Status Survey and Conservation Action Plan

The African Wild Dog

Compiled and edited by
Rosie Woodroffe, Joshua Ginsberg and David Macdonald

IUCN/SSC Canid Specialist Group

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Contents

Preface

To nominate one sight as the most beautiful I have seen might, in a world filled with natural marvels, be considered disingenuous. Yet, of images jostling for supremacy in my memory, it is hard to better the bounding forms of African wild dogs, skiffing like golden pebbles across a sea of sunburnt grass at dusk. For the wild dogs, it was a moment of social turmoil, impenetrable to me, but chillingly clear to the vanquished dog that fled the ferocity of the pack. What was it about those African wild dogs that seared a glimpse of them so vividly in my memory? It was not just the dappled mosaic of their sinuous bodies whose beauty triggered the soaring elation I now recall; it was the thrilling elasticity of motion with which they scythed grass and air. As we turn, in this book, to consider what can be done to prevent the extinction of the African wild dog, I think it is pertinent to remember why it matters. Of course, it matters because they are an intriguing component of their threatened ecosystem; it matters because they are as unique as any species and – forgive the malapropism – a 'bit more unique' than most; and it matters because, though the tracks of wild dogs and of our ancestors have crossed in the African dust for a million or more years, it has taken just a century of recent human excess to end that coexistence. We have brought them to the brink of annihilation – a responsibility that makes me, for one, feel shoddy. I do not mean to diminish the power of logical, scientific, political or philosophical reasons why the fate of African wild dogs matters, but as readers explore this book with thoughts of scientific triumphs, political rivalries and economic expedience, let me remind you of one other point: African wild dogs are shudderingly beautiful. It would be a shame to obliterate them.

There is another reason why the conservation of African wild dogs is important, especially to those nations who have custody of their surviving populations. It is that wild dogs are so fragile – a flame so easily snuffed out – that their survival is a hallmark of successful reserve management. Like a canary in a coal mine, wild dogs are a barometer of environmental well-being. For those countries which manage to retain healthy populations of wild dogs, their survival is a success of which to be truly proud.

This book, the *Lycaon* Action Plan, has grown out of the *Lycaon* Population Viability Analysis meeting which Joshua Ginsberg and I convened in Arusha, Tanzania, in March 1992. The meeting was sadly memorable as the moment at which the collected wisdom of all concerned revealed that the species' prospects were perilous. It is more happily memorable as the start of a concerted focus on the species' plight that must rival the attention paid to any other endangered species in the 1990s. Our original intention had been to produce this book much sooner; many complications, not least the astounding speed at which the wild dog's predicament unfolded, caused us repeatedly to postpone its completion. Ultimately, the postponements have proven a blessing in disguise, not least because they brought the opportunity for a third member, Rosie Woodroffe, to join our team. Normally, it would be unbecoming for one of its compilers to sing the praises of a book. However, I am freed from that restraint because so much that is good and helpful in these pages stems from the dedication and insight of Joshua and Rosie, while I have added little more than a certain doggedness to keep our craft afloat as we charted the rapids that buffet every undertaking of this complexity. Therefore, in thanking my two friends for the excellence of their work, I can also commend this text to its readers far and wide.

I should also stress that another, albeit unexpected, benefit of the prolonged gestation of this publication is that seminal questions that were unanswered at the outset – for example, what limits wild dog numbers – are now largely resolved, and the answers can thus enlighten our synthesis. However, the resolution of one question remains imperfectly ragged, despite exhaustive attention, and that is whether handling or vaccinating wild dogs had inadvertently contributed to their demise in the Serengeti-Mara ecosystem. Although we know of no data that will ever resolve the historical debate, more information has become available on the seroconversion of rabies vaccines by *Lycaon*. These data enhance a thorough synthesis of this debate presented herein. While all three of us, and many others beside, have played a more or less hefty role in drafting or editing other chapters herein, Rosie Woodroffe has been the sole author of Appendix 1: this is because she is the only one of us not to publish previously on the topic of handling, and therefore, as a new broom, could sweep cleanest. She has brought a fresh view, and synthesized a conclusion from the available data which we believe will not, in the absence of additional data, be significantly improved by further debate on an uncertain past. The only merit of exploring the history was to improve the future; now, unless more historical data can be found, we three can see nothing more we can personally contribute by continuing that exploration. Henceforth we will be looking ahead.

The Lycaon Action Plan is a product of the IUCN/SSC Canid Specialist Group, under whose auspices the Arusha PVA was originally held. I am grateful to all who have been involved since the outset, and especially to Costa Mlay, and the staff of the Tanzania National Parks (TANAPA), who were such gracious hosts to us in Arusha. We also acknowledge the particular role of Gus Mills who coordinates the Lycaon Working Party on behalf of the CSG, and is assisted by Scott Creel. The CSG is in good heart. We employ two staff, Claudio Sillero-Zubiri who is our African Conservation Officer, and Laura Handoca, our Actioner and co-editor of Canid News. We have just published a companion volume to this volume, the Ethiopian Wolf Action Plan, more are in the pipeline, and our developing web page can be accessed via http://users.ox.ac.uk/~wcruinfo. We have exciting plans but, if I may drop a hint, they require sponsorship! We greatly hope that the Lycaon Action Plan will contribute to the survival of African wild dogs. If the book is judged to be interesting, we will be pleased, but that is secondary to its goal of being useful. Conserving wild mammals tends to be difficult, but conserving wild dogs is likely to be especially so. For me, there is a sad message in these pages. It is that the adaptations that suited the African wild dog to its extraordinary lifestyle, and by which we should be enthralled, cannot safeguard it in the modern world. The African wild dog is not of the twentieth century, and we may fear that it will not be for the twenty first. The only hope lies in intense, and probably radical, conservation. The wild dog matters. It will be worth the effort.

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This Action Plan brings together data collected over a ten year period. It is clear, then, that a wide array of people have contributed to its preparation.

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Frame & Fanshawe's survey was followed by the IUCN/SSC Canid Specialist Group's 'Workshop on the Conservation & Recovery of the African Wild Dog' held in Arusha, Tanzania, in 1992 and hosted by Mr Costa Mlay, Director of the Wildlife Department of the Government of Tanzania. We are extremely grateful to the organizations which provided funding for the Workshop: the World Conservation Union (IUCN), the People's Trust for Endangered Species, the World Wide Fund for Nature (WWF), the African Wildlife Foundation, Wildlife Conservation International (now WCS), the Zoological Society of London, Chicago Zoological Society, Philadelphia Zoological Society, the Aspinall Zoos, Perth Zoo and the Taronga Zoo. We would also like to thank the Iris Darnton Trust, the People's Trust for Endangered Species, and Roebuck-Eyot Ltd for contributing funds for the final publication of the Plan.

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Executive Summary

The African wild dog (*Lycaon pictus*) has declined dramatically over the past 30 years. Wild dogs have disappeared from 25 of the 39 countries in which they were formerly recorded, and only six populations are believed to number more than 100 animals. Between 3,000 and 5,500 wild dogs, in perhaps 600–1,000 packs, remain in total. Most of these are in southern and eastern Africa; only small remnant populations remain in West and central Africa.

Wild Dogs as Indicators

Wild dogs are uniquely susceptible to habitat fragmentation. A resident breeding population may therefore provide a 'gold standard' indicating excellent local management of wildlife. Wild dogs' recent decline reflects the expansion of human populations in Africa and the associated fragmentation of habitat available to wildlife:

- Wild dogs range widely, so that even those inhabiting protected areas often contact human activity on reserve borders. Over half the wild dogs found dead in protected areas have been shot, snared, poisoned, killed by road traffic or infected with diseases by domestic dogs outside the reserve.
- Human activity therefore represents a serious threat, even to wild dogs inhabiting large reserves.
- Areas smaller than 10,000 km² contain no safe 'core' where wild dogs are buffered from these edge effects. As a result they will be the first species to disappear as wildlife lands are fragmented.

The Highest Priority: Promoting Connections between Wildlife Areas

Since wild dogs are so susceptible to habitat fragmentation, the highest priority for their conservation is to maintain and promote the contiguity of wildlife areas. Establishing cross-border parks, corridors and buffer zones, and encouraging land use favourable to wildlife on reserve borders, will therefore benefit wild dogs even more than other endangered species. Wild dogs are highly appropriate 'flagships' for the expansion of wildlife areas.

The Second Priority: Mitigating Edge Effects

Most of Africa's remaining wild dog populations inhabit areas substantially smaller than 10,000 km². These are extremely vulnerable due to their small size and exposure to human activity. Protecting such populations requires mitigation of 'edge effects' on the borders of wildlife areas by:

- Working with local farmers to limit persecution. This may involve establishing zones where wild dogs are to be conserved, and areas where farmers are not required to tolerate large predators. Inside predator conservation zones wild dog protection might involve improved livestock husbandry, compensation for livestock losses, local education, and better legal protection.
- Routing of new high-speed roads away from reserves and their border areas.
- Control of snaring inside wildlife areas and along their borders. This may involve local development to provide alternative sources of protein.
- Minimizing wild dogs' contact with diseases carried by domestic dogs. Control of diseases such as rabies will also benefit people and livestock, and may be carried out in collaboration with public health organizations. Domestic dogs should not be permitted inside protected areas. Outside reserves, the numbers and mobility of domestic dogs should be controlled, with unaccompanied dogs being shot on sight. Domestic dogs may also be vaccinated against canid diseases.

Monitoring Population Trends: Continued Information-gathering

Continued monitoring of wild dog populations is crucial to dynamic management:

- Countries such as Algeria, Sudan and the Central African Republic might contain wild dog populations with very high conservation value. Surveys are needed to establish their status.
- Wild dog sightings should be collected continuously by local conservation authorities. Sightings are rare and wild dogs' decline may go unnoticed if data are not collected systematically.
- Threats such as disease vary dramatically from place to place and over time. Continued monitoring of populations under long-term study will identify new threats as they emerge.

Lower Priorities: Re-establishing Extirpated Populations

It is technically possible to re-establish extirpated wild dog populations by reintroduction, but this provides no substitute for the conservation of existing populations. Reintroduction is most needed in West and central Africa, but there are few suitable release sites, and no animals of appropriate genotypes available for release.

In highly fragmented landscapes, wild dogs could be released into a network of small, fenced reserves, each supporting one or a few packs, to establish an intensively-managed metapopulation. This would be prohibitively expensive in most of Africa, but locally valuable if funds were available.

Chapter 1
Introduction

Rosie Woodroffe & Joshua R. Ginsberg

*There can be no doubt that African wild dogs (*Lycaon pictus*) have suffered a dramatic decline over the last 30 years. As human populations have grown and larger areas have been taken over for livestock grazing and cultivation, wild dogs' habitat has become fragmented. Furthermore, wild dogs have been heavily persecuted both inside and outside national parks and game reserves.*

Packs, rather than individuals, represent the basic unit of wild dog populations. Pairs rarely raise pups without assistance, so wild dogs are constrained to living in packs. Wild dogs also cooperate to hunt prey much larger than themselves. Such prey would be inaccessible to them if they hunted alone.

Wild dog packs live at low densities and range over very large areas. As a result, even those living in large protected areas may travel outside reserve borders where they encounter threats associated with human activity.

Later chapters describe the current distribution and status of Africa's remaining wild dog population, and the threats faced by these populations, before recommending measures for their conservation.

Background

There can be no doubt that African wild dogs (*Lycaon pictus*) have declined over the last century, and this decline has accelerated in the last 30 years. They were once distributed through much of sub-Saharan Africa, apart from rainforest areas and deserts (Fanshawe *et al.* 1991; Monod 1928; Schaller 1972). Now, however, they have been extirpated from most of their range – they are extinct in most countries in West and Central Africa, and in the East and the South they are confined to a few areas where human population density remains low (Chapter 3). Today, Africa's wild dog population numbers between 3,000 and 5,500. Most populations outside – and sometimes inside – protected areas may still be declining. Wild dogs are rare compared with other high-profile species in Africa: there are about the same number of wild dogs as there are black rhinos (*Diceros bicornis*, ~3,000 remaining, Cumming *et al.* 1990), fewer wild dogs than cheetahs (*Acinonyx jubatus*, 9–12,000 remaining, Nowell & Jackson 1996), and far fewer wild dogs than African elephants (*Loxodonta africana*, 100–130,000 remaining, Said *et al.* 1995).

The ultimate cause of wild dogs' decline has been a combination of persecution and habitat loss. Like other large predators, wild dogs do kill livestock under some circumstances, and have therefore been shot, snared and poisoned in most livestock areas (Chapter 3). Worse still, they have been persecuted in the name of animal welfare and conservation. Wild dogs kill their prey by tearing it to pieces or disembowelling it (Kuhme 1965), and this earned them a reputation as cruel and blood-thirsty killers. Game managers' attitudes to them are exemplified by Bere's (1955) observation that they "...hunt in packs, killing wantonly far more than they need for food, and by methods of the utmost cruelty... When the Uganda national parks were established it was considered necessary, as it had often been elsewhere, to shoot wild dogs in order to give the antelope opportunity to develop their optimum numbers. Fortunately only a few of these creatures have had to be destroyed and their number in the parks does not seem to be particularly large...".

This last remark of Bere's points to a crucial aspect of wild dog ecology: they always live at very low densities, and are rare even where they live in large well-protected habitats with abundant prey (Chapter 4). This makes them unusually susceptible to habitat fragmentation. Growing human populations have caused wild dog habitat to become discontinuous, as large tracts of land have been taken over for livestock grazing and cultivation. As more people have colonized the land, wild dogs have been persecuted and their prey have been depleted. Wild dog populations have, therefore, become increasingly isolated in fragments of habitat with few human inhabitants. Since wild dogs live at such low densities, even the largest of these fragments could support only small populations, which are vulnerable to extinction (Soulé 1987). Worse still, wild dogs were persecuted inside national parks and game reserves, which represented some of the best remaining habitat. This combination of habitat fragmentation, persecution and prey loss explains wild dogs' dramatic decline across most of Africa. As a result of this process, today wild dogs persist only in countries with relatively low human population densities (Chapter 3).

Although wild dog numbers have declined markedly, it is not too late to prevent their extinction. Viable populations remain in several countries in East and southern Africa and, with adequate protection, there is no reason why these populations should not persist. However, to conserve wild dogs we must understand the factors that have led their numbers to fall across Africa in the past, and determine the threats that might cause further decline or extinction in the future. If we can use this knowledge to halt wild dogs' decline, then we can prevent their extinction without the 'emergency' measures that have been necessary for some other endangered carnivores (Caughley 1994; Clark 1994; May 1986; Phillips 1995).

Wild dogs chase zebras, although they rarely kill such large prey.

Aims and Structure of this Action Plan

Given wild dogs' current circumstances, this Action Plan has the following aims:

1) To assess the size and distribution of the wild dog populations that remain in Africa.
2) To assess the factors likely to lead these populations to decline further – perhaps to local extinction.
3) To use this information to formulate management plans aimed at halting or reversing wild dogs' population decline across Africa.
4) Where we do not have enough information to allow us to make informed decisions about wild dog management, to pinpoint the research needed to provide the necessary data.

The Action Plan is structured to meet these aims. The remainder of this chapter concerns aspects of wild dogs' natural history that are crucial for understanding the threats they face, and the management options that are possible. Chapter 2 deals with genetic factors important in wild dog conservation, especially their taxonomy and the identification of sub-species. Chapter 3 describes the current status and distribution of wild dog populations across Africa. Chapter 4 outlines the threats faced by wild dogs, and Chapter 5 uses demographic modelling to assess the probability that any of these threats might contribute to the extinction of remaining populations. Chapter 6 draws upon this information to propose measures for the conservation of free-ranging wild dog populations, and Chapter 7 discusses the rôle that captive wild dogs might play in this effort. Chapter 8 describes the additional research that is needed to allow us to refine our strategies for wild dog management. Chapter 9 summarizes the recommendations of Chapters 7 and 8 to propose actions for wild dog conservation in each range state.

The Action Plan also has four appendices. Some of the tactics that we discuss for wild dog conservation involve vaccination against infectious diseases, and immobilization for radio-collaring. Such procedures have been the subject of considerable controversy and we have, therefore, included a full discussion of this issue in Appendix 1. Appendix 2 provides details of some techniques used in current research projects on wild dogs, which may be of use to people directly involved with the management of wild dog populations. Appendix 3 is a list of contributors to this Action Plan, and Appendix 4 gives a detailed bibliography of publications concerning wild dogs.

The Natural History of Wild Dogs

Many of the problems faced by wild dogs stem from basic features of their natural history. Here we discuss aspects of wild dog biology which are important in understanding the reasons for their decline, and in devising plans for their conservation.

Diet

Wild dogs mostly hunt medium-sized antelope; their principal prey in several parts of Africa are summarized in Table 1.1. They will chase larger species, such as eland and buffalo, but rarely kill such prey (Creel & Creel 1995; Ginsberg 1992). Wild dogs also take small prey such as hares, lizards and even eggs (Creel & Creel 1995; Ginsberg 1992), but these probably make a fairly small contribution to their diet.

Wild dogs do take livestock in some areas, but this is a fairly rare occurrence. In and around the Masai Mara National Reserve, Kenya, wild dogs ignored livestock (Fanshawe 1989; Fuller & Kat 1990), and in one case in Zimbabwe they ran through a paddock of calves to chase a kudu in the neighbouring paddock (Rasmussen

A kudu, a prey species.

Table 1.1
Principal prey taken by wild dogs in various study sites across Africa. The proportions of prey taken in Serengeti were calculated from data presented in Fanshawe & FitzGibbon (1993); all other data were presented by wild dog biologists attending the IUCN/SSC Canid Specialist Group's Workshop on the Conservation & Recovery of the African wild dog, held in Arusha, Tanzania, in 1992. Data from Hwange provided by J.R.G., data from Kruger provided by M.G.L. Mills, data from Masai Mara provided by P. Kat, data from Moremi provided by J.W. McNutt, data from Namibia provided by L. Scheepers, data from Selous provided by S. Creel, data from Zambia provided by F. Munyenyembe.

Study site	Preferred prey		
	First	Second	Others
Hwange National Park, Zimbabwe	impala (60%)	kudu (30%)	reedbuck (2%)
Kruger National Park, South Africa	impala (52%)	kudu (12%)	reedbuck (15%)
Masai Mara National Reserve, Kenya	Thomson's gazelle (67%)	impala (17%)	wildebeest (8%)
Moremi Game Reserve, Botswana	impala (85%)	kudu	lechwe
Namibia	reedbuck	wildebeest	roan, duiker
Selous Game Reserve, Tanzania	impala (69%)	wildebeest (11%)	reedbuck (3%) warthog (3%)
Serengeti National Park, Tanzania	Thomson's gazelle (57%)	wildebeest (40%)	Grant's gazelle, zebra
Zambia	impala	reedbuck	hartebeest, oribi

An impala, a medium-sized antelope preyed on by wild dogs.

1996). The only study of wild dog depredation on livestock found that the dogs took far fewer cattle than the farmers believed (Rasmussen 1996). Nevertheless wild dogs can occasionally become a severe problem for livestock, especially smaller stock such as sheep and goats (Chapter 4).

Social Organization

Wild dogs are intensely social animals, spending almost all of their time in close association with one other. Packs may be as small as a pair, or number as many as 27 adults and yearlings (M.G.L. Mills, pers. comm., R. Burrows 1993, Fuller *et al.* 1992a) – average pack compositions for various study sites are summarized in Table 1.2. Packs are formed when small same-sex sub-groups – usually siblings – leave their natal groups and join up with other sub-groups of the opposite sex. Thus, in newly-formed packs the females are closely related to one another, but not to the males, and the males are closely related to one another, but not to the females (Burrows 1995; Frame *et al.* 1979; Fuller *et al.* 1992a). Young born into such packs may remain there, or disperse as yearlings or young adults to form new packs.

Cooperative Hunting

Members of wild dog packs hunt cooperatively. By hunting together, they can capture prey much larger than themselves which would not otherwise be accessible to them. Wild dogs weigh 20–25 kg, but their prey average around 50 kg, and may be as large as 200 kg (Creel & Creel 1995; Malcolm & van Lawick 1975).

Wild dog hunts are almost always preceded by a 'social rally' which is believed to coordinate the pack in preparation for hunting (Estes & Goddard 1967; Kuhme 1965). Once prey sight the dogs, they may flee, or stand and defend themselves alone or as a herd (Creel & Creel 1995; Kuhme 1965). During chases, wild dogs may run at speeds of up to 60 km/h, and are specially adapted to deal with the heat stress that this involves (Taylor *et al.* 1971). During such chases, wild dogs are spaced around the running prey so that a member of the pack can intercept the quarry as it turns. After this dog has made the first grab, other pack members cooperate to drag the quarry to a halt (Creel & Creel 1995; Estes & Goddard 1967; Kuhme 1965).

Once the quarry has been brought to bay, one or a few dogs may distract it from the front, while others attack from behind and begin to disembowel it (Kuhme 1965). Alternatively, one pack member may restrain the head of the prey by biting its nose, and holding on while the others make the kill (Creel & Creel 1995; Malcolm & van Lawick 1975). When hunting ungulate calves, some members of a wild dog pack may distract the mother while the remainder attack her calf.

Table 1.2
Pack compositions of wild dogs in various study sites across Africa. Data for Hwange, Kruger, Masai Mara, Moremi and Serengeti are from Fuller *et al.* (1992a), and data from Selous are from Creel & Creel (1995).

Study site	Sample	Adults	Yearlings	Pups
Hwange National Park, Zimbabwe	5 packs	7.8	3.2	5.4
Kruger National Park, South Africa	8 packs	4.8	2.1	5.6
Masai Mara National Reserve, Kenya	6 packs	4.2	4.0	8.8
Moremi Game Reserve, Botswana	8 packs	4.3	2.5	8.3
Selous Game Reserve, Tanzania	6 packs	7.7	4.3	6.3
Serengeti National Park, Tanzania	7 packs	6.6	6.0	11.2

Wild dogs beginning to disembowel a kudu.

the den during early lactation, and relies on other pack members to feed her at this time. Wild dogs deliver food to the mother by regurgitation; later on, they regurgitate to the pups as well (Malcolm & Marten 1982). Some pack members also 'babysit' the pups, and chase predators away from the den (Malcolm & Marten 1982).

Perhaps because so many helpers are available to assist with pup care (Creel & Creel 1991), wild dogs' litters are enormous: litters number 10–11 pups on average and occasionally contain as many as 21 pups (Fuller *et al.* 1992a). Pup mortality may be high, however. There is some evidence to suggest that more pups survive in packs where there are more helpers to assist with their care, but this is certainly not always the case (S.R. Creel pers. comm., Burrows 1995; Fuller *et al.* 1992a; Malcolm & Marten 1982).

As a result of such cooperative hunting, each pack member has a higher foraging success (measured as kg killed per km chased) than it would if it hunted alone (Creel & Creel 1995). Larger packs are also better able to defend their kills against scavenging hyaenas (Fanshawe & FitzGibbon 1993).

Cooperative Breeding

In most wild dog packs, a single dominant female is the mother of all the pups, although two or even three females may breed on some occasions (Fuller *et al.* 1992a). However, all pack members are involved in caring for the pups (Frame *et al.* 1979; Malcolm & Marten 1982; van Heerden & Kuhn 1985). Such additional care is vital if pups are to survive: packs rarely manage to raise any pups if they contain fewer than four members (S.R. Creel pers. comm.).

The pups are born in a den, where they remain for the first three months of life. The mother is confined to the den during early lactation, and relies on other pack members to feed her at this time.

As well as a dominant, breeding female, each pack also has a dominant male (Frame *et al.* 1979; Malcolm & Marten 1982). Both mating behaviour and genetic analysis indicate that the dominant male fathers most (but not all) of the pups (D. Girman pers. comm., Malcolm & Marten 1982). However, dominant males are usually no more assiduous in caring for the pups than are other males in the pack (Malcolm & Marten 1982).

Since wild dog females cannot breed without assistance, in most cases the pack, rather than the individual, should be considered the basic unit within the population.

[illegible] wild dogs in various study sites across Africa. Data for Aitong [illegible] Fuller & Kat (1990), data from Hwange, Kruger, Moremi and Serengeti [illegible] Fuller *et al.* (1992a), and data from Selous are from Creel & Creel [illegible]

[illegible]	Sample	Home range size
[illegible] Masai Mara, Kenya	1 pack	659 km²
[illegible] Park, Zimbabwe	4 packs	423 km² (range 260–633 km²)
[illegible] Park, South Africa	20 packs	553 km² (range 150–1110 km²)
[illegible] Reserve, Botswana	9 packs	617 km² (range 375–1050 km²)
[illegible] Reserve, Tanzania	6 packs	438 km² (SE ± 87 km²)
[illegible] Park, Tanzania	5 packs	1318 km² (range 620–2460 km²)

A wild dog returns to the den to regurgitate food to pups.

Ranging Behaviour

Wild dogs have enormous home ranges (Table 1.3), much larger than would be expected on the basis of their body size (Gittleman & Harvey 1982). Packs are confined to relatively small areas when they are feeding young pups at a den, but outside the denning period they are truly nomadic. For example, in Serengeti home ranges were 50–260 km^2 during denning, but 1,500–2,000 km^2 at other times (Burrows 1995), and a pack in Kruger ranged over 80 km^2 when denning, but 885 km^2 after denning (Gorman *et al.* 1992).

The home ranges of different wild dog packs may overlap considerably, but they rarely enter one anothers' core areas and so their ranges are, to some extent, exclusive (Fuller *et al.* 1992a). As a result, wild dogs' large home ranges translate into very low population densities (Table 1.4). The reasons why wild dogs live at such low densities are not clear, but several studies indicate that their numbers are rarely limited by the availability of ungulate prey (Creel & Creel 1996; Fuller *et al.* 1992a; Mills & Biggs 1993). This issue is discussed in detail in Chapter 4.

Even wild dog packs which inhabit protected areas may travel extensively outside the reserve borders – where they encounter human activity and threats such as roads, snares and livestock farmers likely to persecute them (Chapter 4). Wild dogs dispersing away from their natal packs range even more widely – they have been followed for hundreds of kilometres (Fuller *et al.* 1992b) and single wild dogs, or single-sex groups, are occasionally reported from countries such as the Democratic Republic of Congo and Uganda, where there has been no resident wild dog population for some years (Chapter 3).

Conclusions

In this chapter, we have outlined the background to the problems faced by wild dogs today, and given brief details of their natural history. An important conclusion is that the pack, rather than the individual, should be considered the basic unit of wild dog populations.

The next chapter will discuss wild dog taxonomy and other aspects of wild dog genetics important in their conservation.

Table 1.4

Population densities of wild dogs in various study sites across Africa. Data for Aitong are from Fuller & Kat (1990), data for Hluhluwe, Hwange, Selous and Serengeti are from Creel & Creel (1996), and data for Kruger are from Mills & Biggs (1993).

Study site	Population density (adults/100 km^2)
Aitong, near Masai Mara, Kenya	2.6–4.6
Hluhluwe-Umfolozi Park, South Africa	3.3
Hwange National Park, Zimbabwe	1.5
Kruger National Park, South Africa	2.0
Selous Game Reserve, Tanzania	4
Serengeti National Park, Tanzania	
1967–1979	1.5
1985–1991	0.67

Chapter 2
Genetic Perspectives on Wild Dog Conservation

Derek J. Girman & Robert K. Wayne

Wild dogs are the only extant representatives of a distinct lineage of wolf-like canids. As a result of this phylogenetic distinctiveness, they have a high conservation value.

In the past, wild dogs from East and southern Africa were considered members of distinct sub-species. However, new data suggest that this is unlikely – genetic exchange seems to have occurred between these populations until recently. Unique mitochondrial haplotypes and nuclear alleles are found in wild dogs from South Africa and the north of East Africa, but intermediate populations in Botswana and Zimbabwe contain a mixture of 'eastern' and 'southern' genotypes. Furthermore, we have identified a unique West African mitochondrial haplotype through examinations of museum skins. Although we cannot recognize separate sub-species at present, the genetic differences mean that populations in southern, eastern and West Africa must all be conserved if wild dogs' genetic diversity is to be preserved.

Within populations, wild dogs appear to have strong inbreeding avoidance behaviour. Probably as a result of this, free-ranging populations retain high levels of genetic variability. However, captive populations risk loss of genetic variability. For this reason, efforts geared towards active management and preservation of wild populations is preferable to a strategy of captive breeding and reintroduction.

Background

Studies of wild dog genetics have a great deal to contribute to plans for their conservation. At the largest scale, molecular genetic comparisons of wild dogs with other species can help us to define their phylogenetic uniqueness, an increasingly important component of priority-setting in conservation (Vane-Wright *et al.* 1991). Comparisons among wild dog populations can be used to identify local subspecies or ecotypes, helping us to evaluate the conservation value of different populations. Finally, genetic studies can be used to look for evidence of inbreeding in both wild and captive populations, allowing us to devise the most effective management strategies.

Ancient population fragmentation followed by subsequent dispersal may characterize wild dogs. They are known to be highly mobile, having home range sizes estimated to be as large as 2,000 km² (Frame *et al.* 1979; Fuller *et al.* 1992a). In addition, animals may sometimes disperse over long distances, although the frequency of such events is uncertain (Frame *et al.* 1979; Fuller *et al.* 1992b; Girman *et al.* in press). However, wild dog populations have declined dramatically during the past century, leading to the development of fragmented populations of wild dogs in many parts of their former range (Chapter 3).

Taxonomy

Wild dogs represent a unique lineage within the wolf-like canids. They are the only members of the genus *Lycaon*, and some taxonomists have placed them in a sub-family, the *Simocyoninae*, distinct from most of the other canids (Wozencraft 1989). Although this sub-family division is no longer recognized (Wozencraft 1989), recent phylogenetic analyses using molecular genetics have supported wild dogs' place in their own genus (Girman *et al.* 1993). An analysis of sequence data from 2001 b.p. of the cytochrome *b*, cytochrome oxidase I, and cytochrome oxidase II genes showed that wild dogs are distinct from the wolves and jackals of the genus *Canis* (Figure 2.1, Girman *et al.* 1993). This phylogenetic distinctiveness places a high conservation value upon wild dogs: their extinction would represent the loss of a unique canid lineage several million years old.

Genetic and morphological analyses also show some differences between wild dogs from different parts of Africa. Our initial studies employed an analysis of mitochondrial DNA (mtDNA) restriction fragment length polymorphisms (RFLPs), and direct sequencing of the cytochrome *b* gene of 92 wild dogs from two localities in eastern Africa (the Masai Mara National Reserve, Kenya, and Serengeti National Park, Tanzania) and two localities in southern Africa (Hwange National Park, Zimbabwe and Kruger National Park, South

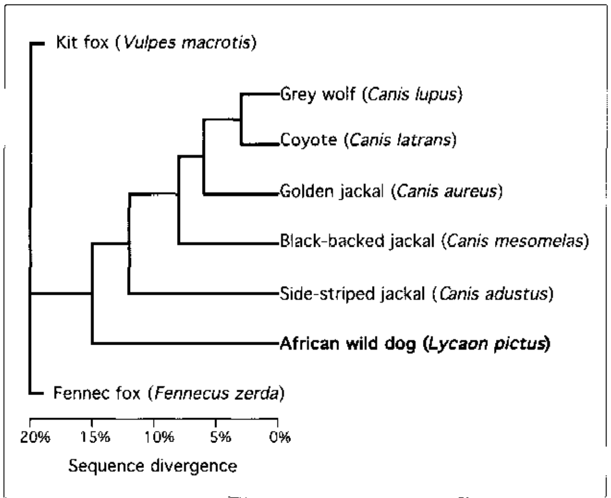


Figure 2.1. The single most parsimonious tree of African wild dog and related canid species generated from phylogenetic analysis of 736 b.p. of cytochrome *b* sequence data.
The kit and fennec foxes are included as outgroups. Modified from Girman *et al.* (1993).

Africa, Table 2.1, Girman *et al.* 1993). In addition, we carried out multivariate analyses of morphological measurements from skulls taken from eastern and southern Africa. Levels of genetic variability in both eastern and southern African populations were similar. In addition, this study suggested that there was a genetic and morphologic distinction between eastern and southern African populations. Based on these results, we recommended separate subspecific designations for eastern and southern African wild dogs (Girman *et al.* 1993).

However, this distinction between eastern and southern populations of wild dogs was surprising, given the dispersal capabilities of wild dogs. Consequently, we sought many more genetic samples from a greater portion of wild dogs' range in eastern and southern Africa (Table 2.1). We also used the most variable portion of the mtDNA genome, the control region, to develop a more fine-scaled analysis of these populations. In addition, since the maternal inheritance of mtDNA may provide a biased picture of gene flow and population differentiation, we carried out further investigations using nuclear loci to develop a complete understanding of the genetic structure of African wild dogs. In our follow-up study we assessed the patterns of gene flow and genetic differentiation of 270 African wild dogs from seven wild populations in eastern and southern Africa, and two captive populations in South Africa, through the analyses of mitochondrial DNA control region sequences and eleven dinucleotide repeat loci (microsatellites) (Girman 1996). We used an AMOVA (analysis of molecular variance) approach to conduct parallel analyses of both the mtDNA and microsatellite data (Excoffier *et al.* 1992). This parallel approach allowed us to examine the hierarchy of population subdivision, and to estimate the patterns and rates of gene flow among the seven sampling localities.

The control region sequences revealed two groups of

Table 2.1
Sampling localities for captive and free-ranging wild dog populations in eastern and southern Africa. Museum skins were collected from populations existing 50–100 years ago. Sources of skins: [1]: Smithsonian Museum of Natural History, Washington D.C., U.S.A.; [2]: British Museum of Natural History, London, U.K.; [3]: Transvaal Museum of Natural History, Pretoria, South Africa.

Locality	Sample size
Samples from wild populations	
Masai Mara National Reserve, Kenya	15
Serengeti National Park, Tanzania	13
Selous Game Reserve, Tanzania	32
Moremi Game Reserve, Botswana	45
Hwange National Park, Zimbabwe	28
Angola	1
Etosha National Park, Namibia	6
Kruger National Park, South Africa	94
Sub-total	***234***
Samples from captive populations	
De Wildt breeding colony, South Africa	20
Kapama breeding colony, South Africa	16
Sub-total	***36***
Samples from museum skins	
Kenya[1]	1
Sudan[1]	1
Nigeria[2]	1
Malawi[2]	2
Botswana[2]	1
Zimbabwe[3]	1
South Africa[1,2,3]	7
Sub-total	***14***

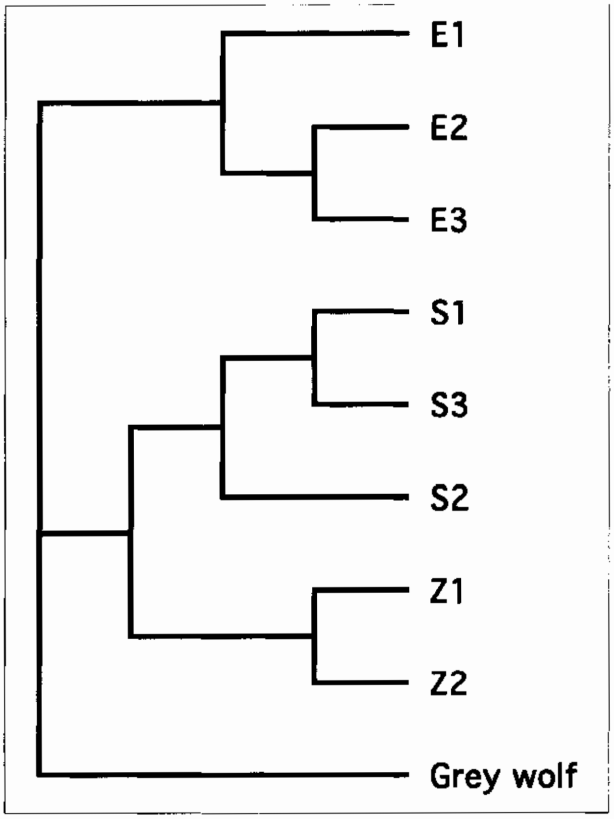


Figure 2.2. One of four most parsimonious trees generated from 381 b.p. of mtDNA control region sequence data from African wild dogs and the outgroup (grey wolf).
E1 and E3 genotypes were found only in eastern African populations while S1, S2, Z1, and Z2 genotypes were found only in southern African populations. Differences in the trees occur with respect to which of the 'S' genotypes is basal.

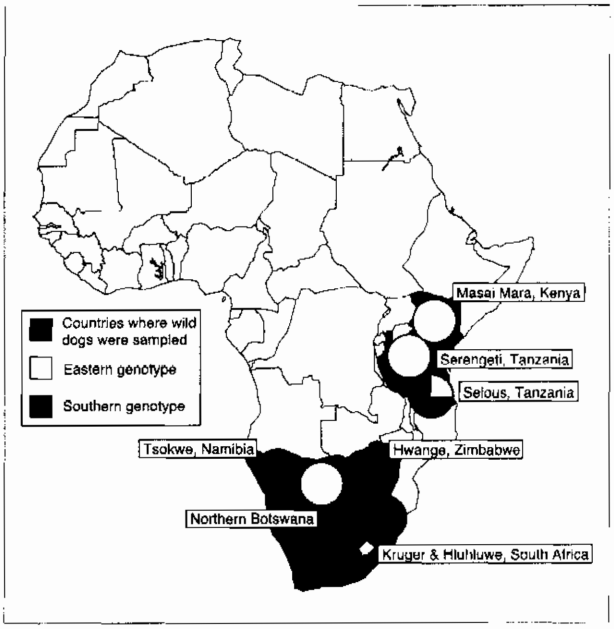


Figure 2.3. The proportion of mtDNA haplotypes from the eastern African and southern African clades are depicted in the circles at each sampling locality.
Black shading represents southern African haplotypes and white represents eastern haplotypes.

haplotypes, forming two distinct clades in a parsimony analysis (Figure 2.2). However, the geographic distribution of haplotypes did not coincide entirely with the divisions suggested by the mitochondrial tree (Figure 2.3). The new mtDNA data suggest a pattern of past separation of eastern and southern populations: there are unique haplotypes from different clades at either end of the geographic range. However, there also appears to be recent mixing of haplotypes from the different clades in the intervening populations in Botswana and Zimbabwe (Figure 2.3).

Our study shows that the population in the Selous region of southern Tanzania is particularly interesting. In this population there appears to be a predominant haplotype that is most closely related to a haplotype so far found only in the Kruger National Park, South Africa (Girman 1996). The only other mtDNA haplotype found in our sample of 31 individuals from this population is found in Botswana and Zimbabwe. No mtDNA haplotypes are shared between the Selous population and the Serengeti and Masai Mara populations, which are also in eastern Africa. Thus the Selous population represents a distinct and interesting population that requires further sampling and analysis. These initial results suggest it may have an affinity with South African wild dogs.

Our analysis of microsatellite data showed that gene flow among all populations was significantly higher than that measured with the mitochondrial data (Girman 1996). The microsatellite data suggest a pattern of differentiation with geographic distance. Differences between the nuclear and mitochondrial datasets may indicate higher levels of long-distance dispersal by males. This is consistent with previous behavioural and genetic studies, which found that males tend to have longer dispersal distances (Frame *et al.* 1979; Fuller *et al.* 1992b; Girman *et al.* in press). The Kruger population contains one unique mtDNA genotype and three unique microsatellite alleles, suggesting some degree of distinction from the other populations. Likewise, unique microsatellite alleles are found in the East African populations (Selous, Serengeti, and Masai Mara), and the Masai Mara and Serengeti populations share a unique mtDNA haplotype (Girman 1996). These results suggest that only populations in Serengeti-Masai Mara and Kruger have a high level of genetic isolation. Those populations in between represent admixture zones. Since most management and captive breeding efforts have focused on southern African populations, we recommend increased effort focusing on the preservation and management of north-eastern African wild dog populations.

An examination of control region sequences from museum skin samples suggests that West African wild dogs have a unique haplotype (Girman 1996; Roy *et al.* 1994). For example, a museum sample from Nigeria (provided by the British Museum of Natural History) contains a unique mtDNA haplotype that is distinct from the two clades containing the eastern and southern African mtDNA haplotypes (Figure 2.2). Clearly, much more investigation of West African wild dog populations is warranted to determine the degree of distinction of these populations. West Africa may contain populations that are quite distinct from the eastern and southern populations that we have studied thus far.

