Chapter 10
Modelling the Effect of Fences on the Viability of Spatially Structured Populations of African Wild Dogs

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Introduction

Fences have become a common management tool to counteract the increasing pressure on protected areas and their animals from encroachment of an expanding human population, increased prevalence of diseases and increased spread of alien invasive species. However, although fences often have positive effects by protecting land from urban sprawl, and from poaching or encroaching livestock, they may also have negative effects on animal movement and demographics (reviewed in Hayward and Kerley 2009). Of these negative effects, one of the most important is that fences often restrict the movement of the enclosed animals (Newmark 2008), thereby creating a network of isolated populations. If fences are impenetrable, there will be no interpopulation movement, which has demographic consequences (e.g. Somers et al. 2008).

Movement between subpopulations is an important process in the dynamics of spatially structured populations, because it provides the linkage between subpopulations and enables the colonization of unoccupied areas by dispersing individuals (Brachet et al. 1999; Thomas 2000; Revilla and Wiegand 2008). Movement also ensures the long-term persistence of metapopulations (Hanski 1998). Because conservation areas cover only a small fraction of the total land area, the management of matrix habitat in between isolated populations becomes increasingly important

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M.J. Somers and M.W. Hayward (eds.), *Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes?*,
DOI 10.1007/978-1-4614-0902-1_10,

(Prugh et al. 2008; Franklin and Lindenmayer 2009; Prevedello and Vieira 2010; Watling et al. 2011). For instance, Akçakaya et al. (2007) emphasized that the viability of a population may depend on surrounding populations, in which case metapopulation processes influence or determine reserve design and management options.

Large carnivores are often persecuted in rural areas because of the damage they do to livestock, the fact that they compete with humans over game or the direct threat they pose to humans (Kruuk 2002). This has led to heavy persecution, and subsequently for many species to local, regional or global extinction (Dalerum et al. 2009). Because of their body size and potential conflict with humans, many populations of large carnivores are enclosed by fences, which often have led to detrimental levels of population fragmentation (Hayward and Kerley 2009). This fence-driven fragmentation process has been accentuated by an increase in large carnivore reintroductions (Hayward and Somers 2009). Although substantial efforts are devoted to keep fences secure, many large carnivores are able to penetrate them, possibly decreasing the negative demographic effects of fences. Such breakouts often occur following floods when fences placed across rivers are washed away, when poachers break fences to gain access to conservation areas or simply through holes made by other species such as warthogs *Phacochoerus africanus* (Somers, unpublished data).

The African wild dog *Lycaon pictus* is a large (20–30 kg) canid that lives in complex social groups of up to 24 individuals (Creel and Creel 2002; Somers et al. 2008). It occurs throughout central, eastern and southern Africa. Following heavy persecution, the species became endangered during the twentieth century and it remains at a fraction of its previous population size. In South Africa, wild dog conservation has focused on reintroducing packs within fenced conservation areas and on facilitating movement between these isolated populations through translocations (Davies-Mostert et al. 2009; Gusset 2010). Wild dogs usually disperse in single-sex groups at the age of 1–2 years. Individuals rarely breed if they remain in their natal packs beyond this age because wild dogs usually do not breed with close relatives (Somers et al. 2008; Spiering et al. 2011). Therefore, unless animals of dispersal age are actively translocated (Gusset et al. 2009), they are effectively demographically lost to the South African managed metapopulation.

Although persecution of wild dogs outside of conservation areas in South Africa may be substantial (Gusset et al. 2008), it is potentially beneficial if dispersing wild dogs manage to penetrate fences since they then may meet unrelated dispersers of the opposite sex and form new packs. This may be inside conservation areas or elsewhere. If such spontaneous dispersal is sufficiently common, a natural metapopulation will form (Hanski 1998). This has large demographic and genetic benefits compared to isolated populations where the only method of dispersal between subpopulations would be by human translocation (Frankham 2009). Therefore, evaluating the influence of fences on wild dog demography and population persistence is central to the conservation of the species particularly in southern Africa, where fences are prevalent and populations are fragmented. Here, we use stochastic population models to investigate the demographic effects of varying levels of fence penetrability on the viability of spatially structured wild dog populations.

