CHAPTER 3

Area and prey requirements of wild dogs *Lycaon pictus* under varying habitat and land use conditions: implications for reintroductions

3.1 Introduction

Habitat loss is the most significant factor behind ongoing global species extinction (Fahrig 2001). Increasing land use competition for remaining habitat, coupled with insufficient funding for conservation necessitates the conservation of maximal species diversity in minimum areas (Gurd et al. 2001; Restani & Marzluff 2002). Effective conservation planning for activities such as reserve design and endangered species reintroductions is dependent upon understanding species' minimum area requirements. Area considerations are of particular importance to the conservation of large carnivores, whose large spatial requirements have resulted in their being disproportionately affected by habitat loss, and correspondingly difficult to conserve (Linnell et al. 2001). This is complicated by the fact that successful carnivore restoration entails not only the reintroduction of the species, but also the restoration of the ecological relationships between predator and prey and between the predators (Pyare & Berger 2003). Reserve size extinction thresholds for large carnivores are high, but extremely variable. Snow leopards *Panthera uncia* (>116 km^2) and tigers *Panthera tigris* (>135 km^2) for example, require relatively small reserves for persistence, while brown bears *Ursus arctos* (>3,981 km^2 require large areas for persistence (Woodroffe & Ginsberg 1998).

Across all ecosystems wild dogs occur at low densities relative to competing carnivores (Creel & Creel 2002) and are affected by substantial edge effects in all but the largest reserves, as a result of their ranging behaviour (Woodroffe & Ginsberg 1998). It has been suggested that the long-term viability of wild dog populations and the ecological processes that characterise them may require protected areas as large as 10,000 km^2 (Woodroffe & Ginsberg 1999). Using Vortex modelling techniques however, Mills et al (1998) showed that single packs representing sub-populations within a meta-population could be maintained at desirable levels given realistic levels of manipulation through management. In South Africa, the decision was taken to establish a meta-population through the reintroduction of wild dogs into geographically isolated reserves, linked through management, to complement the single viable population occurring in Kruger National Park (henceforth referred to as "Kruger"). Six sub-populations have been established to date: Hluhluwe-Umfolozi Park (960 km^2); Karongwe Game Reserve (120 km^2); Madikwe Game Reserve (750 km^2); Marakele National Park (900 km^2); Pilanesberg National Park (550 km^2); and Venetia Limpopo Game Reserve (370 km^2). Effective predator proof fencing has reduced edge effects and dispersal from the release sites, and enabled the utilisation of reserves smaller than protected areas in which naturally occurring wild dogs persist (550 km^2, Woodroffe & Ginsberg 1998). However, due to high human population densities and intensive agriculture, few suitable state or privately owned areas of this size exist in South Africa, despite the recent increase in the number of areas where wildlife rather than livestock farming is the major form of land use (Falkena 2000). For expansion of the meta-population, the reintroduction of wild dogs into yet smaller areas, as has recently been carried out in the 120 km^2 Karongwe

Game Reserve, could be considered, although in the long term, the formation of large collaborative nature reserves through the cooperation of neighbouring private land owners, is more ecologically desirable.

Several factors may contribute to the large home range areas of wild dogs under natural conditions, including predation by lions *Panthera leo*, interference competition by spotted hyaenas *Crocuta crocuta*, and human-related mortality (Creel & Creel 1998; Mills et al. 1998; Vucetich & Creel 1999). Although each of these factors can be controlled through management to some extent, it is not clear whether wild dogs can be successfully maintained in areas smaller than naturally occurring home ranges. Wild dogs appear to be rarely limited by food availability (Creel & Creel 1998) despite a positive correlation between wild dog density and prey density across ecosystems (Fuller et al. 1992). If wild dog reintroduction is attempted in areas smaller than observed home range sizes, however, prey availability may become a limiting factor. In this study, the minimum areas required to support packs of varying sizes are estimated for different habitat types, based upon prey requirements. The purpose of this is to provide guidelines for minimum area requirements for wild dog reintroductions, and to provide seed values for the adaptive management of sub-populations post-release.

3.2 Methods

The prey population size required to provide a maximum sustainable yield equal to the number of individuals of a given prey species killed by wild dogs in a year was determined, using the following equation, derived from Caughley (1977):

$$MSY = \frac{r_m}{2} \times \frac{K}{2} = \frac{r_m K}{4}$$

Where *MSY* is the maximum sustainable yield, r_m the intrinsic growth rate of the prey population, and *K* the carrying capacity for the prey population. *MSY* becomes N_{prey}, the number of individuals of a prey species killed per year by a pack of wild dogs, and *K* becomes N_{min}, the minimum population size required to support the predation by a pack of wild dogs of a given size over a year:

$$N_{min} = \frac{4N_{prey}}{r_m}$$

The area required to support N_{min} for a given prey species was determined by multiplying N_{min} by the density at which that prey species occurs in a given area.

