No reaction to carrying the collar was observed on any dog, and most were observed hunting normally within a few hours of the procedure. Occasionally other pack members would show interest and chew the collar antenna for the first few days.

2.3.1.2 Disease tests
Disease testing was carried out opportunistically when samples could be obtained from immobilised dogs. Pathogens tested for had been previously identified in wild dog populations (Woodroffe, Ginsberg et al. 1997) and consisted of: canine distemper virus, canine parvovirus, canine adenovirus, canine herpes virus, and canine para-influenza virus. All but canine para-influenza virus are known to have severe effects on either adult or juvenile wild dogs or, where wild dog data is lacking, on domestic dogs (Woodroffe, Ginsberg et al. 1997). Serology tests were carried out using indirect fluorescent antibody tests (Dept of Veterinary Tropical Diseases, Faculty of Veterinary Science, University of Pretoria, RSA). Rabies was not included due to the logistics and expense of testing at the time of the study.

2.3.1.3 Radio-collars and telemetry equipment
Radio-collars were manufactured to design specifications by Sirtrack Ltd (Havelock, New Zealand). The transmitters were micro-controlled, with a base pulse of 50 pulses per minute (ppm), which changed to 30ppm after 15 seconds of inactivity and then returned to 50ppm after subsequent movement. Mortality was indicated by a pulse rate of 15ppm and occurred after 24 hours of inactivity. Two AA lithium cells gave a minimum transmission life of approximately two years. Stainless steel plates with protruding rivets were fitted to the collar as an anti-snare device (see Figure 2.3). Wild dogs typically catch snares around the neck (see Results 2.4) and the purpose of this device was to trap the wire snare in the rivets on the collar where it would either
break during the dog’s struggles, or fasten onto the metal plate of the collar between the rivets, thus protecting the dog’s neck. The dog would generally break free from the tree or branch the snare was fastened to, and the snare could later be removed. The collar and rivet design was modified from collars originally designed by G. Rasmussen (Painted Dog Research Project, Zimbabwe). Each collar was custom fitted to the appropriate neck size for each animal, fastened with locknuts and any excess trimmed off.

![Figure 2.3. Adult male wild dog fitted with an anti-snare radio-collar.](image)

Each collared dog was tracked using a Telonics TR-4 receiver (Telonics Inc., Mesa, A.Z. USA) and a directional hand-held 3 element yagi antenna (model FANT150, Sirtrack Ltd Havelock, New Zealand).

### 2.3.1.4 Data collection

**i) Direct Observation**

Tracking generally began half an hour before first light and continued until following became impossible due to terrain or loss of signal. Tracking sessions ran from a minimum of one day to usually several consecutive days. The dogs were followed until they settled for the night, then again at first light the next morning when any change in position during the night was recorded. The use of a spotlight appeared to disturb them, particularly when hunting, so this was kept to a minimum. Moonlight was used for night tracking when conditions were suitable. Numerous other studies have found wild dog activities fell between the times of 5.00 to 9.00 hours and 17.00
to 20.00 hours (Fuller and Kat 1990; Mills and Biggs 1993; Creel and Creel 2002), within the tracking periods of this study.

When a signal was obtained but the dogs were inaccessible their position was estimated by triangulation, using direction and signal strength from two or more points. This method took into account the effects of different densities of vegetation and signal bounce caused by the escarpment, and from experimental trials was found to be accurate to within 100-400m. Error in GPS readings taken prior to May 2000 was approximately 30m due to intentional signal degradation by the US Department of Defence. Later readings taken on the Etrex model GPS were accurate to <15m. For this analysis a consistent error of 30m is assumed. Although triangulation error was greater, the dogs were only inaccessible when within thicket or escarpment vegetation as these were the only physical barriers to access, therefore the increased error would not alter the recorded habitat type for that location. Habitat type was recorded directly from all observations, rather than from mapping.

For each observation the following data were recorded; date, time, location details, GPS coordinates, number of adult males and females present (2 years old or more), number of yearling males and females present (12 to 24 months old), number of male and female pups present (1 year old or less), identification codes, belly score, whether the dogs hunted, whether they killed, prey species and sex, the presence of spotted hyaenas or lions, vegetation type, and details of film footage or photos taken. Additional behavioural notes were also taken. More details on definitions of these behaviours and their analysis is given in the following chapter (3). GPS locations were taken either side of a period of movement as either resting sites or kill sites. If no kill was confirmed and/or the pack was only seen on the move locations were recorded as either hunting or travelling.

Intrapack and interspecific interactions and behaviour were recorded. The alpha pair of each pack was identified by dominance behaviour and the incidence of increased double urine marking during the breeding season (Hradecky 1985), and additionally for females by signs of pregnancy, lactation and parturition. Relationships were confirmed with microsatellite analysis where DNA samples were available. Faecal
samples were collected opportunistically in and around known den areas, or when following a pack.

   ii) Survey Forms
Booklets containing photographs of identified wild dogs, pack composition information, and sightings questionnaire forms were compiled at the beginning of each field season and distributed to all the safari operators in the study area. Sightings were collected only from qualified safari guides employed by the camps or Zambian Wildlife Police Officers on patrol, through collection of the forms and also direct reports via VHF radio. Data collected by this method included: vegetation type, pack composition at each sighting, presence or absence of the competitive predators, lion and/or spotted hyaena, prey species and sex, belly scores if known, and any observed activities. Photographic identification kits of recorded wild dogs were distributed to safari guides at the beginning of each field season to increase reliability. Faecal samples were occasionally collected and submitted by guides, as were photographs of new litters or immigrant dogs. Submission rate increased when a reward of a bottle of whiskey was offered in reward for a sample and/or accompanying identification photograph of new dogs.

There were some irregularities in the quantity of wild dog data for the 1999 and 2001 field seasons as no radio-collars were fitted during these years. This was due to a difficult organisational transition period for the Zambia Wildlife Authority which resulted in failure to renew permits for immobilization and radio-collaring. In these years the dogs were tracked by spoor, and via reports from the safari camps. Although field work ceased at the end of 2003, photographic identification records were collected remotely to update population status until July 2005.

2.3.2 Data Analysis
Visual contact was frequent enough to document changes in pack composition through photographic identification of all study animals. Detailed life history records for each dog were obtained and used in demographic data analysis. Frequent annual sightings of all individuals in the study area indicated that data is representative of the true population within the study area.
2.3.2.1 Survival analysis

Survival analysis was carried out on the population based on life history records which provided age at death for analysis. Updates on pack status during 2004 were obtained by remote collection of sightings forms and confirmation photographs submitted by safari guides and were included in this section of analysis. Survival analysis takes into account right-censored values, for example dogs that emigrated and left the study area, and those that survived beyond the term of the study. This method prevents the underestimation of survivorship which may otherwise result from excluding censored values in a small study population. Using the program GenStat 8.1 (2005) Kaplan-Meier estimates of survival curves were plotted using data grouped by sex and area, the latter to test whether survival differed inside or outside of the National Park. Time was specified by age at death, using an entry time of 0 age, and analysis was carried out according to the methods of Kalbfleisch and Prentice (1980). Non-parametric log-rank tests were run to test differences in survivorship for males and females, and to compare between survivorships in different areas; this test ranks all cases equally rather than weighting early events, and gives a test statistic with a $\chi^2$ distribution (Collett 1994). Effects of rank were not analysed here due to small sample sizes.

Annual survivorship was based on each year ending on May 30\textsuperscript{th} to coincide with the annual breeding cycle. Data were grouped by age class and graphed to compare annual survival rates. Yearlings are largely independent of adult care and have been pooled with adults in other studies (Fuller, P.W Kat et al. 1992a; Burrows, Hofer et al. 1994) so they were pooled in this comparison to increase sample size. Differences in average pup and adult survivorship were compared using a Students unpaired t-test.

Pups remained underground at the den until approximately three weeks of age, so pup survivorship was difficult to estimate accurately. Some litters were not counted until after the pups had left the den and moved to an accessible area at approximately two to three months of age. Data therefore represents a minimum estimate of litter size, and may underestimate pup mortality. In the case of the GMA pack litter of 2001, pups were first seen at five months of age. Survival for this litter was conservatively based on a litter size of seven pups, the smallest litter size observed in this study and also in 18 litters studied in Kruger NP (Maddock and Mills 1994).
For classification of survival for animals of unknown fate, animals which disappeared were assumed to be dead under the following criteria:

1. Dominant (alpha) dogs that disappeared, except if pack dissolution or same sex immigration had occurred.
2. Pups less than 8 months of age which disappeared.
3. Dogs of five years of age or older who disappeared alone, with no preceding behavioural indications of conflict or changes in pack hierarchy, and who were not seen after separation from their pack.
4. Dogs last observed with neck snares that disappeared before the snare could be removed.

Other studies have adjusted survival data for undetected emigration by assuming the number of undetected emigrants of a given age, sex, and rank was equal to the number of previously unknown immigrants of the same age, sex and rank (Creel and Creel 2002). However, for a small population with limited samples of different age, sex and rank classes this method was unreliable. Additionally, this method assumes no edge effects are acting on the population, which if present could result in under-estimation of emigrants as few immigrants enter the study population. In this study, observed immigration was substantially less than observed emigration, suggesting edge effects, therefore mortality rates were based on the available descriptive data.

Where unknown, ages were estimated by pelage, overall condition, tooth wear and social rank. With the exception of 5 adults which disappeared in the first year of study, a dog from each unknown age cohort was darted and closely examined at sometime during the study, so age estimates were considered accurate up to 2 years of age and accurate to within 2 years in older dogs. Ages were estimated for a total of 18 out of the 69 dogs. Removal of these individuals would have removed a substantial amount of adult mortality and dogs of alpha rank, so the data were included.

### 2.3.2.2 Pack dynamics

A pedigree tree was constructed for the population using observational field data for birth, death, rank and dispersal for each individual. Rather than using a traditional pedigree tree program which is limited to sire and offspring information, the tree was
drawn over a timeline incorporating the duration of the study. This format provides
details on seasonal survival as well as data on immigration and emigration which did
not necessarily result in successful pack formation and breeding.

2.3.2.3 Dispersal and sex ratios
Definitions of emigration in African wild dogs have differed to fit behavioural
variations observed across study sites (Frame, J.R. Malcolm et al. 1979; Fuller, P.W
Kat et al. 1992a; McNutt 1996a; Creel and Creel 2002). Emigration was defined here
as the movement of individuals or groups of same sex individuals out of an
established pack. In the case of pack dissolution, only the individuals which moved to
a new home range were counted as emigrants (although home ranges often
overlapped), as these individuals bear the risks associated with moving to a new area
to find new mates. In this study emigration was not defined as dependent on the
successful establishment of a new pack because this would have excluded individuals
who dispersed and then either died, left the study area, or remained as a single sex
group until observations were censored at the end of the study. Emigration was
recorded if: i) Same sex siblings separated from the main pack and were subsequently
observed as an independent group for 48hrs or more. If the group later returned to the
natal pack this was recorded as attempted emigration. ii) Individuals or a group
separated from their natal pack before disappearance from the study area. iii) If dogs
were aged between 18 months and 4 years old and disappeared along with, or within 7
months of, other same sex siblings. Although these criteria are not comprehensive
they covered all observed situations for the study population.

Immigration was recorded where previously unidentified same sex groups appeared in
the study area, regardless of whether they formed a successful breeding pack. Pack
dissolution here is the same as defined by Reich (1981), the breakdown of an extant
pack through combined adult and juvenile age classes permanently splitting into same
sex groups.

Sex ratio data were tabulated and graphed according to age class. Annual means and
standard errors were calculated for the adult/yearling age classes for comparison with
other studies. Annual adult sex ratio data was not independent as adults often
contributed data to more than one year, therefore data could not be pooled.
Contingency table analysis was used to test for any significant annual bias. The program GPOWER (Erdfelder, Faul et al. 1996) was used to assess power in analysis. Pup litters were independent samples, therefore data was combined and tested for bias using a non-parametric Wilcoxon matched-pairs signed-ranks test.

Because wild dogs are obligate cooperative breeders, the pack is the important ecological unit, therefore general analysis was conducted at the pack level rather than the individual level to avoid pseudo-replication.
2.4 RESULTS

2.4.1 Demography

The study population consisted of 69 African wild dogs over the duration of the study, 47 of which obtained yearling or adult status. Data were collected for 12 pack years. Mean annual density of adults in the study area was 1.7 dogs/100km² (±SE 0.1) ranging from a maximum of 2.2 dogs/100km² to a minimum of 1.5 dogs/100km² in any one year.

Data collected during immobilisation showed slight sexual dimorphism in the Lower Zambezi wild dogs, with mean weights of 27.42kg (±SE=1.29, n=7) in males and 23.0kg (±SE=1.52, n=3) in females.

2.4.1.1 Survival analysis

Figure 2.4a and 2.4b below show Kaplan-Meier survivorship function estimates for the Lower Zambezi African wild dog population between October 1998 and May 2004. Decline in survivorship was steepest during the first year, the survivorship function stabilised from yearling age through to almost 4 years old, then steadily declined over time. No dogs over the age of 8.5 years were observed. The probability of survival to adulthood (2 years) in the population was approximately 60%.

![Figure 2.4a](image1.png)  
**Figure 2.4a.** Kaplan-Meier estimate of the survivor function for the Lower Zambezi population. Survival time is in years.

![Figure 2.4b](image2.png)  
**Figure 2.4b.** Kaplan-Meier estimate of survival by area grouping. Survival time is in years.
There was no significant difference in survivorship between males and females (Log-rank, $\chi^2 =0.196$, d.f.=1, $P=0.658$). Survivorship within the National Park was not significantly different from that in the GMA (Log-rank, $\chi^2 =0.574$, d.f.=1, $P=0.449$). However, as shown in Figure 2.4b, the survivorship curve is steeper for the National Park after the age of about three years. Under the Kaplan-Meier model, dogs had a 50% probability of survival until the age of 3.5 years in the National Park, compared to a 50% probability of survival until 5 years in the GMA.

Figure 2.5 Annual survivorship by age class. N ranged from 12 to 18 adults/year, and 5 to 18 pups/year.

Figure 2.5 shows annual survivorship of pup and adult age classes across the study population. Mean survivorship of adults was high compared to pup survivorship, at 73.4% (±SE 3.9) and 47.0% (±SE 12.6) respectively. The difference was not statistically significant (Students t-test; $t=2.0$, df=10, $p=0.073$) Pup survivorship was highly variable, ranging from 0.0% to 71.4%.

2.4.1.2 Causes of mortality

Confirmation of the causes of mortality was restricted to cases where death was actually observed or the carcass was found before consumption by other predators. Given the dogs’ nomadic movement patterns, only carcasses of collared dogs could be located soon after death. In this study the cause of death was confirmed for only 5 wild dogs. However, there was often a good indication of the cause of death from circumstances observed during sightings just prior to death or disappearance. Table 2.1 contains a summary of data of confirmed and suspected causes of mortality in
adults and yearlings. Mortality data was omitted for dogs that did not fall into any of the following categories:

1) Predation was suspected if disappearance occurred during a period when the pack was observed to be harassed by lions or spotted hyaenas and/or the dog suffered injuries characteristic of an encounter with predators. In two cases dogs with injured legs were killed and consumed by predators; these were included here since predators were the final cause of death, although the cause of original injury was unknown.

2) Natural causes were suspected where the dog had been observed to be deteriorating in condition prior to disappearance, with no obvious causes (included dogs over 8 years old).

3) Snaring was suspected as a cause of death when dogs who were not potential emigrants disappeared between December and March and surviving pack members were found carrying snares at beginning of the dry season in April. Due to the number of surviving dogs observed carrying snares during the dry season (see below, Section 2.4.1.2.i.) this was considered a reasonable estimate of snaring mortality.

4) Unknown cause of death was recorded whenever a carcass was found with no obvious cause of death, and for any animals that disappeared but did not fit any criteria above. No signs of infectious disease was observed in any age group during the course of the study therefore disease was not included in the causes of death.

Table 2.1. Number of suspected and confirmed causes of mortality in adults and yearlings.

<table>
<thead>
<tr>
<th>Cause of death</th>
<th>Suspected</th>
<th>Confirmed</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural</td>
<td>3</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Snare</td>
<td>13</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>Predator</td>
<td>4</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Unknown</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

As shown in Table 2.1 above, snaring accounted for 54% of adult mortality, predators for 19%, and unknown and natural causes combined accounted for 27%.

i) Observed Snaring.

Adult mortality from poaching was reduced by this project which was part of an ongoing conservation program. In addition to the disappearances attributed to snaring in Table 2.1 above, neck snares were observed on 29% (n=14 dogs) of the adult wild dog population, and almost certainly would have had a substantial effect on
population persistence if not removed. Four snares were found on alpha dogs, the death of whom can result in pack dissolution due to inbreeding avoidance (McNutt 1996a; Creel and Creel 2002). Two snares were removed from a two year old female, one of a group consisting of only two sisters, who later became alpha female of the GMA pack. This female produced three litters, one of which had a survival rate of 72% (8 of 11 pups) despite having only four adults in the pack to raise them. It is conservatively estimated that at least nine dogs would have eventually died from severe snare injuries if they had not been treated. This data alone suggests that snaring was the major cause of adult mortality in the adult-yearling population.

There was no difference between the occurrences of snares observed on dogs from packs based inside the National Park compared to those based in the GMA, 64% of snares were observed inside the National Park. The eastern Chiawa GMA is reserved for photographic safari activities and is under the protection of the Zambia Wildlife Authority, therefore all pack ranges fell inside protected areas.

**ii) Predators**

Adult mortality from predators was rare, however there is strong circumstantial evidence of competing predator interference at some dens. Signs of large predators (spoor and droppings) were observed within the immediate vicinity (<30m) at 3 out of 7 den sites. Packs often moved considerable distances between dens while pups were young. In 2000 the Mushika pack shifted dens when the pups were 6 weeks old, to an initial distance of 11.6 km over two days, then another 16 km over the following week. Despite the long-distance moves, five out of nine pups survived to yearling age. In 2003 the GMA pack shifted dens continuously; with pups at approximately 4 weeks of age the pack moved 4.5 km, then averaged 2.4 km every two days as they moved east along the escarpment ridge for another 15 days, to a total of 22.5 km from the original den site. Dens were accessible only on foot or by aerial tracking since they were located in the escarpment, and the continuous shifting made access difficult, nevertheless spotted hyaenas were encountered at two separate den sites for this pack. By the age of 3 months only three of the eight pups had survived, and none survived to yearling age. Two yearling males who were left to baby-sit at these dens on separate occasions also died during the same time period, and the carcass of one of these dogs was observed being eaten by a spotted hyaena. These events also coincided
with an increase in observed kleptoparasitism by spotted hyaenas in the same year (2003). The impact of competing predators on wild dog population dynamics is discussed further in Chapter 4.