Methods

We modified a stochastic population model previously described in Dalerum et al. (2008). The model is temporally discrete with a simple sex and age structure, and can be formalized as:

$$\mathrm{P_i} = \mathrm{AM}_i + \mathrm{AF}_i + \mathrm{SM}_i + \mathrm{SF}_i + \mathrm{J_i}, \tag{10.1}$$

where P_i, AM_i, AF_i, SM_i, SF_i and J_i are population size, number of adult males and females, number of subadult males and females and number of juveniles at year *i*, respectively. For our purposes, we regarded adults as animals 2 years or older, subadults as animals from 1 to 2 years and juveniles as young of the year (Somers et al. 2008). We calculated the number of animals in each age and sex category as:

$$\mathrm{J_i} = \mathrm{AF}_i \times \mathrm{f}_i, \tag{10.2}$$

$$\begin{aligned} \mathrm{SM}_i &= 0.5 \times \mathrm{J_{i-1}} \times js_i + \mathrm{IMS}_i - \mathrm{EMS}_i, \\ \mathrm{SF}_i &= 0.5 \times \mathrm{J}_{i-1} \times js_i + \mathrm{IFS}_i - \mathrm{EFS}_i, \end{aligned} \tag{10.3}$$

$$\begin{aligned} \mathrm{AM}_i &= \mathrm{AM}_{i-1} \times mas_i + \mathrm{SM}_{i-1} \times mss_{i-1} - \mathrm{EMA}_i + \mathrm{IMA}_i, \\ \mathrm{AF}_i &= \mathrm{AF}_{i-1} \times fas_i + \mathrm{SF}_{i-1} \times fss_{i-1} - \mathrm{EFA}_i + \mathrm{IFA}_i, \end{aligned} \tag{10.4}$$

where f_i is annual birth rate (number of pups per female per year after weaning; weaning sex ratio is estimated to be 1:1), js_i is juvenile survival, mss_i and fss_i are subadult survival for males and females, mas_i and fas_i are adult survival for males and females, respectively, EMS_i, EFS_i, EMA_i and EFA_i are the net number of subadult and adult emigrating males and females, and IMS_i, IFS_i, IMA_i and IFA_i are the net number of subadult and adult immigrating males and females.

We ran the model with discrete 1-year time steps, and for each year we drew female fecundity from a normal distribution, and survival from a binomial distribution. We calculated the number of emigrants by multiplying the number of animals in each age and sex category with binomial probabilities of dispersal. We calculated the number of immigrants from emigrating individuals from connected populations.

To evaluate the effect of fences, we multiplied the number of immigrants from a particular population with a scaling factor ranging from 0 to 1, so that a scaling factor of 0 would result in no immigrants and a scaling factor of 1 would result in all potential immigrants entering the population. We regarded this scaling factor as a theoretical proxy for fences of varying penetrability, so that a scaling factor (i.e. fence penetrability) of 0 would represent a completely wild dog proof fence and a fence penetrability of 1 would represent an unfenced population boundary. This approach controlled only the net number of immigrants, but not the number of emigrants. We used this "one way" fence approach (i.e. restricting immigration but not emigration) since we modelled relatively small populations and any prospective

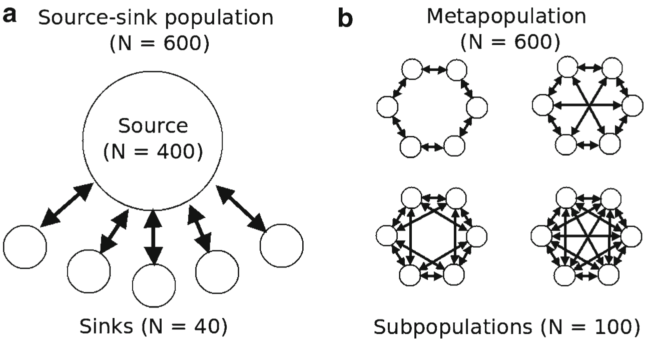

Fig. 10.1 Conceptual description of model scenarios. We explored the effect of fences on (**a**) source–sink populations consisting of one source population with 400 individuals and five sink populations with 40 individuals each, and (**b**) four different metapopulation scenarios, each with six subpopulations consisting of 100 animals each but with varying connectivity (ranging from each subpopulation being connected to its two nearest neighbours to each subpopulation being connected to all subpopulations in the metapopulation)