The following parameters are required to estimate minimum area requirements:

a) Pack size. Estimates were made for the prey requirements of a range of pack sizes (4 - 26 dogs).

b) An estimate of the likely annual increase in wild dog numbers following a reintroduction event. There is likely to be a lag between the birth of additional wild dogs and management action to maintain the desired numbers in a reserve. Subsequently, prey requirements were calculated for a given pack size and one set of offspring. Demographic patterns in packs following reintroductions in South Africa have been extremely variable (e.g. Maddock 1999) with no consistent patterns. Consequently, to be conservative, published (high) survival rates were used to estimate the potential increase in wild dog numbers following one set of offspring. Given average pack structure for Kruger as a whole (five adults and two sub adults), mean litter size (nine pups), and good survival rates (0.8 for adults, 0.7 for sub adults and 0.7 for pups), an initial pack size of seven adult and sub adult dogs would be expected to increase to ~ 12 dogs within the first year (Fuller et al. 1992), as follows:

$$PSt+1=(Ad\times 0.8)+(S.ad\times 0.7)+(Pt+1\times 0.7)$$

Where $PSt+1$ is equal to pack size at the end of year 1, where Ad, and $S.ad$ are equal to adults and sub adults at the beginning of year one respectively, and where $Pt+1$ is equal to the litter of pups born during year one.

c) An estimate of the likely post-release prey-profile of wild dogs for a given area. Documented prey-profiles from three ecosystems: 1) southern Kruger (Mills & Gorman 1997); 2) Save Valley Conservancy in southeastern Zimbabwe (Pole 1999); and, 3) Hluhluwe-Umfolozi Park in Kwa-Zulu Natal (Kruger et al. 1999), were used as approximations of the likely prey-profile of wild dogs in the three areas in which reintroductions are most likely to occur in South Africa: a) the Lowveld in Mpumalanga, and Limpopo (northeastern South Africa); b) northern Limpopo (northern South Africa); and c) northern Kwa-Zulu Natal (eastern South Africa), respectively. Detailed age and sex breakdowns were unavailable for the eastern and northeastern South Africa prey profiles, and consequently standard unit mass was used for each prey species (Coe et al. 1976). From an estimate of the total biomass of prey killed per year by a pack of a given size, the proportion of this made up by each prey species, and the standard unit mass for each species, the number of individuals of each prey species expected to be killed per year by a pack of a given size was calculated. Minimum area estimates were based upon the two dominant prey species in each prey-profile - impala *Aepyceros melampus* and kudu *Tragelaphus strepsiceros* in northeastern and northern South Africa, and nyala *Tragelaphus angasi* and impala in eastern South Africa (Table 3.1).

d) An estimate of the annual biomass of prey killed by a pack of a given size. Adult male wild dogs require a food consumption rate of 3.04 kg / day (Nagy 2001), from which the daily requirements of an average sized individual were estimated, based upon 0.75 mean adult mass for wild dogs (Coe et al. 1976). As a rule, 61% of the body mass of ungulates is made up of flesh (Blumenschine & Caro 1986) and based on this, the daily food requirement estimate was adjusted to yield an estimate of prey biomass killed / dog / day (3.2 kg), approximating to field estimates of 1.8 - 3.5 kg / dog / day (Fuller & Kat 1990; Mills & Biggs 1993; Creel & Creel 1995).

e) An estimate of the density of prey species in the relevant area. Density estimates of the prey species in the three prey profiles considered were taken from census data in each area (southern Kruger - Mills & Gorman 1997; Hluhluwe - KZN Wildlife unpubl. data 1998; Save Conservancy - Pole 1999).