**iii) Infectious Disease**

*Table 2.2 Titre results for indirect fluorescent antibody tests for a range of canine pathogens.*

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>Pack</th>
<th>Canine distemper virus</th>
<th>Canine parvovirus</th>
<th>Canine adenovirus</th>
<th>Canine herpesvirus</th>
<th>Canine parainfluenza virus</th>
</tr>
</thead>
<tbody>
<tr>
<td>P21099F6</td>
<td>Mushika</td>
<td>negative</td>
<td>1:10</td>
<td>1:40</td>
<td>positive</td>
<td>1:40</td>
</tr>
<tr>
<td>P21099M3</td>
<td>Mushika</td>
<td>1:10</td>
<td>1:20</td>
<td>1:40</td>
<td>positive</td>
<td>1:20</td>
</tr>
<tr>
<td>P10498F3</td>
<td>Jeki &amp; GMA</td>
<td>1:40</td>
<td>1:10</td>
<td>1:40</td>
<td>positive</td>
<td>1:40</td>
</tr>
<tr>
<td>P30602M3</td>
<td>Simwenzenze</td>
<td>1:20</td>
<td>negative</td>
<td>1:20</td>
<td>positive</td>
<td>1:20</td>
</tr>
<tr>
<td>P41201M4</td>
<td>GMA</td>
<td>negative</td>
<td>negative</td>
<td>1:40</td>
<td>positive</td>
<td>1:20</td>
</tr>
</tbody>
</table>

Results from indirect fluorescent antibody tests (Table 2.2) suggest previous population exposure to all pathogens tested for, but low titre levels (1:10 to 1:40) imply infections were not recent prior to sampling. The test for canine herpesvirus was only run at a single serum dilution so no conclusions can be drawn about the level of infection or timeframe involved.

Individual P41201M4 was a yearling when tested; all the other individuals were adults. All packs had previous exposure to canine distemper virus, including a male immigrant to the area (P30602M3). No symptomatic evidence of current infectious disease was observed in either pups or adults in the Lower Zambezi study population.

**2.4.1.3 Breeding**

Breeding was seasonal, with all litters born between 1st May and the first week of September. The latest litter was that of a subordinate female who became dominant immediately after the death of the alpha female, who had been pregnant. Excluding this late litter all breeding fell between May and July. Mean litter size for the population was 8.0 (±SE 0.58, n=7) and ranged from 7 to 11 pups.
Table 2.3 summarises the data on litter size, survival rates and the number of adult and yearling carers in the pack. There was a moderate positive correlation between the number of adults and pup survivorship to yearling age ($r= 0.59$, df=6, p=0.16) although it was not significant. There was no association between the number of combined adults and yearlings against pup survivorship ($r= 0.067$, df=6, p=0.87).

Table 2.3 Litter size, survival to one year of age, and associated number of adults and combined adults-yearlings in the pack.

<table>
<thead>
<tr>
<th>Litter size</th>
<th>Proportion survived</th>
<th>Adults</th>
<th>Adults &amp; Yearlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>0.7</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>11</td>
<td>0.7</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>8</td>
<td>0.0</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>7</td>
<td>0.7</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>9</td>
<td>0.6</td>
<td>6</td>
<td>11</td>
</tr>
<tr>
<td>7</td>
<td>0.6</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>7</td>
<td>0.1</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

There was no strong association between litter size and the number of adults or litter size and the number of adults and yearlings ($r=-0.33$, df=6, p=0.47; and $r=0.12$, df=6, p=0.79 respectively).

Only one subordinate female was observed to breed during the course of the study. This female reached parturition two weeks after the alpha female and denned less than 50m away. The fate of her litter is unknown but all pups had disappeared by 3 weeks of age, when she returned to the alpha female’s den to help care for the pups with the rest of the pack.

2.4.2 Pack Dynamics

Mean annual adult pack size was 7.2 ($\pm$SE 1.7, range 3 to12, n=12 pack years). Appendix 1 contains a figure showing the life history of each individual and pack dynamics for the duration of the study period. Two matriarchal lineages over four packs were followed throughout the study. In this study population, females showed higher philopatry; in two of two cases of new pack formation (GMA pack and Simwenzenze pack, Appendix 1) females remained in their natal home range and males immigrated into the area.
The first pack observed was the Jeki pack, which originally consisted of 7 adults and 5 new pups. During the first year of study, this pack was dramatically reduced to 5 orphaned pups, at the age of 10 months old. The Jeki pack was not collared in 1999 so there is limited hunting data available. It is possible the pups survived on small prey items, although they were observed successfully killing impala at regular intervals from the age of twelve months. The Jeki females survived to found the GMA pack in 2001, joined by males from the Mushika pack. The Jeki males emigrated from the study area in two separate groups. When the first alpha female of the GMA pack died her only surviving sister became the new alpha.

The second matriarchal line originated in the Mushika pack. Mushika pack dissolution occurred after the disappearance of the alpha male, whereby the remaining Mushika males joined the Jeki female siblings to form the GMA pack. The Mushika females were joined by new immigrant males to form the Simwenzenze pack. When the Simwenzenze alpha female died one of her daughters became the new alpha. No inbreeding was observed in either pack.

Although field work ceased at the end of 2003, photographic sightings records were collected from the safari operators until the end of July 2005. These data indicate that the three females from the GMA pack emigrated from the study area. The remaining GMA pack in 2004 raised only 1 pup to yearling age from a minimum litter size of 7 (first observed after they left the den), and failed to breed in 2005. By the end of data collection this pack consisted of; the alpha female, 3 adult males, one of which became the new alpha and bred successfully in 2004, and one yearling male.

2.4.2.1 Dispersal
Pack home ranges overlapped extensively in the Lower Zambezi population (see Chapter 3, section 3.4.2.1), which made the extent of movement away from the natal home range by emigrants difficult to quantify. Where pack dissolution occurred, the emigrating sex was defined as the sex that moved away from the core areas occupied by the natal pack that year.

Seven dispersal events were observed, summarised in Table 2.4. Four single sex groups and two individual males were observed to emigrate. Two of the emigrant
groups included dogs of more than one age cohort (Mushika 2001, 3 males; and Mushika 2001, 4 females). One group of males immigrated into the area in 2002.

Table 2.4 Summary of dispersal events and group composition.

<table>
<thead>
<tr>
<th>Year</th>
<th>Natal Pack</th>
<th>No./Sex</th>
<th>Ages (yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>Jeki</td>
<td>2 M</td>
<td>1.4</td>
</tr>
<tr>
<td>2001</td>
<td>Jeki</td>
<td>1 M</td>
<td>2.5</td>
</tr>
<tr>
<td>2001</td>
<td>Mushika</td>
<td>1 M</td>
<td>5</td>
</tr>
<tr>
<td>2001</td>
<td>Mushika</td>
<td>3 M</td>
<td>2, 2.5, 1.4</td>
</tr>
<tr>
<td>2001</td>
<td>Mushika</td>
<td>4 F</td>
<td>2, 2, 2, 2.2</td>
</tr>
<tr>
<td>2002</td>
<td>Simwenzenze</td>
<td>4 M</td>
<td>3.5</td>
</tr>
<tr>
<td>2004</td>
<td>GMA</td>
<td>3 F</td>
<td>2.1, 2, 1.3, 1</td>
</tr>
</tbody>
</table>

Two of the recorded dispersal events resulted in successful pack formation. After Mushika pack dissolution occurred, 3 males consisting of an adult (6 years), a two year old and a yearling male emigrated and formed the GMA pack with the Jeki females. Four immigrant males joined the Mushika females within 6 months of pack dissolution to form the Simwenzenze pack, and were the only immigrants observed in the population. A single subordinate male emigrated from the Mushika pack and joined the Jeki females, nine months prior to Mushika pack dissolution. The male was observed with a badly broken leg and died weeks later. The remaining four dispersal events involved emigrants who left the study area and were not seen again, including the two female groups.

2.4.2.2 Sex ratios

Figures 2.6a and 2.6b summarise the results for age sex ratios in different age classes. There was a consistent trend of female sex bias in all age classes. Average sex ratios for different age classes are shown in Figure 2.6a (n=6 years data). Since individuals generally contributed data points for several years of data, samples were not independent and means were not compared statistically. Although there was a higher mean proportion of females in adult, yearling and pup age classes (1.3F:M, 2.3F:M, 2.4F:M respectively), 95% confidence intervals suggest there was no significant difference between mean values.

Previous studies have pooled yearlings into the adult age class to investigate population sex ratios (Frame, J.R. Malcolm et al. 1979; Maddock and Mills 1994; McNutt 1996a; Girman, M.G.L. Mills et al. 1997) therefore yearlings and adults were
also pooled here for analysis. For a total of 47 dogs which were observed to reach 1 year of age or more, 44% were male. Figure 2.6b shows a consistent female bias in adults throughout the study, with the exception of one year where there was no bias (2002). Contingency table analysis showed no significant difference between expected and observed sex ratios ($\chi^2=2.47; \text{df}=5, p=0.78$).

![Figure 2.6a Mean sex ratio of age classes over six years. (error bars = 95% confidence interval)](image1)

![Figure 2.6b Annual sex ratio of combined adults and yearlings (N from 14 to 22).](image2)

For five of seven litters the mothers’ parity was known, three of which were primiparous. Due to limited accessibility and visibility at den sites, which were inevitably located in thick vegetation in the foothills of the mountains, each litter contained some pups which died/disappeared before they could be sexed. Assuming equal probabilities of these unsexed pups being male or female, four litters of five litters contained more female pups, and the remaining multiparous litter contained equal numbers of male and female pups (see Appendix 1). There was no significant difference in sex ratios over seven litters (Wilcoxon matched-pairs signed-ranks test; $p=0.0625$, $W^+=1.50$, $W^-=19.50$, $n=6$). However, out of 56 pups, 20 were of unknown sex, 23 were female and 13 were male. Power analysis showed that in order to detect a small effect in sex ratios using a chi-squared contingency table at the 95% confidence level, for six years of data ($\text{df}=5$), 1,979 samples would be required compared to the 96 dog-years used here. A sample of this size would only be obtainable from a very large population and this highlights the problems associated with obtaining reliable estimates of sex ratio bias for a low density predator.
2.5 DISCUSSION

The density for the Lower Zambezi wild dog population (1.7 dogs/100km²) falls within the lower estimates of wild dog densities observed in other study populations, which ranged from 1.5 to 4 dogs/100km² (Fuller and Kat 1990; Maddock and Mills 1994; Creel and Creel 1996b; Woodroffe, Ginsberg et al. 1997). Given the small size of the Lower Zambezi population, density alone should not be used to indicate the robustness of the population. The maximum number of adults recorded in any one year was 18 (31 dogs including pups). At less than 50 adults, the Lower Zambezi population is representative of the majority of extant populations in Africa (Woodroffe, Ginsberg et al. 1997), and particularly susceptible to extinction through environmental stochasticity and genetic factors due to its small size (Gilpin and Soulé 1986).

2.5.1 Survival Analysis

Adult survivorship has been shown to be an important determinant of population persistence, in all populations, but particularly small populations; using the program VORTEX to model populations, Woodroffe et al. (1997) predicted the probability of extinction of various population sizes using demographic data from a wide range of previously studied wild dog populations. More recent studies implicated that pup mortality was the most important factor in determining population persistence (Cross and Beissinger 2001; Creel, McNutt et al. 2004). In a small population any increases in either adult or juvenile mortality will have a detrimental effect on population persistence, since every individual is of value. Adult mortality may reduce pack sizes below the optimum number required to successfully raise a litter, thus affecting juvenile survivorship (Courchamp and MacDonald 2001) and in turn maintaining small pack and population sizes.

Both adult and pup survival rates in the Lower Zambezi population were comparable to rates found in other larger populations. Pup survivorship was highly variable, partly due to small sample sizes; however it has been found to be similarly variable both between and within other wild dog study populations (Reich 1981; Malcolm and Marten 1982; Fuller, P.W Kat et al. 1992a; Van Heerdan, M.G.L. Mills et al. 1995; Creel and Creel 2002). Annual survival rates in the large populations in Kruger National Park in the Republic of South Africa and in northern Botswana were 0.35.
and 0.48 respectively (Creel, McNutt et al. 2004), comparable to the mean annual pup survival rate in the Lower Zambezi (0.47). It is often difficult to identify the causes of pup mortality since pups are not collared and tend to disappear from the population. Data collected from three large wild dog populations in Tanzania, South Africa and Zimbabwe found 83% of pups deaths were attributed to natural causes of predation and disease, predation being the most common cause (Woodroffe, McNutt et al. 2004). Regardless of overall survival rates, in a small population with limited ability to recover from demographic stochasticity, pup survivorship declining as low as 14% and 0% (Figure 2.5) could have important implications for population persistence.

The survivorship curves for the Lower Zambezi population stabilised from the age of one year to approximately 3.5yrs. Yearling survivorship was observed to be stable in other populations, ranging from 64% to 92% over 4 populations (Creel and Creel 2002; Creel, McNutt et al. 2004). This study may provide the first record of orphaned wild dog pups surviving in the wild alone. Based on previous studies, the five 10 month old Jeki orphans should not have been expected to survive without adult support. Age estimates here were conservative because data was limited during the wet season when the pack adults disappeared; the pups may have been orphaned as early as the age of 8 months. Wild dogs are generally still learning to hunt and have priority access to kills made by adults until the age of 10 to 12 months, and then play an increasing role in hunts as yearlings (Malcolm and Marten 1982; McNutt 1996a). Even yearling contributions to hunting appear variable, and they have been generally classified as dependents based on their effects on hunting efficiency, although not on hunting success (Creel and Creel 1995a). However, dispersal events have been recorded from the age of 13 months (McNutt 1996a), which suggests hunting skills are sufficiently developed for survival by this age. As mentioned in results, the orphans may have partially survived off smaller prey, which is likely to be consumed quickly and therefore less likely to be observed.

The probability of survival to adulthood (2 years) in this population was relatively high at 60%. A recent study compared survivorship between three of the largest extant wild dog populations in Africa; the Selous Game Reserve in Tanzania, Kruger National Park, and the study population in northern Botswana (Creel, McNutt et al. 2004). In Kruger and Botswana only 16% and 35% (respectively) of dogs reached
adulthood. Lower Zambezi results are comparable to those of the Selous, which had a much higher rate of survival to adulthood of 63%. At between 64% and 84%, Lower Zambezi annual adult mortality rates were within the range found in other study populations (reviewed in Creel and Creel 2002).

Although there was no significant difference in survival rates between protected areas, comparison of the curves indicates lower survivorship inside the National Park. Although the Chiawa GMA is closer to human settlement than the National Park, the Park is likely to have a higher density of competing predators which may affect wild dog movements and interact with mortality rates. This is further addressed in the following Chapter (3).

Large populations have an increased ability to recover from perturbations, but this is compromised in small populations (Woodroffe, Ginsberg et al. 1997). Identifying key causes of mortality is therefore a management priority, particularly the presence of deterministic threats that can drive a population to decline regardless of vital rates.

2.5.2 Causes of Mortality
Snaring was confirmed or suspected in 54% of mortality (Table 2.1). Although evidence for the impact of snaring on adult and yearling mortality was circumstantial, 50% of adult mortality occurred during the wet season, a four month period of the year (December to March). This is a period where poaching by snares is generally acknowledged by local safari operators and residents to increase; due to weather conditions restricting accessibility and the activities of anti-poaching patrols, including aerial patrols. The impact of snaring on adult mortality was reduced by this study, which was part of an active conservation effort to protect and preserve the local population of wild dogs. The data on the number of snares removed from badly injured dogs confirms that snaring was a major threat to population persistence.

The effect of predators on adult mortality was minor, but data suggests they played an important role in pup survivorship in the last year of the field study (2003) when an entire litter of pups was lost. Behavioural evidence implies that harassment at den sites caused large den shifts in two breeding years. Other studies have found average den moves to be a few hundred meters (Reich 1981), to a maximum distance of 1.2km
in the Selous (Creel and Creel 2002), compared to moves of over 20km observed in this study. Predation is a natural part of pup mortality and not necessarily an avoidable threat to be managed, but nevertheless as a stochastic factor it played an important part in this population’s decline between 2003 and 2005.

No outbreaks of infectious disease were observed in the study population. From seroprevalence results it appears that all packs had prior exposure to nearly all diseases tested for (only canine parvovirus was absent from the Simwenzenze pack). Whether or not these diseases impacted on population mortality in the past is unknown, but surviving individuals are likely have some resistance to further outbreaks. Canine parvovirus and canine herpes virus are known to affect pup mortality (Woodroffe, Ginsberg et al. 1997), and may have played an undetected role in pup survivorship in this study, particularly since pups could not be observed or counted for several weeks after birth.

Disease has reduced wild dog populations in other areas (Durchfeld, W. Baumgartner et al. 1990; Fanshawe, Frame et al. 1991; Alexander, P.W Kat et al. 1996; Woodroffe and Ginsberg 1999a) and the presence of domestic dogs at the western edge of the study area indicates that there may be a potential threat to this population, since domestic dogs are likely disease reservoirs (Alexander, P.A Conrad et al. 1993; Gascoyne, M.K. Laurenson et al. 1993; Ginsberg, Mace et al. 1995; Woodroffe, Ginsberg et al. 1997; Woodroffe and Ginsberg 1999a). Future studies in the area should certainly continue to monitor this potential threat.

2.5.3 Breeding

The breeding season observed in the Lower Zambezi coincides with that observed in southern Africa where breeding corresponded with the dry season and increased prey density, particularly around water sources (Reich 1981; Maddock and Mills 1994; McNutt 1996a). The Zambian wet season falls between November and March, and prey densities begin to concentrate during winter. Although the Zambezi river is a constant water source for the area, prey has been observed to disperse during the rains and increase in concentration on the alluvial terraces of the valley floor during winter (Dunham 1994). Impala drop their lambs in November each year following the main rutting season in May {(Estes 1991); personal observation} which provides easy
hunting for the dogs. This would be an additional benefit for the dogs that have increased feeding demands from larger, but still dependent pups at that time of year.

There were no significant correlations between pack size and litter size or pup survivorship. This may be partly a result of small sample size leading to a lack of power to detect a significant result. The results contrast with other studies of larger populations where litter size and pup survivorship have been correlated positively with pack size, based on the number of yearling and adults (Courchamp and MacDonald 2001; Creel and Creel 2002; Creel, McNutt et al. 2004). The benefits of increased pack size on pup survivorship derive from increased hunting efficiency as well as increased vigilance. Larger packs kill more frequently, kill larger prey and have more success defending kills from interpredator competition (Fanshawe and Fitzgibbon 1993; Fuller and Kat 1993; Creel and Creel 1995a; Creel, McNutt et al. 2004). This increased hunting success is likely to influence litter size (Creel, McNutt et al. 2004) as well as the ability to raise pups to independence.

The limited results available here indicated that yearling contributions to pup survivorship in this population were negligible. When yearlings were included with adults in pack size, sample size increased, but correlations weakened further. In fact one of the two packs with the largest annual number of yearlings and adults (maximum of 10) failed to raise any pups to yearling age, and were also observed to suffer from increased kleptoparasitism by spotted hyaenas. Only four adults were present in this pack year, a ratio of 0.5 adults:yearlings. In the second pack of 11 which raised five of nine pups successfully, there was a higher ratio of 1.4 adults to yearlings. Thus the number of more experienced dogs may have played a more important role in breeding success than overall pack size in this population.