emigrants that would have been locked in by a fence would most likely not be demographically active (Somers et al. 2008). We repeated each subset of simulations over the full range of fence penetrability values 1,000 times, and for each simulation we coded population size at 25 years as either below the initial population size or not, or extinct or not-extinct. Based on these binary codes we used logistic regression models to calculate probabilities of population decline and extinction over varying levels of fence penetrability (e.g. McCarthy et al. 1995, 1996; Cross and Beissinger 2001; Dalerum et al. 2008).

We considered two different scenarios of wild dog populations. Both are relevant from a conservation perspective (see Davies-Mostert et al. 2009). First, we considered a source–sink scenario with one large source and five small sink populations, with each sink population being 10% of the size of the source population (Fig. 10.1a). Secondly, we considered a metapopulation scenario with six evenly sized subpopulations (Fig. 10.1b). For the metapopulation scenario, we altered the connectivity of the subpopulations to range from one to five (i.e. the number of connected populations for each subpopulation), and also the number of connected populations that were affected by the fence variable (ranging from one to the maximum number of connected populations for each scenario).

Fecundity, survival, demographic structure and dispersal parameters underlying the simulations are given in Table 10.1. To avoid unlimited exponential growth, we capped source and sink populations at a carrying capacity of 500 individuals, and subpopulations within the metapopulaton at 200 individuals (see below for descriptions of the two demographic scenarios). However, for simplicity we did not include density-dependent effects on demographic parameters until the carrying capacity was reached.

Table 10.1 Parameters underlying our modelling approach to evaluate the effect of fences on the viability of spatially structured wild dog populations

Parameter	Value	Source
Adult males (%)	29.86	Creel and Creel (2002)
Adult females (%)	27.09	Creel and Creel (2002)
Subadult males (%)	8.03	Creel and Creel (2002)
Subadult females (%)	9.84	Creel and Creel (2002)
Juveniles (%)	25.18	Creel and Creel (2002)
Fecundity mean (offspring/female/year)	2.4	Estimated from Creel and Creel (2002)
Fecundity SD (offspring/female/year)	1.2	Estimated from Creel and Creel (2002)
Juvenile female survival (annual)	0.75	Creel and Creel (2002)
Juvenile male survival (annual)	0.66	Creel and Creel (2002)
Subadult female survival (annual)	0.84	Creel and Creel (2002)
Subadult female survival (annual)	0.99	Creel and Creel (2002)
Adult female survival (annual)	0.69	Creel and Creel (2002)
Adult male survival (annual)	0.73	Creel and Creel (2002)
Subadult male migration (proportion animals)	0.30	Creel and Creel (2002)
Subadult female migration (proportion animals)	0.49	Creel and Creel (2002)
Adult male migration (proportion animals)	0.10	Creel and Creel (2002)
Adult female migration (proportion animals)	0.11	Creel and Creel (2002)
Sink population size mean	40	Estimated from Davies-Mostert et al. (2009)

Results

In the source–sink scenario, completely wild dog proof fences (i.e. with zero penetrability) generated substantial probabilities of population decline in all five sink populations (>75%), and over 20% probability of having up to three sink populations going extinct within 25 years. Fences with less than 25% penetrability generated almost 100% probabilities of population decline in at least one of the sink populations over 25 years (Fig. 10.2a), and generated associated risks above zero of having at least one sink population going extinct (Fig. 10.2b). There appears to be a threshold of fence penetrability at about 50%; populations enclosed by fences with higher penetrability had substantially lower probabilities of decline and almost zero probability of extinction (Fig. 10.2).