Table 3.1 Percent biomass made up by each prey species in the diet of wild dogs in three ecosystems

Prey species	Eastern SA [a]	Northeastern SA [b]	Northern SA [c]
Bushbuck *Tragelaphus scriptus*	0	2.0	1.2
Cattle *Bos spp.*	0	0	1.0
Grey duiker *Sylvicapra grimmia*	0.1	4.4	0.4
Eland *Taurotragus oryx*	0	0	0.2
Impala *Aepyceros melampus*	16.3	**81.0**	**61.0**
Kudu *Tragelaphus strepsiceros*	0.8	8.1	36.0
Nyala *Tragelaphus angasi*	**76.1** [d]	0	0.2
Red duiker *Cephalophus natalensis*	0.3	0	0
Reedbuck *Redunca arundinum*	0.9	2.0	0
Steenbok *Raphicerus campestris*	0	2.5	0
Waterbuck *Kobus ellipsiprymnus*	2.0	0	0
Wildebeest *Connochaetes taurinus*	3.5	0	0
Total	100	100	100

[a] Kruger et al. (1999).
[b] Mills & Gorman (1997).
[c] Pole (1999).
[d] Bold figures highlight the dominant prey species in the wild dog prey-profile.

f) An estimate of the intrinsic growth rate (r_m) of each prey species. This was estimated as follows (Caughley & Krebs 1983):

$$r_m=1.5W^{-0.36}$$

W represents the mean adult live body mass (Bothma 1996; Baker 1999).

Calculation of the minimum area requirements of wild dogs in this fashion assumes: 1) that the prey-profile of wild dogs in small protected areas will be similar to that observed in large protected areas; 2) that the numerical impact of wild dogs upon prey populations is not influenced by age or sex-based prey selection; 3) that carrying capacity remains constant for prey populations, and 4) that the prey populations in the three reference ecosystems were stocked at ecological carrying capacity.

3.3 Results

The estimated minimum area required to support wild dogs is greatest in northeastern South Africa, followed by eastern South Africa (Table 3.2). An estimated minimum area of 354.2 km^2 is required to support an average pack of seven adult and sub adult dogs, and one set of offspring (12 dogs in total) in northeastern South Africa, compared to 172.8 km^2 in eastern South Africa, and 158.5 km^2 in northern South Africa. Nyala in eastern South Africa, impala in northeastern South Africa and kudu in northern South Africa set the greatest minimum area requirements.

Table 3.2 Minimum population sizes and areas required to support predation by a pack of 12 wild dogs (pack of seven dogs, plus one year's offspring at one year of age), given three prey-profiles

Ecosystem / Species	N_{prey} [a]	r_m [b]	N_{min} [c]	Prey density / km^2	Area required (km^2)
Eastern SA					
Impala	56	0.38	591	0.09	65.4
Nyala	144	0.30	1904	0.11	172.8
Northeastern SA					
Impala	281	0.38	2950	0.08	354.2
Kudu	8	0.23	143	0.008	173.1
Northern SA					
Impala	211	0.38	2223	0.15	148.4
Kudu	37	0.23	638	0.04	158.5

[a] Estimated number of individuals of a prey species killed per year by a pack of 12.
[b] Estimated intrinsic growth rate of the prey population.
[c] Estimated minimum prey population size required to support predation by a pack / year.

A pack size of five adults represents the statistical threshold above which pack survival is likely, and below which pack extinction is likely (Courchamp & Macdonald 2001). The predicted minimum area requirements for a pack of five wild dogs in northern South Africa are comparatively low at 130.8 km^2 (given five adults and one set of offspring - 10 dogs in total, Figure 3.1). In comparison, estimates for eastern and northeastern South Africa are higher, at 144.3 km^2 and 294.6 km^2, respectively. At large pack sizes, the predicted minimum area requirements are much higher. In northern South Africa, 18 wild dogs are predicted to require a minimum area of 235.6 km^2, compared to 259.7 km^2 in eastern South Africa, and 530.0 km^2 in northeastern South Africa.

Observed home range areas are 1.2, 2.0 and 3.5 times larger than the estimated minimum areas required to support a pack equal to the mean pack size observed in eastern, northeastern and northern South Africa, respectively (Table 3.3). In keeping with this, the density at which wild dogs occur in the three reference areas is markedly lower than the theoretical maximum potential density that each area could support, if wild dogs were regulated by density dependent resource limitation (Table 3.4). The observed density of wild dogs is 0.21 that of the maximum potential density in eastern South Africa (taking the density of dogs within Hluhluwe-Umfolozi Park as a whole), 0.31 that of the potential density in northern South Africa, and 0.61 of potential density in northeastern South Africa.