2.5.4 Pack Dynamics and Dispersal

With an average adult pack size of 7.2 the Lower Zambezi pack estimates were slightly lower than pack sizes in most studies. Average adult (>1yr old) pack sizes ranged between 8 and 11 dogs for study sites in the Zimbabwean Zambezi Valley, the Serengeti National Park, Hwange National Park, Kruger National Park, and the Selous Game Reserve (Frame, J.R. Malcolm et al. 1979; Childes 1988; Fanshawe, Frame et al. 1991; Mills and Gorman 1997; Creel, McNutt et al. 2004), but ranged between 2 to
50. Constant annual adult mortality from snaring in this population is likely to have limited pack size and population size.

Unsuccessful dispersal appears to be the other most important factor in limiting population size. Woodroffe et al. (1997) discussed an unpublished report which suggested that inbreeding avoidance (rather than inbreeding depression) may halt breeding in small populations. However, Woodroffe et al. (1997) concluded that this had not been demonstrated and that relatives had been observed to breed in captivity. Data here does in fact provide evidence that inbreeding avoidance reduced fecundity in this population. In all four cases involving emigrants of known natal origin, the dogs left the study area when no unrelated opposite sex dogs were available, and were not seen again. This included female groups, which in two other studies with larger home range sizes dispersed mean distances of 19km and 27km (McNutt, 1996a and Creel and Creel 2002 respectively). If females in this study had remained in home ranges adjacent to, or overlapping, their natal home range it is highly likely they would have been detected. In the two cases of successful pack formation observed here, when unrelated mates were available, the females were philopatric and did not leave their natal home ranges.

The loss of adults through dispersal contributed to maintaining the population at low density, and thus to increased difficulty in finding a mate. This suggests the presence of an inverse density dependence and Allee effect in the population (Courchamp, Clutton-Brock et al. 1999). The Allee mechanism occurs when individual fitness is related to numbers of conspecifics in a positive manner (Stephens and Sutherland 1999). Boukal and Berec (2002) gave a definition of a “positive relationship between any measurable component of individual fitness and population size, quantified by the number or density of conspecifics”. The most cited cases of Allee effects in many species are based on the limited probability of finding mates in small populations (Boukal and Berec 2002). Courchamp et al (2000) identified three processes through which the Allee effect can lead to extinction in wild dogs. The first is an increased probability of pack extinction through small pack sizes, which in turn increases the probability of population extinction. The second is the effect on dispersal success. Smaller populations suffering Allee effects generally have smaller packs, and therefore smaller dispersing groups which would have less probability of successful
pack formation due to increased mortality risk, and create smaller founder packs which have less chance of success. Therefore, lack of successful dispersal and colonization further reduces the population and increases extinction risk. Larger populations with direct density dependence, in contrast, have better success rates from dispersing cohorts to balance pack extinction. Lastly, less colonisation leads to fewer packs, and again to fewer dispersers, further demonstrating Allee effects at the population level. Empirical data from this study fits this model, with a dispersal group size ranging from only one to four dogs. The impact of Allee effects on population survival and its relevance to conservation management are discussed further in Chapter 6.

Woodroffe and Ginsberg (1998) assessed the impact of edge effects, or increased mortality outside reserve borders, on wide ranging carnivore populations. They suggested that if population size determines extinction probability, then critical reserve size should be related to density, as this determines population size. If edge effects determine extinction probability, then critical reserve size would be related to home range size. The study found critical reserve size was related to home range size and that edge effects play an important part in population persistence. This theory could be further extended to include the Allee effect on dispersal. Although home ranges may lie within reserve borders in larger protected areas, in populations of species which exhibit inbreeding avoidance behaviour dispersal distance may increase if population size is reduced and mate choice becomes limited. If based only on home range size, edge effects may still be underestimated in small populations since dispersal and recruitment are critical to population persistence.

While sex bias in larger populations has been related to mate choice and different dispersal distances between the sexes (McNutt 1996a), in smaller populations inbreeding avoidance may play a key role in determining dispersal distances for both sexes. Evidence from this study is limited since actual dispersal distances and the fate of emigrants are unknown. The Zambian Escarpment provided a barrier to tracking of uncollared dogs, so detection of emigrants in that area was unlikely. However, range data from study packs suggests that the escarpment also provided a barrier to wild dog home range movements, and dogs would be unlikely to remain in the mountainous areas when high prey densities are available on the valley floor (see Chapter 3, section
3.4.1). Dispersers may travel over it, so this physical barrier could also increase dispersal distances. The effect of inbreeding avoidance in smaller populations is an important area for further study in other small populations.

2.5.5 Sex Ratio
Other wild dog studies have encountered either a male biased adult sex ratio (Frame, J.R. Malcolm et al. 1979; McNutt 1996a), or no sex bias at all (Maddock and Mills 1994; Girman, M.G.L. Mills et al. 1997; Creel, N.M. Creel et al. 1997c). There was no significant sex bias in the Lower Zambezi population, nevertheless all age classes displayed a constant trend of a higher proportion of females. The data from this study must be interpreted with caution due to small sample sizes resulting in lack of power. However, lack of power is likely to be a constantly limiting factor for detecting small changes in populations when investigating the dynamics of small and declining populations.

Alongside a shortage of receptive mate encounters, demographic stochasticity is another main category of the Allee effect in small populations (Courchamp, Clutton-Brock et al. 1999), and this provides one explanation for the unusual trend in sex bias observed in the Lower Zambezi population. Additionally, in long lived species such as wild dogs there may be large temporal autocorrelation in sex ratios (Engen, Lande et al. 2003). Nevertheless, female bias was present in pups here, and 40% of adults only contributed data to the adult age class. There is also evidence of sex bias following maternal lines in other canids (Beketov and Kashtanov 2002) which would be exaggerated in wild dogs by the pack breeding structure limiting the number of maternal lines in a population. The number of pups of unknown sex may mean that the trend in female sex bias observed here is the result of differential juvenile survivorship rather than birth ratios, however this would also be the case for comparative wild dog studies since pups do not emerge from the den for three weeks.

Data from large population studies of wild dogs suggested that males contribute more to raising young and improving natal pack success (Malcolm and Marten 1982), but by emigrating further they also reduce resource competition with the natal pack compared to females. Therefore both local resource competition theory and resource enhancement theory (Hardy 1997) would predict a male bias in stable wild dog
populations. Given the size and instability of the Lower Zambezi population there is no evidence here to contradict these theories.

However, it is plausible to consider that any female sex bias may be an artefact of small population dynamics. Based on small pack size and Allee effects on hunting success, it can be hypothesised that maternal condition might play a role in sex bias. Although sexual dimorphism in wild dogs is not as pronounced as in other species, adult males were found to be approximately 16% heavier than females in two previous studies (Woodroffe, McNutt et al. 2004) and 17% heavier in this study. Myers (1978) adapted the Trivers-Willard hypothesis on maternal condition and birth sex ratios to suggest that the production of more of the least expensive sex allows the mother to maximise the number of offspring produced. Myer’s assumption that reducing litter size does not enhance the survival of the mother is likely to hold in this case; in wild dogs larger litter sizes are important for small packs due to expected higher mortality in pups, and due to inverse density dependence in small packs. Nutritional stress has been found to result in production of the least expensive sex in various mammal species (Smith, Robbins et al. 1996; Andersson and Bergstrom 1998; Fisher 1999; Kruuk, Clutton-Brock et al. 1999) and the number of helpers was found to have an effect on maternal health in cooperatively breeding meerkats (Russell, Brotherton et al. 2003). As Creel et al (1998b) suggested, if sex ratio bias was due to one zygote being more susceptible to stress, one would expect a bias in one direction only and an overall population wide bias, a trend which was observed here in all age classes.

In conclusion, inbreeding avoidance and mate competition, proposed as important factors in large wild dog populations, may play an important part in small and fragmented populations by contributing to a migration-mediated Allee effect, which in turn has subsequent impacts on breeding success and population demography. High adult mortality rates from snaring compounded Allee effects on dispersal and pup survival, leading to a continuous state of population decline.
CHAPTER 3: ECOLOGY AND HABITAT UTILISATION

3.1 INTRODUCTION
Loss of habitat continues to affect many species, particularly those with large home ranges. Growing human development has had steadily increasing impacts on the survival of African wild dog populations, due to the species’ far ranging, nomadic habits (Woodroffe & Ginsberg 1999a; Woodroffe et al. 2004b). Once they leave the protection of National Parks and Game Reserves wild dog mortality rates are likely to increase. Ecological factors may interact to increase the probability of wild dogs leaving protected areas. In previous studies wild dogs were shown to avoid high densities of lions (Creel & Creel 1996; Mills & Gorman 1997), while lions tended to concentrate in protected areas with high prey density (Creel & Creel 1997; Spong 2002; Stander 1993). Wild dogs may therefore be pushed out of favourable habitats into higher risk areas.

This chapter investigates the home range movements of the Lower Zambezi wild dog population, and their utilisation of habitat in relation to vegetation density, prey density and hunting success. The effects of interpredator competition on wild dog range movements are addressed in the following chapter.

3.1.1 Home Ranges and Habitat Preferences
Wild dogs typically have large home ranges, although range sizes vary considerably in differing habitats. In the free-ranging population in Kruger National Park home ranges averaged 537 km² (Mills & Gorman 1997), similarly, in other wooded areas such as Hwange National Park and Selous Game Reserve, ranges averaged 423 km² and 379 km² respectively (Creel & Creel 2002; Woodroffe et al. 1997). In the fenced Hluhluwe Umfolozi Game Reserve in South Africa (96000 ha), wild dog home ranges fell to 242 km² (Andreka et al. 1999) and were concentrated away from the highest lion density areas. Average home ranges in the more open habitats of the free-ranging Serengeti and Aitong (Kenya) populations averaged 665 km² and 650 km² respectively (Fuller & Kat 1990; Schaller 1972). Home ranges often overlap, in some areas by 50-80% (Fanshawe et al. 1991; Mills & Gorman 1997). In Kruger National Park it was thought that packs rarely met (Mills & Gorman 1997), however, in the Serengeti Frame et al. (1979) never recognised one pack deliberately avoiding
another and observed larger packs chasing smaller packs from an area. The thicker vegetation cover and subsequently reduced visibility in Kruger National Park may have reduced the likelihood of observing packs interacting.

Wild dog habitat preferences vary; they appear to be able to utilise a variety of vegetation types. Dogs in the area of the Serengeti and Masai Mara have been observed to prefer short and medium grass habitats for hunting and resting (Fuller & Kat 1990; Maddock 1993), while dogs in southern Africa thrived in closed bush and hilly woodland habitats (Mills & Gorman 1997; Reich 1981). Hunting success has been shown to be just as successful in areas of moderate and low prey density (Creel & Creel 1998; Fanshawe & Fitzgibbon 1993), therefore wild dog habitat selection is not necessarily determined by prey density alone.

3.1.2 Hunting and Prey Preferences
African wild dogs generally prey on medium sized antelope species, often favouring the most abundant species in their area. The dogs hunt in cooperative groups, which allow them to take prey much bigger than themselves (Fanshawe & Fitzgibbon 1993; Fuller & Kat 1993; Woodroffe et al. 1997). The dogs weigh on average 20-25kg but may take prey up to 200kg (Creel & Creel 1995; Frame et al. 1979). Chases often continue over distances greater than 5km and reach speeds of up to 60km/hr (Malcolm & Marten 1982; Woodroffe et al. 1997). Prey species include impala (*Aepyceros melampus*), Thompson’s gazelle (*Gazella thomsoni*), reedbuck (*Redunca arundinum*), wildebeest (*Connochaetes taurinus*) and kudu (*Tragelaphus strepsiceros*) (Woodroffe et al. 2004b). In areas of mixed bush habitat in Southern Africa impala play a large part in the dogs’ diet as they are generally the most abundant medium sized prey (Creel et al. 2004; Fuller & Kat 1990; Kruger et al. 1999; Mills & Gorman 1997). In a study in east Africa the dogs took mostly adult Thompson’s gazelles, but killed more juveniles of larger species, including impala (Fuller & Kat 1990). More male Thompson’s gazelles were killed than females in two studies in east Africa, which may reflect the male antelope’s reluctance to leave his territory, and decreased alertness in comparison to the female breeding herds (Fanshawe & Fitzgibbon 1993; Fuller & Kat 1990). In southern Africa wild dogs did not favour male or female prey (Kruger et al. 1999).
It should be kept in mind that kill data may be biased toward larger prey species, since smaller prey would be consumed very quickly with little evidence left of kills (Childes 1988). Wild dogs have been observed taking springhare (*Pedetes capensis*) and *Lepus* species in east Africa, and bat-eared foxes (*Otocyon megalotis*) in Zimbabwe (Fuller & Kat 1990; Rasmussen 1996).

While some studies have suggested that the advantages of cooperative hunting may be its evolutionary cause (Estes & Goddard 1967; Kruuk 1972), others have indicated that communal hunting is more a consequence of sociality (MacDonald 1983; Packer & Ruttan 1988b). It has been suggested that communal hunting benefits wild dogs by increasing the prey base available to them (Fanshawe & Fitzgibbon 1993). In a study of one pack in the Serengeti, Fanshawe and Fitzgibbon (1993) found that wild dog’s hunting of larger prey such as wildebeest maximised their food intake in groups of three to four, while dogs hunting gazelles did best alone. They concluded that communal hunting was beneficial in increasing the range of prey species that could be hunted, and that hunting in groups reduced interspecific competition from spotted hyaenas. In contrast, Fuller and Kat (1993) studied a single pack and found that in an area of abundant prey and low predator competition wild dog pack size remained large, confounding theories about the evolutionary cause of pack size. In data from 404 kills from six packs Creel and Creel (2002; 1995) found that hunting success, prey mass and the probability of multiple kills increased with the number of adult dogs in a pack. These studies overall suggest that the energetics of cooperative hunting favour group living in African wild dogs.

In addition to studies on the benefits of sociality in wild dogs, one study also focussed on assessing the factors that influence the coursing hunting methods of the dogs, especially in comparison to the stalking cheetah and lion (Fanshawe & Fitzgibbon 1993). Coursing predators approach prey openly, flush it and then give chase often over long distances (Estes & Goddard 1967; Kruuk 1972; Schaller 1972). Fanshawe and Fitzgibbon (1993) found that wild dogs tended to either approach prey slowly with the pack grouped together and heads lowered, or run straight up to the prey in full view. Although hunting success was influenced by pack size, it was not affected by the amount of available cover, the size of prey groups, or the distance at which prey groups fled, in contrast to the hunting of stalking predators.
Hunting success in wild dogs is generally high compared to other large carnivores (Schaller 1972) but actual success rates vary depending on the area in which they are found. In an eastern African study data indicated that the dogs were never unsuccessful on two consecutive hunting sessions, and they hunted twice a day (Fuller & Kat 1990), however this was based on hunting sessions rather than the number of individual hunts within each session. Consumption rates were estimated at 1.7kg prey/dog/day. Success rates over eastern and southern Africa range from 39% to 85%, seem to be similar in high and low density populations, and independent of prey density (Creel & Creel 1998; Fuller & Kat 1993). The exception to this independence from prey density would be when packs are denning and movements are restricted, particularly if they are dependent on migratory prey (Creel & Creel 1998).

Adults and yearlings contribute similar amounts of food to dependent pups at the den. However, yearlings play a smaller role in killing larger prey and tend to be more successful hunting juvenile prey (Fanshawe & Fitzgibbon 1993; Fuller & Kat 1993; Malcolm & Marten 1982). Approximately one third of a meal is fed to pups, even in times of food scarcity (Malcolm & Marten 1982). On rare occasions wild dogs have been observed to cache food. This has only been recorded during food scarcity and when the dogs were returning to a breeding den (Malcolm 1980). In wooded areas the dogs rarely hunt at night, but have been observed to travel on moonlit nights (Creel & Creel 1995).
3.2 OBJECTIVES
The objective of this section of the study was to determine the role of ecological factors on wild dog home range movements and population dynamics. Specifically, aims were to:

1. **Assess the vegetation structure and classify the main habitats within the study area.**

2. **Estimate the density of prey within each habitat.**

3. **Determine the size and distribution of wild dog home ranges and habitat utilisation.**

4. **Determine wild dog hunting success rates and prey preferences in relation to habitat characteristics.**
3.3 METHODS

3.3.1 Habitat and Prey Species

GPS coordinates for wild dog activities and home ranges were collected using the general methodologies for field work outlined in Chapter 2. Surveys were carried out to provide background ecological information on habitat and prey densities within the study area.

Human settlement areas inside the study area were also mapped using ArcGIS 8.1 (1999-2001, ESRI™ Inc., USA), from GPS field data and additional boundary data provided by Conservation Lower Zambezi (I. Stevenson, unpublished data).

3.3.1.1 Vegetation classification

Due to a lack of information on vegetation within the study area, a preliminary vegetation survey was carried out during the course of the study to classify habitat types. The objective of the survey was to obtain a general classification of habitats by means of field surveys and remote sensing classification. The analysis was not intended to provide a comprehensive vegetation survey of the area.

i) Field surveys

Four habitat categories were surveyed within the African wild dog home range area: 1) grassland, 2) *albida* woodland, 3) ecotone (transitional zone of grassland or woodland to thicket), and 4) thicket. Habitats were sampled by line transect methods. Transects were randomly spaced within each habitat, with the restriction that sites were limited to those within 1km of an existing road or track due to park regulations on walking. Vehicle tracks were little more than game trails in most cases so vegetation was not disturbed more than 10m either side. Tracks were sufficiently distributed throughout each habitat type for equal sampling to be carried out. GPS locations for potential transect areas were identified from satellite maps and preliminary ground observations, given a number, then 4 numbers from each habitat were chosen randomly.

In each habitat four replicate 300m line transects were laid out. A 20X20m quadrat was pegged out on each transect at 100m intervals from 0 to 300m, giving a total of 4 quadrats per transect and 16 per habitat. Within this 20m quadrat all species present were identified. Percentage ground cover for each species within each quadrat was
estimated by two to three individual observers, averaged and then recorded. To ensure consistency in estimates I was principal observer at every site. All species with greater than 1% cover were included in the species description list. Since large trees were often sparsely distributed and fell outside of quadrats, a list of all dominant tree species for each habitat was composed by walking each transect and identifying all observed species within 30m either side of the transect line.

Canopy cover was visually estimated at the centre of each quadrat using a vertical projection method, through a viewing square of 30cm by 30cm, held 190cm (researcher arm height) from ground level. Cover was recorded as a percentage estimate of the area at canopy height, bordered by the viewing square, which was covered by foliage. Ten percentile intervals were used for coverage estimates. Digital photographs of sample canopy areas were taken and used as reference.