Genetic Variation within Wild and Captive Populations

Levels of genetic variability in the eastern and southern African wild dog populations are similar (Girman 1996). All of the free-ranging populations sampled appeared to have relatively high levels of genetic variability (heterozygosity levels ranging from 0.56 to 0.66) with an average of 0.603 over all seven populations measured (Table 2.2). Also, allelic variability was relatively high among free-ranging populations of African wild dogs, with the average number of alleles per locus ranging from 3.4 to 4.1 (Table 2.2). High levels of variability may be due to strong inbreeding avoidance behaviour. A study of a single population in Kruger National Park demonstrated that male and female wild dogs that formed new packs did so only with unrelated members of the opposite sex (Girman *et al.* in press). This was true even though most males and females dispersed to territories very near their close relatives. We found no evidence for inbreeding in the Kruger population.

To examine the genetic status of captive wild dogs, we compared the levels of genetic variability in two captive populations with those in seven free-ranging populations. The captive populations had lower genetic variability than all of the wild populations (Girman 1996). This suggests that careful genetic management is needed in captive populations to maintain variability levels similar to those found in the wild. In addition, pedigree information provided by the the managers of captive groups were not consistent with parentage analyses using microsatellites (D. Girman, Unpublished data) suggesting that accurate assessment of parentage is difficult in captivity without genetic analyses. The only way to regulate breeding is to break up the natural pack groupings through the isolation of breeding pairs. In contrast, wild dogs in natural populations are extremely effective at inbreeding avoidance and naturally maintain high levels of genetic admixture without compromising the natural structure of wild dog packs. Therefore, from a genetic perspective, active management of wild populations is preferable to captive breeding and reintroduction by humans where possible.

Table 2.2
A comparison of genetic variability between wild and captive wild dog populations. The numbers of individuals sampled are given by *n*, and the ranges of population sizes are given in parentheses.

	Wild populations *(n = 217 dogs)*	Captive populations *(n = 36 dogs)*
Average population size	24 (range 6–94)	18 (range 16–20)
Average H_E per population	0.603	0.431
Average number of alleles per locus per population	3.75	2.55
Number of mtDNA haplotypes per population	2.7	1.0

Chapter 3
The Status & Distribution of Remaining Wild Dog Populations

John H. Fanshawe, Joshua R. Ginsberg,

Claudio Sillero-Zubiri & Rosie Woodroffe

In order to make plans for effective wild dog conservation, we need to know where the remaining populations are located. This chapter combines data from a number of surveys to give an up-to-date picture of wild dogs' status and distribution in Africa today.

We estimate that there are between 3,000 and 5,500 wild dogs, in perhaps 600–1,000 packs, remaining in Africa. More than half of these are in southern Africa, where the largest population occupies northern Botswana, north-east Namibia and western Zimbabwe. There are other populations in the Kruger National Park, South Africa, and Kafue National Park and the Luangwa valley, Zambia, all of which are probably viable. The only substantial wild dog population in East Africa is in southern Tanzania. Kenya and Ethiopia have small populations, but it is not clear whether these are viable in the long term. Wild dogs have been extirpated across most of West and central Africa, although there are populations in Sénégal and Cameroun which might be viable.

Countries where wild dogs have been extirpated are characterized by having relatively high human population densities. This points to the fact that it is very difficult for wild dogs to coexist with people in the long term. This issue is discussed in more detail in the next chapter.

Background

An important first step in devising strategies for wild dog conservation is to survey their distribution and status. In order to set priorities for action, we need to know (i) where wild dogs occur, (ii) roughly how many are left in each population, and (iii) the threats they are facing. Only by gathering these basic data can we determine where conservation effort should be focused. Furthermore, comparing the areas where wild dog populations have been extirpated with those where they have persisted may help us to identify – and halt – the factors leading to local extinction.

The first pan-African survey of wild dogs' status and distribution was carried out in 1985–1988 (Frame & Fanshawe 1990). Updates to this survey were presented for several countries at the IUCN/SSC Canid Specialist Group's 'Workshop on the Conservation & Recovery of the African Wild Dog' held in Arusha, Tanzania, in 1992 (Ginsberg 1992). In this chapter, we combine these updates with data from the 1990 survey, as well as data from additional surveys carried out by ourselves and other authors (*e.g.* Buk 1994; Hines 1990; Jennings 1992; Malcolm 1995). The result is a compilation of the most up-to-date information available to us on wild dogs' distribution and status throughout Africa.

The chapter is divided into sections for North, West, central, East, and southern Africa. For each country, we have given details of wild dogs' distribution and population status, based upon postal and field surveys. Most of these data were gathered through extensive correspondence with park staff, field workers, tourists and others. In the interests of brevity we have not cited sources for data taken from this correspondence, although sources are available from the authors on request. In the 1990 survey, respondents were asked to characterize wild dogs as absent, rare, uncommon or common. These measures are necessarily subjective – 'common' sometimes means that the same dogs are seen repeatedly. For many areas, we simply have isolated reports of wild dog sightings. To make the country-by-country data more accessible, we have also included maps and summary tables. In addition, we have summarized wild dogs' status in each country with the following symbols:

☹ = Countries with no viable wild dog population. There are either no sightings, or very few isolated sightings, in the past 10 years. Some of these countries may be used by wild dogs, but they seem to have no resident population large enough to be viable in the long term.

😐 = Countries with wild dog populations which might be viable. Wild dogs are sighted reasonably regularly in the same small area, indicating that a population consisting of a few packs is resident there. Alternatively, data may be very sparse, but suggest that a viable population might exist in the country.

☺ = Countries in which wild dogs inhabit extensive areas of land, and where the population appears large enough, at present, to be viable in the long term if environmental circumstances do not worsen.

For areas which still seem to support wild dogs, we have provided some details about the habitat, as well as the potential threats to wild dogs. Most of these data were provided by people who responded to the questionnaire surveys, although additional data on the distribution of lions were taken from Nowell & Jackson (1996).

For each country, we have also provided information on the legal protection offered by the national government – most of these data were provided by the IUCN Environmental Law Centre.

Distribution of Wild Dogs in North Africa

Wild dogs' status in North Africa is very poor. There are rumours of wild dogs in a few North African countries, but any remaining population must be very small. If still extant, however, they are likely to be genetically distinct from other wild dog populations and would have a very high conservation value.

Algeria

Status ☹

The outlook is very poor. Most respondents believe that wild dogs are extinct in Algeria, although it is possible that a relict population still exists in the south of the country. Wild dogs have probably always been rare in Algeria, and have been driven out of most of their former northern range by a combination of persecution, drought and dwindling food supplies.

Distribution

The only recent report of wild dogs in Algeria comes from Tuareg tribesmen in the Teffedest mountains. These sightings come from an area of *c.* 60,000 km², mostly above 1500 m ASL.

Wild dogs were formerly seen in the Mouydir Arah Mountains to the north of Teffedest, and the Tuareg used to trap and poison wild dogs in this area. There are no recent sightings. Tuareg also reported wild dogs from Ahaggar National Park in 1989, but they were considered very rare and, again, there are no recent reports.

Mauritania

Status & Distribution ☹

There are probably no wild dogs in Mauritania. There is one unconfirmed sighting from the coastal area of Mauritania in 1992, and hunters living in the coastal areas of Western Sahara, to the north of Mauritania, described an animal resembling the wild dog, which hunted in packs. However, in neither of these cases is it clear that the animals reported really were wild dogs.

Western Sahara

Status & Distribution ☹

There are probably no wild dogs in Western Sahara. Hunters interviewed in the coastal region reported an animal resembling a wild dog, known to hunt in packs. However, it is not clear whether these really were wild dogs, and the hunters had not seen any for thirty years.

Distribution of Wild Dogs in West Africa

Wild dogs are faring very badly in most of West Africa. As far as we are aware, there is only one potentially viable population, in and around Niokolo-Koba National Park, Sénégal (Figure 3.1). Occasional sightings come from other parts of Sénégal, Guinea and Mali, but there are no recent reports from the rest of West Africa. This means that the Niokolo-Koba population has an extremely high conservation priority.

Benin

Status ☹

Wild dogs are probably extinct in Benin. Respondents to the 1990 survey thought it extremely unlikely that any population remained, and we have received no further information.

Distribution

Wild dogs might still be present in the Parc 'W' (5,600 km²; see also under Niger), although they were considered to be either extinct or declining in 1988. All

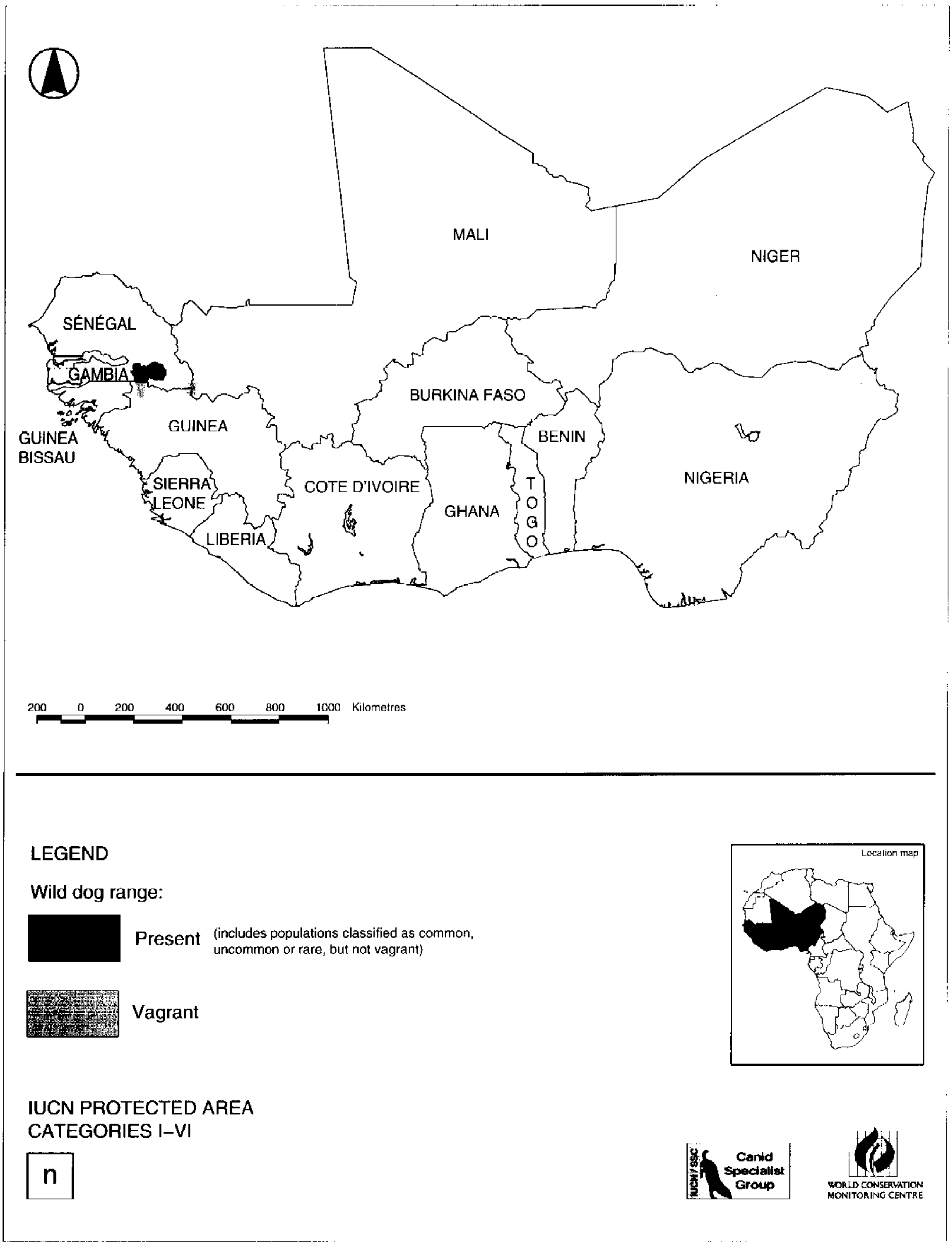


Figure 3.1. Wild dog distribution in West Africa.

Table 3.1
A summary of wild dog distribution in Burkina Faso. Burkina Faso [illegible] wild dog population.

Site	Area (km²)	Abundance	[illegible]
Arli National Park	1,143	extinct?	[illegible]
'W' National Park	1,900	extinct?	[illegible]
Pô Forest Reserve	–	extinct	[illegible]
Nazinga Game Ranch	757	1 sighting	[illegible]

large carnivores are rare in the area – although lions are recorded as present – and no livestock losses are reported.

It is also possible that wild dogs still occur in the Pendjari National Park (6,037 km² including contiguous game reserves), but they are almost certainly declining if they are still present. Domestic dogs are very common inside the reserve, and spotted hyaenas are common. No livestock losses have been reported recently.

We have received no information from Djona and Atakora Hunting Zones, but these areas are contiguous with Pendjari and 'W', and are probably similarly affected.

Burkina Faso

Status ☹

Wild dogs may well be extinct in Burkina Faso. There was only one recent sighting recorded by the 1990 survey, and since then none of our correspondents has reported any sightings. Burkina Faso is one of the poorest countries in the world, and there are not sufficient funds to protect wildlife effectively – although wild dogs receive partial legal protection. People interviewed in the north of the country said that, unlike spotted hyaenas, wild dogs did not hunt cattle – but did attack people. They were, therefore, very hostile to wild dogs.

Distribution

Wild dogs' distribution in Burkina Faso is summarized in Table 3.1.

The most recent wild dog sighting in Burkina Faso was of three individuals, possibly vagrants, seen in 1985 in the Nazinga Game Ranch (940 km²) in the central south, bordering Ghana. Domestic dogs are officially excluded from this area, although visitors sometimes bring their pets. Spotted hyaenas – and all large carnivores – are rare.

It is possible that wild dogs still occur in the Arli National Park (1,143 km²), which borders the Pendjari National Park in Benin, where wild dogs might still exist; however, all carnivores are rare and poaching is unchecked.

We have no information from the part of the Parc 'W' complex in Burkina Faso (1,900 km²), but see the entry under Niger.

Wild dogs might still be present in Komoe Region, in the extreme south-west of Burkina Faso, although there are no recent sightings and all large carnivores are rare. Dogs might also still occur in the central-west part of the country, but, if present, they would be very rare. One dog was seen crossing the Bobo-Dioulasso – Ouagadougou road in the late 1970s.

Wild dogs are probably extirpated from Pô Park: surveys in 1972–74 yielded no evidence of their presence (Heisterberg 1977) and we have received no further sightings since then.

Table 3.2
A summary of wild dog distribution in Côte d'Ivoire. Côte d'Ivoire [illegible] wild dog population.

Site	Area (km²)	Abundance	[illegible]
Comoé National Park	11,500	extinct?	[illegible]
Marahoue National Park	1,038	extinct?	[illegible]

Côte d'Ivoire (Ivory Coast)

Status

☹

The outlook is poor. There are very few sightings of wild dogs, and most of the general public have never heard of them. Wild dogs' legal status is recorded as 'noxious'. If a population exists, it is unlikely to be substantial or survive for much longer.

Distribution

Wild dogs' distribution in Côte d'Ivoire is summarized in Table 3.2.

Dogs might still be present in Comoé National Park in the north of the country. The most recent sightings are from 1985 and 1987. They were considered very rare by 1988, and one correspondent believes that they are now extinct. Spotted hyaenas are very rare (*c.* 100) for the size of the park (11,500 km²), and lions are recorded to be present.

Wild dogs might still be present in the Marahoué National Park (1,038 km²), and northward to Mankono, although the most recent sightings are from the 1970s and there is no new information. They are now extinct in the south of the country, where local Baoulés hunters have not seen wild dogs ("les chiens avec beaucoup de couleurs mélangées") for 20 years.

Gambia

Status & Distribution

☹

The only report we have received from the Gambia is a pack sighted on the northern border with Sénégal in 1995. Wild dogs were also sighted recently on the Senegalese side of this border, suggesting that a small population of wild dogs uses the area.

Ghana

Status

☹

The outlook is poor – wild dogs may well be extinct in Ghana. There is growing appreciation of the need to conserve wildlife, but effective conservation has yet to take place. Poaching is rampant: most of the well-armed commercial poachers operating in southern Burkina Faso are Ghanaians. The heavy off-take of ungulates, combined with a traditional hostility towards all carnivores, has resulted in *Lycaon* becoming all but extinct in the country – although it does receive partial legal protection.

Distribution

Wild dogs' distribution in Ghana is summarized in Table 3.3. They might be present in the Bui National Park (2,100 km²), and the Digya National Park (3,478 km²), although there are no recent sightings from either.

Wild dogs have been reported by hunters in the area of the Kyabobo Range National Park, which is adjacent to the Fazo-Malfacassa National Park in neighbouring Togo. They would, however, be extremely rare.

Wild dogs are now extirpated from Mole National Park (4,840 km²), where the last sighting was in 1978, and absent from the Kalakpa Game Production Reserve, where they were eradicated around 1960.

Wild dogs have also been extirpated from the Gbele Game Production Reserve, where there have been no sightings for 20 years.

Guinea

Status & Distribution

☹

The outlook is poor, although there still seems to be a small population using parts of Guinea, and the species is listed as protected. Wild dogs occur in the Niokolo-

Table 3.3
A summary of wild dog distribution in Ghana. Ghana has no viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Bui National Park	2,100	extinct?	1987
Digya National Park	3,478	extinct?	1987
Mole National Park	4,840	extinct	1995
Kyabobo Range National Park	–	rare?	1994
Gbele Game Production Reserve	–	extinct	1995
Kalakpa Game Production Reserve	–	extinct	1987

Table 3.4
A summary of wild dog distribution in Guinea. Guinea has no viable wild dog population.

Site	Area (km^2)	Abundance	Date of estimate
Badiar National Park	380	uncommon	1996
Ndama Forest Reserve	500	1 sighting	1996
Sankarani River	n/a	2 sightings	1990/91

Koba National Park in Sénégal, which is adjacent to Badiar National Park in Guinea. Suitable habitat is available in Badiar, and along a corridor to the south joining the Ndama Fôret Classée to Hafite Niger National Park. There is one report of a pack of wild dogs' killing three cattle in the Ndama Fôret Classée in early 1996. In addition, a pack was photographed in eastern Guinea, along the Sankarani River near the border with Mali, in 1991.

Wild dogs' distribution in Guinea is summarized in Table 3.4.

Liberia

Status & Distribution ☹

There is no reference to *Lycaon* in the folklore, and the species has probably never occurred in the heavily forested areas such as Sapo National Park. Wild dogs might possibly have been present in the north at one time, but they are certainly absent now.

Mali

Status & Distribution ☹

The outlook is poor – wild dogs are now extremely rare in Mali, although they may once have been widespread. For example, they were seen in the Forêt Classée de la Faya in 1959. However, by the 1980s an observer making extensive ground surveys for primates in western Mali saw virtually no ungulates, and only one lion. The overall impression was one of a severely depleted and threatened wildlife population.

A population of wild dogs might remain in the south and west of the country, crossing to and from Sénégal and Guinea: a pack was sighted along the Baoule River in the south in 1988, another was photographed in the extreme east of Guinea in 1990, and two dogs were seen in south-eastern Sénégal close to the Mali border in 1997.

Niger

Status ☹

The outlook is poor – wild dogs are almost certainly extinct in Niger. In the 1960s there was a campaign to exterminate *Lycaon*. and, although the species is now legally protected, game guards shot them as recently as 1979. The country's wildlife has been seriously affected by drought over the last twenty years. Loss of prey, as well as persecution, means that wild dogs have very little chance of surviving.

Distribution

Wild dogs' distribution in Niger is summarized in Table 3.5. They are possibly still present in the cross-border Parc 'W' (3,340 km^2) although, as in Benin and Burkina Faso, there have been no recent sightings. There are some rumours of their presence, but others consider them extinct there.

Wild dogs might still be present, in very low numbers, in the extreme north and in the Sirba region. Although dogs were once common in this area, they were largely eradicated in the late 1960s and early 1970s.

In Aïr et Tenéré (the Air Mountains) wild dogs were extirpated in the 1950s.

Nigeria

Status ☹

The outlook is poor: there is probably no resident population of wild dogs in Nigeria although occasional vagrants may be sighted. Over most of Nigeria, the situation for large mammals is pretty hopeless, and carnivores are rare throughout. Wild dogs have declined as a result of persecution by hunters and drastic reductions in their prey as a result of poaching. Disease may also be a factor. Although wild dogs are totally protected under the law, in practice there is no effective protection.

Distribution

Wild dogs' distribution in Nigeria is summarized in Table 3.6.

Wild dogs might still be present, although in very low numbers, in Gashaka-Gumti National Park. However, any dogs here would be poorly protected and probably on the verge of extinction. There were no sightings in 1982–1986, but one unconfirmed report in 1988. This park is fairly close to Faro National Park in neighbouring Cameroun, where wild dogs are known to persist.

Similarly, there are very occasional reports of wild dogs in Chingurmi-Duguma National Park in the far north-east of Nigeria. The most recent sighting was in 1995. This park is close to the border with Tchad, and it is possible that the dogs are vagrants from there.

Wild dogs are probably extinct in the Kainji Lake National Park (5,300 km²) and contiguous Borgu Game Reserve – although they were common in Borgu until 1969. Game scouts reported a few sightings from the area in the 1980s, but there have been no sightings in the 1990s and poaching in the Park is extremely intense. It seems unlikely, therefore, that any wild dogs remain.

Wild dogs are extinct in Yankari National Park (2,244 km²), where the last sighting was in 1978 – although they were once common enough in Yankari for the authorities to consider control shooting. Researchers spent two years in Yankari between 1988–91 but saw no wild dogs. There was, however, one confirmed sighting of a single individual in 1991 in Lame Burra Game Reserve, some 200 km north-west of Yankari.

Wild dogs are now extinct in Sambisa Game Reserve (518 km²), where they were present until the early 1970s.

Sénégal

Status

The outlook for wild dogs in Sénégal is fair. Although sightings were very sparse in the 1980s, since 1990 numbers seem to have increased in and around Niokolo-Koba National Park (Sillero-Zubiri 1995; Sillero-Zubiri *et al.* 1997), indicating that this area represents the best hope for wild dogs in West Africa. As a result, the Canid Specialist Group, in collaboration with the Licaone Fund, has set up a new wild dog project in this area. Elsewhere in Sénégal, however, wild dogs have dwindled although there are occasional sightings (Sillero-Zubiri 1995).

Wild dogs receive only partial legal protection in Sénégal.

[illegible] wild dog distribution in Nigeria. Nigeria has no viable [illegible]

[illegible]	Area (km²)	Abundance	[illegible]
[illegible]	5,300	extinct	[illegible]
[illegible]	–	vagrant?	[illegible]
[illegible]	–	extinct?	[illegible]
[illegible]	2,244	extinct	[illegible]
[illegible]	–	1 sighting	[illegible]
[illegible]	518	extinct	[illegible]

Distribution

Wild dogs' distribution in Sénégal is summarized in Table 3.7 and in Figure 3.2.

Wild dogs are present in and around Niokolo-Koba National Park (9,130 km²), where the frequency of sightings, both by park staff and by tourists, has increased since 1990 (Sillero-Zubiri 1995). The species was once thought to be "very common" in Niokolo-Koba, but sightings were very infrequent (*c.* 1 per year) throughout the 1980s (Sillero-Zubiri 1995). Reasons for this decline, and the subsequent recovery (to 8–9 sightings per year in the early 1990s) are not known, although it is possible that the apparent variation might reflect varying numbers of park staff and tourists using the Park. The Park is composed of soudano-guinean savannah and dry woodland, and is bordered by a large buffer area, and the Falemé hunting area: together these make up a protected area of nearly 25,000 km² which borders the Badiar National Park in Guinea (380 km²). Wild dogs have been sighted in all parts of the protected area on the Sénégal side of the border (Sillero-Zubiri 1995). The population is currently believed to stand at 50–100 animals, and is being monitored by CSG in association with the Licaone Fund. Spotted hyaenas, lions, leopards and side-striped jackals are all present in the Park, although lion density is low (0.5–1.5/100 km², Sillero-Zubiri *et al.* 1997). Domestic dogs are absent from the Park itself, but are common in the unprotected areas outside. Livestock losses are rare (much less common than losses to lions and hyaenas), but public attitudes towards wild dogs remain negative, mainly because people are afraid of them (Sillero-Zubiri 1995). An additional threat to wild dogs in Niokolo-Koba is a new tarmac road through the Park: road traffic accidents are a major cause of wild dog mortality elsewhere in Africa (Chapter 4).

Wild dogs were present elsewhere in the Tambacounda and Kolda regions in the 1980s, but may now be absent. They are probably close to extinction in all other parts of Sénégal, although there are occasional sightings. A pack was sighted near Delta de Seloun, north of the border with the Gambia, in 1995.

Sierra Leone

Status & Distribution

Wild dogs are almost certainly extinct in Sierra Leone. There were reports from the northern part of the country in the 1980s, but these were all second-hand and must be regarded as tentative. The local people in the northern savannah-woodland areas do have names for wild dogs, suggesting that they were once present there. There is a small chance of a few remaining in what is now the proposed Outamba-Kilimi National Park, although staff saw no dogs or spoor in the period 1980–1984 and the local conservation body considers them extinct there. However, there is one unconfirmed report from the area, suggesting that a few might still be present.

Togo

Status

The outlook is uncertain, but poor: wild dogs are probably extinct in Togo. Although few data were received, like all the western African states, Togo has severely depleted wildlife. Wild dogs are certainly extinct in the north of the country, and are likely to be extirpated from the whole of Togo. They do, however, receive partial legal protection.

Distribution

Wild dogs may still be present in the Fazao Malfacassa Game Reserve (2,169 km²) although, if so, they are very rare. There are rumours of groups of 2–5 wild dogs on the Mazala, Kpeya, and Kibidi mountain-sides, where they are thought to take refuge in caves or holes. Heavy poaching on the lower grasslands is thought to have caused their decline.

Table 3.7
A summary of wild dog distribution in Sénégal. Sénégal has a potentially viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Niokolo-Koba National Park	9,130	uncommon	1997
Falemé Hunting Area	13,360	uncommon	1997
Ferlo-Nord Faunal Reserve	49,700	extinct?	1995
Ferlo-Sud Faunal Reserve	63,400	extinct?	1995
Delta de Seloun	n/a	1 sighting	1995

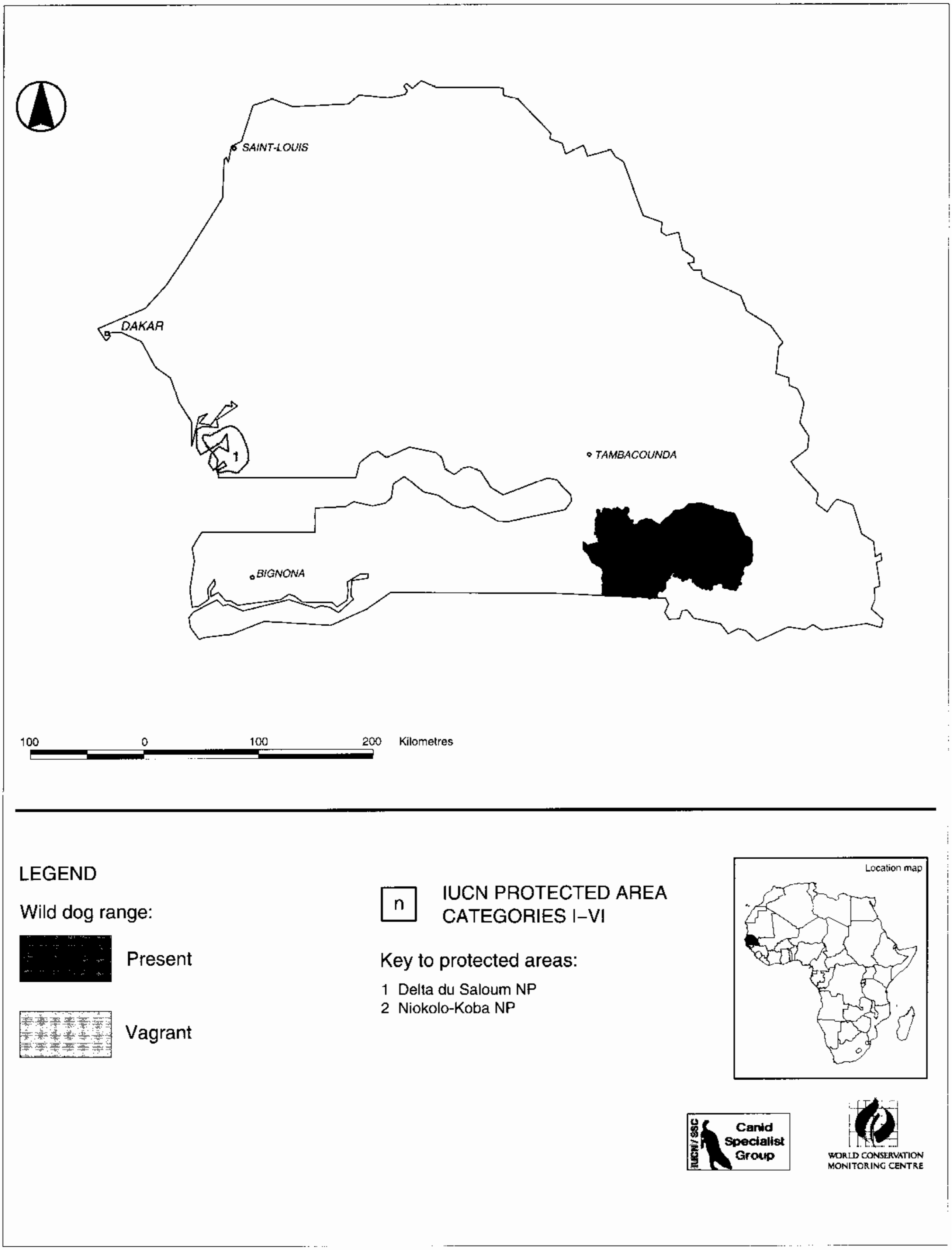


Figure 3.2. Wild dog distribution in Sénégal.

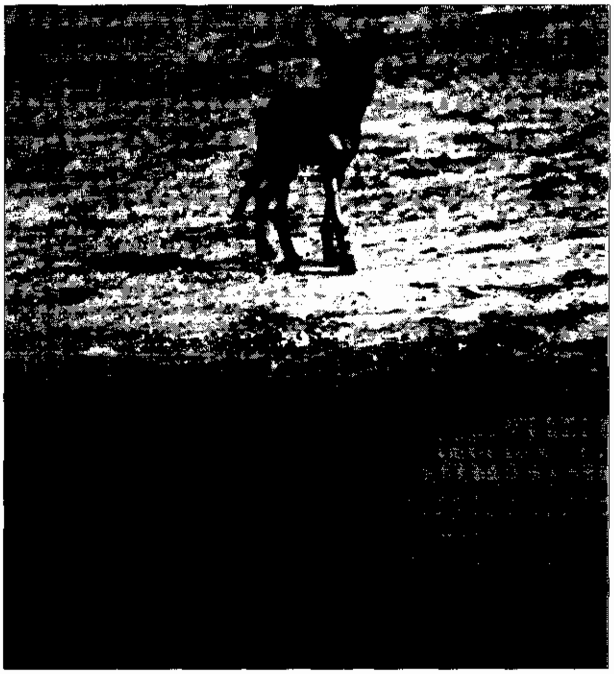
Distribution of Wild Dogs in Central Africa

Wild dogs are doing rather poorly in most of central Africa. A potentially viable population remains in Cameroun, with smaller populations in the Central African Republic and Tchad (Figure 3.3). These populations, especially the one in Cameroun, have a very high conservation priority. We have few quantitative data on these populations; further surveys are needed to assess their size and status. Wild dogs are extinct in Gabon, the Democratic Republic of Congo, and in the Republic of Congo.

Cameroun

Status

The outlook is uncertain. Wild dogs still occur in three parks in the north of Cameroun, and the country's population may be viable, but urgent conservation action is required. Apart from the Central African Republic and southern Tchad, northern Cameroun is the only possible refuge for wild dogs remaining in central Africa. Conservation efforts in Cameroun have so far focused on the rainforest reserves in the south of the country, largely ignoring the savannas to the north. However, a new biodiversity project in Cameroun may help to redress this balance. Meanwhile, hostility towards wild dogs continues around the reserves. Hunters believe them to be a "plague which must be killed until the last", and one was found dead in Faro National Park after it had been severely wounded by shepherds. Government records show that professional hunters killed 25 wild dogs in northern Cameroun in 1991/2, and the government quota for the season December 1995–May 1996 was 65 dogs. This indicates that wild dogs are poorly protected in Cameroun,



although we have no official data on their legal status.

Distribution

Wild dogs' distribution in Cameroun is summarized in Table 3.8 and Figure 3.4.

Wild dogs are still sighted regularly in and around Faro National Park (3,410 km²), where at least four packs are present. The habitat is wooded and bushed grassland, and both domestic dogs and spotted hyaenas are common. Local people are hostile towards wild dogs, which sometimes hunt goats and sheep.

Wild dogs are also present in and around the nearby Bénoué National Park (1,780 km²), although they are probably less common here than in Faro. Nevertheless, in 1989 they were sighted several times in the lands between the two parks, indicating that the population is probably contiguous. The habitat in Bénoué is wooded

Table 3.8
A summary of wild dog distribution in Cameroun. Cameroun has a potentially viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Benoue National Park	1,781	uncommon	1995
Bouba-Njida National Park	1,940	uncommon	1993
Faro National Park	3,410	common	1995
Kala-Naloué National Park	–	absent	1987
Waza National Park	1,700	absent	1987
Kimbi River Fauna Reserve		absent	1987

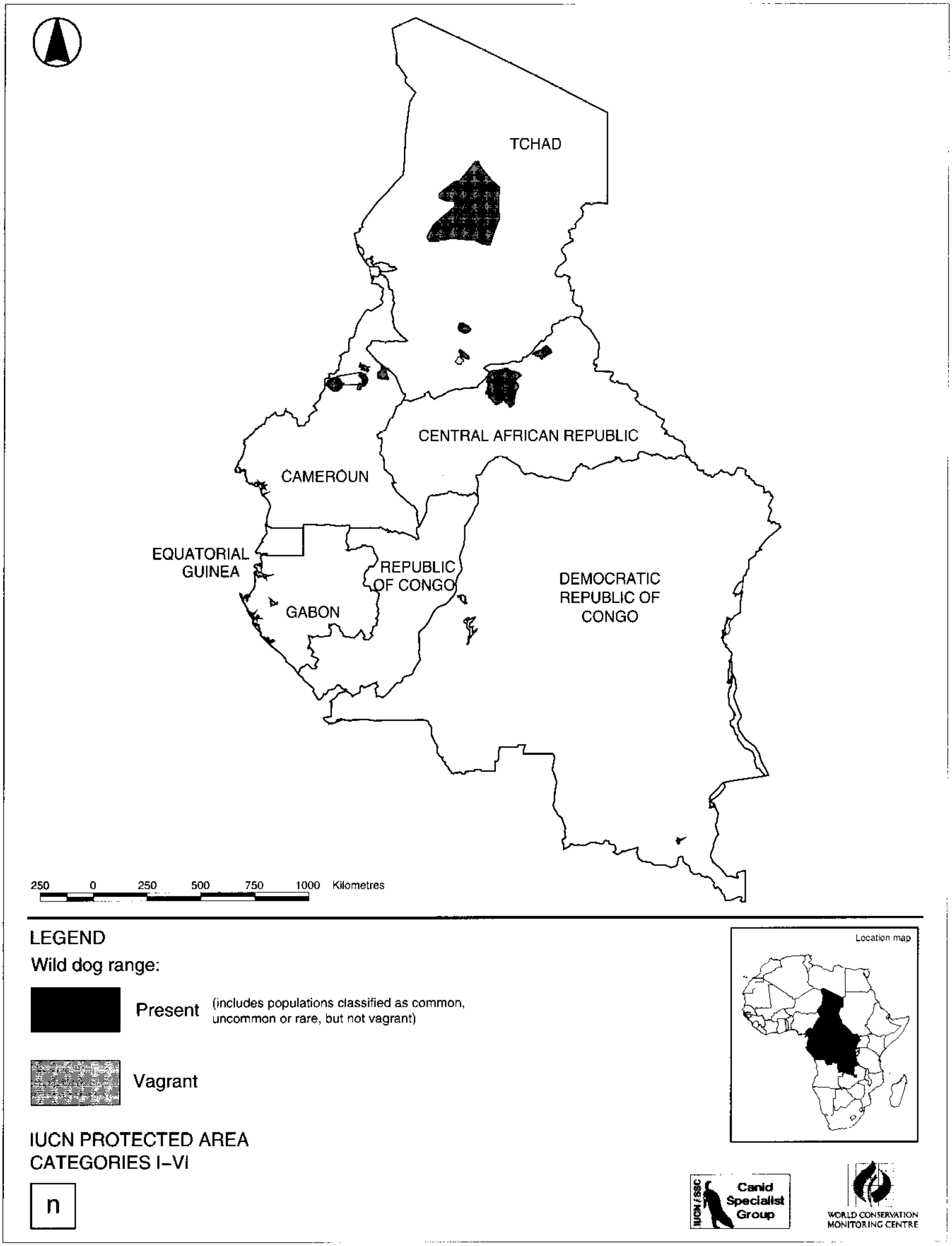


Figure 3.3. Wild dog distribution in Central Africa.

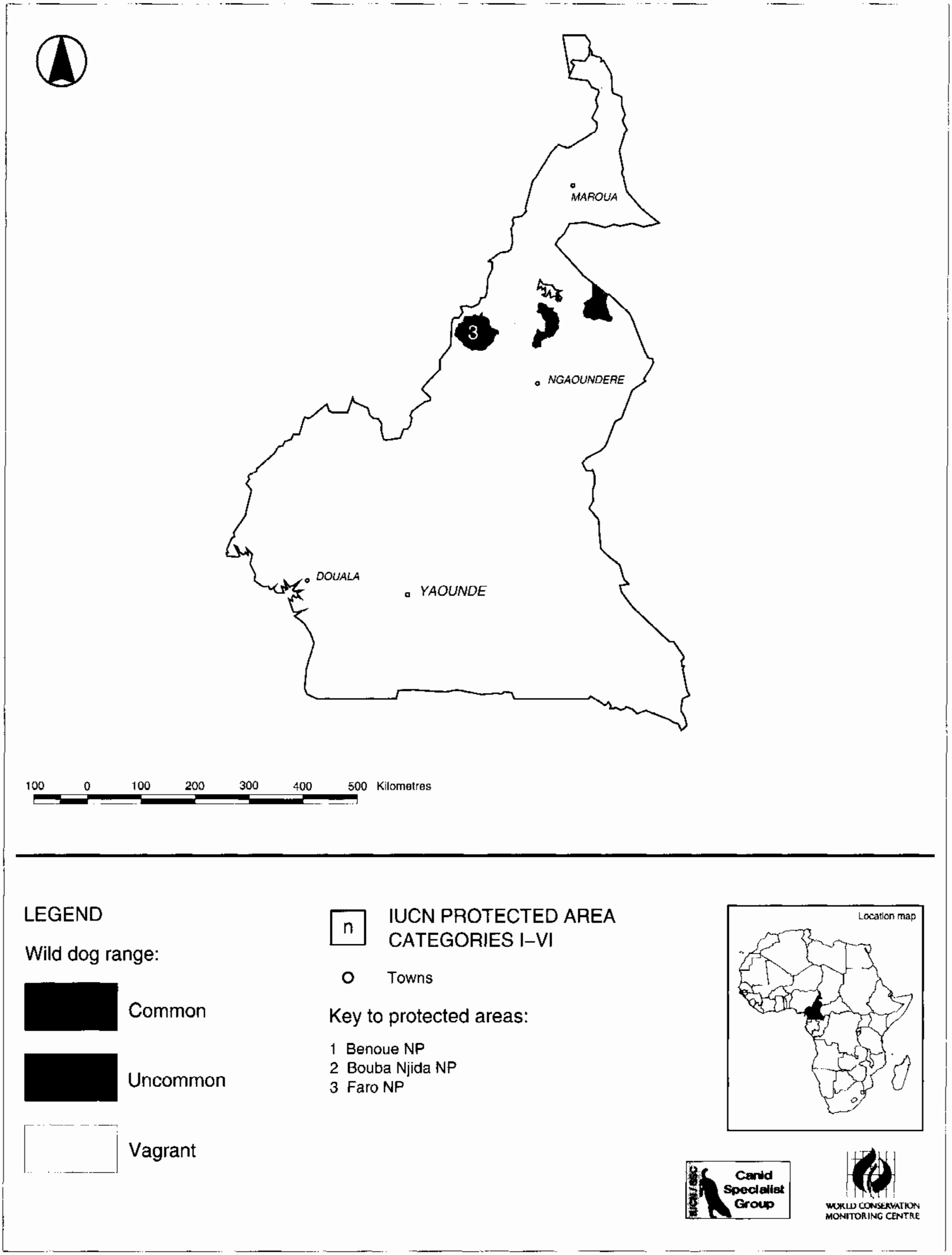


Figure 3.4. Wild dog distribution in Cameroun.

grassland; domestic dogs are absent but lions are present and spotted hyaenas are common.