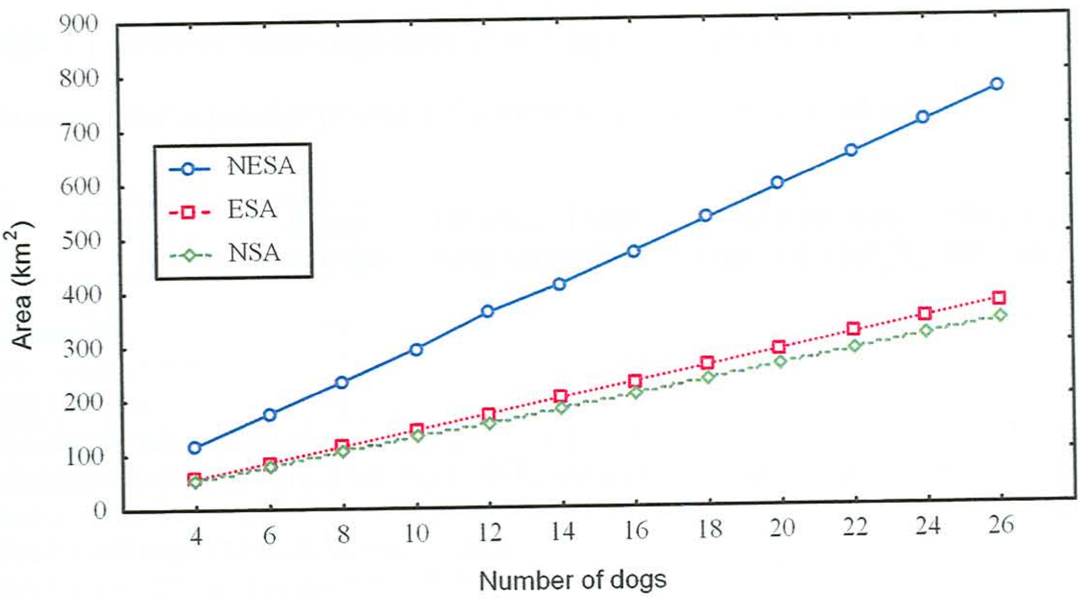

Figure 3.1 Minimum areas required to support predation by varying pack sizes, based upon the dominant prey species in three different prey profiles (ESA, eastern South Africa - nyala; NESA, northeastern South Africa - impala; NSA, northern South Africa - kudu)

Table 3.3 Observed home range areas of wild dogs in three ecosystems, versus estimated minimum areas required to provide sufficient prey to support equivalent pack sizes

Area	[a] Mean pack size	Observed home range areas (km^2)	Estimated area required (km^2)	Observed : estimated
[b] Eastern SA	13	218	188	1.2
[c] Northeastern SA	9	537	265	2.0
[d] Northern SA	9	414	117	3.5

[a] Adults, sub adults, and number of pups divided by 2, after Mills & Gorman (1997).
[b] Hluhluwe-Umfolozi Park (December 1994 pack size – Maddock 1999, 1993 - 1994 home range size - Andreka et al. 1999).
[c] Southern Kruger (Mills & Gorman 1997).
[d] Save Valley Conservancy (Pole 1999).

Table 3.4 Observed density of wild dogs in three ecosystems, versus estimated maximum density (dogs / 100 km^2) at which wild dogs would occur if they were regulated by density dependent resource limitation across three ecosystems

Area	Observed density	Estimated maximum density	Observed : Estimated
Eastern SA [a]	1.44	6.93	0.21
Northeastern SA [b]	2.07	3.39	0.61
Northern SA [c]	2.40	7.64	0.31

[a] Hluhluwe-Umfolozi Park (1994 density data, Maddock 1999).
[b] Southern Kruger (Maddock & Mills 1994).
[c] Save Valley Conservancy (Pole 1999).

3.4 Discussion

The validity of minimum area estimates presented in this chapter is dependent upon the validity of the underlying assumptions. It was assumed that the prey-profile of wild dogs reintroduced into small areas would approximate to that observed in large areas of similar habitat. Wild dogs usually prey upon the most abundant medium to large prey species and typically take prey in proportion to abundance (Reich 1981; Fuller & Kat 1990; Pole 1999), suggesting that approximate prey-profiles can be predicted. Experience from recent reintroductions, however, suggests that wild dogs reintroduced into small areas learn to utilise perimeter fencing during hunting, enabling the capture of larger prey (Hofmeyr 1997; van Dyk & Slotow 2003). There is also the possibility that in the short term after a reintroduction, naïve prey will be more susceptible to predation (Hunter 1998). Given this scope for variation in prey-profiles, monitoring prey population trends as well as prey selection following a reintroduction is important to guide the regulation of wild dog or prey numbers in line with management objectives and ecological conditions.

