

# Area and prey requirements of African wild dogs under varying habitat conditions: implications for reintroductions

P.A. Lindsey<sup>1\*</sup>, J.T. du Toit<sup>1</sup> & M.G.L. Mills<sup>1,2</sup>

<sup>1</sup>Mammal Research Institute, University of Pretoria, Pretoria, 0002 South Africa.

<sup>2</sup>South African National Parks Board and Endangered Wildlife Trust, Private Bag X402, Skukuza, 1350 South Africa

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In South Africa efforts are currently being made to manage several sub-populations of African wild dogs (*Lycaon pictus*) occurring in isolated, fenced reserves, as a meta-population. This study represents an attempt to estimate the minimum reserve size for the reintroduction of a pack of wild dogs, as a sub-population. Minimum area requirements were based on the area required to support an adequate population of the most important prey species in the diet of a pack of wild dogs. A pack size of five is the threshold below which reproductive failure is likely, and the area requirements of five wild dogs are estimated to be 65 km<sup>2</sup> in northern, 72 km<sup>2</sup> in eastern and 147 km<sup>2</sup> in northeastern South Africa. The presence of perimeter fencing at release sites is a potentially complicating factor, however, as in some cases wild dogs learn to use fences as a hunting tool, permitting the capture of larger prey than is normal. In the event of this happening, larger areas may be required to prevent local population declines in preferred prey species. In general, the use of larger areas is advisable to allow for variation in prey population sizes and the prey profile of wild dogs post-release, and would also be necessary if wild dogs are to be reintroduced into an area with existing populations of lions and spotted hyaenas.

**Key words:** canid conservation, conservation management, *Lycaon pictus*, meta-populations.

## 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 maximum 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 on 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).

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 characterize them may require protected areas as large as 10 000 km<sup>2</sup> (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 (hereafter referred to as 'Kruger'). The average home range size of wild dogs in Kruger is 537 km<sup>2</sup> (Mills & Gorman 1997) and wild dogs have been reintroduced into four reserves of a similar or larger size: Hluhluwe-Umfolozi Park (960 km<sup>2</sup>), Madikwe Game Reserve (750 km<sup>2</sup>), Marakele National Park (900 km<sup>2</sup>) and Pilanesberg National

\*To whom correspondence should be addressed. Present address: Samburu-Laikipia Wild Dog Project, Mpala Research Centre, P.O. Box 555, Nanyuki, Kenya. E-mail: wilddogs@mpala.org.

Park (500 km<sup>2</sup>). However, due to high human population densities and intensive agriculture, few additional 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, could be considered given effective predator-proof fencing to reduce edge effects and dispersal from the release sites, and if meta-population management is practiced. Wild dogs have been reintroduced into four reserves that are substantially smaller than the average home range size of wild dogs in Kruger: Venetia Limpopo Game Reserve (370 km<sup>2</sup>); Shamwari Game Reserve (200 km<sup>2</sup>); Shambala Game Reserve (120 km<sup>2</sup>); and Karongwe Game Reserve (85 km<sup>2</sup>). However, it is not yet clear how successful reintroductions into such small areas will be in the long term, and the formation of large conservancies through the cooperation of neighbouring private landowners, is more ecologically desirable.

Several factors may contribute to the large home range areas of wild dogs under natural conditions, including avoidance of dominant competitors, lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), and deaths caused by humans (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. Furthermore, although wild dogs appear to rarely be limited by food availability (Creel & Creel 1998), if wild dog reintroduction is attempted in areas smaller than observed home range sizes, 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 on prey requirements. The aim is to provide guidelines for minimum area requirements for wild dog reintroductions, and to provide a basis for the adaptive management of sub-populations post-release.