Field data were then used to describe the four major habitats by growth form, height class, cover and dominant species, based on methods adapted from Walker and Hopkins (1990). The classification tables used are contained in Appendix 2. Both crown canopy structure and percent cover were used to determine cover class for all growth forms.

Vegetation density in each habitat was estimated based on relative visibility, using truncation distances from impala density surveys (see section 3.1.2 below). The examination of perpendicular distance histograms showed no decrease in the frequency of prey sightings with increasing distance below the chosen truncation distance for each habitat, therefore the truncation distance was judged to be a reasonable scale to use as a measure of vegetation density.

ii) Vegetation classification by remote sensing
The satellite image containing the study area was a Landsat-7 image (P171/R71), taken on 24/09/2001, which was ortho-rectified and pan-fused with Enhanced Thematic Mapper (ETM) bands 7-4-2 (Intec Americas Corp. USA). This raster map of the area was used for all spatial analysis of wild dog home range movements and activities, and competing predator densities. A raw version of the satellite image (“Raw” Fast L7-A.fst) was used to carry out a supervised vegetation classification,
using 7 spectral bands, performed in IDRISI Kilimanjaro (version 14.02, Clarke Labs, Worcester, MA, USA).

To classify vegetation on the satellite image, spectral signatures of each vegetation category were created using calibration sites (training sites). This process correlates pixel distribution and characteristics with vegetation cover, and was based on information obtained from the ground transect locations and at least two other known areas for each habitat. The combined training sites resulted in a training class of a minimum of 200 pixels for each habitat. Classification accuracy was assessed from ground-truthing and extensive knowledge of the study area, rather than In-process Classification Assessment procedures. Based on the spectral signatures created, twenty additional ground-truthed sites (five for each habitat) were used for accuracy assessment and 100% were correctly classified.

The hard classifier method MAXLIKE was used to assign pixels. This method is the most powerful hard classifier method and uses Bayesian probability theory to assign pixels to each class based on training site information. It also accounts for correlation between bands. All pixels are assigned to a category using this method so additional habitat categories were created to allow for areas with spectral properties that were not previously allocated to any habitat. The additional habitat categories were derived from ground-truthing from direct observation, and included categories outside the wild dog home range areas. The additional categories were; miombo woodland, burnt miombo woodland, Zambezi River, and sand bars.

### 3.3.1.2 Prey density

Prey counts using line transect sampling methods were used to assess relative densities of impala, the wild dogs’ main prey species, in each of the four major habitats described above. Transect sampling methods do not effectively sample rare or shy animals with low detection probabilities (Thomas et al. 2003), including species such as bushbuck and kudu (*Tragelaphus strepsiceros*) which made up a small proportion of the wild dogs’ diet. These species were recorded during prey counts but due to the low encounter rates and subsequent lack of data they were dropped from density analysis. Due to limited field time the density of these species in each habitat was considered in-line with previously published literature.
Prey counts were carried out during the dry season, between August and October in 2003. Visibility and detection of animals was maximized at this time of year because vegetation had been reduced by annual die off, animal trampling and foraging pressure. Line transect counts were carried out on the existing dirt-track network for ease of access and to minimize vehicle impact and prey disturbance. Transects were randomly allocated along straight sections of road in each vegetation type. Due to spatial fragmentation of habitats, two to four transects of varying length were used in each habitat, which were then pooled to give a total average transect length of 13.7km (SE: 0.31km) in each. Four temporal counts were carried out on each transect, divided into two morning and two afternoon counts, each separated by several days. To avoid double counting within a transect due to prey movements, sampling was restricted to between 5.00-9.30 hours in the morning and 16.00-18.30hrs in the afternoon.

Counts were carried out within a maximum distance of 300m either side of the transect, by one to two observers in a vehicle driven at 10-15km/hour. I was always principal observer to standardise counts. The vehicle was stopped whenever prey was observed, and 8x30 binoculars were used to identify species, sex and herd size. Perpendicular distance from the transect line was calculated by recording distance from the vehicle to the centre of the herd/animal where it was first sighted using laser rangefinders (Yardage Pro Legend, Bushnell, USA), and angle from the road which was estimated using a compass.

Due to lack of independence of temporal samples, a single transect from each vegetation type (average length 14.4km, range 13.5 to 15.2 km) was used to estimate density in each vegetation type. Impala count data was imported into the program DISTANCE 4.1 (Thomas et al. 2003). DISTANCE 4.1 (Thomas et al. 2003) relaxes the assumption found in other strip transect methods that all objects within a pre-defined strip are detected, and can also test and adjust for cluster size-bias; the increased probability of detection of larger groups which would affect density calculations (Thomas et al. 2002). A best fit detection model function was chosen by plotting and examining histograms of recorded distances, to set data filters and truncation distances, and by comparing AIC (Akaike Information Criteria) values between different model definitions. This preliminary assessment investigates the
distribution of the data and trends in detection distances. There was little difference between model combinations, however the half-normal detection function with a simple polynomial expansion model generally resulted in lower AIC’s and smaller confidence intervals, so this model was used for most analysis. In the case of the “thicket” sample the uniform detection function with simple polynomial expansion model gave a lower AIC and smaller confidence interval so was used for this stratum, which differed due to low sample size. Plots of group size against perpendicular distance showed no correlation, indicating, for instance, that there was no decrease in detection probability with increasing distance, within the chosen truncation distances. Therefore mean group size was used in density analysis. Default settings in DISTANCE 4.1 (Thomas et al, 2003) were used except where specified.

Coefficient of variation increased with larger sample sizes, so density results were log-transformed for further analysis. Log D was used for density estimates. DISTANCE 4.1 (Thomas et al, 2003) outputs the percentage coefficient of variation in the form of CV=(SE/D*100), therefore SE was transformed by the equation log (1+(cv/100)). One-way ANOVA was used to test for differences between densities and cluster size in each vegetation type. If ANOVA gave significant results, post-tests were carried out using the Bonferroni test to correct for multiple comparisons between the four vegetation groups.

To estimate overall impala density of the study area, density was calculated in DISTANCE 4.1 (Thomas et al, 2003) using one transect from each vegetation type, entered as different samples within the one stratum. Temporal patterns in impala density within each vegetation type were investigated by calculating density in DISTANCE 4.1 (Thomas et al, 2003) using the detection function parameters as above. For each vegetation type a morning and an afternoon density was calculated using the two replicate morning or the two afternoon counts combined, giving a total sampling effort of between 25km and 30km for each density estimate. Since density figures are output only as summary data (mean, SE, 95% CI) from DISTANCE 4.1 (Thomas et al, 2003), raw densities were calculated, based on the area of each transect within truncation distances, and differences between AM and PM densities were tested using the Wilcoxon Matched-Pairs Signed-Ranks Test.
Temporal transects for each vegetation type were pooled to assess the relationship between herd (cluster) size and perpendicular distance from the transect line. Pearson's product moment correlations were used to investigate the relationships between impala density and herd size in relation to vegetation density.

3.3.2 Wild Dog Home Ranges and Habitat Utilisation

GPS locations collected from field observations were used to calculate wild dog pack home ranges and habitat selection. For details of field methodology refer to general methods section on Data Collection, 2.3.1. All wild dog fixes were separated by a period of movement such as hunting or travelling so they are assumed to be independent. A maximum of two data points per pack per day was used in analysis. Triangulation from radio signals (see section 2.3.1.3) was used rarely and only when a later sighting confirmed the dogs had been in the area, for example as they left an inaccessible thicket. For habitat selection analysis triangulation readings were removed and only direct observations were used.

3.3.2.1 Home range analysis

Home ranges were calculated using the Minimum Convex Polygon (MCP) method in the program CALHOME (Kie et al. 1994). This basic method of home range calculation is commonly used and allowed comparison with other wild dog study areas. One limitation of the MCP technique is that home ranges may include areas which are not actually utilised by the study animals. A 95% MCP contour is often applied to compensate for overestimation of home ranges due to outlying points (Lawson & Rodgers 1997), however a 100% MCP contour was retained here. Outliers in this dataset were invariably in thicket and mountainous areas at breeding times. Limited accessibility, signal bounce and resource restrictions on aerial tracking may have resulted in underestimation of the use of these areas, therefore all location points were included in home range calculations.

MCP methods have been shown to have a positive correlation between home range size and the number of data points (Gautestad & Mysterud 1993). The minimum required sample size for accurate home range estimates was calculated by plotting MCP home range size against sample size for the two annual home ranges with the highest number of observations, GMA-2003 and GMA-2002 (n>100). Both curves
appeared to plateau at approximately 40 observations (see results section 3.4.2.1). Four annual home ranges were then plotted based on 40 or more observations. For the remaining six pack-years, two years of observations for each pack were combined to establish three home range areas based on 35 or more observations. A correction was then applied; nonlinear regressions of the GMA-03 and GMA-02 data sets provided an asymptote value where extra data points had little effect on home range size. This value was used to estimate the percentage of total home range area generated by each number of observations, at intervals of 10 observations. The regression curve resulting from the mean percentage values of both datasets was used to adjust all home range area estimates, based on the number of observations. All MCP home range areas were further adjusted for non-utilised areas by removing the Zambezi river from the home range polygons using ArcMap 8.1. Correlations of pack size against MCP home range sizes were carried out in GenStat 8.1 (2005).

MCP methodology was also used to calculate breeding home range sizes for each pack that was observed to den. Data was used over a three month denning period, less where a pack was disturbed by predators (see section 2.4.1.2).

Adaptive kernel density analysis methods were used to provide more detailed information on space use within the annual home range area boundaries. The kernel density function is a robust nonparametric method, which allows the user to avoid assumptions about the distribution of data (Seaman & Powell 1998; Worton 1987, 1989). Bandwidth (equivalent to a histogram's binwidth) is the most important parameter in kernel analysis, and determines the amount of smoothing of the data (Seaman & Powell 1996; Worton 1989). Least-squares cross-validation was initially used here to select optimum bandwidth using the program CALHOME (Kie et al. 1994). However, this method gave poor data fit and overestimated home range area. This is often the case with non-normally distributed data where the study subject is using two or more core areas (Kie et al. 1994). In this case a bandwidth below the optimum is recommended. The least-squares cross-validation method is also inappropriate where there are multiple observations at identical locations (Seaman & Powell 1998; Tufto 1996), which occurred in this data set at den areas.
An alternative technique of selecting bandwidth was used by graphing several densities using different bandwidths and then choosing the most suitable bandwidth for best fit (Mugdadi & Ahmad 2004). Smaller bandwidths are generally more appropriate for revealing small-scale patterns in the utilization distribution (Seaman & Powell 1996), and after several trials an arbitrary bandwidth of 65% of the optimum bandwidth produced in CALHOME was used on all home ranges. Density was calculated and mapped using the Spatial Analyst extension in ArcMap (ArcGIS 8.1), with an output cell size of 200m. The Spatial Analyst kernel density function uses a quartic approximation of a Gaussian kernel. This method produced volume contours that outlined the minimum contours in which the study subject spent a specified proportion of time, based on probability under a bivariate probability surface. Contours were calculated at 50%, 75% and 95% intervals.

3.3.2.2 Habitat utilisation and prey selection

i) Habitat utilisation

Wild dog habitat selection in this study was first analysed at a population level using pooled wild dog GPS locations over the entire study area. Habitat selection was then analysed at an individual pack level, within each pack’s home range area. Annual ranges for each pack were combined for this analysis which provided data for three to five years per pack. Analysis assessed whether dogs utilised habitats more than would be expected from the proportion of each habitat available to them. Habitat selection was then investigated in relation to prey density and interspecific competition.

Wild dog habitat selection was analysed using Duncan’s (1983) method which gives an index of preference (PI), as previously used for wild dogs by Mills and Gorman (1997).

\[ PI = \frac{Uh}{Ut} \times \frac{Ah}{At}, \]

where; Uh is the number of wild dog observations in one habitat, Ut is the total number of wild observations in all habitats, Ah is the area for the habitat, and At is the total area.

1) \[ \log_{10}(PI+1) \] then gives an index of preference for wild dog usage within each area of different lion density.

Duncan’s (1983) method gives a preference index where 0.3 is parity, values above 0.3 show preference for that area, and below 0.3 demonstrates avoidance. Duncan’s normalisation of the preference index removes the compression of avoidance values.
relative to preference values that otherwise would occur, since avoidance is restricted to between values of 0 and 1.0 using only formula number 1) above.

Data from sightings reports submitted by safari guides and ZAWA Wildlife Police Officers was included where sufficient information was provided. This data was tested for bias before inclusion in this section, as there may be an increased likelihood of observing wild dogs in more open areas when not using telemetry methods and data may have been biased towards open habitats. The proportion of sightings in each habitat was tested against the proportion of the road network in each habitat. Although there was a significant difference between the proportion of sightings expected from each habitat ($\chi^2=172.6$, df=3, $P<0.0001$), more sightings than expected were observed in thickets and less than expected in woodland, so no relative visibility bias towards open areas was apparent. No data were available on the relative road usage in each habitat so no adjustments to data were made. Wild dogs were frequently observed using roads for travelling and resting in all habitats, which may cancel out visibility limitations.

**ii) Prey selection**

Each prey species identified was presented as a proportion of the total observed hunts, kills and its total biomass contribution to the wild dogs’ diet. Data for age and sex distribution of prey was incomplete so biomass was estimated for impala and kudu according to Mills and Gorman (1997), using weights of 40kg and 136kg respectively. Bushbuck weights were estimated visually from kills and an average of 50kg was used. Hunt data was then used to calculate the hunt effort spent on each prey species in each habitat and overall wild dog hunting success in each habitat. This was then compared to general wild dog habitat selection (PI) and prey density.

A hunt was defined as a chase in which dogs reached a run and where one adult or more pursued the prey. Pups and yearlings often participated in short “warm up” chases of a variety of prey including warthog and herds of fully grown buffalo and zebra. However, these chases were short, unsuccessful (often the prey did not even flee) and the adults did not participate so they were not considered a serious hunt. Consecutive individual hunts were difficult to observe due to limited visibility and accessibility in some habitats, so hunting success (kills/hunt) was determined from the
number of observed hunting periods, (morning, evening or night) and whether each period resulted in one or more kills.

GPS locations were taken for each wild dog hunt or kill observed, however prey was not always identified as carcass remains were often removed by spotted hyaenas before they could be identified. To calculate the proportion of prey species in the wild dogs’ diet only observations where prey were identified were included, however to calculate hunting success in each habitat all hunt and kill data was used.
3.4 RESULTS

3.4.1 Habitat and Prey Species

3.4.1.1 Vegetation classification

The study area was classified into dominant habitats according to vegetation type. Table 4.1 below describes the four major valley floor habitats by growth form, height class, cover and dominant species, based on methods by Walker and Hopkins (1990). Vegetation species lists for each habitat are described in Appendix 2. Truncation distances from DISTANCE 4.1 (Thomas et al. 2003), analysis (section 3.3.1.2) were included with each habitat as a relative measure of vegetation density based on the visibility of prey.

The grassland habitat was characterised by isolated trees and shrubs, and a variety of grasses and forbs. This habitat also included sections of sodic soil relatively bare of growth, and other areas heavily dominated by tussocks and grasses more typical of savanna grasslands. In the groundcover structural layer grasses are listed as “mixed grass species” because vegetation surveys were carried out during the dry season and this made identification of many grass species difficult, since few were flowering. Groundcover was highly seasonal in all habitats except grasslands, with little groundcover remaining by the end of the dry season.
Table 3.1 Vegetation structure and composition for dominant habitats in the study area.

<table>
<thead>
<tr>
<th>Habitat (visibility)</th>
<th>Growth Form</th>
<th>Dominant species</th>
<th>Average Height (m)</th>
<th>Cover class</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Grassland (250m)</strong></td>
<td>Tree</td>
<td>Acacia nigrescens, Acacia tortilis, Hyphaenae petersiana, Combretum imberbe</td>
<td>6-12</td>
<td>isolated plants</td>
</tr>
<tr>
<td></td>
<td>Shrub</td>
<td>Caparis tomentosa, Salvadora persica</td>
<td>1-3</td>
<td>isolated clumps</td>
</tr>
<tr>
<td></td>
<td>Ground cover</td>
<td>Duospermum quadrangularis, Sphaeranthus flexuosus, Vernonia glabra, mixed grass spp.</td>
<td>0.25-0.75</td>
<td>mid-dense</td>
</tr>
<tr>
<td><strong>Albida Woodland (140m)</strong></td>
<td>Tree</td>
<td>Faidherbia albida</td>
<td>12-20</td>
<td>sparse</td>
</tr>
<tr>
<td></td>
<td>Shrub</td>
<td>Senna singueana</td>
<td>1-3</td>
<td>very sparse</td>
</tr>
<tr>
<td></td>
<td>Ground cover</td>
<td>Senna obtusifolia, Solanum panduriforme, Sphaeranthus flexuosus, mixed grass spp.</td>
<td>0.5-1</td>
<td>mid-dense</td>
</tr>
<tr>
<td><strong>Ecotone: grassland/woodland to thicket (80)</strong></td>
<td>Tree</td>
<td>Acacia tortilis, Combretum imberbe, Philenoptera violacea,</td>
<td>6-12</td>
<td>very sparse</td>
</tr>
<tr>
<td></td>
<td>Shrub</td>
<td>Dichrostachys cinerea, Diospyros sinensis, Boscia mossambicensis,</td>
<td>1-3</td>
<td>sparse</td>
</tr>
<tr>
<td></td>
<td>Ground cover</td>
<td>Crossandra spinescus, Duospermum quadrangularis, Vernonia glabra, O. canum, O. americanum, Sphaeranthus flexuosus, mixed grass spp.</td>
<td>0.5-1</td>
<td>dense</td>
</tr>
<tr>
<td><strong>Thicket: shrubland (35)</strong></td>
<td>Tree</td>
<td>none</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Shrub</td>
<td>Acacia ataxacantha, Boscia mossambicensis, Combretum elaeagnoides, Combretum adenogonium, Colophospermum mopane, Holmskioldia tettensis, Markhamia zanzibarica</td>
<td>1-3</td>
<td>mid-dense</td>
</tr>
<tr>
<td></td>
<td>Ground cover</td>
<td>Crossandra spinescus, Dicoma anomela, Duospermum quadrangularis, mixed grass spp.</td>
<td>0.25-0.75</td>
<td>sparse</td>
</tr>
</tbody>
</table>

The *albida* woodland habitat was an open woodland generally monodominant with *Faidherbia albida*, a sparse shrub layer of *Senna singueana* which was often associated with termite mounds, and a variety of forbs and grasses. Young *albida* forest with a closer canopy cover was included here, which otherwise had the same floral characteristics. The ecotone habitat was a heterogeneous transitional zone between grassland and thickets or open woodland and thickets, forming open
woodland at the tree canopy with an understory of open shrubland which was composed of a diverse array of species at different transect locations. The dense groundcover contained an equal prevalence of forbs to grasses. This habitat included areas of termitaria vegetation. Thicket habitats (shrublands) were composed of a variety of species, including some areas dominated by *Acacia ataxacantha* and *Combretum elaeagnoides* (jesse bush), and others by *mopane* scrub. Much of the *mopane* woodland in the valley floor had a thicket understory, so it was included in this habitat.