It was also assumed that prey populations in the reference areas were at carrying capacity and that prey population sizes were estimated correctly. Estimates of wildlife densities are often inaccurate (Bell 1986) and liable to underestimate numbers of small species such as impala (Creel & Creel 2002). In addition, prey densities used to derive minimum area estimates represent densities after off-take by a large predator guild, including wild dogs. Both factors are likely to result in conservative minimum area estimates.

In estimating minimum required prey populations, no consideration was made for sex or age selection by wild dogs. The effect of this is likely to be further conservatism in minimum area estimates. Mills & Shenk (1992) showed that lion predation had a lower impact upon zebra *Equus burchelli* than wildebeest *Connochaetes taurinus* populations in Kruger, as a result of selection for juveniles in the former species. In keeping with this, wild dogs select for juveniles when hunting larger species (Kruger et al. 1999; Pole 1999; Creel & Creel 2002) and as a result, are likely to have a lower impact on populations of these species. Furthermore, wild dogs select for impala in poor condition (Pole 1999, Pole et al. in prep.), and subsequently, a portion of predation by wild dogs may compensate for animals that would have died anyway.

It is also assumed that carrying capacities for prey populations are constant. In reality, however, carrying capacities vary continuously and markedly with environmental conditions (Bell 1986). Ungulate numbers are likely to drop during times of drought, and wild dog numbers are likely to increase due to improved conditions for hunting (Mills 1995). During drought in Kruger between 1981 - 1983 for example, impala and kudu populations declined by 30 - 40% (Walker et al. 1987), and in a drought in the early 1990s, wild dog numbers increased (Mills 1995). Despite reduced prey availability, weakening caused by food shortages in a drought is likely to make alternative prey species available to wild dogs, and improve hunting success (Mills 1995). In addition, the logistical model used to determine minimum required prey population sizes is conservative and likely to cater for some variation in carrying capacity (Caughley & Sinclair 1994). In wet years, ungulate numbers are likely to increase, and wild dog numbers might be expected to decrease, as occurred in Kruger between 1995 - 2000, probably due to poor conditions for hunting (Davies 2000). These patterns stress that if reintroduction into a small area is carried out, it is necessary to monitor wild dog and prey numbers to evaluate population trends, to learn how and when to manage these processes. One way that this could be accomplished would be to set limits of acceptable change, although these are always subjective.

The results of this chapter suggest that in the absence of other factors, smaller areas than those typically considered for wild dog reintroductions provide sufficient prey resources to support wild dog packs. Supporting this, wild dogs reintroduced into three reserves in South Africa have utilised smaller home range areas than typically recorded in large protected areas (Fuller et al. 1992): Hluhluwe-Umfolozi Park (218 km^2, Andreka et al. 1999); Pilanesberg National Park (13.4 km^2 during the first 8 months post-release, van Dyk & Slotow 2003); and Madikwe Game Reserve (180 km^2, Hofmeyr 1997). My study suggests that in areas of high prey density, protected areas as small as 130 km^2 have the potential to support a small pack of wild dogs and one year's offspring. Reserves of this size are comparatively common in South Africa (Chapter 4, van Dyk & Slotow 2003), suggesting that the number of sites potentially available for wild dog reintroduction might be greater than previously thought (Mills et al.1998). Given the dynamic nature of wild dog packs and other aspects of their ecology (Creel and Creel 1998), the practical application and management of this needs to be studied in more detail.

The predicted maximum density at which wild dogs could occur in northeastern South Africa given density dependent resource limitation (3.39 dogs / 100 km^2), is markedly lower than the observed density of some other large carnivores (approximately 10 lions and spotted hyaenas / 100 km^2, Mills & Gorman 1997) in the same habitat. This indicates that wild dogs require large areas simply to meet prey requirements. Wild dogs have extremely high rates of daily energetic expenditure (Gorman et al. 1998; Nagy 2001) and consequently high daily food consumption rates (Fuller & Kat 1990; Creel & Creel 1995; Fuller et al. 1995). Furthermore, in contrast to lions and spotted hyaenas, wild dogs do not exploit carrion, utilise a narrow range of prey species (Ginsberg & Macdonald 1990; Fuller et al. 1992; Mills & Biggs 1993), and because of their cursorial hunting technique, appear to be selective for individuals (Pole 1999; Pole et al. in prep.). Wild dogs are rate-maximisers (Kruger et al. 1999; Pole 1999) and it is possible that they range widely in order to attain a constant food supply with minimal effort (Schaller 1972).