Wild dogs are present in and around the Bouba-Ndjida National Park (1,940 km²) where, in 1993, they were very often sighted near the Park headquarters. The groups reported from Bouba-Ndjida are fairly small (range 4–6 individuals) and the total population size is not known. The habitat is wooded grassland; domestic dogs are common, but spotted hyaenas are rare. There have been no livestock losses since the early 1980s, but the public attitude is still very negative.

Wild dogs are absent from the Kala-Naloué National Park, Waza National Park, and Kimbi River Faunal Reserve; they may never have occurred in these areas.

Central African Republic (C.A.R.) 😐

Status

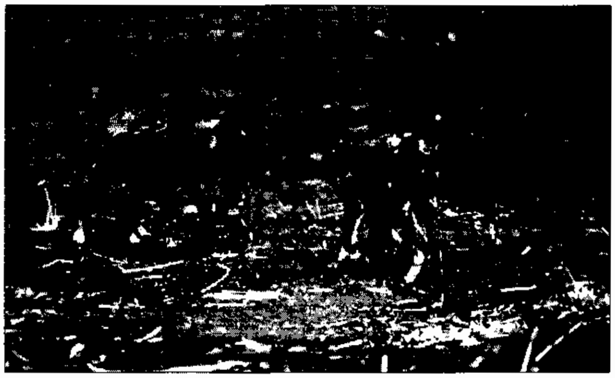
The outlook is uncertain. Although present in the country, wild dogs urgently need support. This sub-population is not far from the one in Cameroun, and, together, they might represent a potentially secure Central African reservoir. However, rabies was confirmed in one population in 1984. Wild dogs receive total legal protection in C.A.R.

Distribution

Wild dogs' distribution in C.A.R. is summarized in Table 3.9 and Figure 3.5.

Wild dogs are present, but very rare, in the Manovo-Gounda-St. Floris National Park (32,400 km²). Eight sightings were reported between 1979 and 1986, including one of a pack of 23, and Wildlife Conservation Society staff reported that they were still sighted in northern C.A.R. in 1992. The Park consists of savannah woodland, floodplains, and salt pans. Lions are present, but we have no information on hyaenas or domestic dogs. However, at least one wild dog is known to have died from rabies in this park in 1984.

Wild dogs were believed to be fairly common in the Bamingui-Bangoran National Park (32,000 km²) and neighbouring reserves in the 1980s. However the chief game warden saw just one pack in two years in



1988–90, and there were no other reports of wild dogs in this period, suggesting that the pack might have been vagrant. The habitat is bushed and wooded grassland. Domestic dogs are rare, lions are present and spotted hyaenas are common. There have been no confirmed livestock losses, but Bororo herdsmen, who frequently enter the Park illegally, are hostile.

Republic of Congo

Status & Distribution ☹

Wild dogs are extinct in the Republic of Congo, with no confirmed sightings since the 1970s. Interviews with local people suggest that *Lycaon* may once have occurred in and around Odzala National Park many years ago, but they are now extinct. Most of the dogs apparently lived outside protected areas, where they took sheep and goats and were therefore extremely unpopular with local people. Although wild dogs are extinct in Congo they are, nevertheless, offered total legal protection there.

Democratic Republic of Congo (former Zaïre)

Status ☹

The outlook is poor: wild dogs are probably extinct in the Democratic Republic of Congo, although the country once supported healthy populations.

Any remaining wild dogs would be given partial

Table 3.9
A summary of wild dog distribution in the Central African Republic. The Central African Republic has a potentially viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Bamingui – Bangoran Complex	32,000	rare	1995
Manovo Gounda – St Floris Complex	32,400	rare	1993

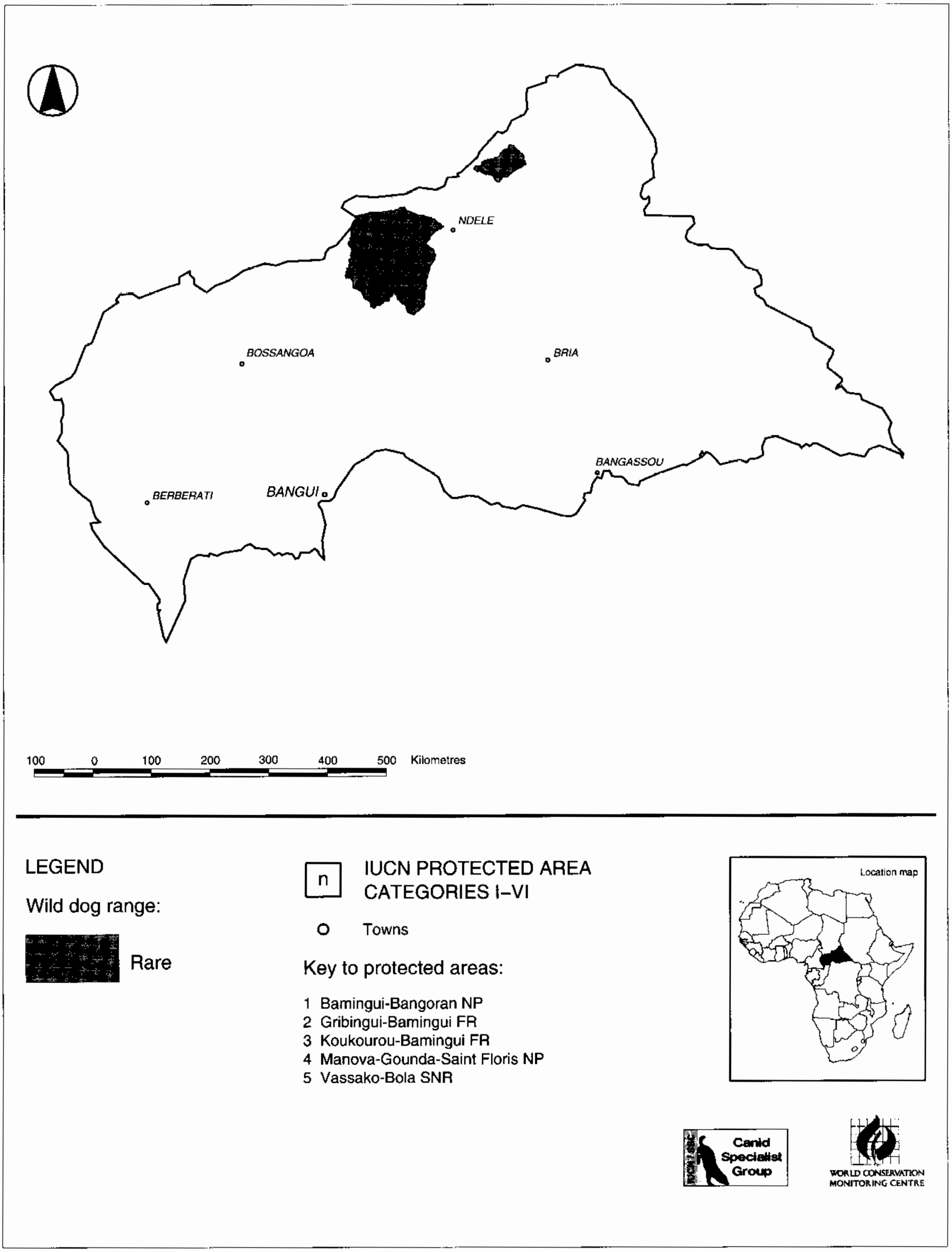


Figure 3.5. Wild dog distribution in the Central African Republic.

Table 3.10
A summary of wild dog distribution in the Democratic Republic of Congo (former Zaire). The Democratic Republic of Congo has no viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Garamba National Park	15,125	extinct	1995
Upembe National Park	11,700	vagrant	1986
Virunga National Park	7,506	extinct	1987

legal protection.

Distribution

Wild dogs' distribution in the Democratic Republic of Congo is summarized in Table 3.10.

The most recent confirmed sighting of wild dogs in the Democratic Republic of Congo was of two individuals seen in the Upembe National Park (11,700 km²) in 1986. This was the first sighting in the area in over 15 years.

Wild dogs are probably now absent from Ango area, south of the Central African Republic, where there have been no sightings for over ten years. They are also absent from the Garamba National Park (4,900 km²) where they may never have been common. They are extinct in the Parc National des Virungas (7,506 km²), and the adjacent Queen Elizabeth National Park in Uganda, where they did occur some 30 years ago.

Equatorial Guinea

Status & Distribution

The island of Bioko (Fernando Po) and Rio Muni are tropical forest and there are no records of *Lycaon* there.

Gabon

Status & Distribution

Wild dogs are probably now extinct. A respondent from the Petit Loango National Reserve said that dogs "used to exist in the great plains bordering the sea" but have not been seen for years. Nevertheless, there are occasional rumours of their presence.

Tchad (Chad)

Status

The outlook is uncertain. Southern Tchad might form an important passageway between sub-populations in Cameroun and the Central African Republic, possibly forming a larger, more viable, population. However, we have no recent reports of wild dogs from Tchad, and no information on the degree of legal protection afforded to wild dogs there.

Distribution

Wild dogs' distribution in Tchad is summarized in Table 3.11 and Figure 3.6.

In the 1980s, wild dogs were considered rare in the Ouadi Rimé-Ouadi Achim Game Reserve (80,000 km²) where they were sighted in well-wooded wadis and adjacent dunes. We have, however, no recent records.

Wild dogs might still be present in Zakouma

Table 3.11
A summary of wild dog distribution in Tchad. Tchad has a potentially viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Manda National Park	1,100	uncommon	1987
Zakouma National Park	3,156	extinct?	1987
Oudai Rimé – Ouadi Achim GR	80,000	rare	1987
Siniaka-Minim Game Reserve	–	uncommon	1987

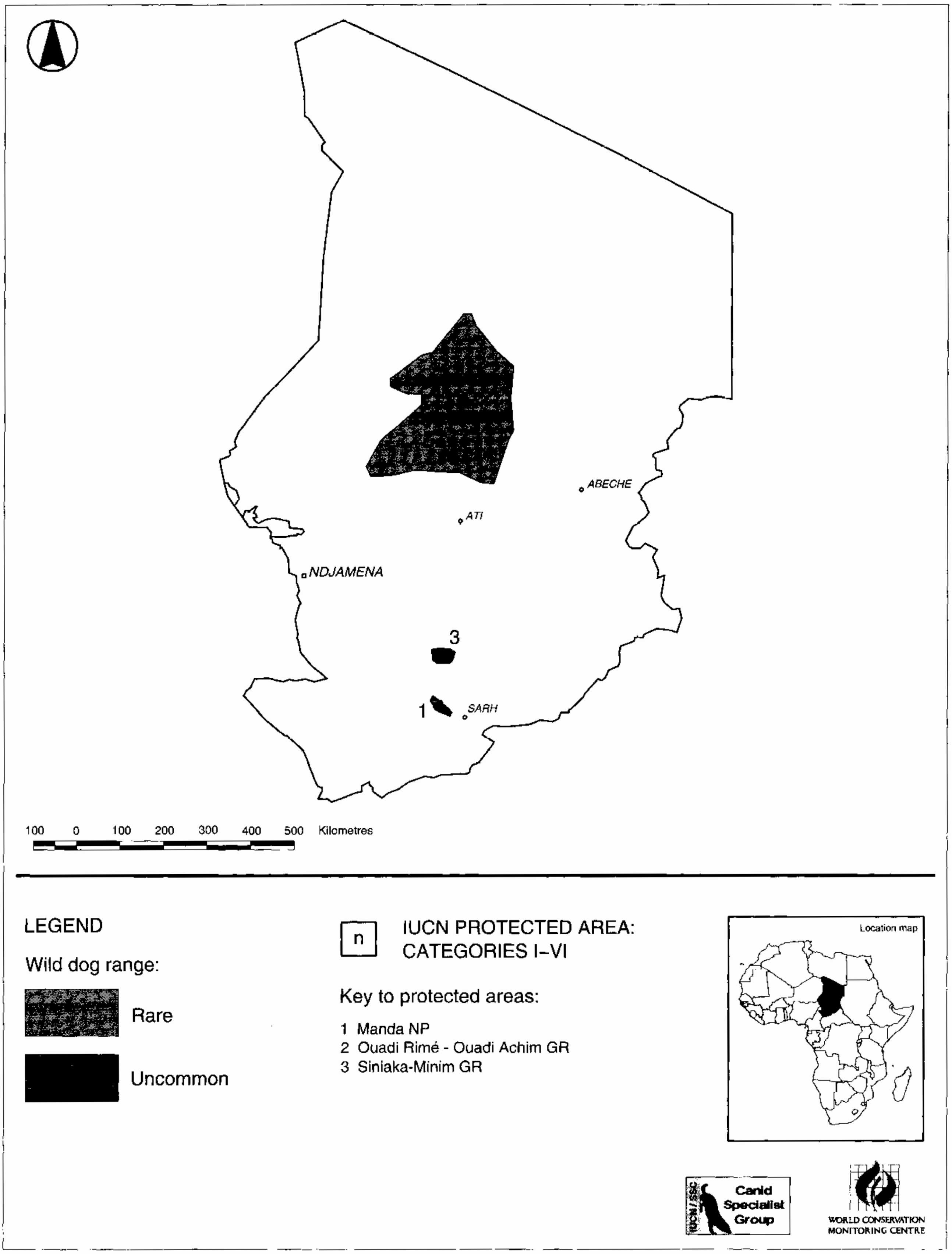


Figure 3.6. Wild dog distribution in Tchad.

National Park and the Bahr Salamat Game Reserve that encircles it, although one respondent to the 1990 survey considered them extinct there.

Wild dogs occurred in reasonable numbers in Manda National Park (1,100 km²) and Siniaka-Minim Game Reserve in the 1980s, although we have no recent records.

Distribution of wild dogs in East Africa

Wild dogs' distribution in East Africa is now rather patchy. They have been eradicated from many of the areas where they were once common, such as Uganda and much of Kenya, but a stronghold remains in southern Tanzania (Figure 3.7). This population, which occupies the Selous Game Reserve and Mikumi National Park, is one of the largest remaining in Africa. The conservation value of this population cannot be stressed too highly: it may be the only long-term viable wild dog population left in East Africa. Another population exists in northern Tanzania, on the Maasai steppe. A far smaller concentration of wild dogs exists in southern Ethiopia, which may spread into southern Sudan, northern Kenya and even northern Uganda – more surveys are needed to assess the status of this population. There seem to be very few wild dogs left in other parts of Sudan. A few may still live in southern Somalia, but it seems unlikely that they will persist. Wild dogs are almost certainly extinct in Rwanda, Burundi and Eritrea.

Burundi

Status & Distribution

Wild dogs were considered extinct in Burundi by 1976.

Most protected areas are too small to support wild dogs, and we received no data from the larger protected areas of Kibira and Ruvubu.

Djibouti

Status & Distribution

We have no information concerning wild dogs in Djibouti. However, only one protected area exists – the Fôret du Day, a forested area isolated within desert – which is unlikely to support wild dogs.

Eritrea

Status & Distribution

Wild dogs were reported from some remote areas of Eritrea in the early part of this century, including the area that is now the Nafka Wildlife Reserve (Yalden *et al.* 1980). However, we have no recent records (Malcolm & Sillero-Zubiri in press), and it seems likely that wild dogs are extinct in Eritrea.

Ethiopia

Status

Ethiopia has been endeavouring to strengthen its network of protected areas and, if this continues, wild dogs' position may improve. Nevertheless, they are everywhere uncommon. Early records give the impression that wild dogs may never have been widespread (Yalden *et al.* 1980), yet most respondents to the 1990 survey reported that wild dogs were less common than they had been in the past. Indeed, the species has been all but extirpated in three national parks. A recent survey suggests that most hope exists in the south (Malcolm & Sillero-Zubiri in press) and more extensive surveys are needed in that region.

Wild dogs receive total legal protection in Ethiopia.

Distribution

Wild dogs' distribution in Ethiopia is summarized in Table 3.12 and Figure 3.8. They are recorded occasionally in and around the Gambela National Park (4,800 km²), although the last confirmed sighting was in 1987 (Malcolm & Sillero-Zubiri in press). The habitat is wooded grassland. Domestic dogs and spotted hyaenas are common, and lions are present. Pastoralists use the park constantly and livestock losses are reported; as a result, public attitudes are hostile. A pack was seen to the south of the park, in Ilubabor Province, in the late 1980s (Malcolm & Sillero-Zubiri in press).

Wild dogs are sighted fairly frequently in the Omo-Mago National Parks complex (6,031 km²). The most

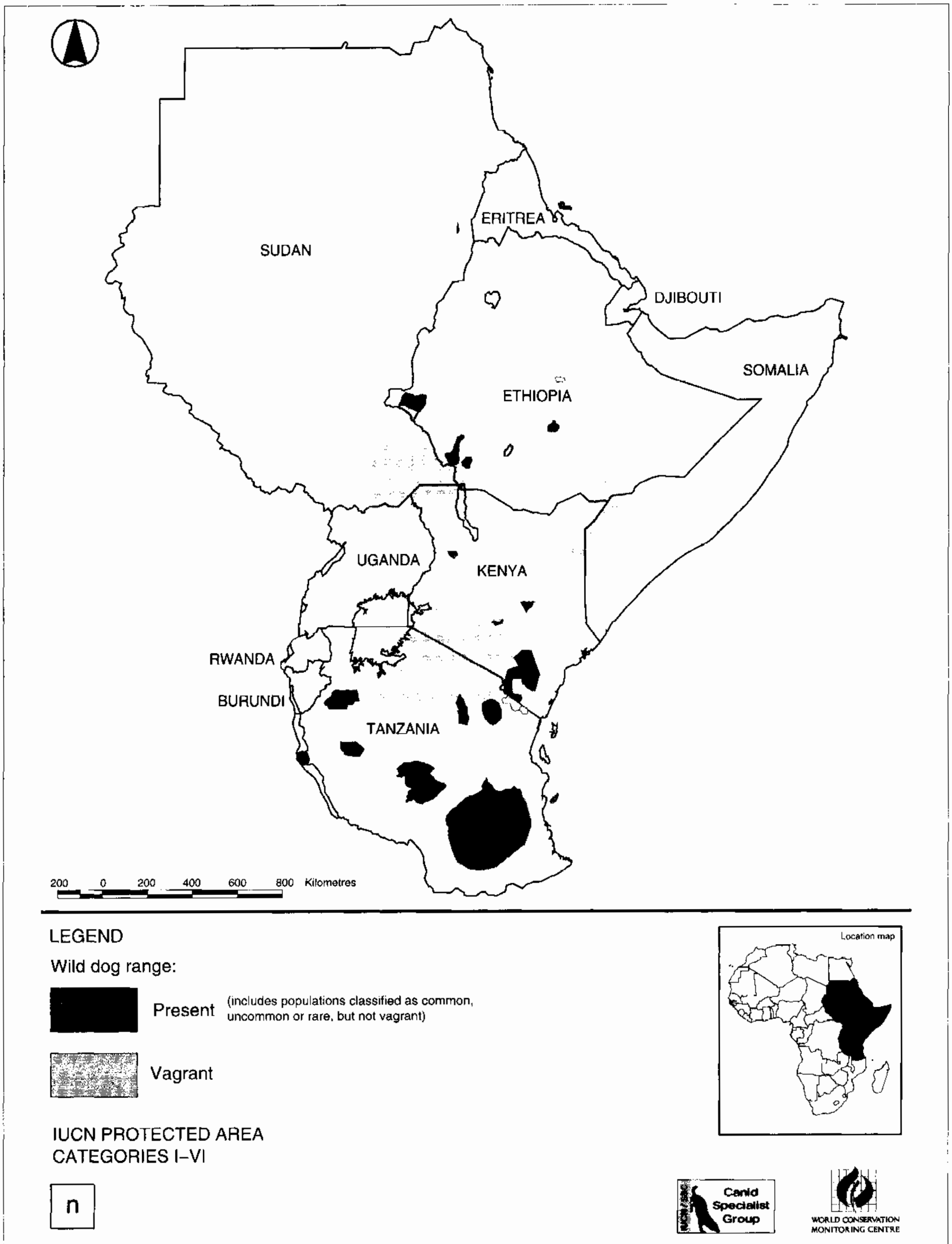


Figure 3.7. Wild dog distribution in East Africa.

Table 3.12
A summary of wild dog distribution in Ethiopia. Ethiopia has a potentially viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Abijatta-Shalla Lakes National Park	400	extinct	1992
Awash National Park	750	vagrant	1990
Haenna-Bale Mountains National Park	2470	rare	1995
Gambela National Park	5,060	rare	1987
Mago National Park	2,200	common	1992
Nechisar National Park	500	vagrant	1992
Omo National Park	3,000	rare	1995
Simien Mountains National Park	180	absent	1987
Yabello Sanctuary	2,500	uncommon	1996
Yangudi Rasa National Park	4,700	extinct	1987
South of Jigjiga	n/a	uncommon	1995
Sof Omar	n/a	1 sighting	1994
Filtu	n/a	1 sighting	1995
South-East of Bale Province	n/a	uncommon	1995
Mehal Meda, Shoa	n/a	uncommon	1994

recent sighting of wild dogs reported from Omo was in early 1995 (Malcolm & Sillero-Zubiri in press). In 1992–3 the Wardens of the two parks estimated that there were one or two packs in Omo, and up to five packs in Mago seen hunting in different parts of the park. These animals were seen repeatedly. On one occasion a pack of five dogs was seen feeding from the carcass of a female Defassa waterbuck in Mago. The habitat is short grassland, bushland, and wooded grassland. Domestic dogs are rare, but lions are present and spotted hyaenas are common. Pastoralists make frequent incursions into the parks, blame livestock losses on wild dogs, and are reported to shoot them.

Wild dogs are recorded occasionally in the Bale Mountains National Park. They were seen from time to time in the Harenna Forest (1,500–3,000m ASL) in the south of the park during the period 1984–90, and a pack was reported by local people in the area in 1994 (Malcolm & Sillero-Zubiri in press). One wild dog was found dead on the Sanetti Plateau (4,000m ASL) in 1995, and another was found in Harenna in 1997. The habitat is afroalpine grassland grading into montane forest and thornscrub, with most wild dog sightings in the forested areas. Lions are sighted occasionally, and both domestic dogs and spotted hyaenas are common. Rabies is widespread. All wildlife is officially protected in the park, but protection is nominal – any animal molesting livestock would be killed. According to one source, wild dogs were once much more common in the park. A pack was also sighted near Sof Omar, some 65 km east of the Bale Mountains National Park, in early 1994 (Malcolm & Sillero-Zubiri in press).

Wild dogs are sighted occasionally in Awash National Park; biologists working in Awash with the Ethiopian Wildlife Conservation Organization saw a pack once in three years (Malcolm & Sillero-Zubiri in press). Occasional sightings also come from Nechisar National Park, most recently in 1992 (Malcolm & Sillero-Zubiri in press). A group of 3 wild dogs was seen in the Yabello Sanctuary in 1996. Wild dogs are almost certainly absent from Simien Mountains National Park, Abijata-Shalla Lakes National Park and Yangudi Rasa National Park, although they have occurred in some of these areas in the past.

Wild dogs have also been seen outside of protected areas. Reports come from dry scrub country south of Jigjiga in the east and Filtu in the south (Malcolm & Sillero-Zubiri in press). Local people around Filtu said that wild dogs were common over a large tract of country between the Ganale and Wabe Shabelle rivers. Perhaps most interesting are reports from Mehal Meda, an intensively cultivated area some 125 km north of Awash National Park. Local people described wild dogs reliably and told visiting biologists that they lived in the ravines which dissect this area of the central plateau, hunting sheep and goats (Malcolm & Sillero-Zubiri in press).

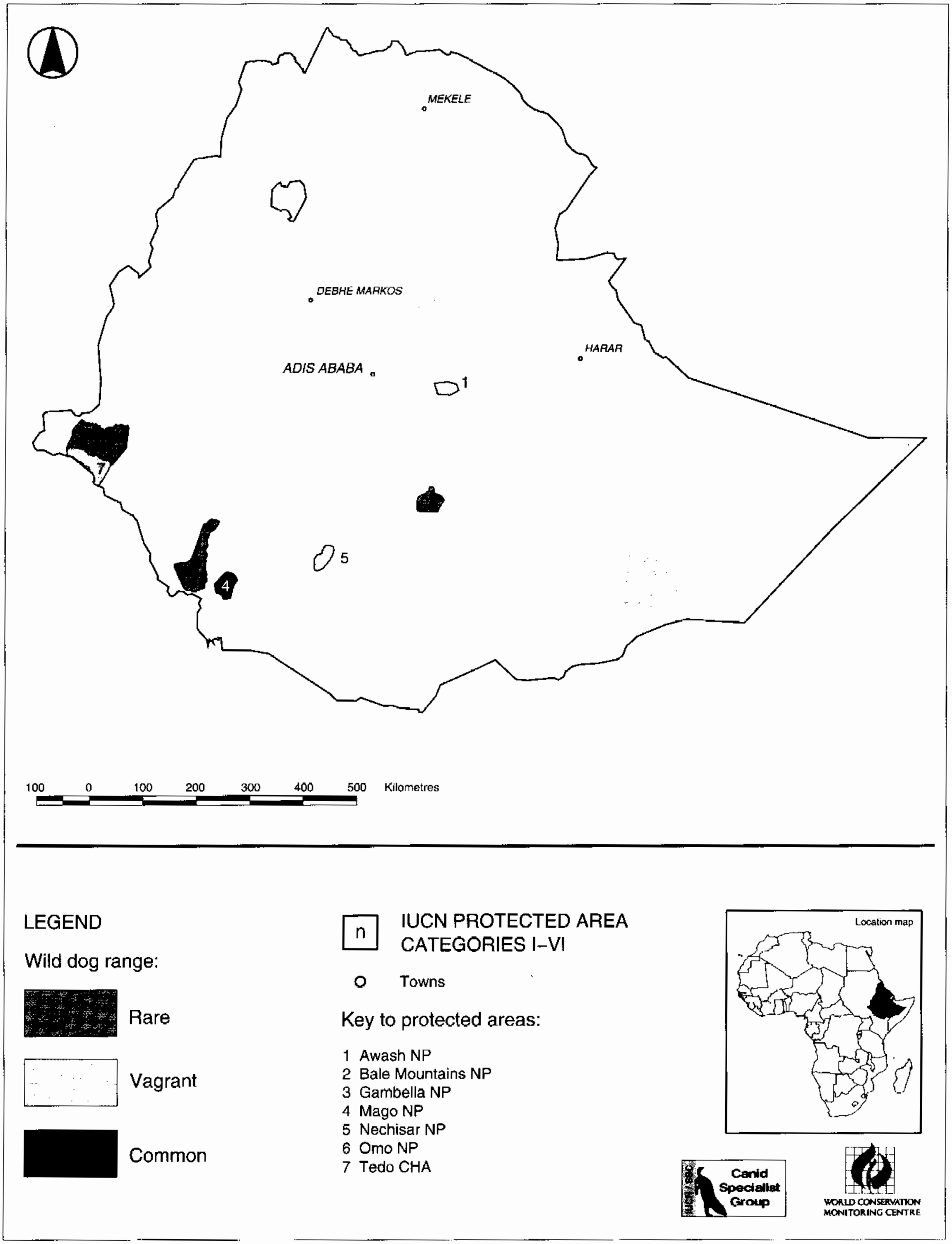


Figure 3.8. Wild dog distribution in Ethiopia.

Kenya

Status

The outlook for wild dogs in Kenya, while not hopeless, is not good. The species is reasonably widespread but there are no strongholds with high population density, and many sightings come from outside protected areas. The population has declined, and become locally extinct in some areas, since the 1990 postal survey (Alexander & Kat 1992; Jennings 1992). More recent surveys suggest that as few as fifteen packs may be present in the whole country. In livestock areas, wild dogs generally are not tolerated and there are fairly frequent reports of their being shot. Increased ranching and cultivation mean that wild dog populations are likely to become increasingly fragmented. Whether wild dogs can persist in Kenya will depend upon how well protected areas can be managed. However, wild dogs receive only partial legal protection in Kenya.

Distribution

Wild dogs' distribution in Kenya is summarized in Table 3.13 and Figure 3.9.

Wild dogs are sighted occasionally in the South Turkana National Reserve (1,000 km²) and in the surrounding Turkana District. Domestic dogs are rare in the District, but spotted hyaenas are abundant. Officially protected, wild dogs prey on livestock, and pastoralists would like to see them eliminated. Wild dogs are not present in the nearby Nasolot National Reserve, but have been reported from the surrounding area (Alexander & Kat 1992).

Occasional sightings of wild dogs come from the extreme north west of Kenya, close to the Sudan border (Alexander & Kat 1992). The most recent sighting was near Lokichokio, in 1992. These records are hopeful, because wild dogs have also been seen recently in nearby areas of Sudan and northern Uganda.

Wild dogs are also reported to be present in the north east of Kenya, around Mandera and Wajir, and also near

Table 3.13
A summary of wild dog distribution in Kenya. Kenya has a potentially viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Aberdare National Park	2,000	extinct	1987
Amboseli National Park	365	extinct	1993
Lake Nakuru National Park	57	extinct	1992
Mount Kenya National Park	1,367	extinct	1987
Nairobi National Park	117	extinct	1987
Tsavo East National Park	20,574	uncommon	1992
Tsavo West National Park		rare	1992
Masai Mara National Reserve	1,672	extinct	1991
Buffalo Springs National Reserve	339	extinct	1992
Dodori National Reserve		uncommon	1991
Kora National Reserve	1,787	rare	1992
Nasolot National Reserve	4,000	extinct	1987
Samburu National Reserve	225	vagrant	1991
South Turkana National Reserve	1,000	rare	1987
Tana River National Reserve	169	vagrant	1993
Kajiado district	n/a	uncommon	1992
Timau, Laikipia	n/a	uncommon	1996
North-West Kenya	n/a	uncommon	1992
Garsen	n/a	1 sighting	1993
Lokichokio	n/a	1 sighting	1992
Manda Island	n/a	1 sighting	1991
Wamba	n/a	1 sighting	1993

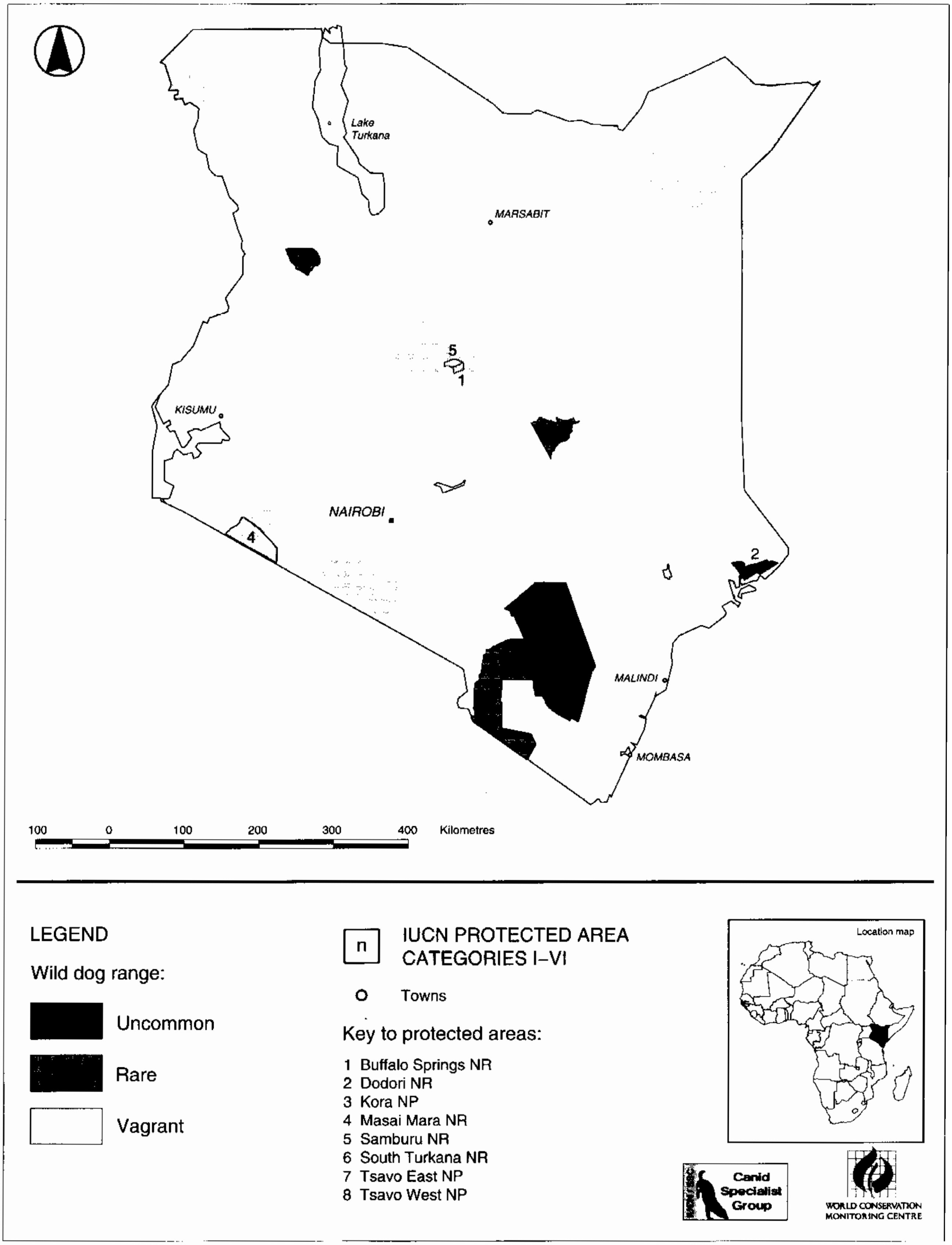


Figure 3.9. Wild dog distribution in Kenya.

Marsabit (Alexander & Kat 1992; Jennings 1992). However, these areas are little visited and information is sparse.

Wild dogs are now very rarely seen in the Samburu National Reserve (225 km²); the most recent sighting was in 1991 (Jennings 1992). Domestic dogs are excluded, and spotted hyaenas are rare to common. Pastoralists are officially excluded, but the Reserve is too small to support wild dogs alone, and the attitudes outside are hostile. A pack of 21 dogs was seen east of Wamba in 1993, and another was sighted between Wamba and Samburu Game Reserve in 1994 (Maggi 1995).

Wild dogs are still present elsewhere in the Samburu District, but are apparently less common than in the 1980s. Village elders interviewed near Maralal in 1993 reported that wild dogs were common in the area, often taking goats, and that a pack was denning nearby. In the 1980s wild dogs were most often seen in Lodokejek, Angata Nanyuki, Lesiriken, Baragoi, South Horr, Kowop, Barsaloi, and Ngilai. Dogs were also seen occasionally in Laikipia in 1993, and in 1996 four females were taken into captivity by the Kenya Wildlife Service after they had killed a number of merino sheep near Timau. Domestic dogs are ubiquitous in these areas, and spotted hyaenas are common. Some 40,000 pastoralists inhabit all but 3,000 km² of Forest Reserves and Samburu National Reserve; many livestock losses are attributed to wild dogs.

Wild dogs are now absent from the Buffalo Springs National Reserve (339 km²), where they have not been seen since the mid-1980s (Alexander & Kat 1992). They probably still use the Kora National Reserve (1,787 km²), although there are no recent records (Alexander & Kat 1992). Wild dogs were observed there twice during an extensive expedition in 1982–3. They are now absent from Mount Kenya, although they were once present there, and were seen regularly at Tree Tops in 1950s. Wild dogs are probably now absent from Lake Nakuru National Park (57 km²). They were very rare here in the 1980s and erection of a game proof fence around the park as part of Rhino Rescue operations will now prevent dogs from entering Nakuru.

Wild dogs have not been sighted recently in the Nairobi National Park (117 km²) since subdivision and fencing of land on neighbouring Kitengela and Athi Kapiti plains, although they were sighted twice in 1986–7 close to the park boundary. Some livestock losses occur, and wild dogs are shot and snared in this area.

Wild dogs are now rare in the area of the Masai Mara National Reserve (1,672 km²), from which they disappeared in 1991 (Alexander *et al.* 1993; Scott 1991), when rabies was confirmed in one pack (Appendix 1). After a serious decline in the Mara during the 1970s (Scott 1980), in 1986 one pack settled in the Aitong District, to the north of the Reserve, and bred successfully for three years. A second group immigrated to Aitong from Serengeti in 1988. The population in this area disappeared, apparently following disease outbreaks, between 1989 and 1991 (Alexander & Kat 1992), although wild dogs are still seen occasionally. Lions and hyaenas occur at high densities in the Mara. Domestic dogs are excluded from the Mara itself, but are common in Aitong district where they are known to carry rabies and distemper (Alexander & Appel 1994; Alexander *et al.* 1993).

The last wild dogs sighted in Buffalo Springs National Park in northern Kenya in the 1980s.

Wild dogs are no longer seen in Amboseli National Park, and local Maasai have noticed how rare dogs have become in the area. They are still seen occasionally in Kajiado district, and might be locally common around Elangata Wuas, to the west of Kajiado, where a wild dog study has been proposed. Dogs were sighted occasionally on the Rift Valley floor close to Mount Susua in the 1980s, and are apparently still present in this area (Alexander & Kat 1992).

Wild dogs are reasonably common in parts of Tsavo National Park (20,000 km² including both Tsavo East and Tsavo West) from where most Kenyan wild dog sightings come. They were sighted repeatedly in the northern part of Tsavo East in 1990–3, although sightings are rare in the south, despite the fact that this area is open to tourists and consequently visited more often (Jennings 1992). Wild dogs are also sighted occasionally in Tsavo West, most recently in 1991 (Jennings 1992). A researcher carrying out aerial surveys for ungulates in Tsavo East and West, and adjacent lands including Mkomazi Game Reserve in Tanzania, saw no wild dogs during a two year period in 1993–5. The habitat is wooded and bushed grassland. Domestic dogs are rare, but lions are present and spotted hyaenas are common. The local attitude is uncompromisingly hostile.

Wild dogs are still present in Lamu District, but are generally rare. Kenya Wildlife Service personnel saw a group of 12 wild dogs on Manda Island in 1991 (Jennings 1992). *Lycaon* was considered common, but declining, in the Dodori National Reserve (900 km²) in the 1980s, and was last sighted there in 1991 (Jennings 1992). Domestic dogs are excluded from Dodori, although pastoralists with dogs do use the area seasonally. There are no complaints of livestock losses. People are afraid of wild dogs and associate them with rabies outbreaks. The local decline in wild dogs has been blamed on disease.

Wild dogs may now be absent from Tana River National Primate Reserve (169 km²) where the last sighting was in 1976, although there is an unconfirmed report from this Reserve in 1993. A group of 8 dogs was seen near Garsen, on the Tana river, in 1993. Dogs are now absent from ranches on the Galana River (Alexander & Kat 1992).