## METHODS

According to Caughley (1977):

$$MSY = \frac{r_m K}{4},$$

where MSY is the maximum sustainable yield,

equivalent to  $N_{prey}$ , the number of individuals of a prey species killed per year by a pack of wild dogs,  $r_m$  is the intrinsic rate of increase of the prey population, and  $K$  is the population size at steady density, equivalent to  $N_{min}$ , the minimum population size required to support the predation by a pack of wild dogs of a given size over a year. Therefore,

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

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

The following parameters were incorporated into the estimation of  $N_{prey}$ :

- Wild dog pack size at re-introduction.*
- Likely annual increase in wild dog numbers following reintroduction.* If small reserves are to be utilized for wild dog reintroductions, should natural mortality not suffice, there is likely to be management to prevent wild dog numbers increasing above what would be considered to be the threshold number that prey numbers could support. However, we assume there will 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 (Fuller *et al.* 1992, five adults and two yearlings), mean litter size (nine pups), and good survival rates (Fuller *et al.* 1992, 0.8 for adults, 0.7 for yearlings and 0.7 for pups), an initial pack size of seven adult and yearling dogs would be expected to increase to ~12 dogs within the first year, as follows:

$$PS(t + 1) = 0.8A + 0.7Y + 0.7P,$$

where  $PS(t + 1)$  is equal to pack size at the end of year 1, where  $A$  and  $Y$  are equal to adults and yearlings at the beginning of year one, respectively, and where  $P$  is equal to the litter of pups born during year one.

- Likely post-release prey-profile of wild dogs (ecosystem-dependent).* Documented prey-profiles from four regions were used (Table 1): i) southern

**Table 1.** Percent biomass made up by each prey species in the diet of wild dogs in four regions.

Prey species	Eastern South Africa <sup>a</sup>	Northeastern South Africa <sup>b</sup>	Northern South Africa <sup>c</sup>	Pilanesberg N.P. <sup>d</sup>
Bushbuck, <i>Tragelaphus scriptus</i>	0	2.0	1.2	0.2
Cattle, <i>Bos spp.</i>	0	0	1.0	0
Grey duiker, <i>Sylvicapra grimmia</i>	0.1	4.4	0.4	0
Eland, <i>Taurotragus oryx</i>	0	0	0.2	2.5
Impala, <i>Aepyceros melampus</i>	16.3	<b>81.0</b>	<b>61.0</b>	10.6
Kudu, <i>Tragelaphus strepsiceros</i>	0.8	8.1	36.0	<b>67.6</b>
Mountain reedbuck, <i>Redunca fulvorufula</i>	0	0	0	0.6
Nyala, <i>Tragelaphus angasi</i>	<b>76.1</b>	0	0.2	0
Red duiker, <i>Cephalophus natalensis</i>	0.3	0	0	0
Reedbuck, <i>Redunca arundinum</i>	0.9	2.0	0	0
Steenbok, <i>Raphicerus campestris</i>	0	2.5	0	0
Waterbuck, <i>Kobus ellipsiprymnus</i>	2.0	0	0	18.4
Wildebeest, <i>Connochaetes taurinus</i>	3.5	0	0	0
Total	100	100	100	100

<sup>a</sup>Adjusted from Kruger *et al.* (1999); <sup>b</sup>Mills & Gorman (1997); <sup>c</sup>Pole (1999); <sup>d</sup>van Dyk & Slotow (2003).

Kruger (Mills & Gorman 1997), representing the likely prey profile of wild dogs in northeastern South Africa; ii) Save Valley Conservancy in southeastern Zimbabwe (Pole 1999), representing northern South Africa; iii) Hluhluwe-Umfolozi Park in KwaZulu-Natal (Kruger *et al.* 1999), representing eastern South Africa; and iv) Pilanesberg National Park (van Dyk & Slotow 2003). Notwithstanding a probable bias in the Pilanesberg data in that most observations of kills were made along the park boundary fence, the recorded diet of these dogs is very different from that observed elsewhere in South Africa, and is included to illustrate the potential effects of deviation from an expected or 'typical' prey profile on minimum area requirements.

Prey profile data for eastern South Africa (Kruger *et al.* 1999) were adjusted from percentage kills to percentage biomass, based on the mass of each prey species of each age and sex category killed (Howells & Hanks 1975; Anderson 1986). Data on the age and sex breakdown of the northeastern South African prey profile were unavailable and the standard unit mass for each prey species was used to estimate the numbers of each species that would be killed in a year (Coe *et al.* 1976). Minimum area estimates for wild dogs were based on one of the two dominant prey species, which had the greatest area requirement.

d) *Estimated annual prey biomass* (dependent on pack 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 (taking into account variation in

feeding requirements between dogs of various ages and sex) were estimated, based on 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). From an estimate of the total biomass of prey killed per year by a pack of a given size (based on 3.2 kg prey biomass killed/dog/day), 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.