However, prey availability explains little of the observed variation in wild dog density between protected areas (Creel & Creel 1998), and wild dogs occur at lower densities than predicted by body mass and available prey biomass (Carbone & Gittleman 2002). Therefore, beyond a threshold of prey availability, other factors are likely to influence wild dog density (Pole 1999). In keeping with this, for the three reference areas considered, observed densities are 2 - 5 times lower than the theoretical maximum densities based on prey availability. Management of the factors responsible for this discrepancy has potential to enable the maintenance of wild dogs at densities closer to the theoretical maximum.

Across ecosystems, there is a negative correlation between the density of wild dogs and the density of lions and spotted hyaenas (Creel & Creel 1996). Spotted hyaenas affect wild dogs through interference competition, and lions are significant agents of mortality (Creel & Creel 1996; Mills & Gorman 1997), causing an estimated 33% of mortality in Kruger (van Heerden et al. 1995). In the presence of intact predator guilds, wild dogs avoid areas of high prey density as a mechanism to avoid high densities of lions (Mills & Gorman 1997; Creel & Creel 2002). In contrast, in an area with low densities of lions, wild dogs were observed to select habitat in a pattern consistent with prey availability (Pole 1999). Lions probably reduce wild dog density through direct mortality and by reducing their access to optimal habitats. In small-protected areas, the potential for spatial niche differentiation between competing predator species is reduced, and subsequently, lion and spotted hyaena numbers are likely to require intensive management to enable wild dogs to persist. It has been suggested that reducing the size of male lion coalitions can increase the success of wild dog reintroductions, by reducing the area covered during the movements of these lions, thus providing more scope for the wild dogs to avoid contact with them (van Dyk & Slotow 2003).

Human-related wild dog deaths represent a major source of mortality in some populations (Creel & Creel 1998) and may limit density in some areas. Most human-related deaths occur as a result of wild dogs leaving protected areas (Woodroffe & Ginsberg 1997) and the maintenance of perimeter fencing has the potential to dramatically reduce this source of mortality. In addition, anti-poaching management and strict speed limits within a reserve are likely to reduce mortality due to snaring and road accidents.

Finally, disease has had a significant impact upon some wild dog populations (Creel & Creel 1998). Although, typically episodic in nature, infectious diseases cause 11% of adult wild dog mortalities across ecosystems (Woodroffe & Ginsberg 1997). Vaccination of wild dogs prior to reintroduction is vital to reduce mortality and to avoid catastrophic outbreaks such as that experienced following the first reintroduction attempt at Madikwe Game Reserve in South Africa (Hofmeyr et al. 2000).

Although it is difficult to determine what is an adequate reserve size for reintroductions (Miller et al. 1999), the results presented in this chapter give estimates and provide seed values for adaptive management of wild dogs and their prey in line with reserve management objectives. Estimating minimum required reserve size is a major focus of conservation biology (Rodrigues & Gaston 2001; Wieglus 2002). Most research has considered the minimum areas required for viable populations, and comparison between the area requirements of wild dogs and most other large carnivore species highlights the difficulties associated with wild dog conservation. Beier (1993) estimated that extinction risk in cougars *Felis concolor* in southern California is low in areas as small as 2,200 km^2, while Sconewald-Cox et al. (1988) estimated that the minimum area required to conserve a viable population of wolves *Canis lupus* indefinitely is as low as 1,080 km^2. By comparison, it has been suggested that wild dogs may require areas as large as 10,000

km^2 for long-term viability (Woodroffe & Ginsberg 1999). Correspondingly, the critical minimum reserve size below which wild dog extinction is predicted (3,606 km^2) is substantially larger than that predicted for their competitors and ecological equivalents (lions – 291 km^2; spotted hyaenas – 179 km^2; wolves - 723 km^2, Woodroffe & Ginsberg 1998).

Increasing habitat loss is likely to increase the need for utilising fragments of natural land cover, and employing meta-population management techniques (Griffith et al. 1989). The methods outlined in this chapter are applicable to the conservation of minimum demographic units or viable populations of any endangered carnivore in remaining habitat fragments. Applicability is perhaps greatest in southern Africa, where the prevalence of fenced reserves and other game areas permits the conservation of large carnivores in small habitat fragments.

In conclusion, the methods developed in this chapter provide a means by which to determine minimum areas required for the reintroduction of wild dogs, or other endangered carnivore species. Given management to reduce the negative impact of other factors upon wild dogs, smaller areas than previously considered may represent potential reintroduction sites.

3.5 References

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