Rwanda

Status ☹

Wild dogs are extinct in Rwanda. Akagera National Park (2,800 km²) once supported a healthy population, and was known as 'Le Parc aux Lycaons', but wild dogs disappeared in 1983–4, perhaps following a disease outbreak. The human population density in Rwanda approaches or exceeds that of most European countries, and it is unlikely that the rather small park would be able to sustain wild dogs, even if they could find their way from western Tanzania. Despite their being extinct, wild dogs receive total legal protection in Rwanda.

A proposal to reintroduce wild dogs to Akagera was put forward in 1989, but, given the current political and economic situation in the country, it seems unlikely that this programme will be implemented in the future.

Distribution

Wild dogs are extinct in Akagera National Park, where they have not been seen since 1983. They are also absent from Volcanoes National Park (228 km²), and may well never have occurred there.

Somalia

Status ☹

The outlook for wild dogs in Somalia is very poor. Deforestation, poaching, drought and over-grazing are rapidly depleting all wildlife. Carnivores are routinely destroyed, sometimes with the assistance of the Veterinary Service, who "flatly refuse to give up the practice in spite of requests from the National Range Agency (which is responsible for wildlife management)". Wild dogs' supposed threat to people has been exaggerated and fuels the pressure to eradicate them. This is surprising, since they officially receive total legal protection in Somalia.

Distribution

Wild dogs' distribution in Somalia is summarized in Table 3.14.

Wild dogs might still be present in the remote northeast of the Central Rangelands in the vicinity of El Hamurra, where there was one sighting in 1982. If a population occurs there it is unprotected and undoubtedly declining.

Wild dogs were once common in Buulu Berde, and were reported to be numerous before the late 1970s, but now they are virtually absent. Apart from warthogs, which are excluded from the Muslim diet, all game in this area is severely depleted.

Wild dogs are believed still to occur in the south near the Juba River (close to the Kenya border) but the population is probably declining. A survey of woodlands south of Mogadishu in 1984 indicated that wild dogs "seem rarer than they were ten years ago" (Fagotto 1985). However, a pack was seen in Bush Bush National Park (4,267 km²) in 1994. It seems likely that this area has the greatest potential for supporting

Table 3.14
A summary of wild dog distribution in Somalia. Somalia probably has no viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Bush Bush National Park	4,267	1 sighting	1994
Juba River	n/a	rare	1994
Buulu Berde	n/a	vagrant	1987

Table 3.15
A summary of wild dog distribution in Sudan. Sudan has a potentially viable wild dog population.

Site	Area (km^2)	Abundance	Date of estimate
Dinder National Park	6,500	1 sighting	1995
Southern National Park	–	uncommon	1987
Bengagai Game Reserve	–	uncommon	1987
Jebel Marra Forest Reserve	–	extinct	1992

viable numbers of wild dogs and other wildlife populations in Somalia.

Sudan

Status

The outlook is poor. Large carnivores are so rare in Sudan that very few livestock are lost to them. Wild dogs are legally protected inside parks and reserves, but lack of funds and the protracted civil war have rendered effective conservation difficult. Nevertheless, there are a few sightings in southern Sudan, as well as in areas of northern Kenya and Uganda close to the Sudan border.

Distribution

Wild dogs' distribution in Sudan is summarized in Table 3.15.

Wild dogs were believed to be "rare to common" in the 1980s in the Sudd, or Eastern Nile Floodplain in the southern part of the country, between Bor and Malakal, although we have no information on the recent population trend. The habitat is short grassland and wooded grassland (*c.* 100,000 km^2). There is no legal protection for wild dogs in the area. Their local name is 'rinderpest dog' because predation becomes more common when cattle are weakened during epidemics. Public attitudes vary from indifferent to hostile.

Wild dogs are probably still present in the zone around Bangagai Game Reserve, and were sighted there several times in 1985–87. The habitat is wooded grassland surrounding the reserve, which is rainforest. Nearby cultivators do not keep livestock. The respondent thought that these dogs might have colonized the area from neighbouring Southern National Park, where they are believed to be present.

A pack was sighted in 1995 in Dinder National Park (6,500 km^2), on the Ethiopia border, by a delegation from the Ministry of Natural Resources of Ethiopia (Malcolm & Sillero-Zubiri in press).

Surveys carried out in Jebel Marra Forest Reserve, in the west of Sudan, report that wild dogs are extirpated there.

We received no data for Radom (12,500 km^2), or Boma (17,500 km^2), although wild dogs may occur in both of these parks. We also received no data for the small Ashana Game Reserve (300 km^2).

Tanzania

Status

In Tanzania, the government is anxious to conserve wild dogs, and there is a good prospect for the long-term survival of a population, at least in the southern protected areas of Selous and Ruaha. In July 1987, the Director of Wildlife imposed a moratorium on all hunting of wild dogs in Tanzania and the species receives total legal protection. One respondent said that the wild dogs' apparent decline in the north had been discussed in Parliament. The long-term prospects for *Lycaon* in the north are uncertain, but in the south it may be said that the tsetse has been the wild dogs' friend. The Selous, and possibly Ruaha, offer enough area of suitable habitat, abundant prey and (so far) freedom from hostile livestock interests, to represent what is probably the best wild dog country remaining in Africa.

Distribution

Wild dogs' distribution in the Tanzania is summarized in Table 3.16 and Figure 3.10.

Wild dogs are common in the Selous Game Reserve (43,000 km^2), where the habitat is mostly miombo woodland. Selous represents an extremely important reservoir for wild dogs: density on a study site of 2,600 km^2 in the northern sector of Selous is unusually high, at around 5.9 individuals/100 km^2 (= 4.0 adults/100 km^2; *cf* 2.0 adults/100 km^2 in Kruger National Park, South Africa and 1.5 adults/100 km^2 in Hwange National Park, Zimbabwe; Chapter 1). Elsewhere in Selous, the density is 1.6–2.4 adults/100 km^2, which is typical for woodland areas. Based on conservative extrapolations to other areas of Selous, the entire population probably numbers about 880 adults. Domestic dogs are uncommon, but may be increasing in the area to the north of Selous, along the road to Morogoro. Morogoro is 70 km from Selous, and domestic dogs there are affected by rabies and canine distemper. Wild dogs in Selous show signs of exposure to canine distemper and parvovirus. The density of both spotted hyaenas and lions are relatively low – estimated at 0.32 adult hyaenas/km² and 0.08–0.13 adult lions/km². Smaller canids are very rare (side-striped jackal, black-backed jackal) or absent (golden jackal, bat-eared fox). Livestock farming was once virtually non-existent due to tsetse, but the numbers of cattle in the area immediately to the north of the Reserve increased in 1994 and 1995. All livestock remain rare further south.

Wild dogs are also present in the Mikumi National Park (3,200 km²), which is contiguous with Selous Game Reserve. The habitat is short grass and wooded grassland. The Mikumi population is monitored as part of the Selous research project, and currently numbers 93–135 adult wild dogs in 4 packs (Creel & Creel 1993). A major cause of mortality are car collisions on the Tanzania-Zambia highway – in one year a total of 11 dogs were hit on this stretch of road (Creel & Creel 1993), although this is probably abnormally high. In other years only 1–2 dogs have been killed. There are also occasional reports of dogs' being snared in this region.

More than 20,000 km² of the Selous ecosystem fall outside the Game Reserve itself. As well as the Mikumi and Udzungwa National Parks, there are two Game Control Areas (Kilombero North and South) and eight open hunting areas (Kisarawe, Tapika, Kilwa, Liwale North, Liwale South, Mahenge North, Mahenge South, and Gonabis). These areas are nominally protected and relatively undisturbed: the Game Control Areas are used for game culling by the government, and the open areas are used for hunting by local people but exclude foreign sport hunters. Although these areas have lower wildlife densities and receive relatively little active protection, wild dogs are seen in all of the areas bordering Selous. This includes ten districts: Kisarawa, Rufiji, Kilwa, Liwale, Tunduru, Songea, Kilombera, Ulanga, Kiloso and Morogoro. These districts fall in four government administrative regions: Pwani, Lindi, Ruvuma and Morogoro. Wild dogs from the Selous Game Reserve often move in and out of these areas, and sometimes even den outside the Reserve. Wild dogs have been seen up to 50 km outside the reserve, and one den was reported 20 km outside the reserve.

Table 3.16

A summary of wild dog distribution in Tanzania. Tanzania has a viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Arusha National Park	137	vagrant	1994
Gombe National Park	52	extinct	1987
Kilimanjaro National Park	760	vagrant	1991
Lake Manyara National Park	325	extinct	1987
Mahale National Park	–	rare	1993
Mikumi National Park	3,200	common	1993
Ruaha National Park	10,400	common	1996
Serengeti National Park	13,000	vagrant	1996
Tarangire National Park	–	rare	1994
Kisigo Game Reserve	14,160	uncommon	1996
Mkomazi Game Reserve	3,509	vagrant	1995
Moyowosi Game Reserve	21,869	rare	1987
Rungwa Game Reserve	–	uncommon	1996
Selous Game Reserve	43,000	common	1996
Ugalla River Game Reserve	6,984	rare	1987
Kilombero Game Control Area	6,928	uncommon	1996
Maasai Steppe	n/a	uncommon	1995

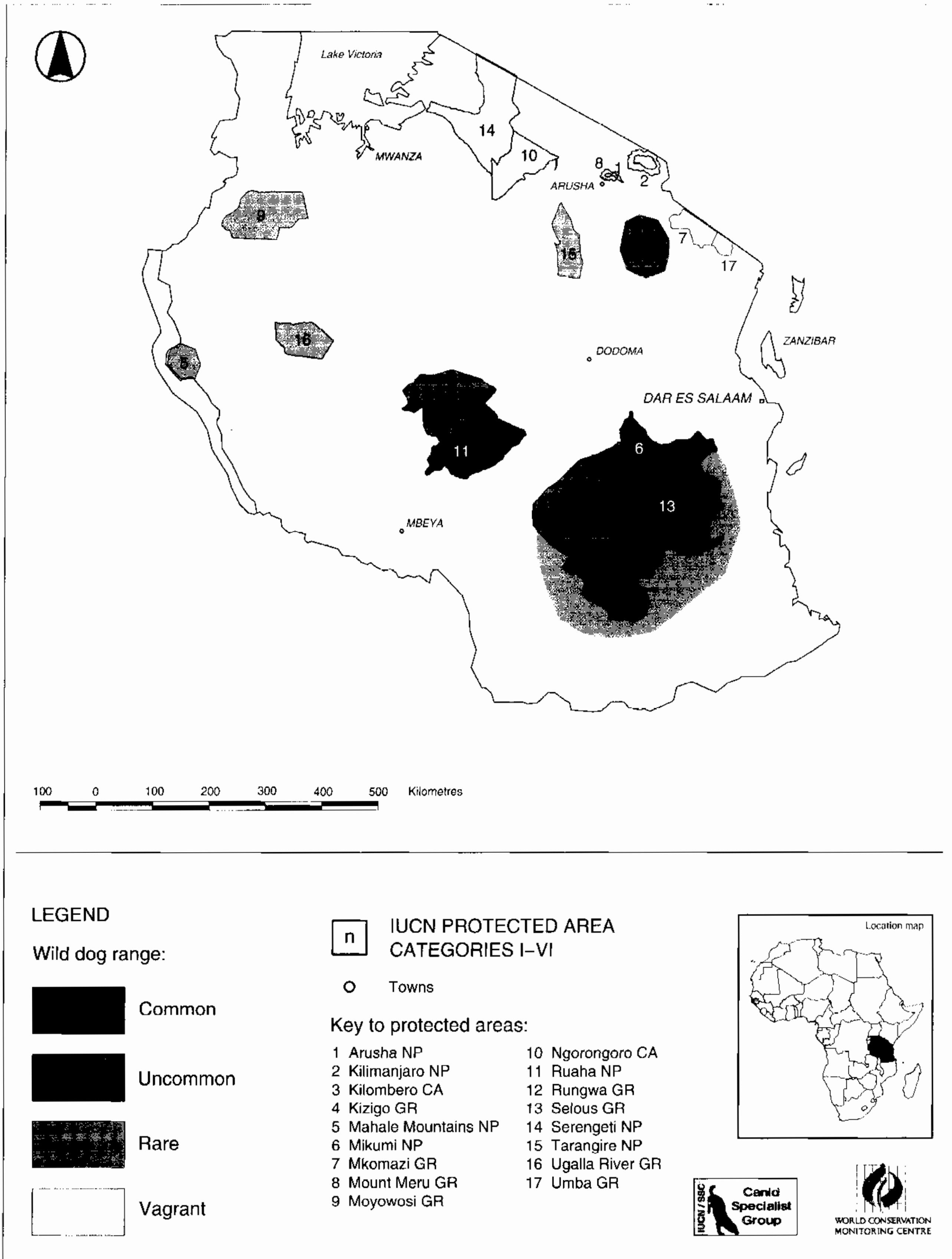


Figure 3.10. Wild dog distribution in Tanzania.

Wild dogs are also present in the Ruaha National Park (10,401 km²), and Rungwa/Kisigo Game Reserve (14,160 km²). This area represents another important refuge for wild dogs. Sightings have been relatively frequent in 1991–6, with several packs, including pups, sighted repeatedly. The population may well be contiguous with the one centred on Selous/Mikumi. The habitat in Ruaha is miombo and wooded grassland. The size of the population is not known, but reports filed by the Project Manager of Rungwa/Kisigo Game Reserve estimate 20 packs for that area (Creel 1992). Domestic dogs are excluded from the area, but spotted hyaenas are common. Wild dogs were occasionally hunted for sport in the Rungwa Game Reserve prior to the 1987 hunting moratorium. Tsetse prevents livestock farming in this area.

There may no longer be a resident population of wild dogs in Serengeti National Park. Serengeti (13,000 km²) is part of a larger ecosystem of approximately 25,000 km² which has a relatively high prey density, yet has supported only a small wild dog population in recent years – the known population size at the end of 1990 was just 34 individuals (Burrows 1995). All of the remaining packs studied by the Serengeti Wild Dog Project disappeared in 1990–1, apparently as a result of disease (See Appendix 1). However, there have been confirmed sightings of wild dogs since then, suggesting that a remnant population remains, and the area might be re-colonized (See Appendix 1).

In the north-east of Tanzania, wild dogs are seen occasionally in and around Kilimanjaro National Park (760 km²), and were sighted in Arusha National Park (137 km²) in 1994. Although the hunting of wild dogs has been banned since 1987, records of the Regional Game Officer for the Kilimanjaro region show that 13 wild dogs were shot as vermin in 1988–9 in Rombo, Moshi and Mwanga. No wild dogs were shot in the area in 1990. Three packs denned near Ngasumet on the Maasai steppe in 1995, but the local people threatened to poison them and the litters were removed with the aim of starting a captive breeding programme for release into Mkomazi Game Reserve (Fitzjohn 1995). A pack of 6 adults was seen in 1994 in Tarangire National Park, and another pack, of seven, was sighted near Handeni in 1993.

Wild dogs are absent from Lake Manyara National Park (325 km²), although they were known to occur there in the past, and are still seen occasionally in the adjacent Marang Forest. They are also absent from Gombe (52 km²) National Park, where there are no records of wild dogs ever having been present. They were observed twice, however, in the Mahale Hills, beside Lake Tanganyika, in 1982 and are still sighted occasionally in the Mahale National Park.

Mkomazi Game Reserve may be visited occasionally by wild dogs from neighbouring Tsavo. Mkomazi is currently being rehabilitated after a period of heavy encroachment by pastoralists and their cattle and, as part of this programme, plans have been considered to reintroduce wild dogs using puppies taken from Tanzanian populations in conflict with man (see Chapter 7, Fitzjohn 1995). Since wild dogs are present at low densities in Tsavo West National Park, Kenya, which is contiguous with Mkomazi, it seems likely that Mkomazi might have been recolonized unaided should circumstances in the area favour wild dogs.

Occasional reports of wild dogs come from several small or otherwise threatened areas, some of which, including the Ugalla and Moyowosi Game Reserves, are protected. Others are unprotected, including Nzega district, Kiteto district in southern Maasailand, Tabora region (including Igrundu, Nzega and Tabora) and areas south of Maswa Game Reserve. Detailed distribution data are being collected by questionnaires which have been distributed to Wildlife Department staff across the country.

Uganda

Status ☹

A directive was issued in 1955 to shoot wild dogs on sight and it appears that there is no longer a resident population in Uganda. Sightings are exceptional: there are occasional rumours of vagrants from Tanzania and the Sudan. Wild dogs were once seen regularly in all the parks and reserves, and it is possible that the ongoing rehabilitation of Uganda's national parks may encourage recolonization. However, a negative public attitude persists.

Distribution

Wild dogs' distribution in Uganda is summarized in Table 3.17.

Mammal surveys conducted inside and outside of conservation areas during 1982–92 suggested that wild dogs were probably extirpated, but scattered sightings in several areas suggest that the species might be recolonizing Uganda. A few sightings of small groups or single dogs in Murchison Falls National Park over the last five years suggest that dispersing individuals may still travel through this area. There are rumours of wild dogs having been seen in the Kidepo Valley National Park (3,346 km²) in 1995, and in 1994 Uganda National Parks staff saw them several times in the Northern Karamoja Controlled Hunting Area, to the south of Kidepo.

Table 3.17
A summary of wild dog distribution in Uganda. Uganda has no viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Kidepo Valley National Park	1,483	vagrant	1996
Murchison Falls National Park	3,346	1 sighting	1990
Queen Elizabeth National Park	1,978	extinct	1987
Northern Karamoja Controlled Hunting Area	–	vagrant	1996

Wild dogs are extinct in Queen Elizabeth National Park (1,978 km²), where they were last sighted in the 1970s.

Distribution of Wild Dogs in Southern Africa

Southern Africa holds wild dogs' best hopes for the future, since it has several potentially viable populations (Figure 3.11). One large population in the north of Botswana is probably contiguous with populations in north-eastern Namibia and western Zimbabwe. Kruger National Park, South Africa, has around 400 wild dogs, some of which seem to move north into south-eastern Zimbabwe. Zambia has a reasonably large population in Kafue National Park, and another in the Luangwa Valley. A smaller population exists in the Zambezi valley, on the Zambia-Zimbabwe border. In contrast, wild dogs are rare in Malawi, and all but extinct in Angola and Moçambique.

Southern Africa may have fairly substantial wild dog populations, but there is no room for complacency. Persecution, road mortality and disease remain serious problems for many wild dogs in the area.

Angola

Status ☹

The outlook for wild dogs in Angola is not hopeful. Political unrest in Angola has prevented the collection of detailed data, but in the 1980s the National Park authorities were forced to withdraw park and reserve administration from the majority of protected areas. Officially, wild dogs receive total legal protection, but there is no effective protection. We have received no further reports since the 1990 survey.

Distribution

Formerly, *Lycaon* was widespread in Angola. It was reported from all of the country's protected areas: Bikuar, Iona, Kameia, Kangandala, Kisama and Mupa National Parks, and Bufalo, Chimalavera, Luando, Luiana, Mavinga, and Mocamedes Natural Reserves. A respondent to the 1990 survey, however, reported that they had always been rare, and had been in decline since the mid-1970s. He saw wild dogs only twice in over 150,000 km² covered by hundreds of hours of aerial survey carried out over four years. However, it is difficult to spot wild dogs from the air and this may not give an accurate picture of the number of dogs present. One of these sightings came from Luando National Reserve, as did another from 1969–70. The last dogs in Iona National Park were reportedly shot by rangers in the late 1960s. Wild dogs may persist in the Cuando-Cubango region in the south-east, near where populations occur in neighbouring Zambia and Namibia, but they were extremely scarce in the 1980s and the population is unlikely to be viable.

Botswana

Status ☺

The outlook for wild dogs in Botswana remains hopeful, and the northern part of the country may contain one of the most extensive populations of wild dogs remaining in Africa. Detailed studies of dogs in the area allow more accurate assessment of the population size and characteristics than is possible in many other areas. The population is by no means without threats, however. Under the Fauna Conservation Act, dogs may not be hunted without a permit. However, such permits are not required if a farmer is defending livestock, and officials rarely investigate reported hunting very closely. Thus, wild dogs receive only partial legal protection – and in practice, wild dogs straying onto farms are shot on sight. Some development schemes in

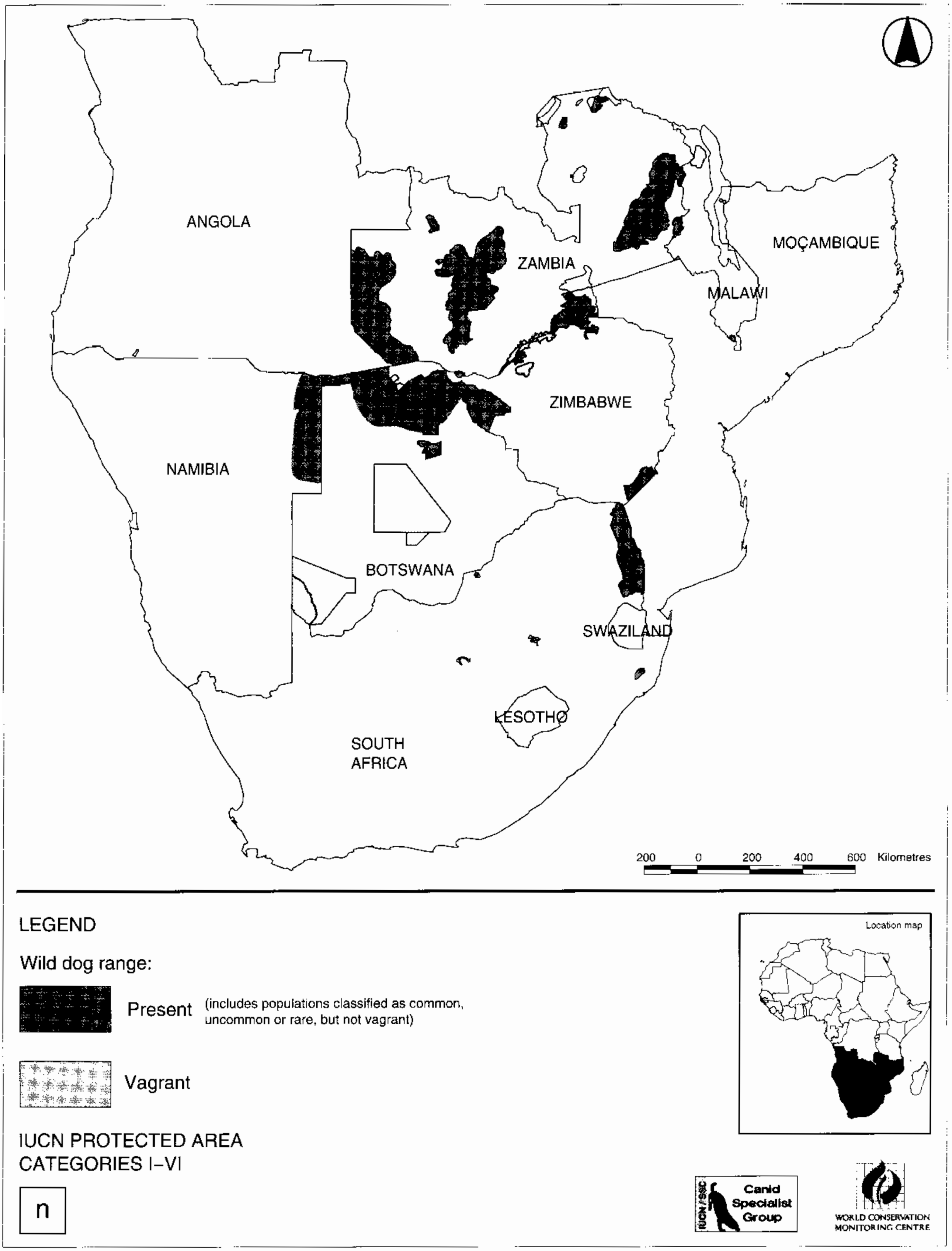


Figure 3.11. Wild dog distribution in Southern Africa.

Botswana, particularly the erection of veterinary cordon fences to control foot and mouth disease, have led to the destruction of large herds of ungulates and many carnivores, and there is growing concern about the effects of livestock policies.

Distribution

Wild dogs' distribution in Botswana is summarized in Table 3.18 and Figure 3.12.

The most important area for wild dogs is in the north of the country, in an area of 176,000 km² in the Ngamiland, Central and Chobe districts. This area includes the Okavango Delta, and the Chobe-Linyanti River system, the Moremi Wildlife Reserve, Nxai Pan National Park, and the Chobe National Park. The estimate of the population for this area is a minimum of 42 packs representing 450–500 individuals.

In 1989, J.W. McNutt began a study of wild dogs in the area in and around the Moremi Game Reserve. His study area, of 2,600 km², is free of livestock. This area has supported as many as 13 packs, totalling 109 yearlings and adults, although the number varies from year to year. Recently, four packs were lost to disease. None of the study packs lives entirely within the boundaries of protected areas. Domestic dogs are excluded from Chobe, but lions are present and spotted hyaenas are abundant. The nearest livestock farming is on the Khwai and Chobe Rivers, where losses to predation might occur, although reports of such losses are rare.

Wild dogs are sighted infrequently in and around the contiguous Makgadikgadi Game Reserve and Nxai Pan National Park. The combined area probably supports no more than two or three packs, and none remains within the borders of the protected area year-round. Domestic dogs are present, and spotted hyaenas are common in the wet season. Hwange National Park in Zimbabwe, which is just over the border of northern Botswana, has a healthy wild dog population and the animals almost certainly cross back and forth.

Wild dogs are also found, at lower densities, in the Ghanzi District (Kalahari Ecosystem). They still occur in the southern part of the Central Kalahari Game Reserve (55,374 km²), which contains an estimated 3–4 packs. The area is wooded grassland; domestic dogs are excluded, spotted hyaenas are rare, and lions are present. Considered common to abundant in the 1970s, wild dogs have suffered depletion in this area through a combination of drought and the activities of the farming lobby. Livestock losses are reported to the west of the reserve, and the local people are hostile. Wild dogs are rare, but still present, in and around the Khutse Game Reserve (2,500 km²) adjoining the south of the Central Kalahari Game Reserve – a pack of eight dogs was sighted there repeatedly in January 1996. Domestic dogs are excluded from the reserve, and spotted hyaenas rare. Livestock losses are reported, however, and wild dogs are persecuted for this reason.

Wild dogs are present, but at very low densities, in the Kgalagadi District, including the Gemsbok National Park and Mabuasehube Game Reserve (total 26,038 km²). The total estimate for wild dog popula-

Table 3.18
A summary of wild dog distribution in Botswana. Botswana has a viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Chobe National Park	–	common	1992
Gemsbok National Park	26,038	rare	1987
Nxai Pan National Park	–	rare	1992
Central Kalahari Game Reserve	55,374	rare	1987
Khutse Game Reserve	2,500	rare	1996
Mabuasehube Game Reserve	–	rare	1987
Makgadikgadi Game Reserve	–	rare	1992
Moremi Wildlife Reserve	–	common	1996
Chobe district	n/a	uncommon	1992
Central district	n/a	uncommon	1992
Ngamiland district	n/a	uncommon	1992
Ghanzi district	n/a	rare	1992

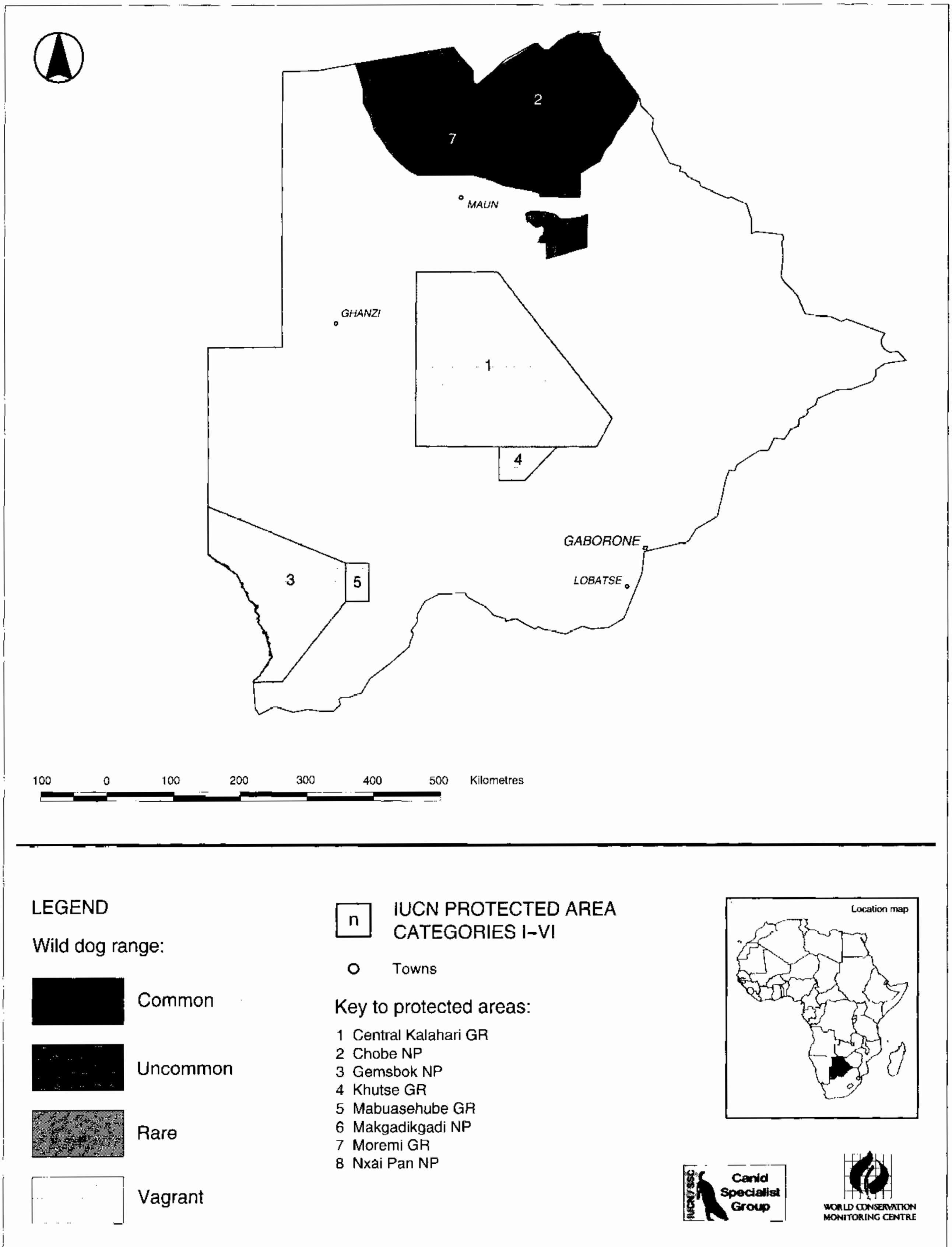


Figure 3.12. Wild dog distribution in Botswana.

tions in the south-west of Botswana (including Ghanzi and Kgalagadi Districts) is 100–200.

These data are based principally upon a pamphletting survey carried out by John Bulger in 1988–9. Comparison of his findings with detailed studies of known individuals in the Moremi study population, which is representative of the population in northern Botswana, suggests that his minimum estimates were realistic, but might represent slight under-estimates. Groups of two or three are probably common in Botswana, and these packs tend to be overlooked by pamphletting surveys. For example, where Bulger estimated a minimum of 7 packs, with an average of 8–9 adults and yearlings, intensive study by McNutt has found 13 packs with an average of 5 adults and yearlings. This trend may be consistent throughout Botswana.

Lesotho

Status

There are no records of wild dogs' ever having occurred in Lesotho. One respondent replied that "In this country most of traditional folklore stories are based on wildlife. Extinct animals appear in these stories, but no wild dogs. It doesn't even have a local (sesotho) name". Thus it seems unlikely *Lycaon* ever occurred there.

Malawi

Status

The outlook for wild dogs in Malawi is uncertain, but might be improving. While there are no new sightings from most of the country, wild dogs have recently been seen regularly in Kasungu National Park. *Lycaon* is officially protected inside reserves; outside they may be taken only by government hunters, and by private citizens with special Minister's licences.

Distribution

Wild dogs' distribution in Malawi is summarized in Table 3.19 and Figure 3.13.

Wild dogs were recorded regularly in Kasungu National Park (2,200 km²) in the early 1990s. They were considered rare there in the 1980s, but there were 18 sightings made by Park staff in 1991, in all parts of the Park, mostly between November and January. As a result, Malawi was the only southern African country to report an increase in numbers of wild dogs at the 1991 CITES meeting (Anon 1992). However, we have no more recent reports. The dogs probably move across the international boundary into the neighbouring Lukusuzi National Park in Zambia. Domestic dogs are excluded from Kasungu, and spotted hyaenas are rare to common. No livestock losses were reported in the 1980s, when most local people were apparently unaware of *Lycaon's* existence.

Wild dogs were seen several times in Nyika National Park (3,040 km²) in late 1992 (Chirwa 1995), although respondents to the 1990 survey reported them as absent. Wild dogs are believed still to be present, but probably very rare, in the Mwabvi Game Reserve (260 km²). They are probably now extinct in Nkhotakota Game Reserve (1,750 km²), where there have been no sightings since the 1970s. Similarly, wild dogs are probably now absent from the Liwonde National Park (586 km²), where the last sighting was in 1975, and from Vwaza Marsh Game Reserve (1,040 km²), where the last pack was seen in 1981. Wild dogs were once a common sight in this area, and the cause of their decline is not known. They are absent from Lake Malawi National Park, Lengwe National Park and Majete Game Reserve, from

Table 3.19
A summary of wild dog distribution in Malawi. Malawi has a potentially viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Kasungu National Park	2,316	uncommon	1991
Lengwe National Park	–	absent	1987
Liwonde National Park	548	extinct	1987
Nyika National Park	3,040	vagrant	1995
Majete Game Reserve	–	absent	1987
Mwabvi Game Reserve	260	rare	1987
Nkhotakota Game Reserve	1,750	extinct	1987
Vwaza Marsh Game Reserve	1,040	extinct	1987

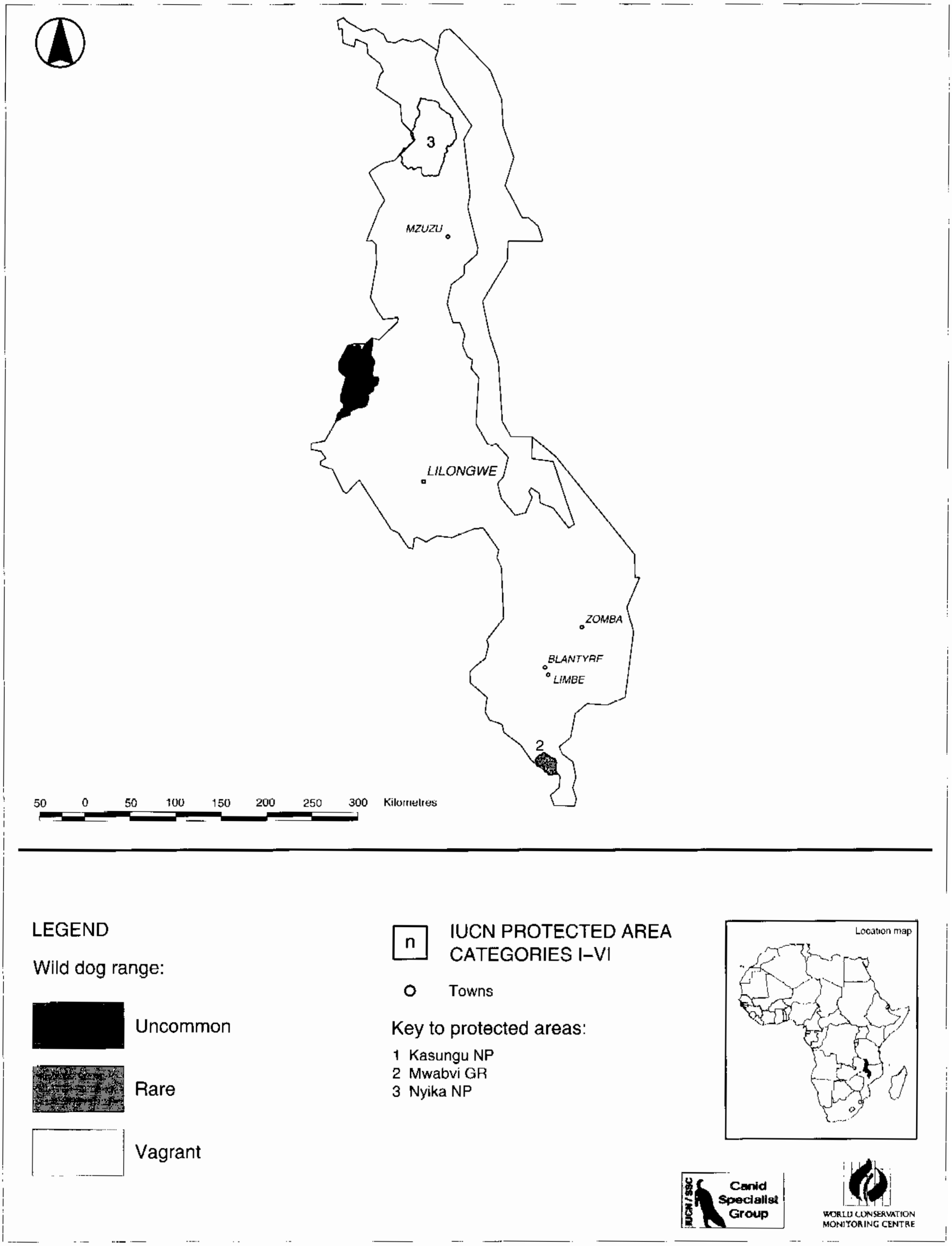


Figure 3.13. Wild dog distribution in Malawi.

where there have never been definite records of presence although the habitat is potentially suitable. Each of these reserves comprises less than 1,000 km².

Moçambique

Status

The outlook is not hopeful, although some wild dogs do seem to remain in Moçambique. Published reports indicate that there was a rapid decline in wild dog numbers after 1975, due to unregulated sport hunting, persecution by cattle farmers, and degradation of habitat. There are no records of disease. *Lycaon* was considered to be on the verge of extinction in Moçambique in 1986 (Lobao Tello 1986) although there are recent sightings from the north of the country. Wild dogs cross the border from Kruger National Park, South Africa in the south, and are also common in southern Tanzania to the north so, should conditions improve, Moçambique might be ideally placed for recolonization. Given the current economic situation, however, any immediate improvement in conditions for wildlife seems unlikely.

Officially, wild dogs receive total legal protection in Moçambique.

Distribution

Although wild dogs were once widely distributed in remote and protected areas of Moçambique (Smithers & Lobao Tello 1976) by 1986 they were considered extinct in most of the western sector of Manica Province, endangered in the Tete and Zambezi Provinces and extinct in the Nampula Province.

In 1986 the Rovuma/Lugenda Valley still sustained a population, and wild dogs were still being recorded in Niassa province in the north of the country. United Nations staff working in this area report seeing several wild dog packs recently, indicating that a population still exists there. A pack with pups was seen in 1996 in the Cabora Bassa area, between the Zambezi and Musengezi rivers. This is close to the Mana Pools area of Zimbabwe, where wild dogs have also been seen repeatedly in recent years.

A pack of wild dogs from Kruger National Park, South Africa, crossed repeatedly into the western part of Gaza Province, but two animals were killed and the pack disappeared. The planned cross-border park envisaged joining Kruger to Moçambique will be of great benefit to wild dogs.

Namibia

Status

The outlook for wild dogs in Namibia is relatively good. Although they have been eradicated by powerful farming lobbies on the commercial farmlands in the centre and south of the country, wild dogs are doing reasonably well in the north-eastern corner of Namibia, an area of low density communal farming where dogs are generally not in conflict with local communities. Outside protected areas, wild dogs are often shot on sight, although they do now have total legal protection.

Distribution

Wild dogs' distribution in Namibia is summarized in Table 3.20 and Figure 3.14.