e) *The intrinsic growth rate of each prey species.* This was estimated as follows (Caughley & Krebs 1983):

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

where  $W$  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 on prey populations is not influenced by age or sex-based prey selection; 3) that density remains constant for prey populations, 4) that the prey populations in the four reference ecosystems were stocked at ecological carrying capacity, 5) that the

**Table 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 each of four prey-profiles.

Region/Species	$N_{\text{prey}}^{\text{a}}$	$r_m^{\text{b}}$	$N_{\text{min}}^{\text{c}}$	Prey density/km <sup>2</sup>	Area required (km <sup>2</sup> )
<b>Eastern SA</b>					
Impala	56	0.38	589	9.0	65.5
Nyala	144	0.30	1901	11.0	172.8
<b>Northeastern SA</b>					
Impala	281	0.38	2958	8.0	354.2
Kudu	8	0.23	139	0.8	173.1
<b>Northern SA</b>					
Impala	211	0.38	2221	15.0	148.4
Kudu	37	0.23	644	4.0	158.5
<b>Pilanesberg N.P.</b>					
Kudu	69	0.23	1196	1.0	1191.7
Waterbuck	19	0.22	343	0.6	579.4

<sup>a</sup>Estimated number of individuals of a prey species killed per year by a pack of 12.

<sup>b</sup>Estimated intrinsic growth rate of the prey population.

<sup>c</sup>Estimated minimum prey population size required to support predation by a pack/year.

kill rate of wild dogs is constant and always sufficient to meet their metabolic needs, and 6) that the area requirements of wild dogs are not significantly affected by competing predator species.

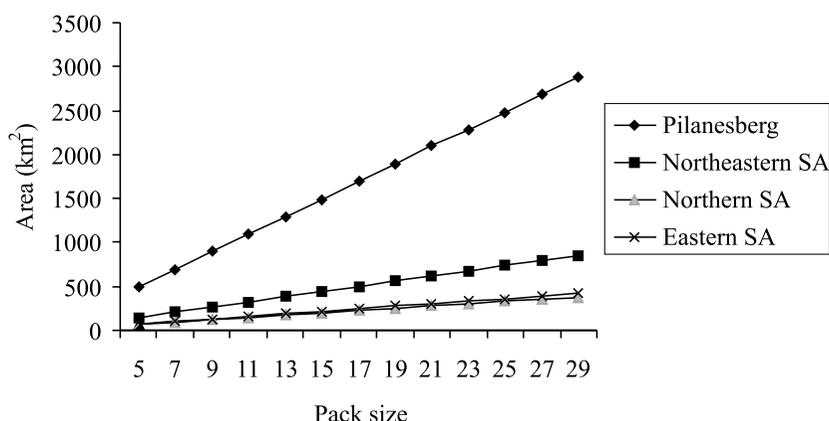
Having calculated  $N_{\text{prey}}$  and  $r_m$  for a given pack size and ecosystem,  $N_{\text{min}}$  could then be calculated. The area required to support  $N_{\text{min}}$  for a given prey species was then determined based on the density at which that prey species occurs in a given area. Density estimates of the prey species in the four 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; Pilanesberg, van Dyk & Slotow 2003). Each of these areas contains other large predators (cheetahs, *Acinonyx jubatus*; lions; leopards, *Panthera pardus*; spotted or brown hyaenas, *Hyaena brunnea*), and as a result prey density estimates take into account the effect of predation by other species.

The effect of variation in the input parameters was investigated. Estimates were made for the area requirements of a range of pack sizes, from five, the statistical threshold above which pack survival is likely, and below which pack extinction is likely (Courchamp & Macdonald 2001), to 29 dogs, the largest pack size observed by Reich (1981) in Kruger. The effect of variation in the prey profiles was investigated by varying the proportion of the two dominant species in the diet. Within

each profile, the proportion of the biomass of the diet comprised by the dominant prey species was increased and decreased by 10, 20 and 30%, and the second most dominant species increased or decreased accordingly. For the Pilanesberg prey profile, the proportion of the dominant species was also varied relative to the proportion of the third most important species (impala) to illustrate the effect of that prey profile approaching wild dog diets elsewhere. The estimated intrinsic rate of increase in prey populations was varied (by  $\pm 10$ –30%) to cater for over- or underestimation in this parameter. Finally, the effect of variation in prey densities was investigated by varying prey densities (by  $\pm 10$ –30%).