In the metapopulation scenario, both connectivity within metapopulations and number of fenced population connections affected how important fences were for wild dog population viability. At least half of the population connections had to be fenced for fences to have a substantial effect on the probabilities of population decline (Fig. 10.3a), and all population connections had to be fenced for fences to have any effect on subpopulation extinction probabilities (Fig. 10.3b). Even with all connections affected by fences, as is typically the case in South Africa, there appears to be a threshold at approximately 50% penetrability for fences to have substantial effects on the

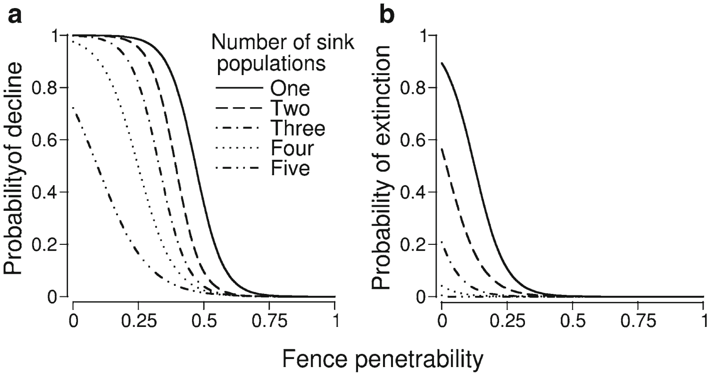

Fig. 10.2 Probability of (**a**) decline and (**b**) extinction after 25 years of simulations of theoretical wild dog populations, each consisting of a source population with 400 animals as well as five sink populations with 40 animals each. Each *line* represents the probabilities of decline and extinction in one to five sink populations. The model assumes that animals not being able to disperse were not demographically active while remaining in their population of origin

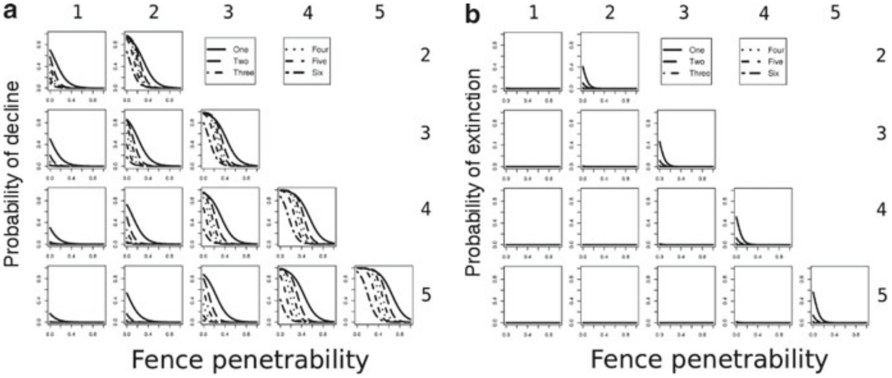

Fig. 10.3 Probability of (**a**) decline and (**b**) extinction after 25 years of simulations of theoretical wild dog metapopulations, each consisting of six subpopulations with 100 animals each. Each *row* represents the number of connecting subpopulations (ranging from two to five) and each *column* represents the number of fenced subpopulation connections (ranging from one to the maximum number of connections for each model scenario)

probabilities of subpopulation decline (Fig. 10.3a), and a threshold at approximately 20% penetrability for fences to substantially affect extinction probabilities (Fig. 10.3b).

The effects of fences on the probabilities of both decline and extinction in at least one subpopulation were higher in the source–sink than in the metapopulation scenario, unless all subpopulation connections in the metapopulation were fenced (Table 10.2). Moreover, metapopulations were more sensitive to the effects of fences if they had a large number of connections, so that fences in metapopulations with a large number of connections could have higher penetrability but still generate substantial probabilities of decline (Table 10.2).