Wild dogs are restricted to the north-east of Namibia, and are extinct throughout the rest of the country. Of the *c.* 61,000 km² area that supports wild dogs, only 6.2% has protected status. However, the population appears to be stable across *c.* 40,000 km² and is probably contiguous with the population in northern Botswana. An integrated carnivore research programme, aimed at creating a carnivore management plan, was started in this region in 1992 and, as a result, a relatively accurate assessment of wild dogs can be

Table 3.20
A summary of wild dog distribution in Namibia. Namibia has a viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Etosha National Park	21,346	extinct	1996
Kaudom Game Reserve	12,492	uncommon	1996
Bushmanland	n/a	uncommon	1996
Caprivi Strip	n/a	uncommon	1996
Hereroland East	n/a	uncommon	1996
Kavango	n/a	uncommon	1996

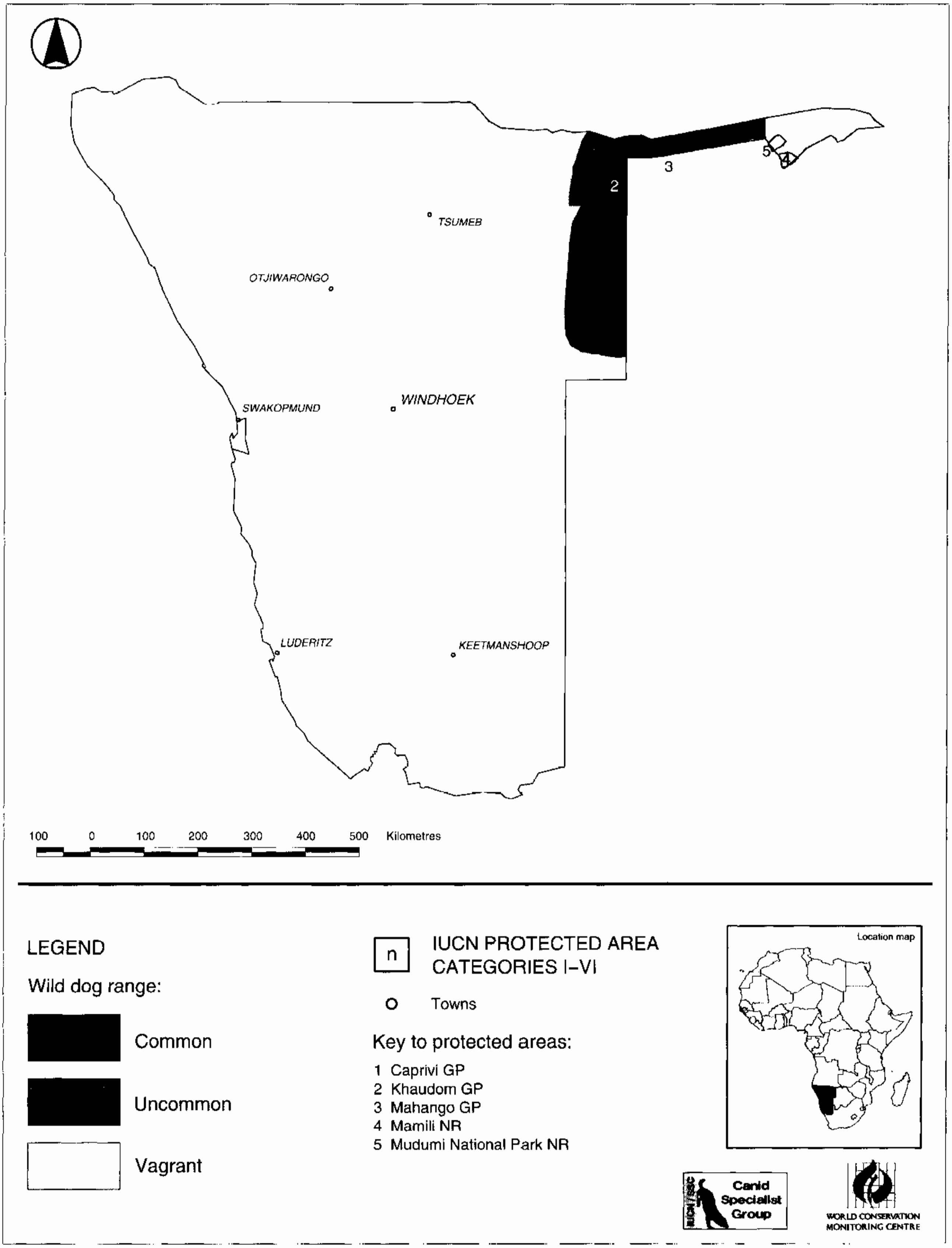


Figure 3.14. Wild dog distribution in Namibia.

made.

In Kavanago, Bushmanland and Hereroland East, wild dogs are sighted fairly often, and occur at a density of approximately 1.9–3.1 animals/100 km² (*cf* 5.9 animals/100 km² in the Selous Game Reserve, Tanzania). Wild dogs in these regions often spill over onto the commercial farms on the western border, where they are shot on sight. Between 150 and 200 animals were shot on farms bordering Bushmanland and Kavango, during 1985–1986 alone. In 1992 at least 124 individuals, in seven packs, were known from Eastern Bushmanland, with a further 49 individuals in the Kaudom Game Reserve on the Botswana border. In total, this area probably supports in the region of 250–1200 wild dogs. Lions and spotted hyaenas also occur in this area. The number of domestic dogs is increasing, and they are known to carry both rabies and canine distemper (Laurenson *et al.* in prep.).

The wild dog population in the western part of the Caprivi strip may also be stable, although the data are sparse since very few people visit the area. An estimated 2–4 packs may occur there.

Very small packs of wild dogs live on cattle farms in the Mangeti block and south-eastern Owambo. These small packs are not in conflict with the cattle farming activities although larger packs are reported to harass cattle. This leads farmers to persecute wild dogs, reducing pack size and putting an end to the cattle depredation problem.

Wild dogs are now extinct in Etosha National Park (21,346 km²), where the last confirmed sighting of a wild pack was in 1986, although they were once seen there fairly consistently. Three attempts have been made to reintroduce wild dogs to Etosha, but none has been successful (Scheepers & Venzke 1995). Instead, the Ministry of Wildlife Conservation and Tourism decided to conserve wild dogs in their natural habitat by the involvement of the community, and create an awareness of their vulnerability.

South Africa

Status ☺

Wild dogs have a stronghold in Kruger National Park, where there is a stable population of 350–400 (Maddock & Mills 1994), but the outlook elsewhere is poor. The South African Red Data Book lists *Lycaon* as endangered, and the species' legal status is 'specially protected'. Several attempts have made to reintroduce wild dogs to a number of small reserves (See Chapter 7). While two of these efforts have been successful, neither of the new populations is large enough to be viable in the long term without intensive management.

Distribution

Wild dogs' distribution in South Africa is summarized in Table 3.21 and Figure 3.15.

Wild dogs are present in three regions of South Africa. In the Northern Cape, very occasional *Lycaon*

Table 3.21
A summary of wild dog distribution in South Africa. South Africa has a viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Addo Elephant National Park	–	extinct	1987
Golden Gate Highlands N.P.	–	extinct	1987
Kalahari Gemsbok National Park	9,500	vagrant	1996
Karoo National Park	–	extinct	1987
Kruger National Park	22,000	common	1996
Mountain Zebra National Park	–	extinct	1987
Hluhluwe Game Reserve	–	uncommon	1996
Itala Game Reserve	300	vagrant	1995
Mkuze Game Reserve	–	extinct	1987
Ndumu Game Reserve	–	extinct	1987
Umfolozi Game Reserve	–	uncommon	1996
Madikwe Game Reserve	720	uncommon	1996
Near Messina	n/a	1 sighting	1996

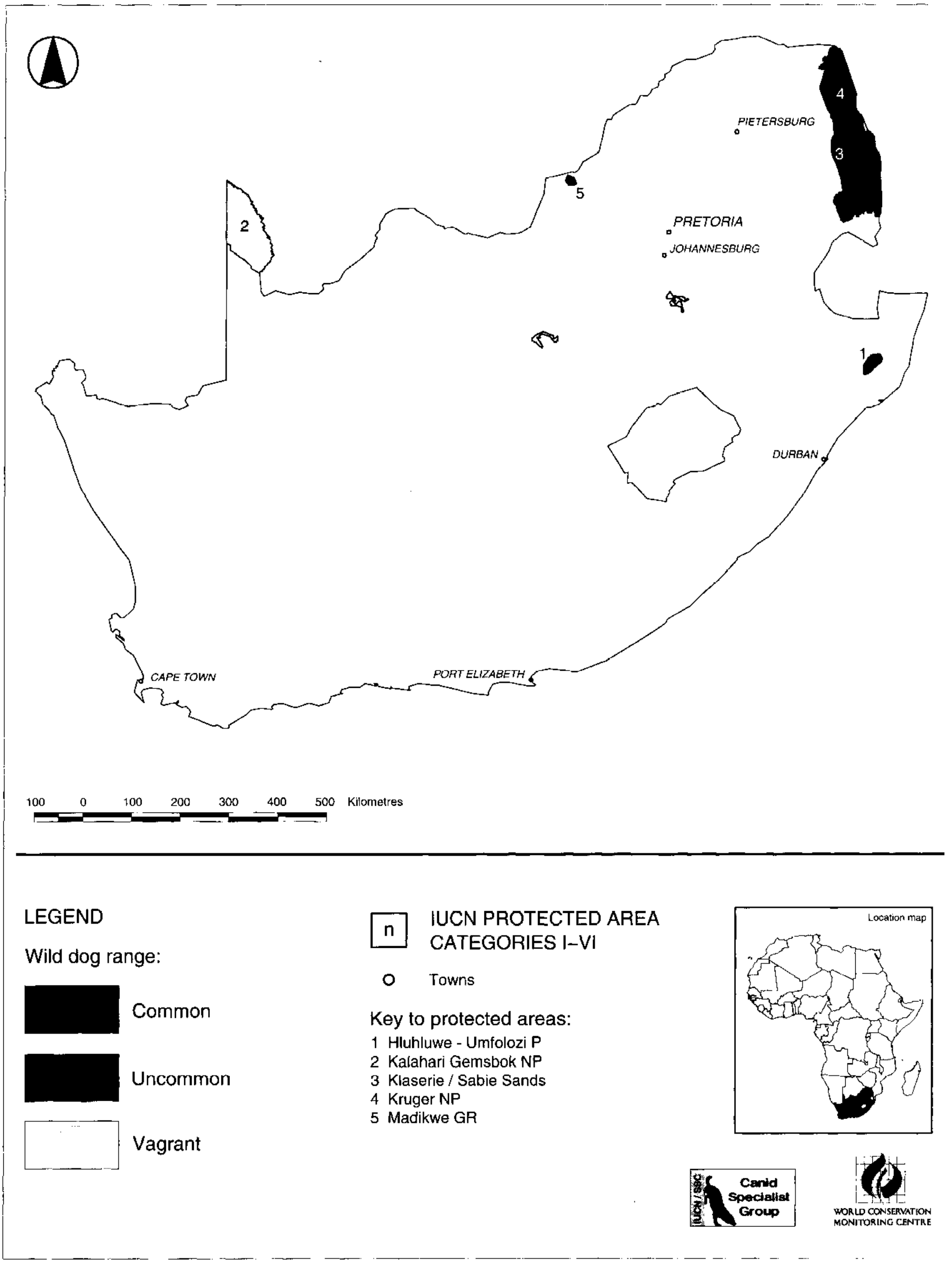


Figure 3.15. Wild dog distribution in South Africa.

sightings come from the Kalahari Gemsbok National Park (9,500 km²). This is marginal habitat and these dogs are almost certainly vagrants from neighbouring Botswana. Protected inside the Park, wild dogs are shot and poisoned on the other side of the Namibian border, and also outside of the park borders in Botswana.

Wild dogs are reasonably common in Kruger National Park (22,000 km²), and the private reserves along its western border (total 2,360 km²). This area of open and closed woodland contains a population that fluctuates between 375 and 450 wild dogs (Maddock & Mills 1994), along with about 250,000 impala, their principal prey. It is not clear what factors control the wild dog population, but it does not appear to be food limited. Lions are an important cause of mortality. Domestic dogs are rare, spotted hyaenas are common to abundant. An ongoing study of demography and mortality factors is being conducted in an area of 4,500 km² in the southern district of the Park. Livestock losses do occur outside the Park, and farmers shoot and poison wild dogs that leave the Kruger. Dogs also get caught in snares. A pack was sighted recently to the north-west of Kruger, along the Limpopo on the Zimbabwe border outside of protected land. However, local game ranchers are intolerant and have tried to shoot this pack.

A pack of 6 wild dogs has recently been released into the Madikwe Game Reserve (720 km²) in North West Province. This pack has bred successfully, but in such a small reserve the population can never be large enough to be viable in the long term without intensive management.

In KwaZulu-Natal, wild dogs are present in the Hluhluwe-Umfolozi Park (960 km²), where they were reintroduced in 1980 81 (see Chapter 7). Since then, the population has fluctuated in the region of 10–30 individuals, and 13 were present, in two packs, in 1994. Eight litters have been recorded between 1982, but there have been no pups produced since 1993. The habitat in Hluhluwe-Umfolozi is grassland, thicket, woodland, and semi-deciduous forest. Domestic dogs are rare except on the boundaries of the reserve, but they do carry canine distemper. Spotted hyaenas are common, and lions are present. Livestock losses have occurred outside the reserve, and farmers are not sympathetic towards wild dog conservation. However, to the north of Hluhluwe-Umfolozi some game ranchers are pleased to have dogs on their properties, and, fortunately, these ranchers appear to be leaders in that community. Negotiations are underway to expand the area available to wild dogs onto surrounding private land, and dogs have bred on neighbouring farms. Wild dogs also move further afield: one dog photographed in Hluhluwe-Umfolozi in September 1993 was photographed again, later the same month, in Itala Game Reserve over 150 km away.

Wild dogs are now extinct in other protected areas in South Africa, including Mountain Zebra National Park, Karoo National Park, Addo Elephant Park and Bontebok National Park, which are all small (< 100 km²) and surrounded by livestock farms. They are also absent from the Golden Gate Highlands National Park, Umlalazi Public Resource and Nature Reserve, Loteni Nature Reserve area, and Mkuzi and Ndumu Game Reserves.

Swaziland

Status & Distribution

The only report of wild dogs from Swaziland comes from Milwane Wildlife Sanctuary, where a group of four males was seen pulling down a blesbok in December 1992. The dogs were seen repeatedly over a period of 1–2 weeks, but then disappeared. One of the individuals had a snare on its neck. These animals were probably vagrants, and there seems to be no resident population in Swaziland.

Zambia

Status

The outlook is uncertain, but could be reasonably hopeful. From the 1930s to the 1950s, wild dogs were shot by vermin control units. Records indicate that these units killed nearly 5,000 between 1945 and the end of 1959, and many more may have been shot by farmers (Buk 1994). Today the species receives total legal protection in Zambia. It may only be hunted legally with a special licence issued by the Minister of Tourism. Such licences cost *c.* US$100 to Zambians in 1991, but few – if any – have been issued in recent years (Buk 1994). Nevertheless, direct persecution is still the most important cause of mortality outside national parks (Buk 1994).

Despite these threats, wild dogs have a fair chance of surviving in Zambia. They are still reasonably widespread and the principal parks are large, if poorly managed. Commercial agriculture and livestock farming are limited in rural areas due to livestock diseases, infrastructure and the past economic and political climate. However, the Zambian wild dog population has declined since the 1990 survey. In 1986, wild dogs had two strongholds, one in and around Kafue National Park, and another in the Luangwa Valley system. However, more recent surveys carried out by Buk (1994) and Munyenembe & Tembo (1992) indicate that wild dogs have declined dramatically in Luangwa since an outbreak of anthrax in 1987. Furthermore, wild dogs are no longer sighted in several of the smaller parks which reported wild dogs as present in the 1980s (Buk 1994; Munyenyembe & Tembo 1992). These declines are a cause for concern about the long-term future of Zambia's wild dogs.

Distribution

Wild dogs' distribution in Zambia is summarized in Table 3.22 and Figure 3.16.

Wild dogs were recorded as present but declining in the Lusenga Plain National Park in 1988, but they have not been reported since then (Buk 1994).

There were two unconfirmed reports of wild dogs from Mweru Wantipa National Park (3,134 km²) in the early 1990s, but they are now probably declining or extinct there (Buk 1994). There is one unconfirmed report from the nearby Tondwa Game Management Area, and no records from Kaputa Game Management Area (Buk 1994). Dogs are sighted occasionally in Sumbu National Park (2,020 km²), most recently in 1993, but are almost certainly declining there (Buk 1994). Rabies was reported from Sumbu in 1991–2 and anthrax in 1992–3. Three wild dogs were found dead in Sumbu in 1991, either diseased or poisoned. Lions are common, and hyaenas, jackals and domestic dogs are present. Livestock losses have been reported, and public attitudes are negative.

North Luangwa National Park (4,600 km²) was thought to contain dogs in the late 1980s, and there were two confirmed reports in 1994 (Buk 1994). Dogs are sighted occasionally in the adjoining Musalangu and Lumimba Game Management Areas (Buk 1994; Munyenyembe & Tembo 1992). One respondent suggested that wild dogs might be declining in Lumimba due to poaching of their prey. Few livestock are present due to tsetse, and there are no reports of livestock losses. Local people, who acquire game meat from wild dog kills, are reported to have a positive attitude. Dogs are sighted rarely in Munyamadzi Game Management Area (Buk 1994; Munyenyembe & Tembo 1992) and are believed to be declining there, perhaps following an anthrax outbreak in 1992 (Buk 1994). There was, however, one confirmed sighting in 1996. There are no reports of livestock losses, but the public attitude is negative.

Wild dogs are now sighted reasonably often in the South Luangwa National Park (8,500 km², Buk 1994; Munyenyembe & Tembo 1992). Most records received from Zambia in the 1980s came from South Luangwa, but the population declined dramatically at the end of the 1980s. A resident elephant researcher saw only one wild dog in two years of fieldwork during 1991–3. This dramatic decline was probably caused by anthrax, which was documented in one pack of wild dogs in 1987 (Buk 1994; Munyenyembe & Tembo 1992). However, the population does seem to be recovering: wild dogs were reported just once in 1993, but 12 times in 1994 (Buk 1994). The habitat is mopane and miombo woodland, with riverine woodland. Domestic dogs are absent, but lions and spotted hyaenas are common. Some poachers enter the Park, and domestic dogs are common in the adjoining areas.

Wild dogs are recorded occasionally in the neighbouring Lupande Game Management Area (Buk 1994; Munyenyembe & Tembo 1992): there were several sightings in 1993, including one pack of 19 on the boundary with South Luangwa National Park. However, several field officers interviewed in 1993 had not seen any in recent years (Buk 1994). These dogs were probably affected by anthrax as in South Luangwa National Park. However, the population may now be recovering: prey are abundant, and the public attitude is indifference. However, there are many human residents, and both small livestock and domestic dogs are present.

Wild dogs are sighted occasionally in the neighbouring Luambe National Park (254 km²): there were three sightings in 1992–3. Two out of three respondents thought that the population was declining, and anthrax was reported from the Park in 1992. Lions, hyenas and jackals are common, and domestic dogs are present. The public attitude towards wild dogs is reported to be positive, and there are no livestock present due to tsetse flies.

Dogs are now rarely sighted in Lukusuzi National Park (2,700 km²): one game scout reported only four sightings between 1983 and 1993, although individuals almost certainly range into the Kasungu National Park, Malawi. Lions, hyaenas and domestic dogs are present, and rabies was reported from the Park in 1989.

We have no records from Sandwe, Chisomo or West Petauke Game Management Areas, although there were three sightings of dogs between Luangwa Bridge and Kachalola on the Great East Road in 1993. They are sighted very occasionally in Luano Game Management Area, although some respondents from this area had heard of no sightings for years (Buk 1994). There are no recent reports of anthrax or rabies, but hyaenas and domestic dogs are common. There are reports of livestock losses to wild dogs.

Dogs are sighted fairly regularly in the Lower Zambezi National Park (4,140 km²); one respondent reported having seen them six times in the previous year (Buk 1994). Wild dogs can cross the Zambezi into Mana Pools National Park, Zimbabwe, where dogs were seen regularly in 1995, and on into Moçambique

Table 3.22
A summary of wild dog distribution in Zambia. Zambia has a viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Blue Lagoon National Park	–	extinct	1994
Isangano National Park	840	extinct	1994
Kafue National Park	22,500	common	1994
Kasanka National Park	390	extinct?	1994
Liuwa Plain National Park	3,660	uncommon	1994
Lochinvar National Park	–	extinct	1994
Lower Zambezi National Park	4,140	rare	1994
Luambe National Park	320	uncommon	1994
Lukusuzi National Park	2,700	rare	1994
Lusenga Plain National Park	–	rare	1987
Mosi-Oa-Tunya National Park	66	extinct	1994
Mweru Wantipa National Park	3,134	extinct?	1994
North Luangwa National Park	4,600	rare	1994
Sioma-Ngwezi National Park	5,276	rare	1994
South Luangwa National Park	8,500	rare	1994
Sumbu National Park	2,020	rare	1994
West Lungar National Park	1,684	uncommon	1994
Bangweulu Game Management Area	–	extinct	1994
Kafue Flats Game Management Area	–	extinct	1994
Kasonso-Busanga G.M.A.	–	rare	1994
Lumimba Game Management Area	2,700	rare	1994
Lunga-Luswishi G.M.A.	13,340	rare	1994
Lupande Game Management Area	4,840	rare	1994
Luwingu Game Management Area	–	extinct	1994
Mulobezi Game Management Area	7,383	common	1994
Mumbwa Game Management Area	3,370	rare	1994
Munyamadzi G.M.A.	2,500	rare	1994
Musalangu Game Management Area	17,350	rare	1994
Namwala Game Management Area	–	rare	1994
Sichifulo Game Management Area	–	common	1994
Tondwa Game Mangement Area	–	1 sighting	1994
West Zambezi G.M.A.	–	rare	1994
Great East Road	n/a	3 sightings	1993

where there was one sighting in 1996. There are no reports from the adjoining Rufunsa Game Management Area.

Dogs were seen occasionally in the Kasanka National Park (390 km²) in the 1980s, but have not been reported since then (Buk 1994; Munyenyembe & Tembo 1992). There are no records from the adjoining Kafinda Game Management Area, or nearby Lavushi Manda National Park or Mansa and Chambeshi Game Management Areas (Buk 1994). They are probably extinct in Kalaso-Mukosa and Bangweulu Game Management Areas, both of which are much affected by poaching. In Bangweulu especially, domestic dogs are common and used by poachers. Wild dogs are probably extinct in Luwingu Game Management Area and Isangano National Park, where they were last seen in

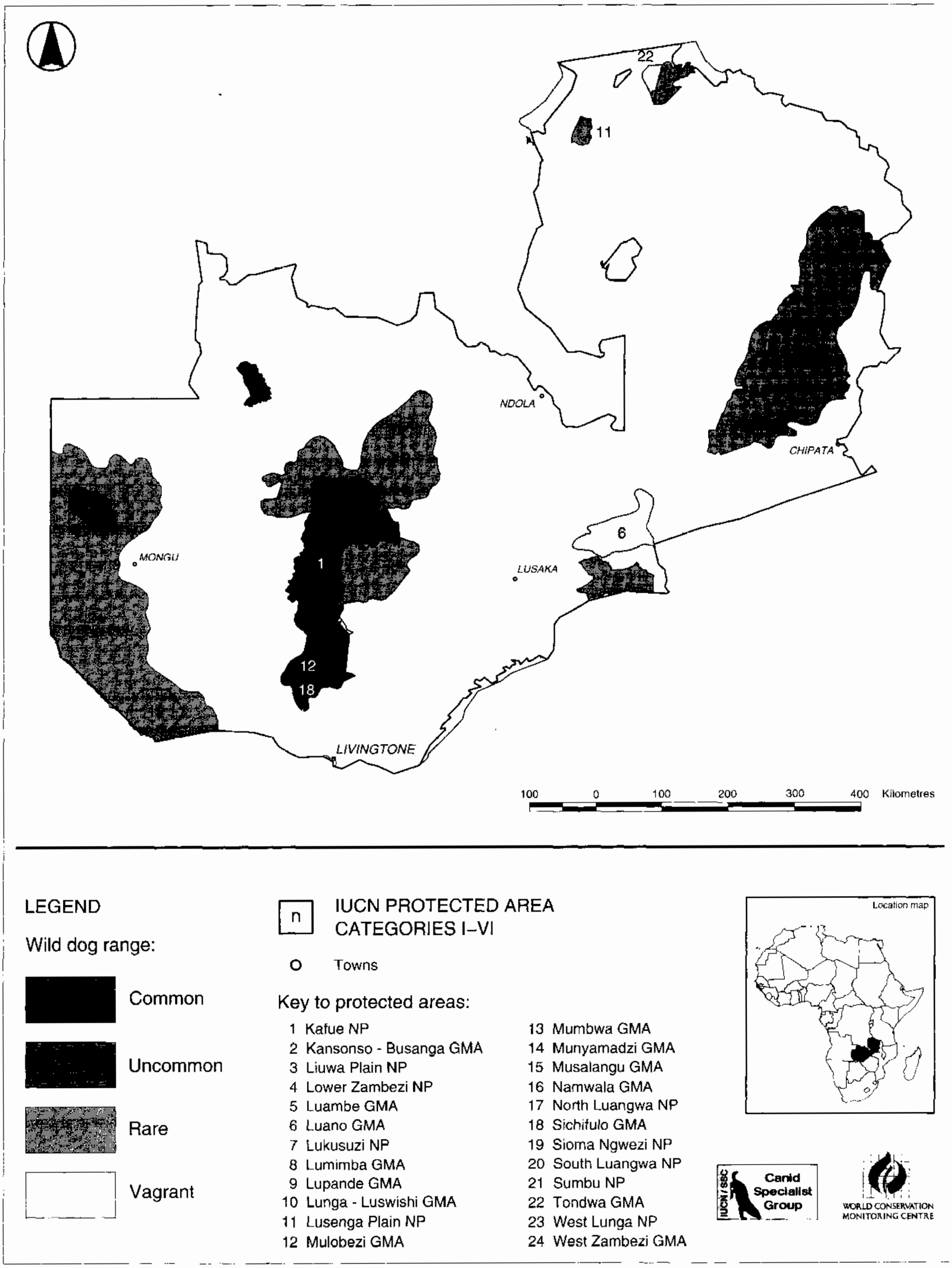


Figure 3.16. Wild dog distribution in Zambia.

the 1970s (Buk 1994).

Wild dogs are fairly common in Kafue National Park (22,500 km²), with frequent sightings in the southern command of the Park, and the southern part of the northern command (Buk 1994; Munyenyembe & Tembo 1992). This is probably the most important wild dog population in Zambia. The population appears to be stable, although prey are subject to poaching, especially along the western border. Furthermore, a road runs through the centre of the Park, causing substantial mortality. The habitat is woodland and open country, and wild dogs are reported to den in thickets. There are no reports of rabies, but there was a suspected anthrax outbreak in the northern command in 1990 (Buk 1994). Domestic dogs are absent, but lions are present and spotted hyaenas are abundant. Avoidance of these competitors might explain why there have been no wild dog sightings from the central part of the northern command where prey are abundant.

There are occasional wild dog sightings in the neighbouring Kasonso-Busanga Game Management Area (Buk 1994; Munyenyembe & Tembo 1992), including one report of a group of > 20 dogs in 1993. Two dogs were found snared in Kasonso-Busanga in 1991. In addition, wild dogs were sighted once in 1993 in the new Mufunta Game Management Area on the western side of Kafue National Park (Buk 1994). There are occasional sightings in Lunga-Luswishi Game Management Area, including one sighting in 1993 (Buk 1994). This population is believed to be declining due to poaching of prey. There are no reports of rabies or anthrax, but domestic dogs are present along with lions and hyaenas. There are no reports of livestock losses and the public are indifferent. No sighting of wild dogs come from Machiva-Fungulwe Game Management Area.

Wild dogs are sighted occasionally in Mumbwa and Namwala Game Management Areas, adjoining Kafue National Park (Buk 1994). Elephants are present in Namwala, which suggests that wildlife is relatively well protected there. National Parks and Wildlife Service Staff occasionally see dogs on the Lusaka-Mongu and Lusaka–Itezhi-tezhi roads (Buk 1994).

There are frequent sightings in Mulobezi and Sichifulo Game Management Areas, adjoining Kafue National Park, and pups were seen in 1994 and 1995. The population trend in this area is uncertain: anthrax occurred in Sichifulo in 1993, and rabies in 1992, and two wild dogs found dead there in 1992 were believed to have died from rabies (Buk 1994). Lions, hyaenas and domestic dogs are present. There have been several reports of livestock losses both inside and outside the borders of Sichifulo Game Management Area, and public attitudes are hostile. One wild dog was found killed by local people in 1992. There are no reports of wild dogs from Bilili Springs Game Management Area.

Wild dogs are probably now extinct in Kafue Flats Game Management Area and Blue Lagoon and Lochinvar National Parks (Buk 1994; Munyenyembe & Tembo 1992). Dogs were last seen in Lochinvar in 1986, in Kafue Flats in 1981, and in Blue Lagoon in the early 1970s. The presence of large numbers of Kafue lechwe in these areas, together with their proximity to the Kafue National Park complex, means that recolonization might be possible, although livestock farming is intensifying and all large carnivores are disappearing fast.

Wild dogs are present in West Lunga National Park (1,684 km²), although it is difficult to assess the sighting frequency because there are no field officers permanently resident in the Park (Buk 1994). There were four sightings in 1993, but respondents agreed that the population was in decline due to depletion of prey and possible persecution. Local people are very hostile to wild dogs. There are no reports from the adjoining Lukwakwa, Chibwika-Ntambu and Musele-Matebo Game Management Areas.

Wild dogs are sighted frequently in Liuwa Plain National Park (3,660 km²). The population trend is uncertain, but dogs were still being sighted in 1994 (Buk 1994; Munyenyembe & Tembo 1992). The habitat is mostly open plain, which may lead to a higher sighting frequency. Protection is poor – antipoaching patrols have neither vehicles nor radios – and there is a great deal of poaching, especially on the western side of the Park which faces Angola (Buk 1994). Roan antelope and buffalo have declined in this area although there are still large herds of migrating wildebeest. Lions are present, and hyaenas and domestic dogs are common. There are many villages both on and inside the Park border to the south-east, and the public are very hostile to wild dogs. Calves are killed occasionally, and there is an unconfirmed report of a woman being attacked by a rabid wild dog. Anthrax and rabies appear to occur frequently. Five wild dogs were shot in February 1993, and two more were found dead from unknown causes. Some additional sightings from the vast West Zambezi Game Management Area which encircles Liuwa Plain National Park (Buk 1994), but these were all very close to the Park borders. Occasional sightings come from Sioma-Ngwezi National Park (5,276 km², Buk 1994; Munyenyembe & Tembo 1992), with the most recent record from 1993. Rabies has occurred in this Park, although there are few or no domestic dogs. There are no reports of livestock losses, and local people are indifferent to wild dogs.

Wild dogs are extinct in the tiny Mosi-Oa-Tunya National Park (66 km², Buk 1994).

Zimbabwe

Status ☺

The outlook for wild dogs in Zimbabwe is uncertain, but hopeful. A survey carried out in 1985 concluded that the country supported between 310 and 430 wild dogs (Childes 1988), suggesting a seriously depleted population. A second survey carried out in 1990–2 estimated the total population at 400–600 individuals indicating that wild dogs have, at the very least, held their own in Zimbabwe (Davies 1992). Indeed, the population in Hwange National Park was increasing in the period 1990–2 (Davies 1992). Wild dogs were classed as 'vermin' between 1961 and 1975, and up to 600 wild dogs were killed by parks staff alone before they were afforded 'protected' status in 1986. Today, those wishing to shoot wild dogs must obtain a permit from the Department of National Parks. Only one such permit was issued in the period 1986–92 (Davies 1992), but livestock farmers continue to kill animals that stray onto their land.

Distribution

Wild dogs' distribution in Zimbabwe is summarized in Table 3.23 and Figure 3.17.

Wild dogs' stronghold in Zimbabwe is the area in and around Hwange National Park, including the Zambezi and Victoria Falls National Parks, Matetsi and Deka Safari Areas, and Kazuma Pan Forestry Area. Together, these comprise an area of *c.* 18,000 km² sustaining an estimated population of 250–300 wild dogs in approximately 35 packs (Davies 1992). The northern part of Hwange and adjacent forestry and game ranching areas contained 137 known individuals in 18 known packs in 1992, in an area of 9,000 km². This gives a density of 1.52 individuals/100 km² (*cf* 5.9 animals/100 km² in the Selous Game Reserve, Tanzania and 2.0 animals/100 km² in Kruger National Park, South Africa). In 1990–2, the Hwange population was increasing by 7% *p.a.* The habitat is a combination of short grassland, mixed scrub and well-developed woodland. Domestic dogs are kept at some camps, and spotted hyaenas are locally abundant. Some livestock losses in the area are blamed on wild dogs, although Park staff believe that most are caused by spotted hyaenas. Road casualties on the Bulawayo-Victoria Falls road constitute an important cause of mortality.

Wild dogs are present, if at low density, in the Zambezi valley in the north of the country, over an area of *c.* 11,000 km². In the period 1990–2 they were reported sporadically from the Charara, Urungwe, and Chewore Safari Areas, as well as the Mana Pools National Park (Davies 1992), where they were still

Table 3.23
A summary of wild dog distribution in Zimbabwe. Zimbabwe has a viable wild dog population.

Site	Area (km²)	Abundance	Date of estimate
Chizarira National Park	2,161	vagrant	1992
Gona re Zhou National Park	5,189	uncommon	1992
Hwange National Park	15,219	common	1992
Mana Pools	–	uncommon	1992
Matusadona National Park	1,343	extinct?	1992
Zambezi National Park	–	uncommon	1992
Charara Safari Area	–	rare	1992
Chete Safari Area	1,237	rare	1992
Chewore Safari Area	–	rare	1992
Chirisa Safari Area	1,498	extinct?	1992
Dande Safari Area	–	rare	1992
Doma Safari Area	–	rare	1992
Matetsi Safari Area	4,399	common	1992
Sapi Safari Area	–	rare	1992
Kazuma Pan Forestry Area	–	uncommon	1992

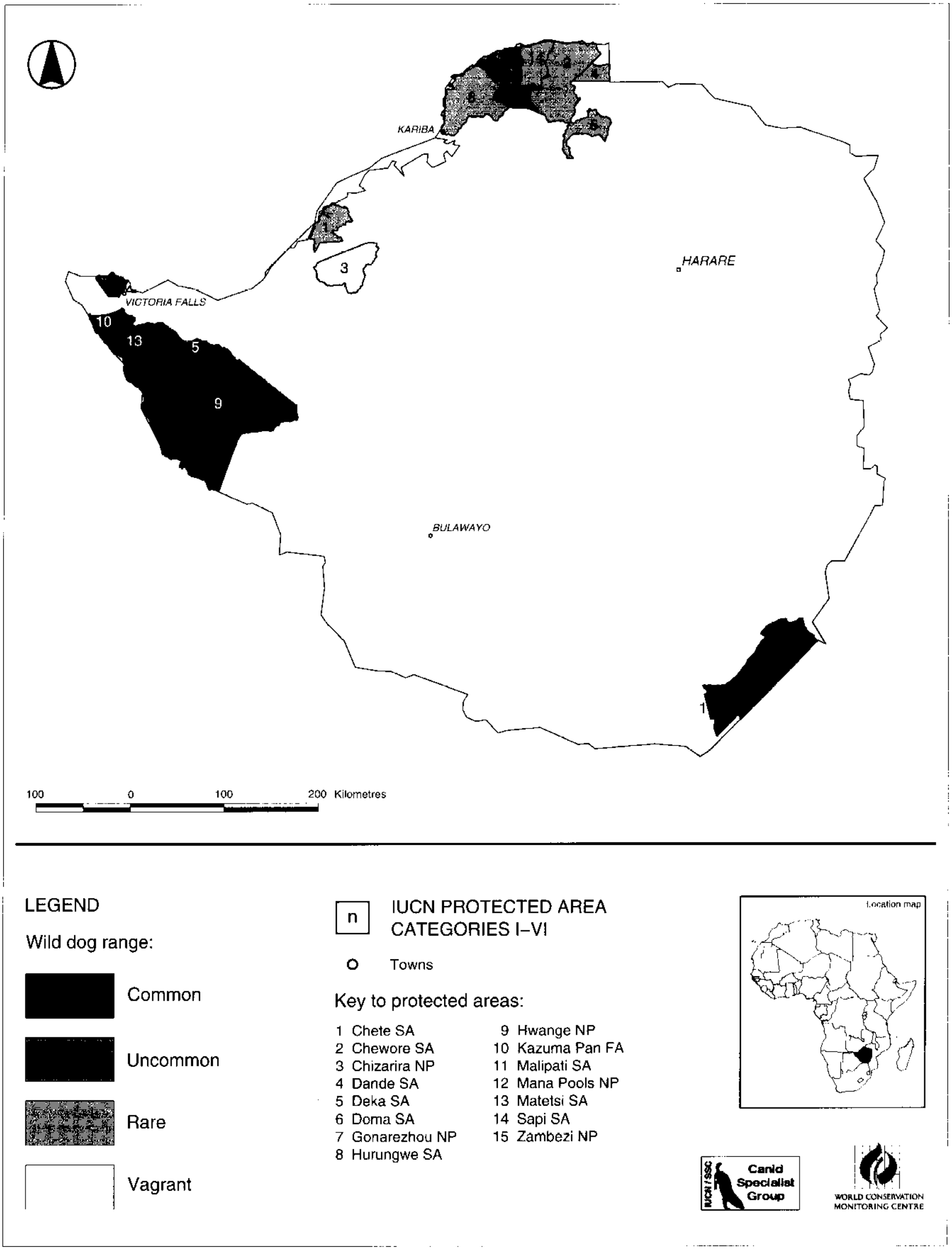


Figure 3.17. Wild dog distribution in Zimbabwe.

sighted regularly in 1995. There are also sightings in this area from neighbouring Zambia and Moçambique. Although no data were received in 1990–2, wild dogs are also believed to persist in the Sapi, Dande and Doma Safari Areas. The distribution of sightings suggests that a minimum of 58 individuals, in 5 packs, remained in this area in 1992 (Davies 1992), compared with an estimated 80–100 individuals in 1985 (Childes 1988). The habitat is a combination of mopane woodland, riverine fringes, deciduous-forest thickets, and *Brachystegia* woodland. Domestic dogs are absent, but spotted hyaenas are common. Livestock losses are blamed on wild dogs and in the 1980s farmers shot them on sight.

A few small packs of wild dogs are believed to persist in the Sebungwe region, where wild dogs were recorded 4 times in 1990–2 from the Chete Safari Area and Omay Communal Area (Davies 1992). The pack present in Chete is also believed to move into Chizarira National Park. Wild dogs were last seen in Chirisa Safari Area in 1984, and in Matusadona National Park in 1985. In 1992 there were an estimated 20 individuals in this area (Davies 1992), compared with 0–5 in 1985 (Childes 1988).

A population of wild dogs also persists in Gona re Zhou National Park (5,000 km²) in the south-east of the country, where there were 6 sightings in 1990–2, of an estimated minimum of 20–40 individuals in 2 packs (Davies 1992). This compares well with the 1985 estimate of 30–40 individuals (Childes 1988). Gona re Zhou is only 40 km from the northern tip of Kruger National Park, South Africa, and wild dogs almost certainly move between the two parks. The habitat is mopane woodland, broad-leafed deciduous woodland and mixed riverine forest/woodland. Domestic dogs are excluded from the Park, but are abundant in the surrounding areas. Spotted hyaenas are also abundant. No livestock losses have been reported. Heavily persecuted in the past, wild dogs are now regarded with indifference by local people.