## RESULTS

Given a typical prey profile, the estimated minimum area required to support wild dogs is largest for the northeastern South Africa scenario, followed by the eastern and northern scenarios (Table 2). Significant deviation from a typical prey profile, as observed at Pilanesberg, greatly increases predicted minimum area requirements. Greater kudu (*Tragelaphus strepsiceros*) in Pilanesberg and northern South Africa, nyala (*Tragelaphus angasi*) in eastern, and impala (*Aepyceros melampus*) in northeastern South Africa set the greatest minimum area requirements. The predicted minimum area requirements for the minimum viable pack size (five dogs and one set of offspring – ten dogs in total) in northern and



**Fig. 1.** Minimum areas required to support predation by varying pack sizes given four different prey profiles.

eastern South Africa are comparatively low at 131 km<sup>2</sup> and 144 km<sup>2</sup> respectively (Fig. 1). In comparison, estimates for Pilanesberg (993 km<sup>2</sup>), and to a lesser extent, northeastern South Africa (295 km<sup>2</sup>) are much higher.

For eastern, northeastern and northern South Africa, observed home range areas are larger than the estimated minimum areas required to support an average-sized pack (Table 3). For Pilanesberg, no published data on home range size outside of the denning season is available. However, the estimated minimum area requirements of the minimum viable pack size (five dogs plus one set of offspring, 993 km<sup>2</sup>) are larger than the park (500 km<sup>2</sup>). The density at which wild dogs occur in eastern, northeastern and northern South Africa is markedly lower than the theoretical maximum potential density that each area could support, if wild dogs were regulated by density dependent resource limitation. At Pilanesberg, the observed density of dogs is greater than the theoretical maximum (Table 4).

For the prey profiles considered, deviation in the proportion of the two dominant species from that

observed generally resulted in increased area requirements (Fig. 2). For the Pilanesberg prey profile, a 10%, 20% and 30% increase in impala, and a corresponding decrease in kudu resulted in a reduction in minimum area requirements by 14.8%, 29.6% and 44.4%, respectively. For a 10, 20 and 30% increase in  $r_m$  or in prey density, minimum area requirements fell by 11%, 25% and 43%, respectively. For a 10, 20 and 30% decrease in these two parameters, minimum area requirements increased by 9%, 17% and 23%, respectively.

## DISCUSSION

The validity of minimum area estimates presented in this paper is dependent on the validity of the underlying assumptions. It was assumed that the prey-profile of wild dogs reintroduced into small areas would approximate that observed in large areas of similar habitat. Wild dogs usually prey on the most abundant medium-sized to large prey species and typically take prey in proportion to abundance (Reich 1981; Fuller & Kat 1990; Pole 1999), suggesting that approximate prey-profiles

**Table 3.** Observed home range areas of wild dogs in three regions, *versus* estimated minimum areas required to provide sufficient prey to support equivalent pack sizes.

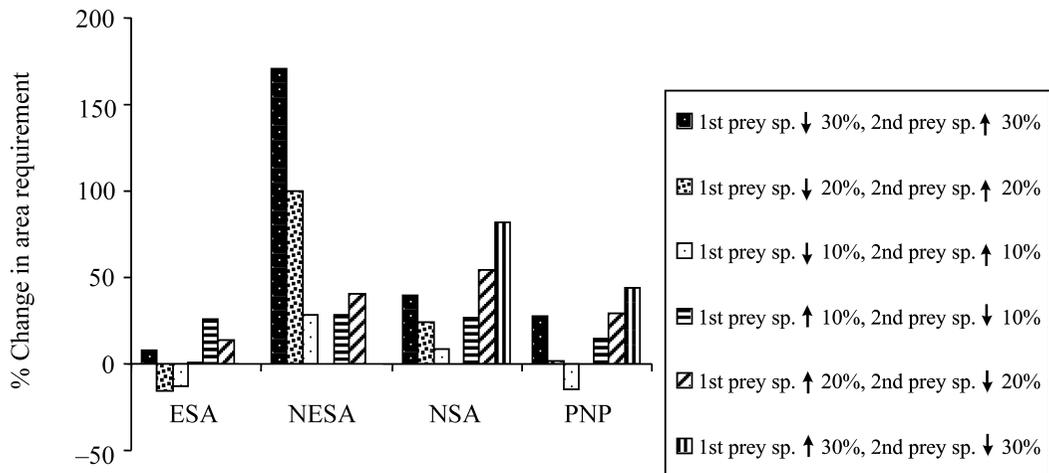
Region	Mean pack size <sup>a</sup>	Observed home range areas (km <sup>2</sup> )	Estimated area required (km <sup>2</sup> )	Observed: estimated
Eastern SA <sup>b</sup>	13	218	188	1.2
Northeastern SA <sup>c</sup>	9	537	265	2.0
Northern SA <sup>d</sup>	9	414	117	3.5