Table 10.2 Fence penetrability (ranging from 0 being complete wild dog proof fence to 1 being no fence), generating 25, 50 and 75% probabilities of decline and extinction after 25 years of simulations in at least one subpopulation of a source–sink population and in metapopulations with varying levels of connectivity and with different numbers of fenced subpopulation connections

Population scenario	Number of connections	Number of fenced connections	Decline			Extinction		
			25%	50%	75%	25%	50%	75%
Source–sink			0.53	0.47	0.41	0.19	0.12	0.06
Metapopulation	2	1	0.23	0.10	0	0	0	0
		2	0.44	0.31	0.18	0.04	0	0
	3	1	0.13	0	0	0	0	0
		2	0.34	0.21	0.09	0	0	0
		3	0.56	0.43	0.30	0.05	0	0
	4	1	0.03	0	0	0	0	0
		2	0.24	0.12	0	0	0	0
		3	0.46	0.33	0.20	0	0	0
		4	0.67	0.54	0.41	0.06	0	0
	5	1	0	0	0	0	0	0
		2	0.15	0.02	0	0	0	0
		3	0.36	0.23	0.10	0	0	0
		4	0.57	0.44	0.32	0	0	0
		5	0.79	0.66	0.53	0.07	0.01	0

Discussion

Our results highlight the fact that fences can substantially affect the viability of source–sink populations of wild dogs through constraints in dispersal, and that fences efficient in limiting wild dog movements can generate substantial extinction probabilities in such populations. Our results further indicate that the connectivity within metapopulations influences the effects of fences on population viability. In both scenarios, there appears to be two crude thresholds of fence penetrability; fences with about 50% penetrability or less seem to generate substantial probabilities of decline, whereas fences with 20% penetrability or less seem to generate probabilities of extinction that are above zero. Although our analyses should be interpreted in a largely qualitative context, these results still suggest that entirely predator-proof fences are detrimental for the conservation of large carnivore species such as wild dogs, unless the animals are periodically translocated between fenced conservation areas (Gusset et al. 2009). However, the penetrability of fences typically varies owing to varying levels of maintenance, flooding or destruction by animals such as elephants *Loxodonta africana*, so that completely predator-proof fences are, in reality, probably absent or very rare.

The demographic impacts of fences will depend both on the level of density-dependent regulation in fenced populations and the mortality rates in unfenced areas. Therefore, fences may not have detrimental effects on all wild dog populations since they might prevent animals from suffering persecution and other human-related mortality outside of fenced areas. For instance, fence length, a surrogate for the level of fence maintenance, was negatively related to the survival of reintroduced wild dogs in South Africa (Gusset et al. 2008). Furthermore, the only reintroduced pack within the South African managed metapopulation that had a mortality risk higher than the population average was released into the only area that was not entirely fenced (Gusset et al. 2010). The major cause for the increased mortality among these wild dogs was snaring immediately outside of the reserve. However, contrasting these results are findings that wild dogs succeed in dispersing over long distances, and occasionally between fenced conservation areas (e.g. 100 km between Hluhluwe-iMfolozi Park to Ithala Game Reserve; Somers, unpublished data). These inconsistent results regarding the effect of fences on wild dog demographics highlight the complexities in evaluating the consequences of fences for populations of large carnivores. Therefore, we stress that our suggestion that a certain level of fence penetrability may be beneficial for large carnivore conservation does not apply to all species and for all management scenarios. Instead, the influence of dispersal barriers such as fences should optimally be evaluated for each species and situation separately. It is only in such context-dependent evaluations that species-specific dispersal behaviour can be considered and weighted against estimated mortality risks in a matrix habitat.

To conclude, our results suggest that fences can generate substantial probabilities of decline and extinction probabilities above zero in both source–sink populations and metapopulations of wild dogs. However, these suggestions of purely negative effects of fences are contradicted by empirical data from South Africa where wild dogs suffered higher mortality in areas with higher fence penetrability due to human-related mortality outside of conservation areas (Gusset et al. 2008, 2010). We argue that these inconsistencies are caused by the relative effects of the levels of density-dependent constraints on population growth inside fenced reserves (Somers et al. 2008) and mortality rates in matrix habitat. However, we still acknowledge that large protected areas probably are the best way to protect biodiversity, especially wide-ranging species such as large carnivores (Mills 2005; Hayward and Kerley 2009).

Acknowledgements We are grateful to Mark Boyce, Matt Hayward and Kyran Kunkel for helpful comments on this chapter.

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