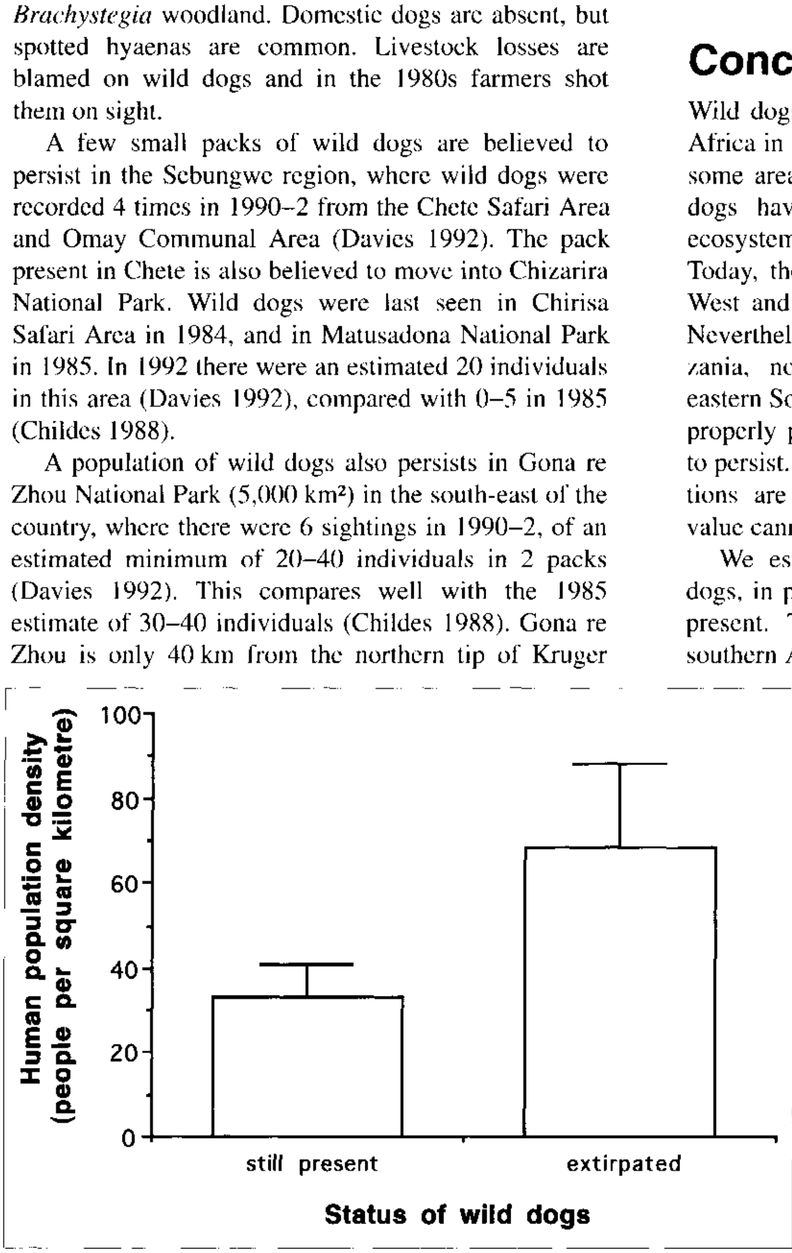


Figure 3.18. Human population densities in 34 countries in wild dogs' historic range, comparing countries where wild dogs have persisted with those from which they have been extirpirated.
Countries where wild dogs have persisted are characterized by having relatively low human population densities ($t_{1,33} = 1.71$, $p < 0.05$, 1-tailed).

Conclusions

Wild dogs have declined dramatically across much of Africa in the last 30 years, and this decline continues in some areas. For example, since the 1990 survey, wild dogs have largely disappeared from the Serengeti ecosystem, and been decimated in the Luangwa valley. Today, they are all but extinct across the majority of West and central Africa, and depleted in East Africa. Nevertheless, the larger populations in southern Tanzania, northern Botswana, western Zimbabwe and eastern South Africa appear relatively safe and stable. If properly protected, these populations ought to be able to persist. Because of this, these relatively large populations are extremely valuable and their conservation value cannot be overstated.

We estimate that between 3,000 and 5,500 wild dogs, in perhaps 600–1,000 packs, remain in Africa at present. The majority of these are in eastern and southern Africa. Both West and central Africa may each have only one reasonable population left: Niokolo-Koba National Park in Sénégal, and Faro & Benoué National Parks in Cameroun. Since these may be genetically distinct from other populations, they also have a very high conservation value.

Apart from these concentrations, wild dogs seem to be spread very thinly across most of Africa: packs, pack fragments and even single dogs are occasionally sighted in countries which have had no resident population for years (*e.g.* Nigeria, Swaziland, Uganda). Such dogs could be important as colonists for areas where wild dogs have become locally extinct. However, since they travel over large areas where wildlife are not protected, we expect that such dogs suffer high mortality and low reproductive success compared with populations resident in and around protected areas. It would be extremely difficult to devise measures that could protect such wide-ranging animals effectively.

What characterizes range states in which wild dogs have persisted? Perhaps the most important factor is human population density: countries which still have wild dogs have fewer people per square kilometre than those where wild dogs have been extirpated (Figure 3.18). This draws attention to the problems which almost always seem to emerge when wild dogs coexist with people: wild dogs are shot and poisoned, human hunting activities and cultivation deplete their prey base, fast-moving vehicles kill them and domestic dogs pass on diseases to them. In the next chapter, we shall discuss the threat that such problems represent to the wild dog populations remaining in Africa.

Chapter 4
Past and Future Causes of Wild Dogs' Population Decline

Rosie Woodroffe & Joshua R. Ginsberg

In the previous chapter we showed how wild dog populations have been extirpated across much of Africa over the last 30 years. This chapter reviews the factors that might cause the few remaining populations to decline or disappear altogether:

Habitat fragmentation, persecution and loss of prey *were the major causes of wild dogs' historic decline, and these factors still represent the principal threats today.*

Competition with larger carnivores *keeps wild dogs' numbers low, so that even the largest habitat fragments may contain populations too small to be viable.*

Contact with human activity *is directly responsible for over 60% of recorded adult mortality through road casualties, persecution and snaring. Even wild dogs living in large protected areas may stray over reserve borders where they are threatened by human activities.*

Disease *represents another serious threat to wild dogs, which has already caused the extinction of one population. The presence of people dramatically increases the disease risk to wild dogs, because domestic dogs provide a reservoir host for canid diseases.*

As a result of these pressures:

- *All of the wild dog populations remaining in Africa are under threat.*
- *In the long term, wild dogs living outside protected areas are unlikely to co-exist with growing human populations without innovative management.*
- *Even in large protected areas, wild dogs' long-term survival will depend on reducing potentially fatal contact with people and domestic dogs on reserve borders.*

Background

In the previous chapter we showed that wild dogs have declined throughout Africa, principally as a result of habitat fragmentation and human persecution. However, a number of authors have remarked that, even in large, well-protected areas, wild dogs always live at very low densities (*e.g.* Mills & Biggs 1993; Schaller 1972). For example, lion densities are 3–20 times those of wild dogs, and spotted hyenas may outnumber wild dogs by factors varying from 8 to over a hundred (Table 4.1, Creel & Creel 1996). In this chapter, we review the factors thought to keep wild dogs' numbers low, and discuss how these problems may be compounded by habitat fragmentation. In the next chapter, we use demographic modelling to assess the extent to which each of these factors might threaten the long-term persistence of wild dog populations.

In the broadest terms, the size of a population will be defined by the rate at which individuals arrive in it – by birth and immigration – and the rate at which they leave it – by death and emigration. Local population decline will occur when recruitment is low and mortality or emigration rates are high. Therefore, to understand why wild dogs are so rare, and to assess whether their numbers are likely to decline still further, we need to understand the factors controlling recruitment, mortality and dispersal. Our efforts to do this are hampered, to some extent, by the availability of data. Relatively little is known about the factors which contribute to breeding success or failure in wild dogs. Similarly, data on the causes of dispersal are rather sketchy: since wild dogs may disperse over very large areas, it is often difficult to distinguish dispersal from death (Burrows *et al.* 1995; Ginsberg *et al.* 1995a). However, reasonably good data are available on mortality of both adults and juveniles – and juvenile mortality represents a very important component of recruitment. In Tables 4.2 and 4.3, we have summarized the available data on causes of mortality in well-studied wild dog populations. These data form the basis of our discussion below. However, they should be interpreted with caution for two reasons. First, most of the study populations live inside or around national parks and

Table 4.1
Population densities of wild dogs relative to other large carnivores. Data taken from: [a]Fuller & Kat (1990); [b]Creel & Creel (1996); [c]Stander (1991); [d]J.R.G. Unpublished data, and Bowler (1991); [e]Mills & Biggs (1993).

	Population density (adults/100km²)				
Study site	**Wild dogs**	**Hyaenas**	**Lions**	**Leopards**	**Cheetahs**
Aitong, near Masai Mara	2.6 – 4.6[a]	20-40[a]	–	–	–
Hluhluwe-Umfolozi Park	3.3[b]	34[b]	–	–	7.8[c]
Hwange National Park	1.5[b]	17[d]	3.5[c]	2.1[c]	0.6[c]
Kruger National Park	2.0[e]	4.5[e]	6.5[e]	2.5[e]	1.5[e]
Selous Game Reserve	4[b]	32[b]	11[b]	–	–
Serengeti National Park					
1967–1979	1.5[b]	17[b]	7.9 – 9.4[b]	5.6[c]	–
1985–199	0.67[b]	82[b]	14[b]	–	2.3[c]

game reserves and may not be representative of populations outside of protected areas. Second, to know the cause of an individual's death one must find the carcass, and this is likely to bias the results. At the extreme, one is more likely to find an adult killed in a road accident than a pup that dies of disease underground. Radio-telemetry greatly improves the probability of recovering a carcass, and therefore provides a less biased assessment of the causes of adult mortality. Indeed, Ginsberg *et al.* (1995a) found that such biases led to significant differences in the causes of mortality observed in collared and un-collared wild dogs.

In this chapter, we first outline the effect of 'natural' factors, such as competition with other large carnivores, likely to limit wild dog numbers. We then discuss the effect of human activities such as road accidents and persecution. The third and final section deals with the diseases that affect wild dogs. Since domestic dogs are the most important reservoir for canid diseases, it is often unclear whether disease represents a 'natural' or a human-induced threat to wild dogs.

This wild dog was hit by a car in Hwange National Park and subsequently died of its injuries underground. This type of incident frequently makes carcasses difficult to locate.

'Natural' Factors that Might Keep Wild Dog Numbers Low

Indirect Competition with other Large Carnivores

The survival and reproductive success of a wild dog pack will depend, at least in part, upon its ability to secure prey. However, no wildlife communities are known to exist in which wild dogs are the only large predators: wild dogs coexist with other carnivores such as lions, spotted hyaenas, leopards and cheetahs. Wherever they have been studied, the spectrum of prey taken by wild dogs is very similar to that of other predators living in the same area (Creel & Creel 1996), raising the possibility that wild dogs might compete for prey with other carnivores. Specifically, other carnivores might reduce prey populations to such low levels that wild dogs are unable to locate and catch sufficient prey.

Where wild ungulates are abundant, such a scenario seems very unlikely. Ecological studies of wild dogs have suggested that their numbers are not limited by the availability of food (Ginsberg *et al.* 1995b; Mills &

An encounter between a hyaena and wild dog. Spotted hyaenas may appropriate kills from wild dogs.

Biggs 1993). Wild dogs are efficient predators: they seldom seem to experience problems finding prey and have a high success rate when hunting (Creel & Creel 1995; Estes & Goddard 1967; Fanshawe & FitzGibbon 1993; Schaller 1972). Furthermore, wild dogs are crepuscular, while their possible competitors are either mainly nocturnal (hyaenas, lions, leopards) or diurnal (cheetahs, Mills & Biggs 1993). Competition might reduce wild dogs' hunting success in areas where ungulate prey are very scarce. However, it seems unlikely that indirect competition with other large predators has a substantial effect upon wild dogs in most areas where there are still resident populations.

Direct Competition with other Large Carnivores

Indirect competition probably has no substantial effect upon wild dog numbers. However, although they are efficient hunters, wild dogs do sometimes lose their kills to scavengers – indeed, a number of authors have suggested that one benefit of sociality for wild dogs is that group living allows for more effective defence of the kill (Kruuk 1975; Lamprecht 1978).

Although wild dogs occasionally lose their kills to lions, spotted hyaenas are much more important kleptoparasites (Creel & Creel 1996). For example, in the Serengeti National Park, Tanzania, hyaenas were present at 86% of wild dog kills and always fed from carcasses eventually (Fanshawe & FitzGibbon 1993). Conversely, in Serengeti wild dogs appropriated just 1% of hyaena kills (Kruuk 1972). Hyaenas seem to find it more difficult to locate wild dog kills in denser vegetation: in the Selous Game Reserve, Tanzania, hyaenas were present at only 18% of kills (Creel & Creel 1996). Nonetheless, wild dogs often go out of their way to mob hyaenas in Selous and elsewhere (Creel & Creel 1996).

Does this direct competition for kills have any detrimental effect upon wild dogs? Again, the answer varies among populations. In Serengeti, where hyaena density was high and wild dog kills highly visible, the presence of four or more hyaenas did reduce the time wild dogs were able to spend feeding from carcasses and, presumably, the amount that they ate (Fanshawe & FitzGibbon 1993). This effect was mitigated when more wild dogs were present: feeding time increased with the ratio of dogs to hyaenas. In contrast, in the thicker vegetation of Selous, where hyaena density was lower and relatively fewer hyaenas were attracted to wild dog kills, the presence of hyaenas had no effect on the time wild dogs spent feeding from each carcass. Hyaenas eventually fed from just 2% of wild dog kills in Selous, and wild dogs seemed to make no effort to avoid using areas frequented by hyaenas (Creel & Creel 1996).

Direct competition with hyaenas might depress wild dog numbers by reducing their feeding success – this might lead to both higher mortality and lower reproductive success, and, thus, to smaller populations. Fuller & Kat (1990) showed that wild dog packs have a relatively high food intake rate when they are feeding pups (average 4.1 kg/dog/day with pups, compared with 1.6 kg/dog/day without), and pointed out that one pack with a food intake rate similar to that of a pack without pups (2 kg/dog/day) subsequently abandoned the litter that it was raising. Thus, it is possible that reduced feeding time as a result of harassment by spotted hyaenas might cause wild dogs to abandon their pups. Creel & Creel (1996) found a negative correlation between the population densities of wild dogs and spotted hyaenas across five study sites in eastern and southern Africa. Unfortunately, areas with high densities of hyaenas also have abundant lions, making it difficult to disentangle the effects of the two larger carnivores on wild dog numbers (see below).

Predation by other Large Carnivores

Although wild dogs are predators themselves, they are also the victims of predation. Twenty-two percent of adult mortality (16/74 deaths) and 42% (19/45) of juvenile mortality across study sites can be attributed to predation by other large carnivores (Tables 4.2 & 4.3). Of those animals killed, 75% (12/16) of adults and 89% (17/19) of pups were killed by lions. Predation by spotted hyaenas is less important: there are reports of just one adult and two juvenile wild dogs being killed by hyaenas (Tables 4.2 & 4.3), and the two pups were debilitated by anthrax (Creel *et al.* 1995). The relative importance of the two predators is reflected in wild dogs' response to them – wild dogs move away from the sound of lions roaring, but they mob hyaenas (Creel & Creel 1996).

Predation by lions is likely to have a marked effect

Table 4.2
Causes of adult mortality in free-ranging populations of African wild dogs. Figures give the percentages of deaths attributed to each cause; numbers in brackets give the total number of known deaths recorded in that study site. References: [a]van Heerden *et al.* (1995); [b]Ginsberg *et al.* (1995); [c]K. Buk, Unpublished data.

	Kruger National Park, South Africa[a]	Northern Botswana[b]	Hwange National Park, Zimbabwe[b]	Selous Game Reserve, Tanzania[b]	Various parts of Zambia[c]	TOTAL
Natural Causes:						
Predators						
Lions	26% (19)	47% (15)	–	0% (4)	0% (36)	**16% (74)**
Spotted hyaenas	0% (19)	7% (15)	–	0% (4)	0% (36)	**1% (74)**
Unknown/others	11% (19)	7% (15)	–	0% (4)	3% (36)	**5% (74)**
Other wild dogs	16% (19)	0% (15)	–	50% (4)	0% (36)	**7% (74)**
Disease	0% (19)	0% (15)	–	0% (4)	22% (36)	**11% (74)**
Accident	0% (19)	33% (15)	–	0% (4)	0% (36)	**7% (74)**
Total natural causes	**53% (19)**	**94% (15)**	**19% (31)**	**50% (4)**	**25% (36)**	**39% (105)**
Human Causes:						
Road kill	5% (19)	0% (15)	52% (31)	0% (4)	22% (36)	**24% (105)**
Snared	21% (19)	0% (15)	10% (31)	25% (4)	6% (36)	**10% (105)**
Shot	21% (19)	0% (15)	19% (31)	0% (4)	14% (36)	**15% (105)**
Poisoned	0% (19)	0% (15)	0% (31)	25% (4)	33% (36)	**12% (105)**
Unknown	0% (19)	7% (15)	0% (31)	0% (4)	0% (36)	**1% (105)**
Total human causes	**47% (19)**	**7% (15)**	**81% (31)**	**50% (4)**	**75% (36)**	**61% (105)**

upon wild dog populations, even though wild dogs form a negligible part of lions' diet. Field studies of community ecology indicate that predators are more likely to suppress the populations of prey that they kill only opportunistically (Erlinge *et al.* 1984). While predators will suffer themselves if they cause a reduction in the numbers of their favoured prey, they will compensate for the loss of less favoured prey by feeding upon other species. This may explain the finding that large predators can often limit the numbers of smaller predators, which form part of their diet (Polis & Holt 1992). African golden cats appear to be limited in part by leopard predation (Hart *et al.* 1996), swift foxes may be limited by coyotes (Carbyn *et al.* 1994), and predation by lions is the single most important cause of juvenile mortality in cheetahs (Laurenson 1994).

Lions are a major source of both adult and pup mortality.

Does lion predation have any effect upon wild dog populations? Several lines of evidence suggest that it does. First, there is a correlation between the population densities of wild dogs and lions across four populations, with wild dog density highest where lions are scarce (Creel & Creel 1996). Unfortunately, areas with high densities of lions also have abundant hyaenas, making it difficult to disentangle the effects of the two larger carnivores on wild dog numbers (see above). Second, an attempt to reintroduce wild dogs to Etosha National Park, Namibia, failed when a pride of lions killed members of the introduced pack (Scheepers & Venzke 1995). Finally, a sudden crash in the population of lions in the Ngorongoro crater in the mid-1960s was followed by the appearance of wild dogs in the area. As the lion population recovered, wild dogs disappeared (Creel & Creel 1996).

Table 4.3

Causes of pup mortality in free-ranging populations of African wild dogs. Figures give the percentages of deaths attributed to each cause; numbers in brackets give the total number of known deaths recorded in that study site. References: [a]van Heerden *et al.* (1995); [b]Ginsberg *et al.* (1995).

	Kruger National Park, South Africa[a]	Selous Game Reserve, Tanzania[b]	TOTAL
Natural Causes:			
Predators			
Lions	37% (38)	43% (7)	**38% (45)**
Spotted hyaenas	0% (38)	29% (7)	**4% (45)**
Other wild dogs	50% (38)	0% (7)	**42% (45)**
Disease	8% (38)	29% (7)	**11% (45)**
Total natural causes	**95% (38)**	**100% (7)**	**96% (45)**
Human Causes:			
Road kill	0% (38)	0% (7)	**0% (45)**
Snared	5% (38)	0% (7)	**4% (45)**
Shot	0% (38)	0% (7)	**0% (45)**
Unknown	0% (38)	0% (7)	**0% (45)**
Total human causes	**5% (38)**	**0% (7)**	**4% (45)**

Human-induced Factors that Might Keep Wild Dog Numbers Low

Road Casualties

The contribution of road traffic accidents to wild dog mortality varies between populations as a result, it seems, of the distribution and quality of roads. Where parks authorities keep speed limits low, and where roads are poor, very few wild dogs are hit by vehicles; only one of 23 adult wild dogs found dead in Kruger and Selous was killed by a vehicle (Table 4.2). However, road traffic accidents may be the single most important cause of adult mortality where wild dogs occupy areas with good roads used by fast-moving traffic. More than half the recorded adult mortality in Hwange National Park, Zimbabwe, is caused by accidents on the road between Bulawayo and Victoria Falls which runs along the northern edge of the Park (Table 4.2). In addition, three wild dogs were killed on a 20 km stretch of the Tanzania-Zambia highway where it passes through Mikumi National Park, Tanzania, in a 15 month period (Drews 1995), and Tanzania National Parks records indicate that in one year 11 wild dogs were killed by vehicles passing through Mikumi (Creel & Creel 1993). In recent years eight wild dogs have been killed on the Lusaka-Mongu highway in Zambia, where it passes through Kafue National Park (K. Buk, pers. comm.).

Outside protected areas, road casualties are likely to cause relatively more wild dog deaths than inside them. For example, very few wild dogs use the area around Bulawayo, Zimbabwe, but two were killed within 30 km of the city within a two year period (J.R.G., Unpublished data). Where roads are available, wild dogs use them to move and hunt. Indeed, road kills constitute an important source of information about the distribution of wild dogs living outside protected areas (See Chapter 3).

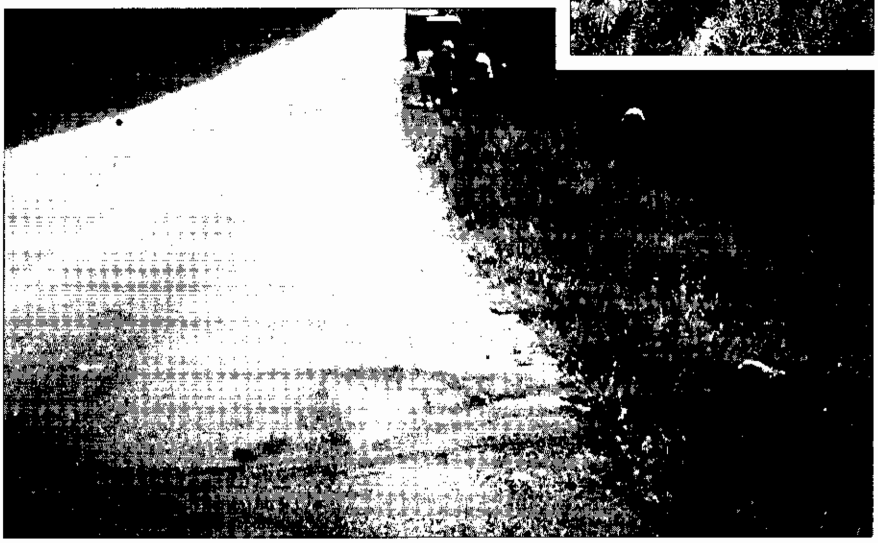
Direct Persecution

Direct persecution by man has, perhaps, been the single most important cause of wild dogs' decline throughout Africa in the last century. Wild dogs were shot as vermin, even in national parks where, as Bere (1955) commented: "...it was considered necessary, as it had often been elsewhere, to shoot wild dogs in order to give the antelope opportunity to develop their optimum numbers...". Such shooting continued for many years; for example, wild dogs were shot by park staff until as recently as 1973 in Tanzania, 1975 in Zimbabwe, and 1979 in Niger (see Chapter 3).

Although persecution of wild dogs is no longer national parks' policy, direct persecution by man remains an important cause of mortality even in populations inhabiting protected areas: Table 4.2 shows that shooting and poisoning accounted for the deaths of 28/105 (27%) adult wild dogs across five areas – and four of these areas are at least partially protected. Local people are also known to poison wild dogs in the Maasai steppe, in Tanzania (Fitzjohn 1995).

Wild dogs are persecuted where they are perceived as a pest which kills livestock, or competes with people for wild ungulates in hunting areas. For example, an unconfirmed report suggests that over 50 wild dogs were shot on a hunting concession outside Hwange National Park between 1987 and 1991. Such persecution represents an important cause of mortality, even for dogs which spend much of their time inside the Park.

The available evidence suggests that wild dogs' reputation as voracious stock-killers is rarely justified (Bowler 1991). Livestock are taken occasionally but, where wild prey are available, losses to farmers seem to be small, especially for lar-



Road accidents are one of the major causes of mortality among wild dogs.

ger livestock. The only systematic study of this problem found that, over a two-year period, wild dogs took just 26 cattle from a herd of 3,132 in the Nyamandhlovu region of Zimbabwe, and all of these were calves and weaners rather than adults (Rasmussen 1996). Losses to wild dogs accounted for just 1.8% of the combined financial cost of all livestock losses. However, losses of small stock may be dramatic: one pack of wild dogs killed 70 ewes and 67 lambs on a single ranch in Laikipia in 1996 (M. Dyer pers. comm.). As for other canids (Ginsberg & Macdonald 1990), levels of stock loss to wild dogs may be low overall, but a few farms tend to suffer disproportionately and local losses may be severe.

Nevertheless, if wild prey are available wild dogs usually ignore livestock (Fuller & Kat 1990) – indeed, on one occasion wild dogs in Nyamandhlovu passed through a calf paddock to chase a kudu in the adjacent paddock (Rasmussen 1996). Despite these low stock losses, farmers in this area of Zimbabwe wanted the wild dogs killed. Thus, persecution remains a serious problem for wild dogs living in unprotected areas. Farmers are known to shoot wild dogs in most places where they occur outside protected areas. In countries where wild dogs survive mostly outside protected areas, such as Namibia, Kenya and Ethiopia, such persecution must represent a very serious threat to their long term survival. Since packs using parks and reserves may also make frequent and extensive forays into unprotected areas, they are also vulnerable to persecution.

Snaring

Snares cause a significant proportion of wild dog mortality, even for populations living inside protected areas: 10/105 (10%) of adult deaths were caused by snares (Table 4.2). Snares are less of a problem for pups, causing the deaths of only 2/45 pups (4%).

In most places, snares are not set to catch wild dogs: they are caught accidentally in snares set for ungulates. Thus, wild dog mortality is an incidental effect of subsistence hunting outside protected areas, and poaching inside them. Wild dogs living in parks and reserves often encounter snare lines as they move out into unprotected areas (S. Creel pers. comm.) – a similar phenomenon is common in spotted hyaenas (Hofer *et al.* 1993).

In some areas of Zimbabwe parts of wild dogs are used for ritual and medicinal purposes – thus snares are set specifically to catch wild dogs (J.R.G., Unpublished data). Such snares may cause very high mortality within individual packs.

Accidental snaring may be an important cause of mortality. This snare was removed by a researcher and the dog survived.

Diseases Affecting Wild Dogs

The threat that disease poses to endangered species has been recognized more and more in recent years (Dobson & Hudson 1986; Karesh & Cook 1995). For example, canine distemper brought the black-footed ferret to the brink of extinction (Williams *et al.* 1988), and a similar disease has been implicated in the extinction of the thylacine (Guiler 1961). Might disease, then, pose a threat to the remaining wild dog populations?

Many authors have noted wild dogs' susceptibility to disease, and suggested that this might help to explain their low densities (*e.g.* Bere 1955; Schaller 1972). This makes it surprising that Tables 4.2 & 4.3 show little evidence of disease-induced mortality: only 8 of 74 adults (11%), and 5 of 45 pups (11%) are believed to have died from disease across study sites. One reason for this apparent paradox is that the mortality from disease is mostly episodic in wild dogs: numbers might remain stable for several years, but then a single epizootic may cause sudden dramatic decline or even local extinction. The data presented in Tables 4.2 & 4.3 come from stable populations unaffected by epizootics at the time of study. Other studies (for which systematic mortality data are not available) show a different picture. Rabies caused the death of 21 of the 23 wild dogs in the Aitong pack outside the Masai Mara National Reserve, Kenya, leading to the extinction of the pack in a period of just 44 days in 1989 (Kat *et al.* 1995). By June 1991, the whole wild dog study population of the Masai Mara and the contiguous Serengeti National Park, Tanzania – a total of eight packs – had disappeared, with disease suspected or confirmed in each case. Disease was therefore believed to have caused the extinction of the wild dog study population in the Serengeti ecosystem (see Appendix 1). Disease also seems to have caused local population decline in other areas. For example, sightings of wild dogs declined dramatically after an outbreak of anthrax in ungulates in the Luangwa Valley, Zambia, which is also known to have killed wild dogs (Turnbull *et al.* 1991), and population declines of wild dogs in north-west Zimbabwe in the early 1980s coincided with an epidemic of rabies in jackals (Childes 1988; Kennedy 1988).

In the following sections, we detail the pathogens which are known to infect free-ranging populations of wild dogs. In Table 4.4, we present data on the prevalence of infection with these pathogens where such data are available. It should be borne in mind that many of these data depend upon serology; that is, the data show which animals have antibodies to the various pathogens or to the toxins they secrete, but give no information about how or when the animals were exposed to the pathogens. The proportion of seropositive animals within a population is affected by a number of factors. A high seroprevalence could indicate that most animals become infected early in life, but that the resulting disease is mild and most animals recover and become immune. Alternatively, the same seroprevalence could indicate that the population has recently experienced an epidemic of a highly virulent disease, and that only those that survived infection (and are thus seropositive) remain in the population. The pattern of seroprevalence in different age classes can help to distinguish between these alternatives (Thrusfield 1986). However, the sample sizes for wild dogs are rarely large enough to allow assessment of such patterns. In the absence of these data, we have inferred the likely impact of each pathogen from observations of wild dogs in the field and in captivity, and from the effect of each disease upon domestic dogs (Table 4.5).

We have designated the pathogens known to cause substantial mortality in wild dogs with the symbol ☠. The effects of the various pathogens are also summarized in Table 4.5. A number of patterns emerge from this survey, which we discuss at the end of the section. The possible impacts of some of these pathogens on population persistence are investigated in the following chapter.

Viral Infections

Rabies Virus ☠

Rabies is a rhabdovirus which may infect all mammals. In North America and Europe, populations of wild carnivores such as racoons and red foxes represent the major reservoir for the virus, but in Africa, as well as Asia and South America, poorly supervised domestic dogs are the principal host (Baer & Wandeler 1987). Rabies represents a major threat to endangered canids: one epidemic halved the population of Ethiopian wolves in the Bale Mountains National Park, Ethiopia (Sillero-Zubiri *et al.* 1996), while another threatened the Blanford's fox in Israel (Macdonald 1996).

Rabies is known to cause high mortality in wild dogs. In 1989, a well-studied pack living at Aitong, outside the Masai Mara National Reserve, Kenya, was decimated by rabies (Kat *et al.* 1995). The following year, at least one wild dog died of rabies in the adjoining Serengeti National Park, Tanzania (Gascoyne *et al.* 1993). Wild dog packs under study in the Serengeti ecosystem disappeared in 1991, and, although the ultimate cause is not certain, rabies is the most likely culprit (Burrows 1992). The circumstances surrounding the Serengeti extinction are discussed in detail in Appendix 1. Rabies is also known to have killed wild dogs in the Central African Republic (A.K. Turkalo pers. comm.) and in Namibia (Scheepers & Venzke 1995), and is believed to have killed dogs in Zimbabwe (C.M. Foggin, cited in Kat *et al.* 1995) and Zambia (K. Buk pers. comm.).

Rabies virus is transmitted principally by biting. In the Aitong pack, infected animals joined in with group activities such as greetings and cooperative hunting, but were often attacked by other group members (Kat *et al.* 1995). This led to biting and, presumably, transmission of the virus. Infected animals became disoriented and lost their appetites, but chewed and consumed non-food items. They became ataxic and progressively paralysed (Kat *et al.* 1995). These symptoms are similar to those of 'dumb' rabies in domestic dogs (Baer & Wandeler 1987).

The few data available on rabies dynamics in wild dogs suggest that the infection would be unlikely to persist in their populations. The disease spread rapidly through the Aitong pack: the time from the first suspected infection of a single pack member to the death of the last of the 21 dogs that died was less than two months (Kat *et al.* 1995). Since transmission of the

Table 4.4

Prevalence of disease in free-ranging populations of African wild dogs. The prevalences marked with an asterisk (*) refer to the proportion of individuals sampled which had antibodies to the pathogen; other prevalences were measured directly. All samples were taken from live animals, apart from those marked †, which were collected *post mortem*. Where samples were taken from both live and dead animals, results are given for both.

	Study Population						
	Kruger National Park, South Africa	**Hluhluwe - Umfolozi Park, South Africa**	**Masai Mara National Reserve, Kenya**	**Serengeti National Park, Tanzania**	**Moremi Game Reserve, Botswana**	**Selous Game Reserve, Tanzania**	**Tsumkwe District, Namimbia**
Viruses							
Adenovirus (infectious canine hepatitis)	84%*[a]	–	present*[b]	25%(16)*[c]	–	–	83%(6)*[d]
African horse sickness virus	36%(11)*[e]	–	13%(15)*[e]	28%(18)*[e]	54%(24)*[e]	–	–
Bluetongue virus	83%(12)*[f]	–	33%(18)*[f]	57%(14)*[f]	96%(24)*[f]	–	–
Canine coronavirus	65%(31)*[a]	–	present*[b]	–	–	–	0%(6)*[d]
Canine distemper virus	0%(43)*[a]	100%(4)*[g]	0%(12)*[h]	0%(16)*[c]	50%(6)*[g]	59%(22)*[i]	67%(6)*[d]
Canine herpes virus	–	–	present*[b]	–	–	–	–
Canine para-influenza virus	68%(31)*[a]	–	–	–	–	–	83%(6)*[d]
Canine parvovirus	0%(43)*[a]	–	7%(15)*[j]	67%(6)*[k]	–	88%(8)*[i]	0%(6)*[d]
Rabies virus	0%(31)*[a]	–	0%(18)*;present†[l]	25%(12)*[m]	–	0%(22)*h;0%(2)†[n]	0%(6)*[d]
Reovirus Type 3	29%(31)*[a]	–	–	–	–	–	–
Rotavirus	53%(31)*[a]	–	–	–	–	–	0%(6)*[d]
Bacteria							
Bacillus anthracis (anthrax)	0% (12)*; present†[a]	–	–	–	–	present†[n]	–
Brucella abortus (brucellosis)	–	–	–	33%(3)[o]	–	–	–
Coxiella burnetti (Q fever)	28% (29)*[a]	–	–	–	–	–	–
Ehrlichia canis	0% (29)*[a]	–	9%(12)[i]	–	–	–	–
Rickettsia conori/africae	93% (29)*[a]	–	–	–	–	–	–
Protozoa							
Babesia canis	7% (29)[a]	–	–	6%(16)[p]	–	–	–
Hepatozoon sp.	90% (29)[a]	–	–	81%(19)[p]	–	–	–
Neospora caninum	suspected[g]	–	–	–	–	–	–
Toxoplasma gondii	100% (16)*[a]	–	–	–	–	–	–
Macroparasites							
Taenia sp.	30% (46)[a]	–	–	–	–	–	–
Ancylostoma caninum	24% (46)[a]	–	present[q]	–	present[q]	–	–
Dipetalonema reconditum	68% (44)[a]	–	–	–	–	–	–
Toxascaris canis	2% (46)[a]	–	–	–	–	–	–

References: [a]van Heerden *et al.* (1995); [b]K. Alexander Unpublished data; [c]M.K. Laurenson Unpublished data; [d]Laurenson *et al.* (in prep.); [e]Alexander *et al.* (1995); [f]Alexander *et al.* (1994); [g]J. van Heerden Unpublished data; [h]Alexander & Appel (1994); [i]Creel *et al.* (in prep.); [j]Alexander *et al.* (1993a); [k]Fuller *et al.* (1992); [l]Alexander *et al.* (1993b); [m]Gascoyne *et al.* (1993); [n]Creel *et al.* (1995); [o]Sachs *et al.* (1968); [p]Peirce *et al.* (1995); [q]van Heerden *et al.* (1994).

Table 4.5
Pathogens that have been recorded in free-ranging populations of wild dogs, and their likely effects. We have also given the effect of each pathogen on domestic dogs where the effects on wild dogs are unknown. Effects marked with asterisks (*) are more severe in mixed infections. Data sources are given in the text.

Pathogen	Known to infect wild dogs?	Known effect on wild dogs	Effect on domestic dogs
Viruses			
Adenovirus	yes	?	severe in pups
African horse sickness	yes	?	some mortality
Bluetongue virus	yes	?	abortion
Canine coronavirus	yes	?	mild*
Canine distemper virus	yes	severe	severe
Canine herpes virus	yes	?	severe in newborns
Para-influenza virus	yes	?	mild*
Parvovirus	yes	?	severe in pups*
Rabies	yes	severe	severe
Reovirus Type 3	yes	?	probably none*
Rotavirus	yes	?	probably none
Bacteria			
Bacillus anthracis (anthrax)	yes	sometimes severe	–
Brucella abortus (brucellosis)	yes	?	abortion?
Coxiella burnetti (Q fever)	yes	?	probably none
Ehrlichia canis (ehrlichiosis)	suspected	less severe	severe
Rickettsia conori/africae	yes	?	probably none
Protozoa			
Babesia canis	yes	occasionally severe	occasionally severe
Hepatozoon sp.	yes	?	none
Toxoplasma gondii	yes	occasionally severe?	–
Neospora caninum	suspected	occasionally severe?	paralysis & abortion

virus between pack members is rapid, the incubation period is short, and mortality seems very high, the virus would probably cause its own local extinction before it could be transmitted to another pack (Kat *et al.* 1995; Mills 1993). Rather than persisting in wild dogs, rabies is probably maintained in the populations of other hosts, which act as a reservoir from which infection occasionally spills over into wild dogs. Rabies is endemic in the domestic dog populations of some areas surrounding the Serengeti ecosystem (Cleaveland & Dye 1995), and the virus which decimated the Aitong pack was genetically indistinguishable from one isolated from local domestic dogs (Kat *et al.* 1995). Thus, in this case domestic dogs appear to have been the reservoir host for rabies. However, in southern Africa wild canids, such as jackals and foxes, may be more important in maintaining the infection (Nel 1993).

Canine Distemper Virus

Canine distemper virus is a morbillivirus related to rinderpest, human measles, and phocine distemper, which is transmitted by inhalation of airborne viral particles (Appel 1987c). The virus attacks most terrestrial carnivores, and in the past it has led to dramatic declines in populations of black-footed ferrets (Williams *et al.* 1988) and lions (Roelke-Parker *et al.* 1996). Wild dogs' susceptibility to canine distemper virus has been demonstrated on several occasions when vaccination of captive animals with live attenuated vaccines has been followed by distemper-like disease and death (Durchfeld *et al.* 1990; McCormick 1983; van Heerden *et al.* 1989).

There is only one confirmed case of free ranging wild dogs' dying of canine distemper – ten died in northern Botswana in 1994 (Alexander *et al.* 1996). However, circumstantial evidence suggests that distemper has caused the deaths of many wild dogs in the past. Schaller (1972) described how members of one pack in Serengeti contracted a disease which resembled "...a typical picture of the gastrointestinal form of distemper...". However, neither canine distemper virus nor antibodies were identified, so this diagnosis remains unconfirmed. Reich 1981 (cited in van Heerden *et al.* 1995) also reported nervous symptoms of a disease resembling canine distemper in wild dogs in Kruger although, again, the diagnosis was not confirmed. A wild dog showing symptoms of canine distemper was seen in Hluhluwe-Umfolozi Park in 1995 (J. van Heerden pers. comm.). Finally, the extinction of wild dogs in the Serengeti/Masai Mara area in 1990–1 has been attributed to an epidemic of canine distemper (Alexander & Appel 1994; Macdonald *et al.* 1992), although other authors have contested this (Burrows *et al.* 1995). This possibility is discussed in detail in Appendix 1.

Serological surveys indicate, however, that canine distemper infection is not always fatal for wild dogs. High seroprevalences have been recorded recently in Hluhluwe-Umfolozi Park, in Northern Botswana, in the Selous Game Reserve, and in Tsumkwe District, Namibia (J. van Heerden & J.W. McNutt, pers. comm., Creel *et al.* in prep.; Laurenson *et al.* in prep.). indicating that some wild dogs had contacted the virus and survived. The mortality caused by canine distemper infection is not clear. No signs of distemper-related mortality or sickness have been recorded in Selous, despite intensive monitoring (Creel *et al.* in prep.). Possible evidence of disease has been seen in Hluhluwe, however (J. van Heerden pers. comm.), and at least one pack in Northern Botswana was decimated by canine distemper (Alexander *et al.* 1996).