<sup>a</sup>Adults, yearlings, and number of pups divided by 2, after Mills & Gorman (1997).

<sup>b</sup>Hluhluwe-Umfolozi Park (December 1994 pack size, Maddock 1999; 1993/94 home range size, Andreka *et al.* 1999).

<sup>c</sup>Southern Kruger (Mills & Gorman 1997).

<sup>d</sup>Save Valley Conservancy (Pole 1999).



**Fig. 2.** Variation in the minimum area requirements of a pack of 12 wild dogs with variation in the proportion of the dominant prey species in the diet in four prey profiles (ESA, eastern SA; NESA, northeastern SA; NSA, northern SA; PNP, Pilanesberg).

**Table 4.** Observed density of wild dogs in four regions, *versus* estimated maximum density (dogs/100 km<sup>2</sup>) at which wild dogs would occur if they were regulated by density dependent resource limitation.

Region	Observed density	Estimated maximum density	Observed:estimated
Eastern SA <sup>a</sup>	1.44	6.93	0.21
Northeastern SA <sup>b</sup>	2.07	3.39	0.61
Northern SA <sup>c</sup>	2.40	7.64	0.31
Pilanesberg NP <sup>d</sup>	1.80	0.75	2.40

<sup>a</sup>Hluhluwe-Umfolozi Park (1994 density data, Maddock 1999).

<sup>b</sup>Southern Kruger (Maddock & Mills 1994).

<sup>c</sup>Save Valley Conservancy (Pole 1999).

<sup>d</sup>van Dyk & Slotow (2003).

can be predicted. Experience from recent reintroductions, however, suggests that perimeter fencing may be a complicating factor. Wild dogs reintroduced into small areas learn to utilize perimeter fencing during hunting, resulting in a higher hunting success rate with large prey species than is typical (Hofmeyr 1997; van Dyk & Slotow 2003). In Pilanesberg, for example, wild dogs utilize the fence-line to kill kudu and waterbuck, and these species are killed more frequently than would be expected from their abundance (van Dyk & Slotow 2003). For this prey profile to be sustainable, a pack of 12 wild dogs in Pilanesberg would require an area of 2.4 times the size of the park. However, the diet data from Pilanesberg is likely to be somewhat biased, as it is based on carcasses collected by fence patrols. Large prey species are more likely to be killed on the fence line than elsewhere, and small carcasses

are more likely to be completely consumed and not seen. Consequently, the minimum area requirement estimates from these data are probably exaggerated. Furthermore, one would expect wild dogs in Pilanesberg to switch to more common prey species such as impala if the dogs move away from the fence line or as the larger prey species become locally scarce, which would reduce area requirements. Nonetheless, the presence of perimeter fencing may increase the ecological impact of wild dogs on non-typical prey species/ages/sexes and thus increase area requirements. This phenomenon is likely to be exacerbated in smaller reserves, and for private reserves this illustrates the desirability of removing internal fencing between neighbouring properties to create large conservancies. In general, variation from expected prey profiles causes an increase in predicted area requirements for wild dogs and to

allow for this, it is advisable that larger areas than the estimated minimum are used for reintroductions.

It was 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 somewhat overestimated minimum area estimates.