The study site also contained strips of riverine vegetation along watercourses and gullies, containing a variety of *Acacia* species and *Trichilia emetica*. However, these areas generally occurred in strips less than 100m wide and resembled the spectral properties and vegetation structure of either the *albida* woodland or ecotone, so they were classified within these general habitats for this study.

Surveys did not extend to the escarpment miombo habitat due to lack of road access. For the supervised vegetation classification this habitat was characterised from the spectral properties of the vegetation in the escarpment, which was clearly visible from the satellite image. Miombo is a specific type of African woodland, dominated by three tree genera; *Brachystegia*, *Julbernadia* and *Isoberlinia*, and covers much of the Zambian plateau (Jachmann 2000). It is generally typified by a closed canopy, but is still considered woodland since it supports an understory of grasses and herbs due to the low density of foliage at canopy level (Bingham 1995). Miombo undergoes regular seasonal burning, which is apparent on the vegetation map derived from the satellite image (Figure 3.1). It should be noted that the escarpment miombo habitat defined for the purpose of this study is more floristically diverse than represented here, particularly in the areas of escarpment where typical woodlands give way to riverine gulleys and steep valleys.
Figure 3.1a and b. Map of habitat distribution in the study area, developed from a supervised vegetation classification. Outlines show the overall study area and the river valley floor. The escarpment, dominated by miombo, is visible to the north of the valley floor.
Figure 3.1 shows the distribution of habitats in the study area. The alluvial terraces of the river valley floor area contain the greatest diversity of habitats, while the northern section of the study area is dominated by the escarpment miombo. Table 3.2 shows the proportion of the study area covered by each habitat. Thicket was the most dominant habitat type on the valley floor, but this was largely due to its prevalence in one north-eastern corner of the study area furthest from the Zambezi River (Figure 3.1a). This area was predominantly *mopane* scrub. *Albida* woodland and ecotone covered a large proportion of the remaining valley floor area on the alluvial terraces.

**Table 3.2** Percentage of study area covered by each habitat. Values are given for both the entire study area, and for only the study area valley floor.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Study Area</th>
<th>Valley Floor</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Km²</td>
<td>% Cover</td>
</tr>
<tr>
<td>Grassland</td>
<td>37.9</td>
<td>2.6</td>
</tr>
<tr>
<td>Albida woodland</td>
<td>118.9</td>
<td>8.2</td>
</tr>
<tr>
<td>Ecotone</td>
<td>131.0</td>
<td>9.0</td>
</tr>
<tr>
<td>Thicket</td>
<td>266.6</td>
<td>18.4</td>
</tr>
<tr>
<td>Miombo</td>
<td>893.7</td>
<td>61.7</td>
</tr>
</tbody>
</table>

### 3.4.1.2 Prey density

Impala density was found to vary between habitats. The highest densities of impala were found in the more open habitats of grassland and *albida* woodland (Table 3.3).

**Table 3.3.** Impala mean density and cluster size within each habitat. Sampling effort and truncation distances are included for each vegetation type. The percentage coefficient of variation is included (% CV). Superscript letters indicate significant differences between habitats (see text).

<table>
<thead>
<tr>
<th>Vegetation Type</th>
<th>Sampling Effort (Km)</th>
<th>Truncation Distance (m)</th>
<th>Mean Density/Km²</th>
<th>% CV (Density)</th>
<th>Mean Cluster Size</th>
<th>% CV (Cluster size)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>13.5</td>
<td>250</td>
<td>174ᵇ</td>
<td>36.9</td>
<td>17.4ᵈ</td>
<td>28.16</td>
</tr>
<tr>
<td>Albida woodland</td>
<td>15.2</td>
<td>140</td>
<td>229ᵃ</td>
<td>23.9</td>
<td>14.0ᶜ</td>
<td>13.92</td>
</tr>
<tr>
<td>Ecotone</td>
<td>14.3</td>
<td>80</td>
<td>66</td>
<td>45.9</td>
<td>8.6</td>
<td>19.78</td>
</tr>
<tr>
<td>Thicket</td>
<td>14.5</td>
<td>35</td>
<td>38ᵃᵇ</td>
<td>52.2</td>
<td>4.2ᵃᵈ</td>
<td>32.45</td>
</tr>
</tbody>
</table>

Analysis of variance showed that there was a significant difference in impala density between habitats (d.f.=3, f=5.23, p=0.0022). Post-tests of multiple comparisons between vegetation types showed that the significant differences lay between the thicket and *albida* woodland (t=3.424, p<0.05, see superscript “a” in Table 3.3), and between thicket and grassland (t=2.857, p<0.05, see superscript “b” in Table 3.3).
Weighting impala density by the proportion of the valley floor covered by each habitat gave an average impala density of 95/km\(^2\) (% C.V = 43.6), and an estimated abundance of 52,600 impala in the study area.

Impala herd sizes in each habitat were assessed as clusters in DISTANCE 4.1 (Thomas et al. 2003). Changes in herd size between vegetation types followed the same trend as impala density, with significant differences in ANOVA results (d.f.=3, f=3.93, p=0.011), found between thicket and *albida* woodland (t=2.790, p<0.05, see superscript “c” in Table 3.3) and thicket and grassland (t=3.133, p<0.05, see superscript “d” in Table 3.3).

The validity of herd size estimates was tested because vegetation density can affect counts as distance increases from each transect. There was no correlation between herd size and perpendicular distance from the transect in grassland (r=-0.12, p=0.07, n=117), *albida* woodland (r=-0.09, p=0.16, n=222), or ecotone vegetation (r=-0.07, p=0.28, n=46). In the thicket classification there was a moderate positive correlation (r=0.65, p=0.001, n=9) between herd size and increasing perpendicular distance. Larger group size may increase the probability of detection, particularly in thicker habitats where smaller groups may be obscured from view. However, thicker vegetation also increases the likelihood of failing to count all members of the group, and these effects are likely to counteract each other, as suggested by Dunham (1994).

Since there was no evidence of decreasing herd size with increasing distance from transects, the truncation distances used in DISTANCE 4.1 (Thomas et al. 2003) were taken as a reliable estimate of vegetation density, as measured by prey visibility. Plots of impala density and herd size against vegetation visibility showed positive relationships, as seen in Figures 3.2a and 3.2b, thus impala density and herd size declined with increasing vegetation density across habitats. Impala density was moderately positively correlated to vegetation visibility (r=0.72, p=0.27, n=4), although not significantly so. Herd size was strongly positively correlated to vegetation visibility (r=0.96, p=0.05, n=4).
Figure 3.2a The relationship between impala density and vegetation visibility. Error bars represent (±)SE.

Figure 3.2b The relationship between impala mean herd size and vegetation visibility. Error bars represent (±)SE.

Impala counts in this study were timed to coincide with wild dog hunting periods, and were tested for temporal differences in impala density between these crepuscular periods, across habitats (Figure 3.3) Wilcoxon Matched-Pairs Signed-Ranks tests showed no differences between morning and afternoon in densities in any habitat; grassland (w+=10, w=11, n=6, p<=1), *albida* woodland (w+=2, w=8, n=4, p<=0.375), ecotone (w+=16, w=5, n=6, p<=0.3125) or thicket (w+=1, w=5, n=3, p<=0.5).

Figure 3.3 Comparison of morning (AM) and afternoon (PM) impala density estimates (impala/km²) within different habitats. Error bars represent (±)SE.
3.4.2 Wild Dog Home Ranges and Habitat Utilisation

3.4.2.1 Home range analysis

Plots of the number of observations against home range area revealed a plateau in increasing home range area at approximately 40 observations, which accounted for 88.5% of estimated home range areas (Figure 3.4). Home range estimates for all pack years were then adjusted based on the number of observations using this non-linear regression curve.

![Graph showing the percentage area of home range generated from an increasing number of observations. Data were based on the mean values from two home ranges with n>100 observations.](image)

Minimum convex polygon (MCP) estimates of wild dog multiyear ranges averaged 378km$^2$, ranging from 184km$^2$ to 665km$^2$ (Table 3.4). Annual home ranges were smaller on average, although not significantly so ($t=0.84$, df=8, $p=0.4$), with a mean size of 273km$^2$. The largest multiyear range occurred as a product of home range displacement as the pack shifted across the river valley floor, combined with large annual home ranges due to remote den locations in the escarpment (see Mushika pack 2000 and 2001 in Figure 3.5a)
Table 3.4 Home range sizes and overlap estimates for wild dog packs. Key: N= number of observations; 100% MCP = maximum home range estimate; Proportion of 50% Contour Area = proportion of 95% probability contour area covered by the 50% probability contour; 100% MCP overlap = percentage of total home range overlap; 50% Contour Overlap = percentage of overlap in 50% contour areas.

<table>
<thead>
<tr>
<th>Pack Year</th>
<th>N</th>
<th>100% MCP (km²)</th>
<th>Proportion of 50% Contour Area</th>
<th>100% MCP Overlap (%)</th>
<th>50% Contour Overlap (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jeki99</td>
<td>50</td>
<td>255</td>
<td>0.18</td>
<td>n/a</td>
<td>0</td>
</tr>
<tr>
<td>Jeki00/01</td>
<td>36</td>
<td>141</td>
<td>0.20</td>
<td>71.5</td>
<td>19.9</td>
</tr>
<tr>
<td>GMA02*</td>
<td>112</td>
<td>74</td>
<td>0.08</td>
<td>0.2</td>
<td>0</td>
</tr>
<tr>
<td>GMA03*</td>
<td>103</td>
<td>442</td>
<td>0.23</td>
<td>32.8</td>
<td>8.6</td>
</tr>
<tr>
<td>Mush00*</td>
<td>58</td>
<td>459</td>
<td>0.17</td>
<td>5.7</td>
<td>0</td>
</tr>
<tr>
<td>Mush01</td>
<td>39</td>
<td>198</td>
<td>0.27</td>
<td>37.6</td>
<td>6.4</td>
</tr>
<tr>
<td>Simwen02/03*</td>
<td>37</td>
<td>345</td>
<td>0.13</td>
<td>42.1</td>
<td>29.3</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td></td>
<td><strong>273.2</strong></td>
<td><strong>0.18</strong></td>
<td><strong>31.7</strong></td>
<td><strong>9.2</strong></td>
</tr>
<tr>
<td><strong>SE</strong></td>
<td></td>
<td><strong>55.9</strong></td>
<td>0.023</td>
<td>9.86</td>
<td>4.3</td>
</tr>
</tbody>
</table>

*indicates breeding pack year.

Fifty percent probability contour core areas covered an average of 18% (SE=2.3%) of the 95% probability distribution (Table 3.4). In general, core areas received two to four times more use than would be expected from a random distribution of observations. In the case of the smallest 50% contour area, the GMA 2002 pack (Figure 3.6e), the core area received six times the expected random use. This was the result of a small home range with a heavily used den area which had many hunts occurring nearby to form the core.

Although spatial overlap in home ranges between packs reached up to 71.5% in any one year (Table 3.4 and see Figure 3.5), dogs were never observed directly encountering each other and are likely to have avoided each other temporally (Mills & Gorman 1997). Packs were observed within one kilometer of each other on only one occasion but typically were observed approximately 30km apart. Overlapping areas were shared with only one pack. Overlap in the 50% probability contour was significantly less (paired t-test, t=2.71, df=5, p=0.042) at only 9% (Table 3.4), further reducing the probability that packs would encounter each other in core use areas.
Figure 3.5a Map of 100% Minimum Convex Polygon home ranges for packs monitored by radio telemetry.

Figure 3.5b Map of 100% Minimum Convex Polygon home ranges for uncollared packs monitored by road tracking and sightings reports.
Home range data for the Jeki pack was limited to the valley floor since this pack was not radio-collared, so their home ranges did not extend into the escarpment. However, of the collared packs, only packs that were breeding were observed in the escarpment and the Jeki pack was a group of siblings (1999-2001) who did not breed. Therefore home range estimates for the Jeki pack are considered reasonably accurate. Thicket usage may be underestimated due to reduced visibility.

Figure 3.6 illustrates the 50%, 75% and 95% contour core areas of wild dog home ranges. Core areas in the escarpment were due to den locations, all other core areas were contained on the alluvial terraces of the valley floor. Packs which denned in the escarpment also maintained core hunting areas in the valley floor throughout the year (Figure 3.6c, e, f, and g).
There was a significant positive correlation between annual home range size and the number of combined adults and yearlings ($r = 0.81$, df=6, $p=0.028$, see Figure 3.7). This relationship became non-significant if only adults were included in the analysis ($r=0.36$, df=5, $p=0.47$).
There was no significant difference in the abundance of the dogs’ main prey species, impala, in pack home ranges (ANOVA, df=11, f=0.27, p=0.77). Pack ranges all included similar sized areas of the two habitats containing the highest impala density, ranging from 24.6 km$^2$ to 28.8 km$^2$ of grassland (mean=26.2 km$^2$, ±SE=1.2), and 66.2 km$^2$ to 97.1 km$^2$ of albida woodland (mean=82.9 km$^2$, ±SE=9.0). There was much greater variation in the size of low prey density habitats; thicket habitat sizes ranged from 17.2 km$^2$ to 173 km$^2$, and miombo from 1.2 km$^2$ to 220 km$^2$ (mean=79.8 km$^2$, ±SE=47.6 and mean=83.5 km$^2$, ±SE=69.1, respectively). Despite larger areas of low density habitats in most breeding packs, there was no significant difference between breeding and non-breeding range sizes (t=0.978, df=2, p=0.38, data not shown).

Data from the wet season (December to March) was extremely limited, due to inaccessibility. All observations of wild dog packs involved locations on the valley floor, although only 5% of sightings utilised aerial tracking or telemetry (from n=22 sightings). There was a range of three to eight wet season sightings per year from the limited number of scouts and staff in the area. Wild dogs were never observed to enter or cross any part of the Zambezi river.
3.4.2.2 Habitat utilisation and prey selection

As might be expected from the high density of impala in the study area, the dominant prey species for the Lower Zambezi wild dogs was impala, with a value of over 80% whether assessed by hunting effort, number of kills or biomass in the wild dogs’ diet (Table 3.5). Bushbuck formed the second largest component of the diet comprising 9.5% of kills, 80% of which occurred in the thickly vegetated habitats of the GMA area.

*Table 3.5 Wild dog prey selection within the study area, showing the proportion of hunting effort spent on each species and the proportion of successful kills and biomass in the diet. *n=165 hunt periods; *n=95 kills.*

<table>
<thead>
<tr>
<th>Prey Species</th>
<th>Hunts (%)</th>
<th>Kills (%)</th>
<th>Biomass (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Impala</td>
<td>81.2</td>
<td>89.5</td>
<td>85.3</td>
</tr>
<tr>
<td>Bushbuck</td>
<td>12.1</td>
<td>9.5</td>
<td>11.3</td>
</tr>
<tr>
<td>Kudu</td>
<td>1.2</td>
<td>1</td>
<td>3.4</td>
</tr>
<tr>
<td>Warthog</td>
<td>2.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Waterbuck</td>
<td>1.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Buffalo</td>
<td>0.6</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

For general habitat selection including all activities, wild dogs showed the strongest preference for grassland habitat (Table 3.6), which comprised only 2.6% of the study area. A preference index below 0.3 demonstrates avoidance, while above 0.3 shows preference for that area. The dogs also had a strong preference for ecotone and *Albida* woodland. Thicket was utilised roughly in proportion to its coverage in the study area, whilst miombo was strongly avoided.

*Table 3.6 Wild dog habitat selection within the study area, expressed as an index of preference (PI).*

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Wild Dog PI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>0.85</td>
</tr>
<tr>
<td><em>Albida</em> Woodland</td>
<td>0.60</td>
</tr>
<tr>
<td>Ecotone</td>
<td>0.66</td>
</tr>
<tr>
<td>Thicket</td>
<td>0.32</td>
</tr>
<tr>
<td>Miombo</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Figure 3.8 illustrates habitat utilisation per pack. The only pack to show a preference for thicket was the orphaned sibling Jeki pack (see section 2.4.1), which also preferred ecotone over grasslands and albida woodland. Overall hunting success was lowest in thicket areas (Table 3.8), which was also where most effort was spent hunting bushbuck (Table 3.7).

![Preference Index Graph]

*Figure 3.8 Habitat selection (PI) for individual packs.*

The GMA pack preferred the escarpment miombo, then grassland and ecotone, but avoided thicket. The Mushika pack was based in the eastern end of the study area inside the National Park and had a strong preference for grassland and ecotone habitats, the two highest prey density habitats. This pack avoided both thicket and miombo. The Mushika and Simwenzenze packs were combined for this multiyear analysis because the Simwenzenze pack was formed from immigrant males and the Mushika females, and maintained the natal home range of the Mushika females.

*Table 3.7 Percentage of hunting effort spent on each of the dominant prey species within each habitat type.*

<table>
<thead>
<tr>
<th>Prey Species</th>
<th>Grassld.</th>
<th>Albida Wd</th>
<th>Ecotone</th>
<th>Thicket</th>
</tr>
</thead>
<tbody>
<tr>
<td>Impala</td>
<td>94.4</td>
<td>82.0</td>
<td>80.3</td>
<td>46.2</td>
</tr>
<tr>
<td>Bushbuck</td>
<td>0</td>
<td>8.0</td>
<td>13.6</td>
<td>53.8</td>
</tr>
<tr>
<td>Other</td>
<td>5.6</td>
<td>10.0</td>
<td>6.1</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3.8. Habitat selection during hunting by wild dogs, compared with hunting success (all prey species) and corresponding impala density in each habitat. Hunting success based on $n=121$ kills, $n=237$ hunts.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Wild Dog Hunting PI</th>
<th>Hunting Success (%)</th>
<th>Impala Density (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>0.55</td>
<td>55.8</td>
<td>174</td>
</tr>
<tr>
<td>Albida Woodland</td>
<td>0.35</td>
<td>57.4</td>
<td>229</td>
</tr>
<tr>
<td>Ecotone</td>
<td>0.39</td>
<td>52.8</td>
<td>66</td>
</tr>
<tr>
<td>Thicket</td>
<td>0.16</td>
<td>25.7</td>
<td>38</td>
</tr>
</tbody>
</table>

Hunting data collected from ground observations were restricted to the river valley floor habitats so miombo habitat was removed to assess wild dog hunting preferences and success in different habitats (Table 3.7 and 3.8). There was little difference in hunting success between grassland, *Albida* woodland and ecotone habitats, which were all preferred by wild dogs, however hunting success was approximately halved in the thicket habitat (Table 3.8) which was strongly avoided. This corresponded to the lower prey density and visibility found in thicket habitat (Table 3.3). There was a strong positive correlation between wild dog hunting preferences and hunting success ($r=0.83$, $p=0.16$, $n=4$), although it was not significant, but the analysis had limited power due to low sample size. The wild dogs showed the strongest preference for grassland, which made up only 7% of the valley floor area. These areas had grasses less than 75cm high (Table 3.2), many of which died off to bare ground by the end of the dry season. There was therefore no restriction on visibility, combined with high prey density in this habitat. General habitat preferences follow the same trend as habitat selection for all activities (Table 3.6), except thicket was not actively avoided (PI =0.32) for general use, only hunting.
3.5 DISCUSSION

3.5.1 Habitat and Prey Species

The study site was naturally divided into an area of miombo escarpment habitat to the north, and the river valley floor which supported a diversity of habitats in the south (Figure 3.1). The vegetation mosaic formed by the horizontal alluvial terraces further divided by erosion gullies and rivers resulted in a large diversity of habitats condensed within a relatively small study area. Other wild dog study sites have generally been more homogeneous in comparison, thus the Lower Zambezi provided an ideal site to obtain more detailed data on wild dog spatial and temporal habitat selection.