It has been suggested that, as for rabies, domestic dogs may act as a reservoir host for canine distemper. Indeed, in areas where wild dogs are known or suspected to have been infected with canine distemper, local domestic dog populations show high seroprevalence for canine distemper virus (Table 4.6). However, wild dogs also show a high prevalence of antibodies to canine distemper in Selous, even though domestic dogs (and other wild canids) are very rare. The nearest concentration of domestic dogs is in Morogoro, some 70 km from Selous, where domestic dogs have experienced canine distemper (S.R. Creel pers. comm.). Thus, it appears that canine distemper may be persisting in Selous without recourse to a domestic dog reservoir. If the infection is persisting in the wild dogs themselves, it is possible that the viral strain has a relatively low pathogenicity for wild dogs (Creel *et al.* in prep.). Alternatively, some other wild carnivore might be acting as a reservoir. More research is needed to reveal the impact of canine distemper infection on free-ranging wild dog populations.

Canine Parvovirus

Canine parvovirus is a virus that replicates only in canids. It appeared, apparently by mutation, in the late 1970s and spread rapidly to domestic dogs world-wide (Appel & Parrish 1987). Antibodies to the virus have

Table 4.6
Seroprevalence of canine distemper virus in sympatric populations of wild and domestic dogs. Figures give the percentage of dogs sampled that were seropositive; numbers in brackets are the sample sizes. References: [a]J. van Heerden Unpublished data; [b]Alexander & Appel (1994); [c]M.K. Laurenson Unpublished data; [d]Roelke-Parker et al. (1996); [e]Laurenson et al.(in prep.).

	Seroprevalence	
Study site	**Wild dogs**	**Domestic dogs**
Hluhluwe-Umfolozi Park	100% (4)[a]	80% (50)[a]
Masai Mara National Reserve	0% (16)[b] (but some deaths suspected)	19% (219)[b]
Serengeti National Park	0% (16)[c] (but some deaths suspected)	48% (297)[d]
Tsumkwe District	67% (6)[e]	44% (70)[e]

Close physical contact during social interaction is likely to facilitate disease transmission within wild dog packs.

been found in wild dogs in Serengeti and Selous (M.K. Laurenson, pers. comm., Creel *et al.* in prep.) and in the Masai Mara region (Alexander *et al.* 1993), but not in Kruger (van Heerden *et al.* 1995) or Tsumkwe District, Namibia (Laurenson *et al.* in prep.).

In domestic dogs, parvovirus replicates principally in the dividing cells of the intestinal epithelium, and the resulting enteritis may be an important cause of mortality in puppies. Infected dogs excrete viral particles in their faeces, and these viruses may persist in the environment for relatively long periods of time (Appel & Parrish 1987).

It is not known whether parvovirus persists in wild dog populations or whether, like rabies, it 'spills over' from domestic dogs. Wild dog populations in the Masai Mara and Tsumkwe had lower seroprevalences than sympatric domestic dogs (Masai Mara: 7% of wild dogs (n = 15) and 25% of domestic dogs (n = 181) seropositive, Alexander *et al.* (1993); Tsumkwe: 0% of wild dogs (n = 6) and 47% of domestic dogs (n = 70) seropositive, Laurenson *et al.* (in prep.). However, in Selous the infection appears to persist in the absence of domestic dogs (Creel *et al.* in prep.).

The impact of parvovirus on wild dog populations remains unknown. Long-term studies of grey wolves show that, while parvovirus infection is an important cause of juvenile mortality, the effect on recruitment is not sufficient to cause a population decline (Mech & Goyal 1995). The virus is, however, believed to have hindered the recovery of some wolf populations (Mech & Goyal 1995). Thus, parvovirus might help to keep wild dog populations small, especially in fragmented populations that have frequent contact with domestic dogs.

Canine Adenovirus (Infectious Canine Hepatitis)

Infectious canine hepatitis is a disease of domestic dogs and other canids caused by Type 1 canine adenovirus, a DNA virus. Antibodies to canine adenovirus have been found in wild dogs in Kruger (van Heerden *et al.* 1995), as well as Serengeti and the Masai Mara (M.K. Laurenson, pers. comm.; K. Alexander, Unpublished data).

A high proportion of wild dogs sampled in Kruger carried antibodies to the virus. Similar patterns of seroprevalence come from infected populations of domestic dogs: most animals become infected early in life and acquire immunity without showing signs of disease (Appel 1987a). However, mortality may be very high in young puppies. Thus, it seems unlikely that canine adenovirus has much effect upon adult wild dogs, but it might be a cause of juvenile mortality.

Canine Coronavirus

Canine coronavirus is a virus that replicates only in canids. Antibodies to the virus have been found in wild dogs from Kruger (van Heerden *et al.* 1995), and the Masai Mara (K. Alexander, Unpublished data). On its own, coronavirus causes a mild gastroenteritis in domestic dogs; however, mixed infections with parvovirus are common and may be fatal (Appel 1987b). Like parvovirus, coronavirus particles are excreted in the faeces and contact with infected faeces represents the most important route of transmission. In domestic dogs, disease occurs mainly in puppies, while infected adults rarely show signs of ill health. Although the effect of coronavirus infection on wild dogs remains unknown, it might be expected to follow a similar pattern.

Canine Herpesvirus

Canine herpesvirus is a DNA virus which replicates only in canids, and may cause high mortality in newborn puppies (Appel 1987d). Adult domestic dogs rarely show clinical signs of disease, although in infected populations most are seropositive (Appel 1987d). Antibodies to canine herpesvirus have been found in wild dogs in the Masai Mara (K. Alexander, Unpublished data). Any effect of the virus on wild dog populations remains unknown although, by extrapolation from domestic dogs, it seems likely that it affects juvenile rather than adult mortality.

Canine Para-influenza Virus

Canine para-influenza virus is a virus affecting domestic dogs, where it is one of the main causes of 'kennel cough' (Appel & Binn 1987). Antibodies to this virus – or possibly the closely related Simian Virus 5 – have been recorded from wild dogs in Kruger (van Heerden *et al.* 1995). In domestic dogs, infection with para-influenza virus alone leads to mild respiratory disease or, more usually, causes no clinical signs. However, under natural conditions infection is often accompanied by secondary infections by other viruses and bacteria (Appel & Binn 1987). The effect of the virus on wild dogs remains unknown, but is likely to be mild.

Reovirus

Three types of reovirus have been isolated from domestic dogs, but none appears to lead to a specific disease (Appel 1987f). Antibodies to reovirus are commonly found in domestic dogs, and have been recorded in wild dogs in Kruger (van Heerden *et al.* 1995). Although reovirus alone seems not to cause disease, dual infection with canine parvovirus and canine distemper does occur in domestic dogs. It is possible that reovirus has an immunosuppressive effect (Appel 1987f). It seems unlikely, though, that infection with reovirus has any marked effect on wild dog populations.

Rotavirus

Rotavirus, like reovirus, appears not to cause disease in domestic dogs (Appel 1987e). The finding of antibodies in wild dogs from Kruger is the first record of rotavirus infection in a wildlife population (van Heerden *et al.* 1995). It seems unlikely that this virus has any marked effect upon wild dog populations.

African Horse Sickness Virus

African Horse Sickness is an important disease of horses and other equids, including zebras. However, other species, including domestic dogs, may also carry the virus. The first survey of wild carnivores revealed antibodies in four populations of wild dogs, as well as sympatric lions, hyaenas, cheetahs and jackals (Alexander *et al.* 1995). African Horse Sickness is caused by an arbovirus which is transmitted between equids by *Culicoides* midges and mosquitoes. However, domestic dogs may contract the virus by eating infected meat (Losos 1986) and this seems the most likely route of infection for wild carnivores – seroprevalences are high in wild carnivores that prey on zebras (hyaenas, lions, wild dogs), but much lower in sympatric populations of domestic dogs (Alexander *et al.* 1995).

It is not known whether infection with African Horse Sickness virus has any effect on wild dogs, but it can cause illness and mortality in domestic dogs. It seems unlikely, however, that this virus has any marked effect upon wild dog populations.

Bluetongue Virus

Bluetongue is primarily a disease of sheep, in which it can cause dramatic economic losses (Losos 1986). The bluetongue virus also affects several wild ruminant species, and antibodies to the virus were recently isolated from wild dogs for the first time (Alexander *et al.* 1994). Antibodies were present in all four wild dog populations that were surveyed. Bluetongue is caused by an arbovirus closely related to the one that causes African horse sickness. Like African horse sickness, bluetongue is usually transmitted by *Culicoides* midges, but eating infected meat is probably the most important route of infection for predators. The virus is fairly resilient and remains viable even in decomposed blood (Losos 1986).

It is not known whether infection with bluetongue virus has any adverse effects on wild dogs, but it has caused abortion in domestic dogs (Alexander *et al.* 1994). It seems unlikely, however, that this virus has any marked effect upon wild dog populations.

Bacterial Infections

Bacillus anthracis (Anthrax)

Anthrax is an extremely important bacterial disease that affects most mammals. Although a serological survey of a small sample of wild dogs in Kruger showed no evidence of exposure to the disease (van Heerden *et al.* 1995), anthrax is known to have killed wild dogs in Kruger, as well as in Selous (Creel *et al.* 1995), and in South Luangwa National Park, Zambia (Turnbull *et al.* 1991).

The spores of *Bacillus anthracis* may survive in the soil for years, so the pathogen can persist in an area even in the absence of a reservoir host (Turnbull 1990). Animals in the final stages of anthrax haemorrhage from the nostrils, mouth and anus, and bacteria in the blood sporulate on contact with the air. As a result, ungulates usually become infected by contact with bacterial spores in the soil or water (Turnbull 1990). However, carnivores become infected by eating the flesh of infected animals. Some carnivores appear highly resistant to the disease: for example, during a serious anthrax epidemic in Etosha National Park, Namibia, lions, spotted and brown hyaenas, and black-backed jackals all fed from the carcasses of animals which had died from anthrax, but showed no signs of the disease themselves (Ebedes 1976). Similarly, during an epidemic in the Luangwa valley in 1987, one area of just 80 km² yielded the carcasses of 101 hippos, 60 buffalo and 20 elephants, along with puku, kudu and other ungulates – but only one spotted hyaena and two leopards (Turnbull *et al.* 1991).

Wild dogs' resistance to anthrax seems to vary. The Luangwa epidemic was accompanied by a marked decrease in the frequency of sightings of wild dogs throughout the Park. Five carcasses of wild dogs were found, and anthrax was confirmed in four of them (Turnbull *et al.* 1991). It seems likely, therefore, that the population decline can be directly attributed to anthrax. However, anthrax does not always have such marked effects upon wild dogs. Anthrax epidemics occurred in Kruger in 1990, 1991 and 1993, but the wild dog population in the area increased during this period, and only 3 of 1538 anthrax-positive carcasses were wild dogs (M.G.L. Mills pers. comm., de Vos & Bryden 1996).

Anthrax has also been reported from a wild dog pack in Selous (Creel *et al.* 1995). Three adults and eight pups, from a group of 18 adults and 24 pups, showed signs of disease. All of the adults recovered, but four of the pups died. Thus, wild dogs can recover from anthrax – indeed, animals which had shown signs of disease were no more likely to die in the six months following the outbreak than were apparently uninfected animals. The outbreak had no effect on the pack's movement patterns or hunting success. Furthermore, there was no transmission of the infection between pack members, although apparently healthy animals licked saliva and ocular discharge from the faces of sick pups. However, this outbreak did not take place during an anthrax epidemic in the ungulate prey base, and was probably caused by some members of one pack killing and consuming a single animal that harboured enough bacilli to transmit the disease (Creel *et al.* 1995). Under epidemic conditions wild dogs would be exposed to prey infected with anthrax repeatedly, and it is possible that a greater proportion of wild dogs in each pack might have been affected. Thus, anthrax may sometimes have a dramatic effect upon wild dog populations, but this is certainly not always the case.


Black-backed jackals in the same area as wild dogs may provide a reservoir of disease.

Ehrlichia canis (Ehrlichiosis)

Ehrlichiosis is a disease of domestic dogs, caused by the rickettsial bacterium *Ehrlichia canis* and transmitted by the brown dog tick, *Rhipicephalus sanguineus*. This disease was believed to have contributed to the decline of wild dogs in Kruger in the 1920s and 1930s (Stevenson-Hamilton 1939). At that time, many domestic dogs living in the park died of "...a disease against which the usual treatment for biliary fever and distemper seemed to be of no avail..." (Neitz & Thomas 1938). Blood slides taken from two domestic dogs that contracted the disease contained *Ehrlichia canis* and also, subsequently, *Babesia canis* (see below). Local people reported having seen wild dogs showing the same symptoms, but ehrlichiosis was not confirmed (Neitz & Thomas 1938). van Heerden (1979) showed experimentally that wild dogs can contract ehrlichiosis, although the disease was less severe in wild dogs than in domestic dogs. Surveys of wild dogs in Kruger and the Masai Mara have found no evidence of exposure to *Ehrlichia canis*, although a few domestic dogs in the Masai Mara were seropositive (Alexander *et al.* 1993; van Heerden *et al.* 1995). Thus, any effect of ehrlichiosis on free-ranging wild dog populations remains obscure.

Rickettsia conorii/ africae (Spotted Fever)

Spotted fevers are a group of tick-borne diseases caused by some of the bacteria in the genus *Rickettsia*. A high proportion of wild dogs in Kruger show evidence of having been exposed to infection, although the two species occurring in Southern Africa, *R. conorii* and

R. africae cannot be distinguished by serological means (van Heerden *et al.* 1995). Domestic dogs and other domestic mammals may become infected, but they show no clinical signs of disease (Marmion 1990). It seems unlikely, therefore, that spotted fever rickettsiae have any marked effect upon wild dog populations (van Heerden *et al.* 1995).

Coxiella burnetti (Q Fever)

Q fever is a disease of man, caused by *Coxiella burnetti*, an intracellular bacterium related to *Rickettsia* (Losos 1986). Many other wild and domestic mammals and birds may sustain infection, and antibodies were found in wild dogs from Kruger in 1990–3 (van Heerden *et al.* 1995). Mammals other than man usually show no clinical symptoms, although infection may occasionally cause abortion in sheep and goats (Losos 1986). It seems unlikely, therefore, that *Coxiella* infection has any substantial effect on wild dog populations.

Brucella abortus (Brucellosis)

Brucellosis is a commercially important disease which causes abortion and infertility in cattle. One of three wild dogs shot in Serengeti in 1965–7 showed evidence of previous infection with *Brucella abortus*, the bacillus which causes brucellosis (Sachs *et al.* 1968). This animal would almost certainly have contracted the infection by eating infected meat: the disease was widespread in zebra, wildebeest and other prey species at the time. *Brucella canis* causes abortion in domestic dogs, but the effect of *Brucella abortus* on wild dogs is not known. It seems unlikely, however, that this infection has any significant impact on wild dog populations.

Protozoal Infections

Toxoplasma gondii

Toxoplasma gondii is a sporozoan parasite which primarily affects cats, although other mammals can become infected. All wild dogs sampled in Kruger were seropositive for *Toxoplasma* (van Heerden *et al.* 1995). Four pups necropsied in Kruger were found to have died from an infection of either *Toxoplasma* or the closely related *Neospora*; 16 other pups from the same den disappeared at the same time (M.G.L. Mills & J. van Heerden, pers. comm.), although adult group members were not affected. Thus, *Toxoplasma* may cause some juvenile mortality, but seems not to affect adult wild dogs.

Neospora caninum

Neospora caninum is a sporozoan parasite related to *Toxoplasma*, which was first discovered in 1978. In domestic dogs it may cause paralysis in pups, and also abortion (Ruehlmann *et al.* 1995). Infection has not been confirmed in wild dogs, but four pups necropsied in Kruger were found to have died from an infection of either *Neospora* or the closely related *Toxoplasma*; 16 other pups from the same den disappeared at the same time. Thus, *Neospora* might cause some mortality in wild dog pups.

Babesia

Babesiosis is a tick-borne disease caused by intraerythrocytic protozoa of the genus *Babesia*. The parasite affects many species of wild and domestic mammals (Losos 1986), and has been recorded from wild dogs in Kruger (van Heerden *et al.* 1995), and probably also Serengeti (Peirce *et al.* 1995). Captive wild dogs usually carry the parasite without showing signs of disease (van Heerden 1980), although one pup died in captivity as a result of acute babesiosis (Colly & Nesbit 1992). Thus, *Babesia* infection might cause disease in wild populations, but it seems unlikely that it has any substantial effect on wild dog numbers.

Hepatozoon

Hepatozoon is a genus of apicomplexan protozoa than infects a wide range of vertebrates. Infestation may be severe in domestic dogs suffering from other infectious diseases such as ehrlichiosis. The parasite has been recorded in wild dogs in Kruger (van Heerden *et al.* 1995) and Serengeti (Peirce *et al.* 1995). It is not known whether *Hepatozoon* infection has any adverse effects on wild dogs, but domestic dogs infected with the parasite usually show no clinical signs of disease (van Heerden *et al.* 1995). However, the parasite infects the white blood cells and presumably causes some impairment of the immune system. Nevertheless, it seems unlikely that *Hepatozoon* has any substantial effect upon wild dog populations.

Macroparasites

As well as the viral, bacterial and protozoal infections discussed above, wild dogs are also hosts for a number of macroparasites. The hookworm *Ancylostoma caninum* has been found in wild dogs from Kruger, the Masai Mara, Moremi and Hwange (Spangenberg & Ginsberg Unpublished data, van Heerden *et al.* 1994). This nematode has caused illness in captive wild dog pups. In Serengeti and Hwange, wild dogs often 'anal dragged' – a typical behaviour of domestic dogs infected with intestinal parasites. One animal which often showed this behaviour in Serengeti also appeared bloated, and lacked stamina when hunting (J.R. Malcolm pers. comm.). Thus, infection with macroparasites might be a contributing factor to mortality of young or malnourished wild dogs. However, it seems unlikely that they have any substantial effect upon wild dog populations.

General Patterns

Two patterns emerge from this survey of wild dog diseases, which point to the need for concern and, in some cases, more research.

First, many of the diseases affecting wild dogs are likely to have been contracted from sympatric domestic dogs. Domestic dogs are believed to act as reservoir hosts, from which diseases 'spill over' into wild dog populations: since wild dogs live at such low densities, it is unlikely that pathogens causing significant mortality could persist in their populations in the absence of such a reservoir. This possibility leads to further concern. Epidemiological models of diseases infecting more than one host within a community usually predict the extinction of species which are more affected by transmission from other species than by transmission from members of their own species (Begon & Bowers 1995). More research is needed in this direction if appropriate strategies for disease control are to be formulated.

Second, most of our knowledge of wild dog diseases is based upon serology, which shows only whether an animal has been exposed to a particular pathogen in the past. Even if an animal is found to be seropositive, the timing of the infection and its effects upon the host remain unknown. Furthermore, animals which die from exposure to the same infection do not, by their very nature, show up in serological surveys. As a result, the effects of many pathogen species on the health of individual wild dogs and the characteristics of wild dog populations remain unknown. For example, canine distemper appears highly pathogenic to wild dogs held in captivity, and yet some free-ranging populations show a high seroprevalence, indicating that animals have survived exposure to the disease. Without knowing the mortality caused by such a disease, it is difficult to assess its likely impact upon wild dog populations.

Similarly, wild dog populations show high seroprevalences for a number of viral infections thought likely to contribute to pup mortality. However, it is difficult to assess their impact since young pups usually remain in the den, making it difficult (and, in all probability, unethical) to sample them.

Conclusions

This discussion has revealed a number of potential threats to the remaining populations of African wild dogs. Perhaps the most important conclusion is that human presence poses a serious threat to wild dogs, even in the largest and best-protected areas: 61% of recorded adult mortality is caused directly by human activity (Table 4.2). Wild dogs using protected areas may range outside the borders and into areas used by people. Here they encounter high-speed vehicles, guns, snares and poisons, as well as domestic dogs which may represent reservoirs of potentially lethal diseases.

The important rôle played by human-induced mortality has two long-term implications. First, it makes it likely that, outside protected areas, wild dogs may well be unable to co-exist with the rising human population unless better protection and local education programmes are implemented. This will be a serious problem for wild dog populations in areas such as Ethiopia and Namibia, where most populations occur outside protected areas. Second, wild dogs' ranging behaviour leads to a very substantial 'edge effect', even in large reserves. Simple geometry dictates that a reserve of 5,000 km² can contain no point less than 40 km from its borders – a distance well within the range of distances travelled by wild dogs in their usual behaviour. Thus, a reserve of this size (fairly large by most standards) would be, from a wild dog's perspective, all edge. As human populations rise around reserve borders, the risks to wild dogs venturing outside are also likely to increase. Under these conditions, only the very largest reserves will be able to provide any level of protection for wild dogs.

Even in large, well-protected reserves, wild dogs live at very low population densities. It seems likely that predation by lions, and, perhaps, competition with hyaenas, contribute to keeping wild dog numbers below the level that their prey base might support. Even within large parks such as Tsavo West in Kenya, wild dogs appear to select certain habitat types in which to live. Such low population density brings its own problems. The largest areas contain only relatively small wild dog populations; for example the Kruger National Park and surrounding reserves, with a combined area of 26,000 km² (about the size of Israel), contain just 375 wild dogs (Maddock & Mills 1994). Most reserves, and probably most wild dog populations, are smaller: for example Niokolo-Koba National Park, at 9,000 km², contains 50–100 wild dogs (C. Sillero-Zubiri, pers. comm.). Such small populations are vulnerable to extinction (Soulé 1987). 'Catastrophic' events such as outbreaks of epidemic disease may drive them extinct when larger populations would recover – such an event seems to have led to the extinction of the small wild dog population in Serengeti (Appendix 1). Such problems of small population size will be exacerbated if, as seems likely, small populations occur in small reserves or habitat patches. As discussed above, animals inhabiting such areas suffer a strong 'edge effect'. Thus, small populations might be expected to suffer disproportionately high mortality as a result of their contact with humans and human activity.

Wild dog carcasses can be used to establish cause of death. [Photograph © John Foster].

Low population density may also cause problems related to disease transmission. Many diseases of domestic dogs appear to 'spill over' into wild dog populations, which probably occur at densities too low to allow the infection to persist. General models of similar systems predict the extinction of the host into which the disease 'spills over' – in this case wild dogs (Begon & Bowers 1995). Similar models designed specifically for wild dogs are needed to examine this problem in more detail.

One further problem related to disease is that wild dogs' social organization might hamper selection for disease resistance. In most animals, naturally resistant animals that survive disease outbreaks will experience reduced competition and high reproductive success after the epidemic. In this way, genes for resistance will spread in the population. However, survivors of local epidemics in wild dogs populations may rarely be able to pass on their genes for disease resistance. If only one or two pack members survive (as, for example, in the rabies outbreak in the Aitong pack, Kat *et al.* 1995), they will have to join or form a new pack if they are to have any hope of breeding. Such dispersing animals are believed to suffer high mortality in some areas (Ginsberg *et al.* 1995a), making it unlikely that pack remnants will survive long after the decimation of their packs. Thus, natural selection for resistance against epidemic diseases such as rabies may be weak in wild dogs.

To conclude, many factors, both natural and human-induced, conspire to keep wild dog numbers low. It seems likely that these threats will be compounded by habitat fragmentation, which will divide wild dogs into smaller populations each at disproportionate risk from human activities. In the next chapter, we use demographic modelling to investigate the likely impact of each of these factors on population persistence.

Chapter 5
Extinction Risks Faced by Remaining Wild Dog Populations

Joshua R. Ginsberg & Rosie Woodroffe

In this chapter we use demographic modelling to assess the probability that the threats to wild dog populations outlined in Chapter 4 might cause local extinction of remaining populations. In constructing our model:

- *We use real data on wild dog biology to develop a standard model.*
- *We estimate that the majority of extant wild dog populations contain ≤ 50 individuals.*
- *Rather than attempting to simulate specific wild dog populations, our models reflect the size of remaining wild dog populations (K ≈ 20, 50, 100 animals).*
- *We employ timescales which reflect the true pace of land use change in Africa.*
- *We examine how population size, fragmentation and inbreeding depression affect the probability of local extinction.*
- *We assess the degree to which both small and larger populations are affected by changing patterns of adult and juvenile mortality to simulate the impact of threats such as persecution, locally endemic and epidemic disease, road accidents, snaring and lion predation.*

It is not our intention to define a minimum size below which populations are likely to become extinct: neither our model, nor the data used to parameterize the model, are adequate to allow such quantitative predictions. The following general conclusions can, however, be valuable for planning management strategies:

Larger populations *(~ 100 individuals) appear remarkably resilient. Wild dogs' large litters allow them to bounce back from catastrophes which cause temporary declines in population numbers. Given protection from fragmentation and a barrage of multiple threats, these populations should persist over the next 50 years. However, such populations require very large areas (≥ 5000 km²). As human populations rise and the African landscape becomes more fragmented, populations of this size will surely disappear without active landscape planning to ensure the integrity and contiguity of current protected areas and wildlife lands.*

Smaller populations *(~ 50 individuals) characterize many remaining wild dog populations. Insulated from threats, such populations stand a decent chance of persisting for the next 50 years. They are, however, extremely vulnerable to change: a small increase in either adult or juvenile mortality greatly increases the probability of extinction. Thus direct persecution, disease, road accidents, accidental snaring and lion predation each represents a serious threat to populations of this size. Increasing connectivity to form larger metapopulations will help such populations to persist.*

Tiny populations *(~ 20 individuals), consisting of just a few packs, face a high probability of extinction. Whether they are remnants of a once larger population, or populations newly founded by reintroduction, tiny populations will be vulnerable to any threat which increases either adult or juvenile mortality. Such populations may occupy relatively large areas (> 500 km²) but are constrained in their ability to grow. Connecting these tiny populations to larger populations greatly improves their persistence.*

Background

In the previous chapter we outlined factors that may cause wild dog numbers to decline, or even drive them to local extinction. Setting priorities for wild dog management, however, demands an assessment of the relative importance of these threats. For example, if accidental capture of adult wild dogs in snares is a major cause of mortality, then better control of snaring inside and outside protected areas could help to protect them. But how does one rank the risk of such snaring with the threat of disease? And is it more important to invest in controlling epidemic rabies or endemic parvovirus? In this chapter we use demographic modelling (Boyce 1992) to simulate how mortality caused by various threats affects wild dog populations, and use these analyses to assess the extinction risks faced by populations of various sizes.

We have chosen to model wild dog populations by using the computer package VORTEX (Lacy *et al.* 1995). VORTEX was developed as a tool for conservation biologists to assess the probability of extinction in small populations. The user specifies a series of population parameters, and the program then uses a modified Leslie matrix to simulate population changes over time, incorporating stochastic variation in those parameters. By running each simulation many times, one can measure the probability that a population will persist under a given set of demographic circumstances. By varying the starting conditions, the user can simulate various factors likely to affect the population's viability, such as its size, degree of fragmentation, inbreeding depression, harvesting, consistent changes in mortality or breeding success, and episodic 'catastrophes'.

The use of such simulations to assess the risk of extinction faced by wildlife populations – termed population viability analysis (PVA) – has been criticized recently because it considers only genetic and demographic effects. Such effects may operate on a timescale of centuries, while habitat loss and persecution can drive a species to extinction within a few decades (Harcourt 1995). We have attempted to make our simulations more meaningful by measuring the cumulative probability of extinction per decade, over a total of 50 years for each simulation. This allows us to assess the impact of various threats to wild dogs on a timescale which reflects the true pace of change of land use in Africa. Rather than using simulations to define the size of a minimum viable population, we are concerned with assessing the relative impacts of various threats upon wild dog populations in an attempt to set priorities for their management. Under these circumstances, PVA can provide an extremely valuable tool in conservation biology (Boyce 1992; Caughley 1994; Harcourt 1995).

Setting Model Parameters

Our modelling exercise required a set of parameters to describe the characteristic features of wild dog populations. We derived demographic parameters using a combination of published and unpublished data on free-ranging populations of wild dogs. Published data were taken mainly from Fuller *et al.* (1992); unpublished data were collected from wild dog researchers at the IUCN/SSC Canid Specialist Group's 'Workshop on the Conservation & Recovery of the African Wild Dog', held in Arusha, Tanzania, in 1992, and through subsequent correspondence. These data allowed us to determine both the average values and the degree of variation in population parameters such as adult and juvenile mortality, litter size, birth sex ratios and the proportion of females breeding. These parameters are summarized in Table 5.1. While many of the data are straightforward, some deserve further discussion.

Population Size

Because threats vary in both space and time, and because we lacked data on the rôle of known threats in regulating wild dog numbers in known populations, we did not attempt to simulate specific wild dog populations. Taking into account the range of sizes of wild dog populations remaining in Africa, we examined the impact of the various factors in populations of three different sizes chosen to reflect the lower end of the range (and therefore the most threatened) of existing populations: tiny (20); small (50); and larger (100). In Table 5.2 we list our estimates of population size for each known wild dog population in Africa, as a guide to determining how our model results relate to real populations.

Mating System

VORTEX contains no direct provision for the inclusion of social structure within population models. While some have therefore questioned the use of VORTEX for modelling wild dog populations (Heinsohn 1992) many aspects of social structure can be incorporated in the demographic parameters that are defined by the user.

Because only one female usually breeds in each pack (Chapter 1), the number of breeding females will be determined, for the most part, by the number of packs in any given population. A factor that increases optimal pack size, thus reducing the number of packs, will therefore reduce the proportion of females breeding in the population as a whole. We simulated the social suppression of reproduction in subordinate female group members by including only 58% of adult (> 3 years) females in the breeding pool. This gives a good approximation to the proportion of females breeding in real wild dog populations (Burrows 1995; Fuller *et al.* 1992). While one might expect this variable to have a relatively strong effect upon population persistence, both sensitivity analyses of VORTEX models (Burrows *et al.* 1994) and a deterministic Leslie matrix model based upon our parameters (G. Mace pers. comm.) suggest that survivorship of adults and juveniles are far more important.

In contrast with earlier simulation models of wild dog populations (Burrows *et al.* 1994; Ginsberg *et al.* 1995), we included 100% of adult males in the breeding pool. All adult male wild dogs are capable of breeding, but usually only the dominant male mates with the dominant female in each pack. Thus, approximately 40–60% of adult males fail to breed because they are socially suppressed (Frame *et al.* 1979; Girman *et al.* in press). Our model simulated this situation by assuming that mating was monogamous: the proportion of males breeding was therefore determined by the number of

Table 5.1
The basic model used for simulations of wild dog populations.

Mating is monogamous:
58% (± 20.15%) of females are in the breeding pool
100% of males are in the breeding pool

Individuals of both sexes first breed as 3-year olds

Breeding is not density dependent

The frequency distribution of litter sizes is:
0.9% of breeding females produce 1 pup
0.9% of breeding females produce 2 pups
0.9% of breeding females produce 3 pups
2.2% of breeding females produce 4 pups
2.2% of breeding females produce 5 pups
4.5% of breeding females produce 6 pups
4.5% of breeding females produce 7 pups
4.5% of breeding females produce 8 pups
6.9% of breeding females produce 9 pups
18.1% of breeding females produce 10 pups
18.1% of breeding females produce 11 pups
9.1% of breeding females produce 12 pups
6.9% of breeding females produce 13 pups
4.5% of breeding females produce 14 pups
4.5% of breeding females produce 15 pups
11.4% of breeding females produce 16 pups

The **sex ratio** at birth is 55% males: 45% females

Juvenile mortality for both sexes is 68% ± 20.49%

Adult mortality for both sexes is:
1–2 years: 20% ± 3%
2–3 years: 15% ± 3%
3+ years: 10% ± 3%
The maximum age any animal can reach is 10 years

Catastrophes
Severe catastrophes occur with a probability of 3%, and:
Reduce adult survival by a factor of 0.5
Do not affect reproduction
Mild catastrophes occur with a probability of 5% and:
Reduce adult survival by a factor of 0.85
Reduce reproduction by a factor of 0.5

Inbreeding depression is incorporated using the lethal recessive alleles model

At the start of each iteration:
Populations are assumed to be at carrying capacity
Population structure is set to give a stable age distribution

Throughout each iteration:
Carrying capacity does not change
Populations are neither harvested nor supplemented

Each model runs for 50 years, and is iterated 1,000 times

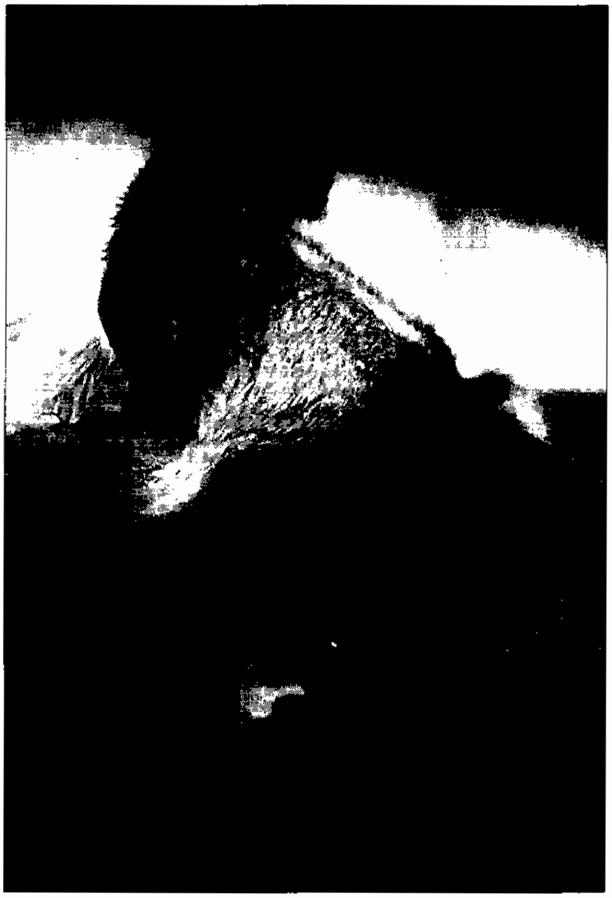
Table 5.2
Estimates of population size for wild dogs remaining in Africa. The estimates are derived by multiplying the area of each reserve or region by indices of wild dog abundance given in Chapter 3. Density was assumed to be 1/60 km² in areas where wild dogs were reported to be 'common', 1/100 km² where they were considered 'present', and 1/500 km² where they were considered 'rare'. All figures are approximate, but estimates are ranked according to their likely reliability.

	Country	Site of wild dog population	Size	Reliability
Tiny populations:	South Africa	Umfolozi/Hluhluwe Park	20	good
	South Africa	Madikwe Game Reserve	10	good
	Zimbabwe	Gona re Zhou N.P. Area	40	moderate
	Zimbabwe	Chizarira N.P. Area	20	moderate
	Zambia	Lunga-Luswishi G.M.A.	30	~ guess
	Cameroun	Benoue National Park	20	~ guess
	Cameroun	Bouba-Njida National Park	20	~ guess
	Ethiopia	Bale Mountains National Park	20	~ guess
	Ethiopia	Gambela National Park	20	~ guess
	Ethiopia	Omo National Park	20	~ guess
	Kenya	Dodori National Reserve	20	~ guess
	Kenya	Kora National Reserve	20	~ guess
	Kenya	South Turkana National Reserve	20	~ guess
	Kenya	Timau, Laikipia	20	~ guess
	Somalia	Juba River	20	~ guess
	Tanzania	Tarangire National Park	20	~ guess
	Tchad	Manda National Park	20	~ guess
	Zambia	Liuwa Plain National Park	20	~ guess
	Zambia	Lower Zambezi National Park	20	~ guess
	Zambia	Sioma-Ngwezi National Park	20	~ guess
	Zambia	Sumbu National Park	20	~ guess
	Zambia	West Lunga National Park	20	~ guess
Small populations:	Ethiopia	Mago National Park	50	moderate
	Kenya	Tsavo East & West N.P.	50	moderate
	Cameroun	Faro National Park	50	~ guess
	CAR	Manovo Gounda-St Floris Complex	50	~ guess
	Ethiopia	South-East of Bale Province	50	~ guess
	Ethiopia	Mehal Meda	50	~ guess
	Kenya	Kajiado district	50	~ guess
	Kenya	Extreme NE Kenya	50	~ guess
	Tchad	Oudai Rimé – Ouadi Achim G.R.	50	~ guess
Larger populations:	Tanzania	Selous Game Reserve	880	good
	Botswana	Chobe Complex	500	good
	Namibia	Northern Namibia Complex	400	good
	South Africa	Kruger National Park	350	good
	Zimbabwe	Hwange N.P. Complex	350	good
	Tanzania	Mikumi National Park	100	good
	Zambia	Kafue N.P. Complex	300	moderate
	Botswana	Gemsbok N.P. Complex	150	moderate
	Tanzania	Ruaha National Park	150	moderate
	Tanzania	Rungwa/Kisigo G.R.	150	moderate
	Sénégal	Niokolo-Koba N.P. Complex	100	moderate
	Zambia	Luangwa Valley System	100	moderate
	Zimbabwe	Zambezi Valley	100	moderate
	Tanzania	Greater Selous Area	400	~ guess
	Botswana	Central Kalahari/Khutse G.R.s	100	~ guess
	CAR	Bamingui - Bangoran Complex	100	~ guess
	Kenya	N. Kenya, Isolo to Marsabit	100	~ guess
	Tanzania	Moyowosi Game Reserve	100	~ guess
	Tanzania	Maasai Steppe	100	~ guess

females breeding. The converse situation – where the number of breeding males limits female reproduction – is unlikely to occur because at all times there is a surplus of reproductively capable males waiting for the chance to breed should a dominant male die. Simulation models will ignore this effect if they restrict the proportions of both males and females that breed. Such models will therefore overestimate the probability of extinction, especially in small populations: in a population with a carrying capacity of 50, reducing the proportion of males in the breeding pool from 100% to 40% nearly doubles the estimated probability of extinction within 50 years, from 2% to 5%.

Density Dependence

Our simulations assumed that breeding is independent of population density (although there has been debate about whether this is universally true, Burrows *et al.* 1995; Ginsberg *et al.* 1995). Female wild dogs' reproductive success is density dependent at one level: a smaller proportion of females breeds in larger packs. However, in an unconstrained population breeding is unlikely to be density-dependent at the population level because animals which cannot breed disperse and attempt to form new packs (Burrows 1995; Fuller *et al.* 1992). In small areas this is likely to lead them into unsuitable habitat where they cannot survive. We therefore considered it more appropriate to truncate population size above a certain carrying capacity – denoted by the letter 'K' – than to simulate density-dependent reproduction. We assumed that the population was at carrying capacity at the start of each simulation.



Modelling Results

In the previous chapter we outlined a series of factors likely to affect wild dog numbers – these are summarized in Table 5.3. We modelled most of these threats by incorporating temporary or sustained changes in adult or juvenile mortality into the VORTEX simulations. We also simulated population fragmentation by using a metapopulation model which broke the population into a number of sub-populations, allowing animals to move between sub-populations, and to re-establish extinct sub-populations.

Inbreeding Depression

Although small populations are expected to face problems associated with inbreeding depression, there is surprisingly little evidence to suggest that inbreeding has deleterious effects in most social carnivores. Indeed, Ralls *et al.* (1988) found that juvenile survival in captive wild dogs increased with the level of inbreeding. The reasons for this relationship are unknown, although there are alternatives to the interpretation that inbreeding is beneficial.

The best evidence for a deleterious effect of inbreeding in communally breeding canids comes from a study of wolves held in captivity (Laikre & Ryman 1991). In this study, founders taken from a small wild population were found to carry a deleterious recessive gene for blindness – an allele which would certainly prove fatal in the wild. This study shows that recessive lethal alleles can persist, even in small populations. In the light of these data, we incorporated a recessive lethal model of inbreeding into our simulations, rather than a more general inbreeding depression model to reduce the survival of highly homozygous juveniles (Lacy *et al.* 1995).

Using this model, our simulations suggest that inbreeding has a small but measurable effect upon the persistence of wild dog populations. Figure 5.1 shows the probability of extinction of populations of three sizes (K = 20, 50, 100) simulated using our basic model, including and excluding the effects of inbreed-

Table 5.3
Threats outlined in Chapter 4, and strategies for simulating them using VORTEX.