In estimating minimum required prey populations, no consideration was made of sex or age selection by wild dogs. The effect of this is likely to be exaggeration of the minimum area estimates. 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 (Mills & Shenk 1992). Furthermore, wild dogs select for impala in poor condition (Pole 1999; Pole *et al.* 2004), and subsequently, a portion of predation by wild dogs may compensate for animals that would have died anyway.

It was 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 in 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). Conversely, in wet years, ungulate numbers are likely to increase, and wild dog numbers might be expected to decrease, as occurred in Kruger during 1995–2000, probably due to poor conditions for hunting (Davies 2000). Given these patterns, it is vital that prey population trends and prey selection are monitored following a reintroduction, to guide the regulation of wild dog or prey numbers in line with management objectives and ecological conditions.

In the calculation of minimum area requirements, the impact of competing predator species was not taken into account. Across ecosystems, there is a negative correlation between the density of wild

dogs and the density of lions and spotted hyaenas (Creel & Creel 1996) and the presence of these species is likely to increase wild dogs' area requirements. Spotted hyaenas affect wild dogs through interference competition, and lions are significant agents of mortality (Creel & Creel 1996; Mills & Gorman 1997). 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; van Dyk & Slotow 2003). 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). Consequently, lions reduce wild dog density both 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 lion and spotted hyaena numbers may require management to enable wild dogs to persist. For example, reducing the size of male lion coalitions may increase the success of wild dog reintroductions by reducing the area covered during the movements of these lions, and providing more scope for spatial avoidance by wild dogs (van Dyk & Slotow 2003). Nonetheless, if wild dog reintroduction into a reserve with existing populations of lions and hyaenas is to be considered, larger areas than the estimated minimum will likely be required.

The results of this paper suggest that given a prey profile related to prey abundance, and 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 utilized smaller home range areas than typically recorded in large protected areas (Fuller *et al.* 1992): Hluhluwe-Umfolozi Park (218 km<sup>2</sup>, Andreaka *et al.* 1999); and Madikwe Game Reserve (180 km<sup>2</sup>, Hofmeyr 1997). In addition, wild dogs have been successfully reintroduced into reserves as small as 85 km<sup>2</sup> (Karongwe Game Reserve), 120 km<sup>2</sup> (Shambala Game Reserve), 200 km<sup>2</sup> (Shamwari Game Reserve), and 370 km<sup>2</sup> (Venetia Limpopo Game Reserve). Our study suggests that in areas of high prey density (for example northern South Africa), given a typical prey profile, protected areas as small as 131 km<sup>2</sup> 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 (Lindsey 2003; 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). Smaller reserves (such as Karongwe Game Reserve) may be suitable for wild dog reintroductions if prey density is high, if wild dog numbers are actively and regularly controlled through translocation (as has occurred at Karongwe), and/or if prey populations are supplemented. However, several factors are likely to increase the minimum area requirements of wild dogs above those estimated from food requirements. The use of larger areas is recommended to provide scope for variation in wild dog prey profile (as may occur due to the use of fences during hunting), to allow for variation in the size of prey populations, and to permit adequate spatial avoidance of dominant competitor species.

The predicted maximum density at which wild dogs could occur in southern Kruger given density dependent resource limitation (3.39 dogs/100 km<sup>2</sup>), is lower than the observed density of some other large carnivores (approximately 10 lions and spotted hyaenas/100 km<sup>2</sup>, 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, wild dogs do not exploit carrion and utilize a narrow range of prey species (Ginsberg & Macdonald 1990; Fuller *et al.* 1992; Mills & Biggs 1993), from which they are selective (Pole 1999; Pole *et al.* 2004).

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, with the exception of Pilanesberg, in the areas considered, observed densities are 2–5 times lower than the theoretical maximum densities based on prey availability.

Although it is difficult to determine adequate reserve size for reintroductions (Miller *et al.* 1999), the results presented in this paper give estimates and provide a basis for adaptive management of wild dogs and their prey. Estimating minimum

required reserve sizes for viable populations is a major focus of conservation biology (Rodrigues & Gaston 2001; Wiegand 2002). However, increasing habitat loss is likely to increase the need for utilizing fragments of natural land cover, and employing meta-population management techniques (Griffith *et al.* 1989). The methods outlined in this paper 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 paper 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 on wild dogs, smaller areas than previously considered may represent potential reintroduction sites.

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