Relative impala distribution over the study area habitats followed expectations based on published data, which found that impala prefer edge habitats between open and closed vegetation types (Leuthold 1970), and light woodland and grassland habitats (Estes 1991). Herd size and impala density may be interdependent and partially explain the finding that impala density and herd size increased with decreasing vegetation density (increasing visibility, see Figure 3.2). However the relationship between herd size and vegetation density also has a behavioural explanation; impala’s preference for more open habitats would leave them more exposed to predation, therefore larger group sizes in open habitats carry the benefits of increased vigilance (Schenkel 1966) and a reduced probability of predation for each animal as group size increases. Impala were observed to congregate on the open grasslands and plains in the evening and disperse into other habitats to feed during the day, thus these open habitats were utilised even when food availability was limited by vegetation die-off during the dry season.

Impala densities for the study area were higher than would be expected, both on average and for the highest density recorded for an individual habitat (at 95/km² and 229/km² respectively). Average population densities at four sites spanning east and southern Africa ranged from 15/ km² to 80/ km² (Estes 1991; Jarman 1979; Leuthold 1970), although a high of 214/ km² was recorded in wooded savannah in Rwanda (Estes 1991). At such high densities the impala population could have adverse impacts on vegetation through overgrazing, and may also affect the species diversity of other antelope species since impala are mixed feeders and compete with more selective feeders for resources. Further study of the impacts of this species on Lower Zambezi
ecology is recommended. Impala densities in each habitat are likely to change seasonally since herbivores tend to disperse back towards the escarpment and ecotone when more water and forage is available during the wet season (Dunham 1994). However, wild dog and prey data were collected simultaneously (during the dry season) so the recorded impala densities remain relevant to the observed wild dog habitat selection.

The Lower Zambezi wild dogs had an abundance of prey. Impala formed the bulk of the wild dogs’ diet which is in agreement with previous studies that found wild dogs preyed upon the most common medium sized prey (Fuller & Kat 1990; Mills & Gorman 1997; Woodroffe et al. 1997). Wild dogs were observed taking larger prey (kudu) only once; instead larger packs made multiple kills of impala in the one hunting session. This strong species preference may partially be a function of pack size, since smaller packs (<10) were observed to take more impala in the Selous (Creel & Creel 2002), while larger packs took more wildebeest and kudu. The mean pack size observed in the Lower Zambezi was 7.8 (range 3 to 12, Figure 3.7). However, in contrast to the Selous, larger prey were limited here; wildebeest are entirely absent from the area while kudu are restricted to localised areas of the Park. Therefore prey selection in this case is more likely to be simply a consequence of the relatively limited abundance of larger species.

Previous studies found that wild dog hunting success was independent of prey density (Creel & Creel 1998; Fuller & Kat 1993) and that wild dogs were found at their highest densities in low prey density areas, suggesting that competing predators were a more important determinant of range movements (Mills & Gorman 1997). In contrast to this, the wild dogs in the Lower Zambezi showed an active preference for high prey density habitats, particularly open grasslands. During hunting they avoided the lowest prey density habitat, thicket, where they had a markedly reduced hunting success (Table 3.8). The reduction of hunting success in thicket is likely to be related to the density of vegetation restricting movement and visibility. The heterogeneous nature of broadly categorised landscapes means that wild dogs can probably avoid thickets in many areas. In fact results suggest that packs who utilised thicket used it mostly for travelling and resting since thicket was avoided during hunting but used roughly in proportion to its coverage for overall usage. Utilisation of thicket may have
been underestimated due to limited access in some areas. However, thicket areas were relatively small and although wild dog kills were not always sighted it was still possible to detect the occurrence or absence of a kill. Telemetry signals indicated if the dogs became stationary to feed, and made it possible to track and observe the dogs leaving the thicket and thereby observe evidence of a recent kill including full bellies and blood on their muzzles.

### 3.5.2 Wild Dog Home Ranges and Habitat Utilisation

Minimum convex polygon (MCP) estimates of wild dog multiyear ranges (from 184 km$^2$ to 665 km$^2$, Table 3.4) were comparable to those observed in similarly wooded areas in Hwange National Park and Selous Game Reserve, at 423 km$^2$ and 379 km$^2$ respectively (Creel & Creel 2002; Woodroffe et al. 1997). There was substantial overlap in MCP home ranges at up to 72% (Table 3.4). Overlap was most likely due to the linear movement of the packs between the geographical boundaries of the river and escarpment, and the wild dogs’ preference for grassland habitats in the valley floor.

Annual home ranges were small (mean = 237 km$^2$) and roughly equivalent to those observed in small fenced reserves such as Hluhluwe Umfolozi Game Reserve in South Africa (Andreka et al. 1999). The smallest home range recorded (74 km$^2$) was for the GMA 2002 pack based in the Chiawa Game Management area where movements to the west were most likely inhibited by village settlements. No home ranges had a 95% probability contour which extended into village areas, several kilometres west of the core study area boundary (Figure 3.6). Packs rarely entered this area and always returned to the photographic safari area within a short period. However, no disappearances or mortalities were recorded during these westerly pack movements, nor reports of livestock losses from the villages. Wet season data was limited and inconclusive, but given the geography of the area and the data from dry season range movements, large seasonal wild dog range movements outside of the valley floor would be unexpected.

Contrary to previous studies, a significant positive relationship was found between pack size and home range size. Results from larger studies in Selous and Kruger found only a weak and non-significant positive correlation between adult/yearling
pack size and home range size using multiyear ranges, and no correlation using annual range data (Creel & Creel 2002; Mills & Gorman 1997). The authors suggested there was no evidence that larger packs defended larger territories and therefore resources, in fact Mills and Gorman (1997) found wild dogs were at their highest density in areas of lowest prey density. Despite the large variation in home range sizes in the Lower Zambezi, the lack of difference between both overall impala abundance, and the area of the highest density habitat in each range, provides no support for the resource partitioning hypothesis and concurs with previous studies.

In this study the correlation between pack size and home range size is likely to be a function of breeding behaviour. Those packs that bred retreated into the escarpment, while still utilising the valley floor to hunt, thereby increasing their home range size. Packs that bred successfully for more than one year had larger pack sizes. There was no significant difference between breeding and non-breeding range sizes largely because the smallest home range was for the first breeding year of the GMA pack of 5 adults. However this pack’s home range increased dramatically the next year (442 km$^2$) when the pack was increased by eight yearlings (Table 3.4). With the exception of this single pack year, home ranges were generally smaller for packs that did not breed. Restricted access to the miombo escarpment habitat may have led to an underestimation of wild dog utilisation in this area, but the wild dogs were only ever located in the escarpment during breeding periods. During these periods the dogs remained in the low foothills of the escarpment and hunted down into the valley floor. The Zambian escarpment rises steeply from the valley floor and due to the slope and vegetation cover some areas may be low in density of preferred prey species (Estes 1991). It is therefore likely the steepest sections of escarpment form a natural deterrent to wild dog movements, except perhaps for emigrating groups who may travel over it to leave the area.

Wild dogs had a strong preference for all valley floor habitats except thickets, but despite impala density being highest in *albida* woodland this habitat was ranked 3\textsuperscript{rd} in both general use and hunting preferences, favoured less than grassland and marginally less than ecotone (Tables 3.6 and 3.8). Ecotone was considerably lower in impala density than grassland and *albida* woodland but it was also preferred (Table 4.2). Ecotone habitat would have a higher abundance of bushbuck which occupies dense
vegetation (Waser 1975b), however densities of this species would be low compared to impala since bushbuck are solitary animals (Waser 1975a) and the lower visibility habitat would make hunting more difficult. Since the relationship between wild dog preferences and prey densities was not strictly linear, this suggests that wild dogs may have selected habitats to minimise interaction with competing predators, for instance when breeding.

The only pack that showed a preference for thickets, and also preferred ecotone over other habitats, was the orphaned sibling Jeki pack. This pack of 3-5 dogs would have been vulnerable to both interspecific and intraspecific competition, which may explain their active avoidance of higher prey density areas. The preference of the GMA pack for miombo was due to this packs’ denning several times in the escarpment. The bulk of the *albida* woodland within their home range was in the National Park, which this pack utilised only in 2003. The GMA area is heavily dominated by ecotone and thicket, however this pack still showed a strong avoidance of thicket. The Mushika pack was based in the eastern end of the study area inside the National Park and had a strong preference for grassland and ecotone habitats, the two highest prey density habitats. This pack avoided both thicket and miombo.

Overall these results show that prey density was not a limiting factor for the Lower Zambezi wild dog population, and that in contrast to previous studies this population showed an active preference for high prey density habitats. Non-breeding home range sizes were small and limited to the river valley floor, but home range size increased during breeding periods to include remote areas of the Zambian escarpment. The effects of competing predators on the range movements of the Lower Zambezi wild dog population are further investigated in the following chapter.
CHAPTER 4: INTERPREDATOR COMPETITION

4.1 INTRODUCTION
Lions (*Panthera leo*) kill both adult wild dogs and pups, and spotted hyenas (*Crocuta crocuta*) often steal wild dog kills and can reduce the feeding success of dogs by harassment, which in turn reduces the dogs’ ability to raise pups (Fanshawe & Fitzgibbon 1993; Fanshawe et al. 1991; Fuller & Kat 1990; Woodroffe & Ginsberg 1999a).

Creel and Creel (1996) compared densities of wild dogs with those of lions and spotted hyaenas across four ecosystems in east and southern Africa. They found strong negative correlations between wild dog and lion densities, and wild dog and spotted hyaena densities, and a positive correlation between lions and spotted hyaenas. Their data supported the theory that wild dog densities are limited by competition with these two carnivores. The significant correlation between lion and spotted hyaenas means that the effect of interpredator competition from these species on wild dog population success is difficult to separate. Diet overlap and subsequently increased competition was used to explain the negative correlation between spotted hyaena and wild dog density, however the competitive relationship between wild dogs and lions was less clear, and the existence of a causal link between the two, rather than a correlation, was not established. Direct predation by lions on wild dogs is a common occurrence in some areas and may explain wild dogs avoiding areas of high lion density (Mills & Biggs 1993; Woodroffe et al. 1997). Wild dogs have also been shown to avoid areas with high lion densities even when these habitats have the highest densities of wild dog prey (Mills & Gorman 1997).

4.1.1 Interpredator Competition from Spotted Hyaenas (*Crocuta crocuta*)
Wild dogs are generally found at considerably lower densities than spotted hyaenas and lions (Creel & Creel 1996). Hyaenas have been found to have a greater impact on wild dog feeding rates in areas where the hyaenas are more common and visibility is good (Creel & Creel 1996). Kruuk (1972) found that hyaenas fed at 60% of wild kills and were present at 74% in the high visibility area of the Serengeti and Ngorogoro.
areas. In contrast, in more wooded areas such as the Selous and Kruger National Park, hyaenas rarely fed at wild dog kills and if present were usually in lower numbers than dogs (Creel & Creel 1996; Mills & Biggs 1993).

By measuring the daily energy expenditure of six wild dogs, Gorman et al. (1998) found the energy costs to wild dogs while hunting to be high, up to 25 times the basal metabolic rate. Therefore a small loss in food due to kleptoparasitism by spotted hyaenas may have a substantial impact on the amount of time the dogs need to spend hunting to achieve energy balance. Measurements were based on a pack which was hunting very intensively due to a high ratio of adults to dependent young, and it was estimated that if the dogs were to lose 25% of their food they would have to hunt for up to 12 hrs a day to maintain energy balance, instead of the observed average of 3.5hrs a day (Gorman et al. 1998).

Successful kleptoparasitism of wild dog kills by spotted hyaenas is mainly dependent on the numbers of hyaenas present. Although hyaenas may be present at a large percentage of wild dog kills, up to 92% (Fanshawe et al. 1991), the hyaenas often only feed after the dogs have eaten their fill (Fanshawe et al. 1991; Fuller & Kat 1990). This level of competition would not be expected to have a significant effect on the feeding success of the dogs. A study in Kenya found there were rarely more than four hyaenas observed at a wild dog kill; dogs often chased single hyaenas and no hyaenas fed before the dogs abandoned the kill of their own volition (Fuller & Kat 1990). Similarly wild dogs were frequently observed chasing and attacking hyaenas in the Selous (Creel & Creel 1996).

In contrast, Carbone et al. (1997) modelled data from a Serengeti study and found that more than four hyaenas at a kill considerably reduced the wild dogs’ access time to that kill, and individual “gut fill” time for a dog often exceeded access time in this situation. An earlier study in the Serengeti (Fanshawe & Fitzgibbon 1993) of an extensively studied single wild dog pack found that the wild dogs’ time at the kill was longer where there was a higher ratio of dogs to hyaenas, and that therefore larger packs of dogs would be more successful in areas of high hyaena density through improved defence of kills (Fanshawe & Fitzgibbon 1993). However, Carbone et al. (1997) suggest that the advantages of a large pack with an increased ability to defend
a kill rarely compensates for the reduction in feeding due to intrapack “scramble competition” for food. Therefore at least three important variables are involved determining the effects of kleptoparasitism: the number of wild dogs, the number of hyaenas, and the prey mass. Intermediate pack sizes of three to ten adults (Carbone et al. 1997) may be most effective in achieving a balance between the defence of kills and meeting nutritional demands for each individual dog.

Direct predation by hyaenas on wild dogs is uncommon and usually opportunistic. In the Serengeti two litters of pups were left unattended at a time of food scarcity and were killed by hyaenas (Malcolm & Marten 1982), while in the Selous two pups were abandoned due to deterioration from anthrax infection and were subsequently killed by hyaenas (Creel et al. 1995). Since pups cannot be collared and remain underground for several weeks, or at inaccessible den sites, it is often difficult to determine causes of mortality. Hyaenas may play an important role as a disease reservoir for wild dogs since they are found at higher densities than wild dogs, and often interact with them (Creel & Creel 1996).

4.1.2 Interpredator Competition from Lions (*Panthera leo*)

The negative effect of lions on wild dog populations has been widely cited (Creel & Creel 1998; Creel & Creel 1996; Mills & Gorman 1997; Vucetich & Creel 1999; Woodroffe & Ginsberg 1999a; Woodroffe et al. 1997; Woodroffe et al. 2004b). In a comparison of wild dog populations in five different countries, predation by lions was the single most important cause of natural mortality in adults, accounting for 12% of adult mortality (Woodroffe & Ginsberg 1999a). These results were an average of values across sites, but in fact high lion predation was only found in two of the five study areas. Another study confirmed the important effects of lions in one of these two sites, Kruger National Park, where lions caused 39% of pup mortality and 43% of adult deaths (Mills & Gorman 1997). It is important to note that these results are site-specific and in some populations, including south-western Zimbabwe and parts of Zambia, direct predation of adult wild dogs by lions has been negligible (Creel & Creel 2002; Woodroffe et al. 1997; Woodroffe et al. 2004b).

In addition to high densities of lions being correlated with low densities of wild dogs (Creel & Creel 1996; Mills & Gorman 1997), in Kruger National Park wild dogs were
also found at their lowest densities where prey was most abundant (Mills & Gorman 1997). Behavioural avoidance of lions could conceivably force dogs out of areas of high prey density and into high risk areas outside of National Parks and game reserves. A case study in the Ngorogoro Crater in Tanzania showed that wild dogs were observed in the area in the 1960s after a crash in the lion population. The lion population recovered, the dogs disappeared, and they have remained absent while the lion population increased five fold then stabilised (Creel & Creel 1996). No causal effects were established.

Reports across study sites suggest kleptoparasitism of wild dog kills by lions is rare compared to that seen by hyaenas (Creel & Creel 2002). In a study in Kenya wild dogs never lost a kill to hyaenas, however Fuller and Kat (1990) observed a single lioness appropriate a juvenile wildebeest killed by wild dogs; the lioness was then joined by another resulting in the dogs abandoning the kill. The lack of observed kleptoparasitism by lions may be at least partly a result of successful avoidance behaviour by wild dogs.

Some studies recommend that in-situ conservation and reintroduction programs should be focused in areas where wild dog population viability, or recovery, will not be compromised by the impact of a dense lion population (Mills & Gorman 1997; Vucetich & Creel 1999). However, since results to date are not consistent across study sites, this suggestion emphasises the need for further collection of site-specific information on the impact of lions and spotted hyaenas to ensure effective management.
4.2 OBJECTIVES

This objective of this section of the study was to determine the role of interpredator competition on wild dog home range movements and population dynamics. Specifically, aims were to:

1. *Estimate the density of competing predators lion and spotted hyaena in the study area.*

2. *Assess the effects of interpredator competition on;*
   
   i) *kleptoparasitism of wild dog kills,*
   
   ii) *wild dog movements and habitat utilisation.*
4.3 METHODS

Annual surveys of lion and spotted hyaena were carried out to establish species density distributions. Density data were then compared to wild dog habitat utilisation.

4.3.1 Lion Surveys

Two methods were combined to assess lion densities in the study area:

i) Annual survey forms were distributed to all safari operators in the study area, who collected data on recognisable individuals and prides in their safari area. Data consisted of opportunistic sightings; lions were regularly tracked by safari guides as they provided a major tourist attraction, and sightings were therefore frequent (approximately once per week). Most individuals and groups were recorded by name and identifying features. A copy of the survey form is contained in Appendix 3.

ii) Photographic and sketch records were collected by AWDC throughout the season. On average, 208 field days per year were spent covering the study area to track the wild dog packs, and all lions encountered during this period were recorded. Individuals were identified using permanent scars, age, body size, mane colour and size for males, whisker-spot patterns, and any other distinguishing features such as missing tail tips and ear notches. This data was then cross-checked against sightings provided by the safari operators to compile a final annual count. Population numbers changed throughout the year; only adults and cubs surviving in September of each year were included in the annual density estimates.

Lion surveys were carried out between April to November each year, from 2001 to 2003. Surveys were restricted to the existing road network and valley floor of the study area. Annual home ranges for each pride or individual were estimated from sighting location data. Data for some animals were insufficient to develop reliable range estimates using minimum convex polygon methods, so home ranges were digitized over satellite images of the study area in ArcMap (ArcGIS 8.1), using biologically meaningful boundaries.

Eastern and western home range boundaries were based on sighting information and often followed natural landscape features, such as ridges and large tributary rivers, and also dry river beds. Although these features do not present barriers to lion
movements, they either corresponded with the limits of pride or group movements, or in some cases lions were seen to patrol and scent mark using the feature as a territory boundary. The Zambezi River was used as the southern boundary and the Zambian escarpment provided a boundary to the north.

Since no lions were collared, sightings data may have been biased towards open areas which would underestimate lion ranges. There was insufficient survey data to test this. Homes ranges were therefore extended to include all habitats up to the base of the escarpment, based on data from Mana Pools showing that lions frequently utilised thickets, jesse bush and mopane habitats on the Zimbabwe side of the Zambezi valley floor (N. Monks, unpublished data). Lions may occur in the escarpment area, however they generally reach highest density in areas of high prey density (Creel & Creel 1997; Spong 2002; Stander 1991, 1993). The research in Mana Pools showed only 3% of prey density occurred in the escarpment, so lion densities would be expected to be correspondingly low in that habitat. Occasionally, lions were observed to cross the river for short stays on small islands or to emigrate, however wild dogs were never observed entering or crossing the river so only mainland areas within the study area boundaries were included to assess interspecific competition.

Annual lion density in each home range was calculated. Overlap occurred in all lion home ranges, up to 100% in some cases where male coalitions overlapped more than one female pride. Once digitized, overlapping ranges created a map of intersection polygons which were partially used by several groups. The proportion of each home range used by each individual or group was used to estimate density in each polygon area. For example, if the home range of a group of four lions overlapped another range by 25%, three lions were used to calculate density in the exclusive part of their range, and one lion was added to density calculations in the 30% overlap area.

Using ArcMap (ArcGIS 8.1) “joins and relates” functions and annual data for both species, the number of wild dog GPS activity points occurring in each lion density polygon was calculated to investigate the effects of lion density on wild dog habitat use. Wild dog activity was broken into three categories, 1) all annual GPS fixes combined 2) the four month breeding season of each pack, and 3) the non-breeding season when
home ranges increased. A four month breeding period was arbitrarily chosen based on
the ten to twelve week observed denning period, plus an additional month when pups
were small and often cached during hunts, thus they still restricted pack movements
and made the pack more vulnerable to predation. Although pups had trouble keeping
up with the pack for some months longer, the packs returned to normal home ranges
soon after denning.

Lion densities obtained from mapping information from the annual lion surveys were
ranked into four lion density categories of equal interval; Low 0-0.045, Low-
moderate=0.046-0.090, Moderate-high=0.091-0.135, and High=0.136-0.180. The
category ranking was based on lion density figures from other regions of Africa with
stable lion populations, which ranged from .086 in a low density open plain habitat in
Serengeti to 0.2 in Ngorongoro Crater in Tanzania, and averaged 0.127 adults/km
(n=5 populations; Creel and Creel 2002). Wild dog habitat selection for ranked areas
of differing lion density was analysed using Duncan’s (1983) index of preference (PI)
as above (3.3.2.2), comparing the number of wild dog observations found in each lion
density area. The far eastern lion home range section (polygon10, see section 4.4.1)
was deleted from analysis as data coverage from lion surveys was poor in this area.

Using the vegetation map composed in ArcGIS (see section 3.4.1.1) and the digitised
lion density polygons, the habitat composition of the four ranked lion density category
areas was calculated. The relationship between lion density and habitat composition
was tested using Spearman Rank correlations.

4.3.2 Spotted Hyaena Surveys

Hyaena density was determined using highly amplified playbacks of noises found to
attract spotted hyaenas (*Crocuta crocuta*), adapted from three methodologies: Mills
(1985), Creel and Creel (1996), and Monks (personal communication). Where
methodologies differed that used by Monks was chosen so that data would be
comparable with that for Mana Pools National Park. Sounds played included noises of
a bleating wildebeest calf, spotted hyaenas mobbing lions, an inter-clan hyaena fight,
hyaenas squabbling on a kill (provided by M.G.L. Mills), and noises of a squealing
pig (provided by N. Monks). The tracks played were varied for each survey.
Four surveys were carried out between May and November, one in 2000, two in 2002 (five months apart), and one in 2003, nine months after the previous survey. No permits were available for a 2001 survey. For the 2000 and 2002 surveys, two RCF 45.7cm, 8 ohm horn speakers wired in series and pointed in opposite directions were connected to a Goldstar TCC-320 High Power Hi-Fi car stereo and a 12V PW-100 Sharp Stereo Power Amplifier. New equipment was used for the 2003 survey consisting of two 40cm Max Trumpet Speakers (40 watts, 8 ohm, Model no. TC-1640) connected to a Sony ESPmax CD Walkman (D-E226CK) and a 12V Max Power Amplifier (Model No. SSB-60).

The sounds were played continuously for 5-minutes at a time. A five-minute pause followed, the speakers were rotated 90 degrees, and the sounds were played for another 5 minutes. The tapes were played 4 times and 50-minutes were spent at each station. Approaching hyaenas were observed by two to eight people in two to three vehicles using high intensity spotlights and binoculars. The majority of hyaenas stayed at the station until the end of the playbacks, and some arrived up to 10 minutes after playbacks were completed. The maximum number of hyaenas simultaneously in view was recorded. Hyaenas less than one year old generally remain at the den, so counts were for animals over one year of age (Mills et al. 2001). All other carnivores that appeared were noted. Hyaenas that were heard whooping but not seen at the time of the count at each station were counted. These hyaenas are thought to be itinerants who may not be members of the local clan and therefore may not be confident enough to confront the intruders (the taped animals) directly and therefore do not come in sight of the calling station, as proposed by Mills (1985).
Figure 4.1 Satellite image of the Lower Zambezi, illustrating hyaena calling station locations (numbered 1 to 8). The valley floor area falling within the study site is outlined in black.

An area of approximately 360km\(^2\) of the Zambian valley floor was sampled, along a transect of 72km of road running southwest to northeast, over eight stations (Figure 4.1). The narrow width of the valley floor meant a single transect sampled the majority of the study area, although the far north east corner of the study area was inaccessible since surveys were restricted by road access. The sample area included the Eastern Chiawa Game Management Area (GMA), from Kayila property to the National Park boundary, then 50km into the Lower Zambezi National Park safari area, to the Mushika river. The first survey was completed during the pilot project in 2000 and was only carried out over the six stations within the National Park (290km\(^2\), over a 50km transect).

The tapes were played at night, beginning 30 minutes after sunset, over two consecutive nights. Three independent experiments were carried out in which hyaenas were located in one vehicle, and a second vehicle carried out playbacks to test the maximum response distance. During these experiments, the longest distance from the calling station in which hyaenas were observed to respond was 3km. Although experiments in this study were limited, this distance is identical to a study which used the same equipment in Zimbabwe (N. Monks personal communication) and comparable to a more comprehensive study by Mills et al. (2001) who found all respondents were within 3.2km in a similar variety of habitats (n=17 experiments).
Survey stations were chosen for good visibility and spaced an average of 9.4 km apart to minimise the chance of double counting.

### 4.3.3 Data Analysis

Spotted hyaena density was calculated from the mean number of respondents at each site and a response radius of 3km established from in-situ experiments. Calling stations were often less than 3km from the Zambezi River, which was not utilised by the wild dogs, so the area for each individual calling station was further adjusted by removing the area of the river, using ArcMap (ArcGis, 8.1). The area for each calling station ranged between 18.1 km$^2$ to 28.3 km$^2$ using a 3km radius. Densities were not adjusted by a probability of failure to respond to playbacks in this study (see Mills et al 2001) because they were intended for comparison with density estimates of spotted hyaenas from other studies, which had not been adjusted for non-response.

A repeated measures ANOVA was used to test for overall differences in hyaena density at each site using the four temporal surveys as dependent observations. An unpaired Students T-test compared the density of hyaenas at sites where lions were present against sites where lions were absent, and Pearson’s product moment correlations were used to investigate the relationship between the density of hyaenas and the number of lions present at call-in sites.

Annual hyaena density estimates at each station were used to test for a relationship between spotted hyaena density and wild dog activity. For year 2002 the mean of the two hyaena surveys was used. Using ArcMap (ArcGIS 8.1), the number of wild dog observations (points) falling with the 3km buffer of each calling station (polygon) was obtained. Ordinary least-squares regression was used to find the model of best fit. Linear relationships were described using Pearson’s product moment correlations.

The number of direct encounters observed between wild dogs and both lions and spotted hyaenas was recorded throughout the entire study, to assess the effect of kleptoparasitism on wild dogs.
4.3.3.1 Comparison across study sites.

Finally, overall densities of the three large carnivore species, wild dog, lion and spotted hyaena were compared to published data from other study sites across Africa, to assess the relative state of the Lower Zambezi populations. Least-squares regression was used to investigate correlations between densities of wild dogs, lions and spotted hyaenas across study sites. Creel and Creel (1996) previously used residual plots to determine that an exponential model of the form $y = e^{a+bx}$ maximised $r^2$ for comparing wild dog density against lion density, and wild dog against spotted hyaena densities. For comparison, the same exponential model was used here in a re-analysis of a modified data set, again comparing wild dog density to lion and spotted hyaena density. The model also gave good data fit in this case. A linear model ($y = a + bx$) was used to test the correlation between spotted hyaena and lion densities.
4.4 RESULTS

4.4.1 Lions

4.4.1.1 Density

Lion population density in the lower Zambezi ranged between 0.06 to 0.086 adults per km$^2$ (Table 4.1). Although overall lion density was moderate, the observed population was small (<50 adults) and declined over three years of study. The population had an unusual mean adult sex ratio of approximately 1:1 males to females (mean=0.97:1, ±SE=0.08). Low cub survival rates were observed, with 0% survivorship from the seven new cubs recorded in 2001 and a single new cub observed in 2002 which by the time of the survey in September was the only survivor from a minimum of three litters recorded during the previous months. There were 5 transient males, observed as singles or pairs, which moved through the area during 2001.

Table 4.1 Lion density estimates (adults/km$^2$) and population structure in the study area, from 3 annual surveys.

<table>
<thead>
<tr>
<th>Year</th>
<th>Males</th>
<th>Females</th>
<th>Cubs</th>
<th>Total Adults</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>2001</td>
<td>18</td>
<td>16</td>
<td>7</td>
<td>34</td>
<td>0.086</td>
</tr>
<tr>
<td>2002</td>
<td>13</td>
<td>14</td>
<td>1</td>
<td>27</td>
<td>0.068</td>
</tr>
<tr>
<td>2003</td>
<td>11</td>
<td>13</td>
<td>9</td>
<td>24</td>
<td>0.060</td>
</tr>
</tbody>
</table>

Maps of lion densities from the annual surveys show a central core of the highest lion densities, from the Chongwe River area on the western border of the National Park (Range number 2, Figure 4.2a-c), and east into the Park. A list of annual lion density figures for each area is included in Appendix 3.
Figure 4.2a

2001 Lion Density

Figure 4.2b

2002 Lion Density

\[ A/d\text{km}^2 \]
- 0 - 0.045
- 0.046 - 0.089
- 0.091 - 0.135
- 0.136 - 0.189
- study areas

10 Kilometers

- 10
- 5
- 0
4.4.1.2 Competition

Analysis of wild dog habitat use in ranked areas of differing lion density showed temporal avoidance of high lion density areas (Table 4.2). During the breeding period, wild dogs showed preference (PI>0.3) for the lowest lion density areas over all three years, with active avoidance of low-moderate through to high lion density areas. There was a significant negative correlation between the wild dog preference index during breeding periods and areas of increasing lion density (r=-0.60, p=0.038, n=12). During the wild dog non-breeding period habitat selection was more varied, with a preference for all levels of lion density occurring at some stage, and no significant correlation between the wild dog preferences and lion density (r=-0.17, p=0.59, n=12). Notably, moderate-high to high lion densities were actually preferred above other areas in years 2001 and 2002 outside of the breeding period. As would be expected from combining these results, annual data show no clear trend of preference or avoidance over the lion density gradient (r=0.08, p=0.80, n=12).
Table 4.2 Index of preference for wild dog use of areas ranked by lion density during wild dog breeding and non-breeding periods, and for annual wild dog data combined. Lion areas are ranked by increasing lion density (adults/km$^2$): Low= 0-0.045, Low-moderate=0.046-0.090, Moderate-high=0.091-0.135, High=0.136-0.180, n= the total number of dog observations, from 6 pack years.

<table>
<thead>
<tr>
<th>Year</th>
<th>Lion Density</th>
<th>Wild Dog Index of Preference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Breeding</td>
</tr>
<tr>
<td>2001</td>
<td>Low</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Low-moderate</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>Moderate-high</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.21</td>
</tr>
<tr>
<td>2002</td>
<td>Low</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>Low-moderate</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Moderate-high</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.12</td>
</tr>
<tr>
<td>2003</td>
<td>Low</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>Low-moderate</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Moderate-high</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0</td>
</tr>
</tbody>
</table>

The ranked categories of lion density are intended as a relative measure for the study area, however they are based on figures from other areas where stable lion population densities ranged from 0.065 to 0.14 adults/km$^2$ for freely dispersing populations, up to the highest density recorded in the geographically isolated Ngorongoro Crater, of 0.24 adults/km$^2$ (see Table 4.5 for details).

Direct encounters between lions and wild dogs were rare. Lions were present at 2.0% of wild dog sightings (n=440), and 2 kills (n=122) both of which were lost to the lions. When lions were encountered the dogs actively moved out of the area, in one case moving 30km in two days. On two occasions a dog pack was seen to interact with lions; once where 8 adult dogs encountered a pair of adult male lions, and another where 6 adult dogs with 10 pups encountered a lone male. In both instances the adult dogs harassed the lions from a safe distance, while the lions occasionally charged them. There was no direct contact or injury during either encounter.
Table 4.3 Percentage habitat composition for areas of ranked lion density.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Very Low</th>
<th>Low</th>
<th>Medium</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>8</td>
<td>5</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>Albida Wd.</td>
<td>14</td>
<td>21</td>
<td>18</td>
<td>31</td>
</tr>
<tr>
<td>Ecotone</td>
<td>29</td>
<td>13</td>
<td>24</td>
<td>38</td>
</tr>
<tr>
<td>Thicket</td>
<td>38</td>
<td>58</td>
<td>44</td>
<td>18</td>
</tr>
<tr>
<td>Miombo</td>
<td>12</td>
<td>4</td>
<td>5</td>
<td>7</td>
</tr>
</tbody>
</table>

Lion survey data was insufficient to establish lion habitat selection within each range, however analysis of habitat composition in areas of differing lion density (Table 4.3) showed a strong correlation between lion density and the proportion of *albida* woodland in lion ranges (Spearman Rank test; $r=0.85$, df=3, $p<0.3$). There was a weak positive correlation between lion density and increasing proportions of ecotone habitat ($r=0.4$, df 3, $p<0.75$), and a weak negative correlation for thicket ($r=-0.4$, df=3, $p<0.75$). All correlations were not significant but levels of significance were limited by the small sample size and the Spearman Rank Correlation test.

In addition to containing the highest proportion of *albida* woodland habitat, the highest lion density areas also had the lowest proportion of thicket areas (Table 4.3). Grasslands contained high impala density, however they made up only a small proportion of all lion home ranges due to their relative scarcity (mean=7.3%, ±SE=0.85). No data was collected on lion prey species, however lions were observed preying on impala as well as larger species including buffalo and zebra. *Albida* woodlands are likely to contain a high density of these larger prey; *Faidherbia albida* pods form an important part of the diet for both browsers and grazers, including buffalo (Dunham 1994; Palgrave 1997), and many areas of this habitat support a seasonal understorey of grasses.

### 4.4.2 Spotted Hyaenias

#### 4.4.2.1 Density

Spotted hyaena density in the Lower Zambezi averaged 0.34 adults/km$^2$ (see Table 4.4 for annual data). A repeated measures ANOVA using the four temporal surveys found no significant differences in hyaena density between any of the eight calling stations (d.f=3, $f=2.02$, $p=0.14$). A table of hyaena densities at each calling station is included in Appendix 3. Each calling station contained a variety of habitats, from...
albida woodlands nearest the river in the south to thickets by the escarpment in the north. Data was therefore insufficient to assess hyaena habitat selection.

Table 4.4 Spotted hyaena population density (adults/km$^2$) in the study area, for three years. 2002 figures are based on the mean of two surveys.

<table>
<thead>
<tr>
<th>YEAR</th>
<th>Mean Density</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>0.35</td>
<td>0.11</td>
</tr>
<tr>
<td>2002</td>
<td>0.34</td>
<td>0.08</td>
</tr>
<tr>
<td>2003</td>
<td>0.18</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Lions responded to the call-ins at a minimum of two sites and maximum of four sites at each of the four surveys. The number of respondents ranged from 1 to 8 lions at any one site. There was no correlation between the number of lions present and the number of hyaenas observed responding to the call-in ($r=-0.16$, $n=30$ calling stations, $p=0.38$). An unpaired Students t-test also showed no significant effect of the presence or absence of lions on the density of hyenas observed at each site ($df=28$, $t=1.48$, $p=0.15$). Although the pride of eight lions which responded was observed to chase 2 hyaenas from the site, its presence did not prevent the hyaenas from initially responding.

4.4.2.2 Competition

Correlations between the annual number of wild dog observations within the hyaena calling station areas (radius 3km) and hyaena density showed weak to moderate positive correlations, but none were significant. In 2000 the correlation was weakest with an $r$-value of 0.46 ($p=0.35$, $n=29$ wild dog observations), for 2002 the $r$-value was 0.47 ($p=0.25$, $n=46$) and for 2003 the $r$-value was 0.56 ($p=0.14$, $n=52$). The strength of the correlation increased with sample size. Therefore there was no evidence of wild dog avoidance of hyaenas in the valley floor based on density figures, however the scale of temporal and spatial data for hyaenas was very limited.

Direct encounters between wild dogs and spotted hyaenas were more numerous than for lions, but rarely affected wild dog feeding success. Spotted hyaenas were observed at 8.6% of wild dog sightings (from $n=440$ sightings), ranging in number from 1 to 5 (mean=1.18, $\pm$SE= 0.12). Of 122 observed wild dog kills, hyaenas were present at 17.2%. Of these the wild dogs lost their kill to hyaenas on only four occasions (3.2%). Three of these occasions involved the same pack of three to four adults and five to six
yearlings (GMA pack 2003, see Appendix 1). In all other cases hyaenas remained at a
safe distance or were successfully fended off by the dogs, and claimed the carcass
remains once the dogs had finished feeding and abandoned the kill.

Wild dogs did not appear to be antagonised by hyaenas when food or young pups
were not present. One pack of 8 adult and yearling wild dogs lying in grassland
habitat in the late evening allowed 2 hyaenas to approach and come into physical
contact 3 times. A single hyaena came into contact with the same adult female wild
dog each time, who initially stood to face the hyaena. On the third occasion the
hyaena approached when the wild dog pack had settled to sleep and the last contact
sniff prompted only a raised head from the wild dog, while the rest of pack ignored
the hyaena’s presence.

4.4.3 Comparison Across Study Sites
Lion and spotted hyaena densities were compared to wild dog data across study sites
to assess inter predator competition. Lower Zambezi lion and hyaena density estimates
both fell within the range of values observed in other study areas, with lion density
comparatively low, and spotted hyaena density in the mid range of observed values (Table 4.5)

<table>
<thead>
<tr>
<th>Study Area</th>
<th>Wild Dog</th>
<th>Spotted Hyaena</th>
<th>Lion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower Zambezi, Zambia</td>
<td>0.018</td>
<td>0.34</td>
<td>0.071</td>
</tr>
<tr>
<td>Selous, Tanzania</td>
<td>0.04a</td>
<td>0.32a</td>
<td>0.11a</td>
</tr>
<tr>
<td>Hwange, Zimbabwe</td>
<td>0.015a</td>
<td>0.17a</td>
<td>0.035a</td>
</tr>
<tr>
<td>Moremi, Botswana</td>
<td>0.04c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kruger, RSA</td>
<td>0.02d</td>
<td>0.45d</td>
<td>0.065d</td>
</tr>
<tr>
<td>Serengeti, TZ (1967-79)</td>
<td>0.015a</td>
<td>0.17a</td>
<td>0.079-0.094a</td>
</tr>
<tr>
<td>Serengeti, TZ (1985-91)</td>
<td>0.0067a</td>
<td>0.82a</td>
<td>0.14a</td>
</tr>
<tr>
<td>Ngorongoro</td>
<td>0a</td>
<td>1.43a</td>
<td>0.16-0.24a</td>
</tr>
<tr>
<td>Aitong, Kenya</td>
<td>0.036a</td>
<td>0.3a</td>
<td></td>
</tr>
</tbody>
</table>


Lower Zambezi figures were taken from the mean of all survey years for wild dogs
and lions, however 2003 data was omitted from spotted hyaena estimates due to
suspected low response rates (see section 4.5.2). Figures from other study sites were
slightly updated from those that appeared in Creel and Creel’s (1996) comparable
analysis. The lion density figure for Kruger National Park was taken from figures published in Mills and Biggs (1993), where previously they were from Pienaar (1969) and personal communication, and corresponding wild dog figures were used from Mills and Biggs (1993) for spatial and temporal consistency. Lion density figures were included from Hwange National Park which were absent from Creel and Creel’s (1996) figures. Correlations between lion, hyaena and wild dog densities were compared across study sites using the updated figures. Comparisons of wild dog density against competing predators only included sites were wild dogs were present.

Least-squares regression found no relationship between lion and wild dog densities across five study sites ($r=0.02$, $t=-0.54$, $p=0.61$, $n=6$, Figure 4.3b). Since wild dogs were thought to have declined due to disease outbreaks in the Serengeti area, figures from this site were then removed and there was a moderate positive relationship between lion and wild dog densities, although this was not significant ($r=0.73$, $t=1.84$, $p=0.16$, $n=5$).

There was a moderate negative relationship between wild dog and spotted hyaena density, but again this relationship was not significant ($r^2=-0.56$, $t=-1.52$, $p=0.19$, $n=7$). There was a significant, positive relationship between lion and spotted hyaena densities ($r=0.91$, $t=4.78$, $p=0.005$, $n=7$).
Figure 4.3a Previous analysis of the relationship between lion and wild dog densities across study sites, figure taken from Creel and Creel (1996). A negative exponential model was fitted (see text).

Figure 4.3b Current analysis of the relationship between lion and wild dog densities across study sites, data from Table 4.5 above. No relationship was found.

The results above prompted re-analysis of Creel and Creels (1996) published data (Figure 4.3a), using their exponential model, to investigate the significant negative relationship that was previously found between lion and wild dog densities across study sites. Where a range of densities for one study site were given in Creel and Creel (1996), the mean was used in analysis here (Table 4.5). Results matched Creel
and Creel (1996) with a strong negative relationship found between lion density and wild dog density across sites ($r=-0.91$, $t=3.72$, $p=0.03$), however standard residuals and leverage for one point were high and therefore were poorly fitted to the equation and also had a large effect upon the curve (Table 4.6). The Ngorongoro population data gave a leverage of 0.85 ($>4/n=0.8$) and a standardised residual of -2.88 ($>±2.0$). Thus one area with no wild dogs present had a significant effect on the predictive relationship.

Table 4.6 Ordinary least-squares regression details, from input data and exponential model as per Creel and Creel (1996).

<table>
<thead>
<tr>
<th>Study site</th>
<th>Density (adults/km$^2$)</th>
<th>Regression analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lion</td>
<td>Wild dog</td>
</tr>
<tr>
<td>Selous</td>
<td>0.110</td>
<td>0.040</td>
</tr>
<tr>
<td>Kruger</td>
<td>0.100</td>
<td>0.017</td>
</tr>
<tr>
<td>Ngorongoro</td>
<td>0.200</td>
<td>0.000</td>
</tr>
<tr>
<td>Serengeti (1967-79)</td>
<td>0.087</td>
<td>0.015</td>
</tr>
<tr>
<td>Serengeti (1985-91)</td>
<td>0.140</td>
<td>0.007</td>
</tr>
</tbody>
</table>
4.5 DISCUSSION

4.5.1 Interpredator Competition from Lions

Lion population density in the lower Zambezi was comparable to lion density in Kruger National Park at 0.065 adults/ km$^2$, but estimates were lower than those in the Selous Game Reserve at 0.11 adults/ km$^2$, and recent estimates in the Serengeti of 0.14 adults/ km$^2$ (Table 4.5). The observed population was small (<50 adults) and declined over the three years of study. The mean adult sex ratio (1 male: 1 female) was unusual since lion populations generally have a higher proportion of females; surveys of the large and stable lion population in the Selous recorded 64% females (Creel & Creel 1997), an estimate similar to the lion population in the Serengeti which had 67% females (Packer & Ruttan 1988).

The high proportion of males was accompanied by low cub survivorship. The dominant male of the central study area died in 2001 and this may account for the high infant mortality observed in the two prides he associated with, the two largest in the study area. His death coincided with a high number of male coalitions and single males moving through the area in 2001, outnumbering the females (Table 4.1). Five of these males were not seen again from 2002 onwards. Infanticide is common in lion populations during male takeovers (Whitman et al. 2004). The immigration of new male groups into the area suggests that dispersal mechanisms in the lion population were not as compromised as those in wild dogs. Lions were often observed crossing to islands in the Zambezi River, and several were identified after crossing to the directly opposite Mana Pools National Park.

Lion density surveys were restricted to the valley floor, so results do not represent density estimates for the entire National Park. However, lions have been shown to reach highest density in areas of high prey density (Creel & Creel 1997; Spong 2002; Stander 1991) and in the study area prey was concentrated on the alluvial terraces of the river valley where vegetation is diverse and water abundant. Research in the Zambezi River valley in Mana Pools, directly across the river from the Lower Zambezi, showed only 3% of prey density occurred in the escarpment and lion densities were correspondingly low in that habitat (N. Monks unpublished data). Therefore, figures presented here are likely to be an over-estimate for lion density throughout the National Park. Lion density was positively correlated with the
proportion of *albida* woodland within each lion range, however grassland areas were relatively small and scattered and therefore any habitat preferences for this area would be probably be difficult to detect using this method. Grasslands generally adjoined *albida* woodlands and lions were frequently observed in both habitats.

In striking contrast to other studies which have shown wild dogs avoid high lion and prey density areas (Creel & Creel 2002; Creel & Creel 1996; Mills & Gorman 1997), wild dogs in the Lower Zambezi avoided high lion density areas only during the breeding season and demonstrated preference for these areas during other times of the year. Lower Zambezi lion densities were positively correlated with the proportion of the highest prey density habitat within each range. Mills and Gorman (1997) demonstrated that wild dogs in Kruger National Park avoided high impala density areas due to high lion density, even though impala was by far their favoured prey (81.0% of biomass). However, in that study lions were a major cause of adult mortality (43%), which was not the case in the Lower Zambezi (see Table 2.1).

Broken hill country was actively preferred by the wild dogs in Kruger National Park (Mills & Gorman 1997), and miombo woodland itself is certainly not unsuitable for wild dogs since this habitat dominates much of Zambia and Tanzania and is one of the major habitats in the Selous Game Reserve, which contains a large and stable population of wild dogs (Creel et al. 2004). In this study the miombo areas would be considerably lower in prey than the river floor, if only due to more limited water availability. Although the escarpment appeared to be a geographical barrier to wild dog movements in this study, there were large areas of low lion density available to the east and west of the high lion density core area (Figure 4.2) which results suggest were under-utilised. Interpredator competition was cited as the most likely cause of wild dogs’ avoidance of high prey density areas in Kruger, through resource competition and the threat of direct predation by lions. The seasonal variation in habitat selection by the Lower Zambezi wild dogs implies a threat of intraguild predation since high prey and lion density areas were avoided during breeding, but it also implies a lack of interpredator competition for resources since these areas were heavily utilised at other times of the year.
These results have important management implications for wild dog populations, by suggesting that wild dogs may successfully compete with other large predators where there are sufficient refuge areas available for breeding. The wild dog habitat selection observed here may be specific to the geography, prey densities and habitat composition in the Lower Zambezi. However, they may also be applicable to other areas in central Africa, including eastern Zambia and portions of the Rift Valley system. The South Luangwa National Park in Zambia is part of the southernmost section of the Great Rift Valley, with the Luangwa River forming its eastern boundary. The Luangwa River valley extends south to meet the Zambezi River in the eastern end of the Lower Zambezi National Park. Reports of wild dog sightings from the South Luangwa National Park suggest seasonal wild dog movements also occur there. The dogs are observed in the valley floor safari area only during periods either side of the breeding season, and quite probably retreat into the escarpment to den. The South Luangwa National Park covers an area of over 9000km$^2$ and is surrounded by adjoining GMAs (Jachmann 2000). This area could potentially support a large and viable population of wild dogs.

Further investigation of the temporal use of refuge areas could be applicable for the management of smaller wild dog populations, particularly in fenced reserves containing populations of other large predators. Instead of focussing wild dog conservation in areas with low overall lion densities or managing interpredator competition, areas containing a combination of poorer prey density habitats and high prey density habitats may provide sufficient refuge for wild dogs, depending on habitat type.

### 4.5.2 Interpredator Competition from Spotted Hyaenas

Spotted hyaena densities in the Lower Zambezi (see Table 4.4), fitted within the range of hyaena densities observed in other study sites across sub-Saharan Africa (0.17 to 0.82 adults/km$^2$). Estimates were similar to those in the wooded habitats of the Selous Game Reserve and Kruger National Park (Table 4.5).

Hyaena response rates appeared to drop by the 3rd survey (Table 4.4), even though the audio tracks used for calling were varied and no more than two surveys per year were carried out (three of the four were at least eight months apart), as recommended by
Mills et al. (2001). Non-response was not determined experimentally, however results for 2003 were probably not representative of total hyaena densities; increases in both the number and frequency of hyaenas sighted in comparison to previous years were reported by safari guides, including up to 43 hyaenas observed on one kill in the area of one calling station. However, only 35 hyaenas responded in total over 8 sites in 2003. 2003 figures were therefore dropped from the population estimate (used in Table 4.5.). Assuming equal probabilities of non-response at each site, figures still give a relative indication of hyaena density per area and were included in analyses of annual data. Although the pride of eight lions which responded at one hyaena playback site was observed to chase two hyaenas from the site, its presence did not prevent the hyaenas from initially responding. These results agree with Mills et al. (2001) who found no effect of lions on hyaena response.

Spotted hyaena densities were not adjusted for non-response so they are a conservative estimate. Future surveys should include more experiments to measure response rates in different habitats to utilise the non-response model proposed by Mills et al. (2001), together with a reward system to avoid habituation and increased non-response to playbacks.

Spotted hyaenas had minimal effect at wild dog kills, stealing carcasses at only 4% of them. These figures are very similar to those from the Selous study, where spotted hyaenas were present at 18% of wild dog kills and ate at only 2% (Creel & Creel 1996). However, a substantial reduction in wild dog feeding rates due to hyaenas was found in the open plains habitat in the Serengeti where hyaenas ate at over 70% of wild dog kills (Kruuk 1972). Previous research suggested that more wooded habitats reduce the impact of interpredator competition by reducing the probability of kill detection (Creel & Creel 1996; Mills & Biggs 1993), and because hyaena density and clan structures differ in these environments and fewer hyaenas generally arrive at wild dog kills. Findings in the Lower Zambezi further strengthen this argument.

Despite the lack of competition at kills, hyaenas appear to have to affected wild dog pup survivorship in the last year of this study, and wild dog habitat selection during breeding periods (see section 2.4.1.2). Predator competition is likely to have caused the long distance den moves observed in the wild dog population, where two packs
shifted over 20km over a two week period (section 2.4.1.2). It was difficult to accurately identify causes of pup mortality due to restricted den access and visibility, so predators may have had a greater effect than detected. Predation is often cited as the main cause of pup mortality in other studies (Woodroffe et al. 1997; Woodroffe et al. 2004b).

There was no significant correlation between wild dog and spotted hyaena densities (section 4.4.2.2), however information on range and habitat utilisation for hyaenas was limited here in comparison to that for wild dogs and lions. Other studies have found lion and hyaena densities are positively correlated (Creel & Creel 1996), so the effect of interpredator competition from these two species is difficult to separate.

4.5.3 Comparison Across Study Sites

Analysis of updated figures on wild dog, lion and spotted hyaena densities showed no significant correlation between wild dog and lion densities, in contrast to previous research by Creel and Creel (1996) who detected a significant negative relationship based on data from four ecosystems. Data analysed in this study used similar figures but added two study sites (Lower Zambezi and Hwange). The main difference in findings was due to the omission of the Ngorongoro data which was not included in this analysis since no wild dogs were present at this site (Figure 4.3). If this data is removed from the data used in Creel and Creel’s (1996) study the relationship between wild dog and lion densities no longer exists ($r=0.047$, $t=-0.07$, $p=0.52$). The cause of the wild dog’s disappearance from the Ngorongoro is not known, therefore it was considered dubious to include data from this site for lack of a causal link and since it becomes the key point in suggesting a predictive relationship between lion and wild dog densities.

The negative correlation between wild dog and lion densities found by Creel and Creel (1996) was later used as a basis for modelling wild dog extinction probabilities (Vucetich & Creel 1999), which then found that wild dogs were extremely sensitive to competition with lions and subsequently recommended management of interspecific competition in wild dog conservation strategies. Since the correlation did not hold due to a difference of one study site and with new data added, caution should be exercised.
in extrapolating those findings into evidence of a sound ecological relationship and a basis for long-term species management.

Creel and Creel (1996) acknowledged that the inclusion of the more recent Serengeti estimates was questionable, and re-ran the correlation without data from this site but found the relationship continued to be strongly negative. Although lion populations were increasing at the time that wild dogs declined to near local extinction in the Serengeti area, there were also viral disease outbreaks which have been cited as one likely cause of the population decline (Alexander & Appel 1994; Ginsberg et al. 1995a; Woodroffe 2001). High densities of sympatric large carnivores may have been a contributing factor through interpredator competition or disease transmission (Creel et al. 2004; Vucetich & Creel 1999), but the population was also small and susceptible to local extinction from stochastic events, its extinction predicted in 1979 (Ginsberg et al. 1995a). In any case, if the figures from the Serengeti site were removed here there was in fact a moderate positive correlation between lion and wild dog densities, although this was not significant (section 4.4.3). The deletion of data points is subjective, however it serves to illustrate that the previous findings of a negative correlation between lion and wild dog densities was effectively based on two sites where wild dogs declined due to unknown causes.

The Selous wild dog population is estimated to be one of the largest remaining in Africa, with the highest recorded density of dogs, although there is a comparable population in northern Botswana. Lion density in the Selous was judged low compared to other populations and this was proposed as an important factor in the wild dogs’ success there (Creel & Creel 2002). In fact the lion density figure published for Selous was almost double that of Kruger National Park, and several times higher than that of Hwange National Park (Table 4.5). Wild dog densities were correspondingly low in Kruger and Hwange compared to the Selous.

There seems to be no consistent relationship across study sites between lion densities and their observed effect on wild dog populations. Lions were identified to be a major cause of wild dog mortality in Kruger NP which had low lion density (Mills & Gorman 1997), while lion density in the Lower Zambezi was higher than Kruger and yet lions were not a major cause of wild dog mortality, and avoidance of high lion and
prey density areas was observed only during the breeding season. More data from a larger number of sites would be required to establish if any type of consistent relationship exists between these two species.

A simpler explanation may be that the relationship changes with variations in other related ecological factors. There is substantial evidence that wild dogs do avoid high lion and prey density habitats in some protected areas (Creel & Creel 2002; Creel & Creel 1996; Mills & Gorman 1997), and this may also be correlated with avoidance of spotted hyaenas since lion and hyaena densities are positively correlated. Although not significant in this analysis, the negative relationship between wild dog and hyaena density was more evident than that for lions. This corresponds with evidence of hyaenas causing a decrease in wild dog feeding rates, which could have important impacts on wild dog energy balance (Carbone et al. 1997; Fanshawe & Fitzgibbon 1993; Gorman et al. 1998; Kruuk 1972), and the more limited evidence of direct predation (Woodroffe et al. 2004; this study), particularly on wild dog pups. Increased resource competition from hyaenas is likely given their larger diet overlap with wild dogs (Mills & Gorman 1997) compared to diet overlap between wild dogs and lions.

Findings from the Lower Zambezi wild dog population suggest that competition theory, where increased resources lead to decreased competition, may explain the seasonal avoidance by wild dogs of high predator and prey density habitats. With sufficient cover from vegetation and a high density prey base, interpredator competition over resources would be reduced in high prey density habitats, while the threat of direct predation may have induced wild dog avoidance of these areas during breeding periods when packs are more vulnerable. Mills (1995) observed a parallel rise in both lion and wild dog densities during a time of drought in Kruger National Park, which further supports competition theory. This conflicts with an alternate hypothesis published by Creel (2001); that higher prey density actually increases interpredator resource competition for wild dogs due to the increased value of a carcass over live prey, combined with the wild dogs’ hunting success and vulnerability to kleptoparasitism by larger predators such as lions. This hypothesis was based on data from two study sites and the previously recorded negative relationship between wild dog densities and lion densities across study sites. More
detailed information on prey densities and related hunting success and kleptoparasitism across study sites is needed to further clarify this supposition.

The evidence suggests that management of interpredator competition from both lion and spotted hyaenas should be assessed on a site by site basis, along with other interacting ecological factors, including the nature and density of habitat and other possible threats to wild dogs. This is an important consideration given the economic value of all large carnivores to ecotourism in Africa, which is intrinsically linked to the conservation value of protected areas. Areas that support a high diversity of large carnivores are generally more appealing to tourists, and wild dog management should not be unnecessarily focussed towards areas containing low levels of competing predators.