Threat	Main effect on wild dog populations	Procedure for VORTEX simulation
Habitat fragmentation	Isolates some parts of the population from others, increasing the impact of demographic stochasticity on each sub-population	Simulate isolated populations, and also metapopulations of equal size that are fragmented into sub-populations
Shooting and poisoning	Causes 0–47% (mean = 27%) of adult mortality	Persistent increase in adult mortality
Road accidents	Causes 0–52% (mean = 24%) of adult mortality Causes 0-50% of pup mortality	Persistent increase in adult and juvenile mortality
Snaring	Causes 0–21% (mean = 10%) of adult mortality Causes 0–5% (mean = 4%) of pup mortality	Persistent increase in adult and juvenile mortality
Diseases of domestic puppies (*e.g.* parvovirus)	Likely to cause some pup mortality, but the amount is unknown	Persistent increase in juvenile mortality
Epidemic disease (*e.g.* rabies, canine distemper)	Cause high or total mortality of whole packs	Simulate occasional 'catastrophic' mortality and breeding failure
Lion predation	Causes 0–47% (mean = 16%) of adult mortality Causes 37–43% (mean = 38%) of pup mortality	Persistent increase in adult and juvenile mortality

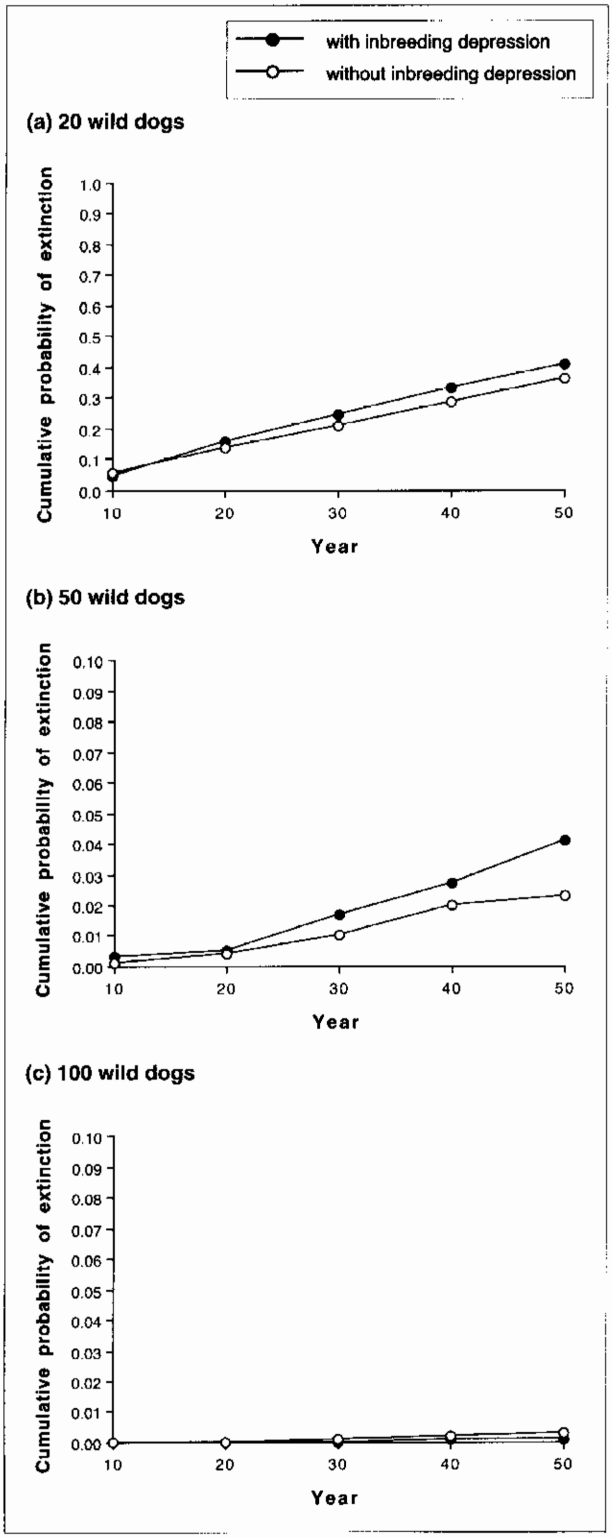


Figure 5.1. The effect of incorporating inbreeding depression, caused by lethal recessive alleles, into the population simulations.
The cumulative probability of extinction is given for model populations which either include or exclude inbreeding depression, for carrying capacities of (a) 20, (b) 50, and (c) 100 wild dogs.

ing depression. In tiny populations (K = 20, Figure 5.1a) our simulations show that inbreeding depression has a moderate effect on persistence, increasing the probability of extinction within 50 years from 36% to 41%. For a population with a carrying capacity of 50 animals (Figure 5.1b), the addition of inbreeding depression raises the probability of extinction from 2% to 4%. In larger populations, the effects of inbreeding are negligible (Figure 5.1c).

A note of caution: when a monogamous mating system is defined in VORTEX, mates are chosen randomly in each year of a simulation, while in wild dog packs, a dominant male and female may breed together for a number of years. VORTEX will therefore underestimate the negative impact of inbreeding, because the proportion of adults contributing to each successive generation will be greater than in the real world. On the other hand, because wild dogs appear to selectively outbreed in the wild (Chapter 2, Girman *et al.* in press) random assignment of mates may not be too great an overestimate the effect of inbreeding. Other factors will also influence the impact of inbreeding on our simulations: for instance, by allowing 100% of males to breed we further underestimate the potential impact of inbreeding, particularly in small populations. We acknowledge the limitations of VORTEX in this regard, but for the sake of completeness, we retained inbreeding depression in our basic model.

Catastrophes

Catastrophes, as defined by VORTEX, are episodic effects which occasionally depress survival or reproduction. We included two types of catastrophes in our basic model. The first, a 'mild' catastrophe, was devised to simulate the effects of environmental factors such as drought or episodic human persecution. These 'mild' catastrophes reduced adult survival for one year by a factor of 0.85 (*i.e.* a 15% reduction), and reduced breeding by a factor of 0.5. Our default model included a 5% chance that such a 'mild' catastrophe would occur in any one year (*i.e.* they occur, on average, every 20 years). Calibrating this type of catastrophe against observed data is difficult, but reproductive failure through environmental effects such as flooding (Malcolm & Marten 1982), through persecution (Ginsberg, Unpublished data), or other causes is not uncommon.

We included a second, 'severe', catastrophe type to simulate the effects of epidemic disease. 'Severe' catastrophes had no effect upon breeding, but reduced adult survival by 50%. Our model included a 3% chance of such a 'severe' catastrophe in any one year. This level of mortality represents an average loss over

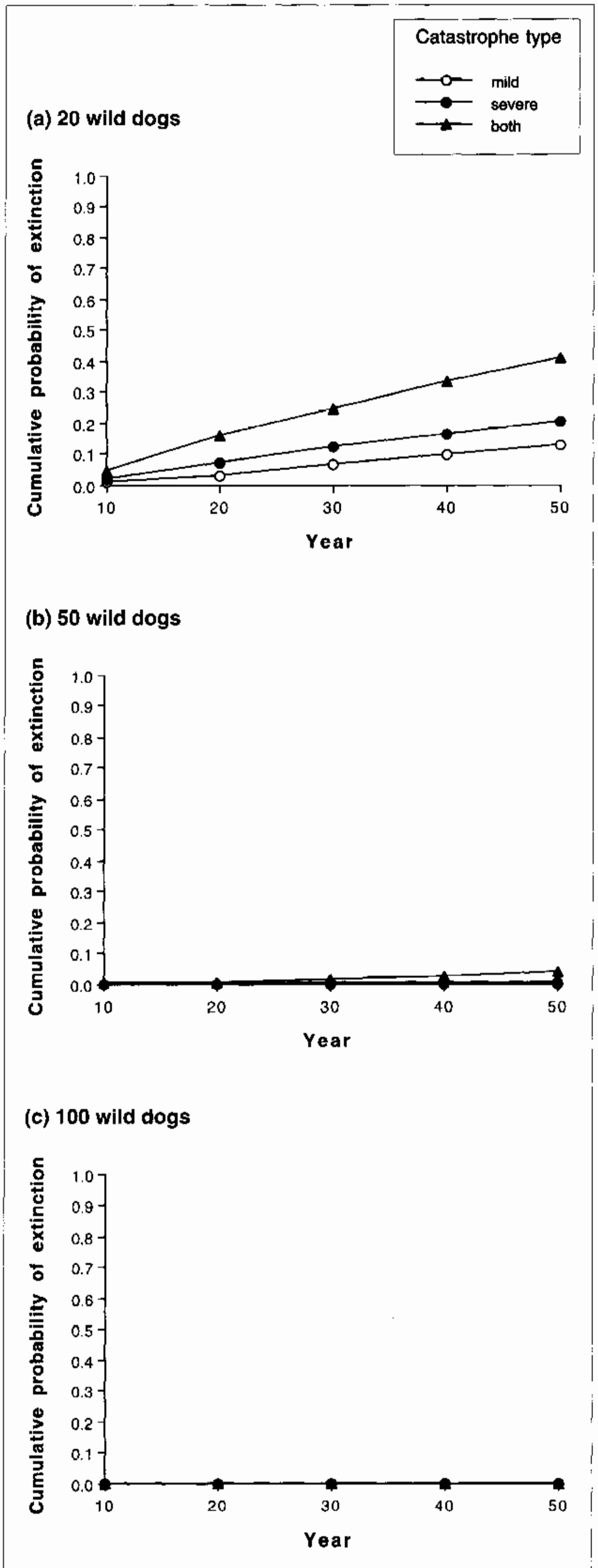


Figure 5.2. The effect of 'mild' and 'severe' catastrophies, and a combination of the two, upon simulated populations. The cumulative probability of extinction is given for populations with carrying capacities of (a) 20, (b) 50, and (c) 100 wild dogs.

an array of diseases such as canine distemper and rabies (Chapter 4). The cyclicity of such infections will vary with a number of factors (Dobson & Hudson 1995) and, while few empirical data are available, catastrophic die-offs are often of this magnitude (Young 1994).

The effects of 'mild' and 'severe' catastrophes, and of the two in combination, are shown in Figure 5.2. The effect of either or both catastrophes is surprisingly unimportant in model populations of 50 or above (Figures 5.2b & c). Presumably, the remarkable fecundity of wild dogs allows them to recover rapidly from such short-term perturbations. In tiny populations (K = 20, Figure 5.2a), however, catastrophes can be devastating. As expected, 'severe' catastrophes have a greater impact upon population persistence than do 'mild' catastrophes: the probability of extinction is 13% within 50 years when only 'mild' catastrophes occur, compared with 20% if only 'severe' catastrophes are included in the model, and 40% if both types of catastrophe are incorporated.

VORTEX only allows the user to define a stochastic probability with which catastrophes occur. Clearly, in small populations, the frequency of catastrophes, and the length of the interval between catastrophes, is critical to determining how they will affect the probability of population extinction. Indeed, Ginsberg *et al.* (1995) found a non-linear increase in the probability of extinction over 25 years as the number of catastrophes increased.

Population Fragmentation

Wild dogs persist only in areas where human population density is low (Chapter 3). As a result, many wild dogs have become isolated in parks or other protected areas, with only limited exchange between populations. We investigated the effects of such fragmentation by simulating two sub-populations linked by dispersal. While animals may move between the simulated sub-populations, VORTEX assumes that stochastic effects such as catastrophes influence each sub-population independently. This assumption may be invalid in many circumstances.

In Figure 5.3 we compare the persistence of a single population with that of a fragmented metapopulation. Each metapopulation is composed of two sub-populations, with a combined size equal to that of the single population. For example, we compare the persistence of a single population of 50 animals with that of a metapopulation made up of two populations of 25. Figure 5.3 shows that tiny populations are more likely to become extinct when they are fragmented than when they remain intact: the probability that a population of

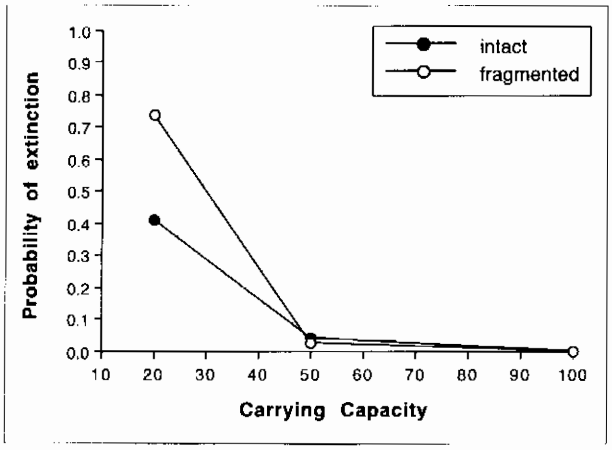


Figure 5.3. The effect of fragmentation upon the probability that model populations will become extinct.
The probability that an intact population will become extinct within 50 years is compared with the corresponding probability for a fragmented metapopulation with the same combined carrying capacity. This graph compares a single population of K = 20 with a metapopulation consisting of two sub-populations each with K = 10, a single population of K = 50 with a metapopulation consisting of two sub-populations each with K = 25, and a single population of K = 100 with a metapopulation consisting of two sub-populations with K = 25 and K = 75. In each metapopulation, the probability of dispersal from the first sub-population to the second is 0.9%, and the probability of dispersal from the second sub-population to the first is 1.5%.

20 animals will become extinct within 50 years rises from 41% to 74% when it is divided into two sub-populations of 10 animals each. This is to be expected: since fragmentation reduces the functioning size of each sub-population, it can lead to increases in both inbreeding and the impact of stochastic effects, making sub-populations more likely to die out despite the opportunity for exchange between them.

In contrast, larger populations persist as well – or even marginally better – when they are fragmented. The probability that a population of 50 animals will become extinct falls slightly from 4% to 2% when it is divided into two sub-populations of 25 each (Figure 5.3). This is not entirely surprising. If sub-populations face different threats, or similar threats at different times, then fragmentation may reduce the probability of metapopulation extinction: a series of catastrophes can cause one sub-population to become extinct, but animals from the other sub-population can re-colonize the extinct sub-population. Extinction/recolonization metapopulation dynamics appear to be relatively unimportant in larger metapopulations (K = 100) with both fragmented and cohesive populations having high persistence (Figure 5.3).

While the persistence of a larger metapopulation may not be seriously affected by fragmentation (as long as sub-populations remain linked), smaller populations within a metapopulation matrix gain tremendously by being linked together. The value of linking small populations can be seen by examining the persistence of a tiny (K = 25) population under three scenarios: alone, linked to another population of K = 25, or linked to another population of K = 75 (Figure 5.4). An isolated population of K = 25 has a 13% probability of extinction within 50 years, but this probability falls to 8% if that population is linked to another of K = 25, and drops still further to less than 1% when it is linked to a population of K = 75. Linking smaller sub-populations into a single metapopulation gives them the persistence profiles of larger populations.

As for all modelling exercises, the value of this finding depends upon the validity of its assumptions. In this case, the important assumption is that catastrophes affect the sub-populations independently. The reason why populations of 50 to 100 individuals persist relatively well when fragmented is that while each sub-population is more likely to become extinct, in most cases the other sub-population persists and re-colonizes the first. However, in the real world, extinction risks within different parts of the same metapopulation are unlikely to be independent. For example, it is very unlikely that linked populations would experience dramatically different weather conditions: a drought

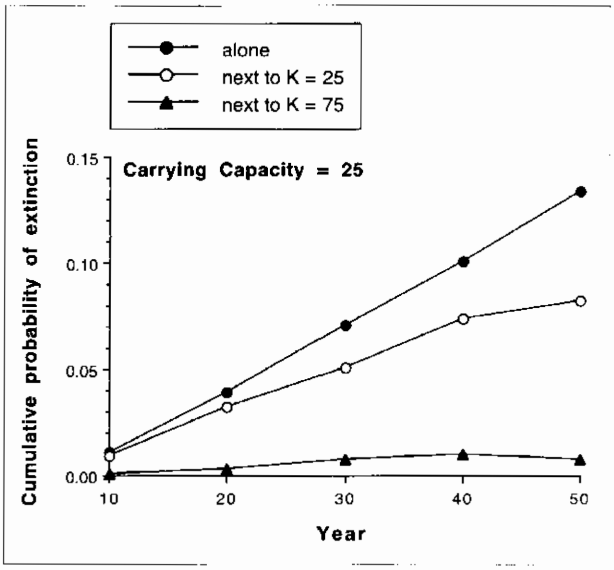


Figure 5.4. The effect of proximity to another sub-population on the probability that a tiny population will become extinct.
This graph shows the probability of extinction of a population of K = 25 when it is alone, when it is linked by dispersal to another population of the same size, and when it is linked by dispersal to another population of K = 75. In each metapopulation, the probability of dispersal from the first sub-population to the second is 0.9%, and the probability of dispersal from the second sub-population to the first is 1.5%.

that affected one sub-population would also be likely to affect the other. A similar argument can be applied to the effects of epidemic disease. Domestic dogs constitute the reservoir host for many diseases that threaten wild dogs (Chapter 4). Wild dogs may be largely confined to islands of low human population density, but the areas between such sub-populations are likely to contain more-or-less contiguous populations of domestic dogs. If an epidemic disease spread from domestic dogs to one part of a wild dog metapopulation, it would also be likely to affect the other sooner or later. In addition, wild dogs themselves could carry infection from one part of a metapopulation to another (as may have occurred in the last population of black-footed ferrets, Seal *et al.* 1989). It seems likely, therefore, that absolute size of a population, or metapopulation, is the single most important variable in the persistence of wild dog populations, and we would certainly not advocate population subdivision as a management strategy. Indeed, every effort should be made to maximize the continuity of habitat available to wild dogs.

Threats which Increase Adult Mortality

Several of the threats summarized in Table 5.3 affect wild dogs by increasing the mortality of animals more than a year old (N.B. in this section we refer to such animals as 'adults', although the model defines separate survival probabilities for yearlings and two-year olds to reflect increased probability of mortality during dispersal). Predation by lions, road traffic accidents, snaring and direct persecution all act in this way. We therefore investigated the effect of sustained changes in adult mortality upon the persistence of simulated wild dog populations.

The results are shown in Figure 5.5, and point to some important effects. First, a small drop in adult mortality generates a marked reduction in the probability that very small populations will become extinct: in a population of 20 animals, reducing adult mortality by a step of 5% causes the probability of extinction within 50 years to fall from 41% to 13% (Figure 5.5a). This effect essentially disappears in larger population (K = 50), where the same reduction in mortality brings the probability of extinction down from 0.3% to zero (Figure 5.5b). Perhaps more important, however, is the finding that increasing adult mortality can have dramatic effects upon the probability that even larger populations will become extinct. For example, if adult mortality rises by a step of 10%, the probability that a population of K = 50 will become extinct within 50 years increases from close to zero to 7% (Figure 5.5c).

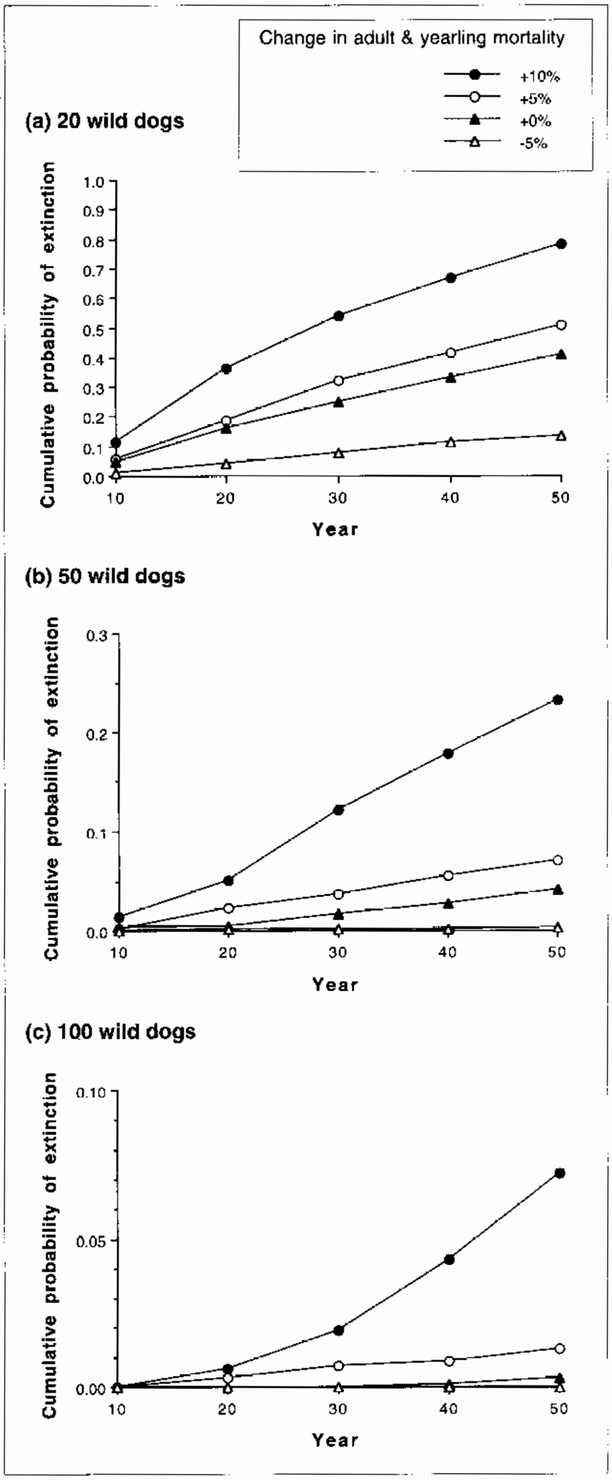


Figure 5.5. The effect of varying adult mortality upon the cumulative probability of population extinction.
In our basic model, mortaility is 20% between the ages of 1 and 2, 15% between the ages of 2 and 3, and 10% thereafter. These simulations increased or decreased adult mortality in steps of 5%: thus for '+5%' adult mortality was 25% between the ages of 1 and 2, 20% between the ages of 2 and 3, and 15% thereafter. Results are given for populations with carrying capacities of (a) 20, (b) 50, and (c) 100 wild dogs.

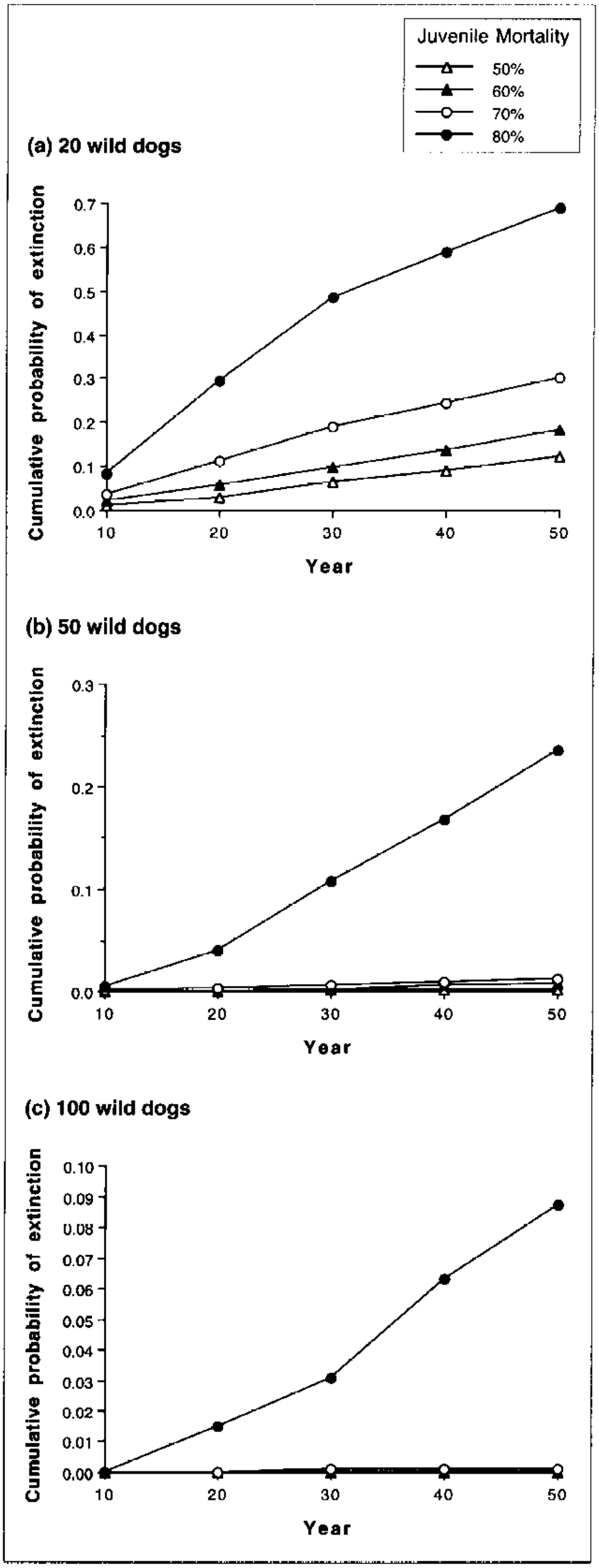


Figure 5.6. The effect of varying juvenile mortality upon the cumulative probability of population extinction.
Results are given for populations with carrying capacities of (a) 20, (b) 50 and (c) 100 wild dogs.

These findings have two important implications for the assessment of threats to real wild dog populations. First, small populations are extremely sensitive to changes in adult mortality. Essentially, in a tiny population every adult will be important in ensuring persistence. The management of such populations – which will include those re-established by reintroduction – will therefore demand that factors which kill adults be minimized. This will mean that measures must be taken to control persecution, road kills and snaring. Lion predation may also represent a very serious threat to tiny populations – lions can cause up to 47% of adult mortality (Table 5.3). While little can be done to control lion predation in free-ranging wild dogs, reintroduction attempts may be more successful in areas which are free of lions. Indeed, lion predation has foiled at least two reintroduction attempts in the past (Chapter 7).

A more important finding, however, is that sustained increases in adult mortality will threaten large populations as well as smaller ones. Thus changes in land use which lead to higher adult mortality – such as the opening of new tarmac roads through national parks, rising human population density generating more intense persecution of wild dogs, or even changes in carnivore management leading to marked increases in lion density – could drive populations of 100 or more wild dogs to extinction.

Threats which Increase Juvenile Mortality

A number of the threats summarized in Table 5.2 affect the mortality of wild dog pups. Juvenile mortality varies substantially within and between populations (Fuller *et al.* 1992). We therefore varied the levels of juvenile mortality in our simulated populations in 5% increments between 50% and 80%. The results – which are shown in Figures 5.6 & 5.7 – indicate that persistent changes in juvenile mortality can have a marked effect upon the viability of wild dog populations, even those which are reasonably large.

In all but the smallest populations (Figure 5.6a), varying juvenile mortality in the region 50–70% has little effect upon population persistence. Above 70%, however, small increases in juvenile mortality generate large changes in population persistence. For example, in a population of K = 50, increasing juvenile mortality from 70% to 80% raises the probability of population extinction within 50 years from 1% to 24% (Figure 5.6b). Likewise, the same increase in juvenile mortality in a population of K = 100 causes the extinction probability to rise from less than 1% to 9%

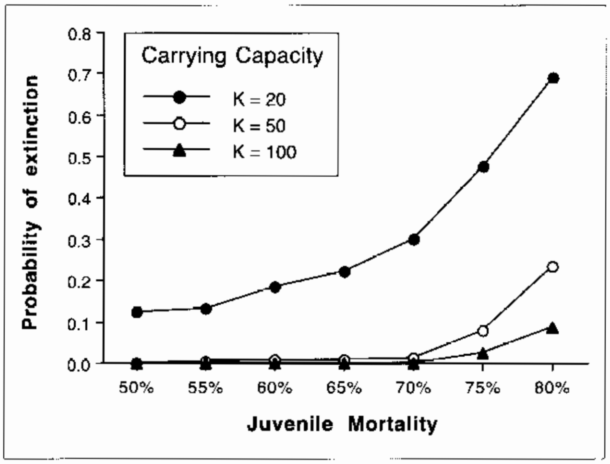


Figure 5.7. The effect of varying juvenile mortality upon the probability of extinction within 50 years, for populations with various carrying capcities.

(Figure 5.6c). These 'threshold' effects of increasing juvenile mortality on population persistence are shown more clearly in Figure 5.7.

These simulations point to two important conclusions. First, although our 'mild catastrophe' models indicate that episodic reductions in the number of pups born have relatively little impact upon population persistence, a persistent change in juvenile mortality has a much more marked effect. Factors which cause short-term breeding failure, such as epidemic diseases affecting only pups, or flooding of dens, are therefore unlikely to drive populations to extinction, but more long-term effects could be devastating.

A second important finding of our simulations is that average juvenile mortality, at 68%, falls just below the threshold where population persistence starts to decline. This means that even relatively small increases in pup mortality could be sufficient to drive some populations to extinction if new causes of mortality act in addition to existing ones. Changes such as the introduction of diseases which kill pups but rarely adults (*e.g.* parvovirus), or falling prey densities leading to frequent breeding failure, could therefore contribute to the extinction of even relatively large wild dog populations. Consistent increases in pup mortality would also be generated by opening new high-speed roads in wild dog areas, poor control of snaring, and increasing lion predation (Table 5.3). All of these factors would also affect adult mortality, causing even more marked effects upon population persistence.

Conclusions

A number of patterns emerge from this modelling exercise. Perhaps the most important conclusion to be drawn is that wild dog populations appear to be remarkably resilient. With their large litters, wild dogs have a high reproductive potential and can, in principal, bounce back from perturbations if their populations are not reduced too far. Our simulations indicate that 'catastrophes' having dramatic short-term effects on breeding and survival affect the persistence of only the smallest populations.

In stark contrast, consistently high mortality of adults or pups can generate an abrupt increase in the probability that simulated populations become extinct. High juvenile mortality negates the effect of high fecundity and prevents wild dogs from bouncing back from perturbations. Thus while wild dog populations are resilient to short-term perturbations, factors which cause consistent increases in adult or juvenile mortality could represent very serious threats.

Our modelling suggests that inbreeding depression is unlikely to have a substantial effect upon most wild dog populations. Indeed, wild dogs have a mechanism for avoiding inbreeding and, probably as a result, large populations show fairly high levels of heterozygosity (Chapter 2). While it has been suggested that inbreeding avoidance (rather than inbreeding depression) might halt breeding in small populations (Maddock 1996), this has not been demonstrated: relatives breed together readily in captivity (J. van Heerden pers. comm.), and inbreeding has been recorded once in the wild (Reich 1978). Our simulations suggest that environmental and demographic effects are more important than inbreeding depression in driving small populations to extinction; this appears to be a general pattern in the biology of small populations (Lande 1988).

As expected, larger populations ($\geqslant 100$ animals) are best able to persist in the face of threats. Populations of this size remain in extensive tracts of land with low human population density, inside protected areas such as Selous ($n > 800$) and Kruger ($n > 300$), in areas which are either mostly privately or communally held such as north-east Namibia ($n > 400$), or in matrices of protected and communal land as found in northern Botswana ($n > 400$). Since populations of this size are likely to persist if they can be protected adequately, their importance for wild dogs' long-term survival cannot be stated too highly.

Small populations (~50 animals) remain resilient to perturbation, and stand a high chance of persisting if they are well protected. They are, however, very sensitive to consistent increases in adult and juvenile mortality. Factors such as persecution, road accidents, accidental snaring, endemic disease and lion predation will therefore represent very serious threats to such populations. Many of Africa's remaining wild dog populations are about this size (Table 5.2), and most inhabit unprotected areas or relatively small protected areas with a correspondingly high perimeter:area ratio. This will bring these animals into contact with human activity. As a result, the populations which are exposed to the most severe threats are likely to be the smaller populations least able to withstand them.

Tiny populations (~20 animals) are still more vulnerable. With so few animals, every individual becomes important in ensuring the survival of the population, so that protection must be intense. All smaller populations stand a much better chance of survival if they can be linked by dispersal to other populations.

These conclusions must be accompanied by a note of caution. Because we have considered each factor independently, in some ways this modelling exercise is extremely conservative and underestimates the extinction risks threatening wild dogs. In the real world, increasing human population density, concomitant increases in the number of domestic dogs and livestock, and resultant reductions in the number of wild prey, would lead simultaneously to increases in threats such as persecution, road casualties and disease. This conservative approach is somewhat mitigated, however, by our assumption that threats themselves are statistically independent of one another, and that an increase in one form of mortality will not lead to a compensatory decrease in another form of mortality. Furthermore, while VORTEX is adequate to enunciate patterns and differences, for modelling to be prescriptive, rather than merely informative, we would advocate a detailed, demographically and spatially structured model be developed for wild dogs.

With these caveats, our results indicate wild dog conservation demands the maintenance of relatively large (⩾ 100 individuals) and inter-connected population. To do this, the decline of some populations must be halted through better protection, while ensuring that future development is both zoned and implemented in such a way as to define areas where wild dogs, and other wildlife, can survive. The statement that protecting wild dogs must involve keeping their numbers high may sound like a truism, but this represents a serious conservation challenge for a species that occurs at such low densities. Specific conservation measures for wild dog populations of all sizes are discussed in detail in the next chapter.

Chapter 6
Measures for the Conservation and Management of Free-ranging Wild Dog Populations

Rosie Woodroffe & Joshua R. Ginsberg

Previous chapters show that fragmentation, persecution, disease and road accidents represent serious threats to small wild dog populations, but that these risks diminish in larger populations. This suggests three paradigms for the management of Africa's remaining wild dog populations:

***(1) Maintaining large (> 10,000 km²) contiguous tracts of land set aside for wildlife** represents the single most important strategy for wild dog conservation. Such areas are large enough to support viable wild dog populations, and contain core areas where wild dogs are fully protected from human activities. Measures that would benefit wild dogs include:*
- *maintaining the integrity of large protected areas*
- *establishing cross-border parks*
- *linking reserves by corridors*
- *establishing networks of smaller protected areas linked by privately, publically, or communally held land managed for wildlife*

Inside such wildlife areas, wild dogs would be protected by routine reserve management including:
- *control of poaching to maintain their prey base*
- *severe restrictions on building high-speed roads in wildlife areas*
- *zero tolerance of domestic dogs – strays must be shot on sight.*

***(2) Integrated carnivore management programmes** should be established to resolve conflicts between people and wild dogs where they coexist. Such programmes could involve:*
- *zoning of lands to define areas where predators will, and will not, be tolerated*
- *assessment of predator impact on livestock and wild prey species*
- *local conservation organizations working with farmers to minimize livestock losses through better husbandry practice*
- *compensation programmes for stock that are killed*
- *control, and perhaps vaccination, of domestic dog populations*
- *a ban on sport hunting of wild dogs*

***(3) Establishing tiny populations in small, fenced reserves** may be the only way to conserve wild dogs in highly fragmented landscapes. Persistence would be improved by managing several such populations together as a metapopulation, periodically translocating animals between reserves. Such intensive management would be expensive and, while valuable for increasing the number of wild dogs in a local area or country, provides no substitute for protection of free-ranging populations.*

Background

In previous chapters, we have described how wild dogs have been extirpated across much of Africa, and discussed the factors which threaten populations of various sizes. In this chapter, we use this information to propose measures for the conservation and management of the wild dogs that remain in Africa. In the next chapter, we discuss the possibilities for re-establishing populations by the reintroduction of wild dogs to areas where they have been extirpated.

Protection of wild dog habitat

Wild dogs only persist in countries with low human population density (Chapter 3). Some wild dog populations do coexist with people – but such coexistence is only likely to be stable under certain circumstances:

1) The density of wild ungulate prey must remain high.
2) The density of domestic dogs must remain low. High density domestic dog populations can act as reservoirs for diseases that threaten wild dogs.

Such conditions mainly occur where human settlement has been curbed, either because the area has been set aside for wildlife, or through some external factor (*e.g.* tsetse flies, Rogers & Randolph 1988). Conservation of wild dogs therefore depends upon the long-term persistence of large areas where human population density remains low.

National Parks and Reserves

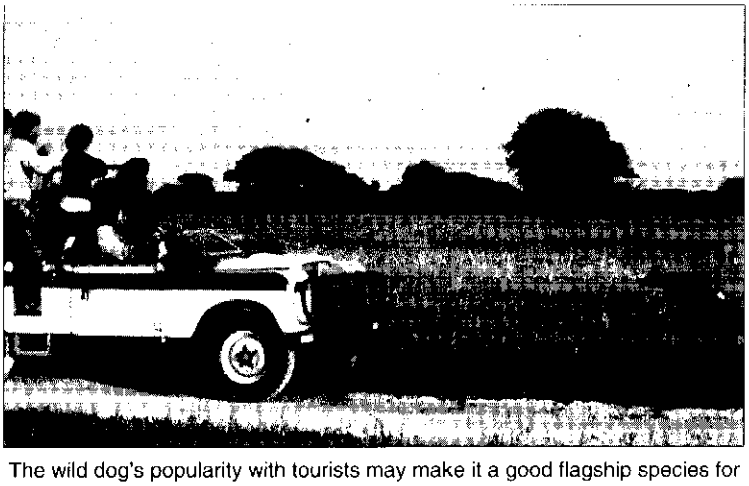
Maintaining protected areas forms the single most important component of a strategy for wild dog conservation. As human populations rise, pressure on wild dogs will increase. Under these circumstances, protected areas will become some of the few areas where threats to wild dogs can be minimized in the long term.

As discussed in Chapters 4 and 5, in most cases only the very largest reserves will provide adequate protection for wild dogs. There are two reasons for this. First, since wild dogs live at extremely low densities, only very large areas can sustain populations large enough to be potentially viable. Second, wild dogs frequently range outside reserve boundaries, where they encounter high-speed traffic, snares, persecution and domestic dog diseases. This means that they experience substantial edge effects, even in reserves which are large by other standards (1,000 km² – 5,000 km²). Only very large reserves (> 10,000 km²) can provide core areas where wild dogs will be protected from hazards on the borders. For this reason, any measures which lead to the expansion and stabilization of protected areas – such as establishing cross-border parks, linking reserves with corridors, maintaining buffer areas around national parks, and encouraging land use favourable to wildlife on reserve borders – will make substantial contributions to the conservation of wild dogs. Such measures have been proposed or implemented in a number of areas. For example, the Niokolo-Koba National Park in Sénégal has recently been linked with Badiar National Park in Guinea, and plans have been put forward to link Kruger National Park, South Africa, with Gona re Zhou National Park, Zimbabwe by establishing further protected areas in neighbouring Moçambique. Programmes of this kind will benefit many wildlife species, but are especially valuable for the conservation of wild dogs. Wild dogs may, therefore, act as 'flagships' for the expansion of protected areas.

Wild dogs travel widely, with home ranges in excess of 1,000 km² per pack, and daily movements of around 15 km. Wild dogs living in small reserves are therefore vulnerable because, no matter where they go, they will cross the edge of a reserve and be exposed to human activity outside. In principal, fencing could protect wild dogs from threats on reserve borders, but fencing is extremely expensive. Some reserves are fenced in parts of southern Africa, but most of these are too small to sustain more than one or two wild dog packs. Neverthe less, a network of such reserves might support a metapopulation of wild dogs if they were protected from threats such as disease, and if some animals were translocated between sites periodically to maintain genetic diversity. Such intensive management is no substitute for protecting truly free-ranging wild dog populations and would, in any case, be prohibitively expensive in most of Africa. Nevertheless, such efforts will aid the conservation of wild dogs in highly fragmented landscapes where funds are available.

Other Wildlife Areas

Protected areas maintained by national or local governments are not the only places where wild dogs persist. Low human population densities and abundant wild ungulate prey also occur on private ranches, game farms and communal lands in many parts of Africa. Indeed, in Namibia, as well as parts of Botswana, Kenya and Ethiopia, there may be more dogs outside protected areas than there are inside them (Chapter 3). In other areas, such as Zimbabwe, even those dogs



The wild dog's popularity with tourists may make it a good flagship species for expansion of protected areas.

which 'live' in protected areas spend much of their time in the buffer zones outside of parks and reserves.

Wild dogs were extirpated from most private ranches and game farming areas earlier this century. However, many farmers that persecuted wild dogs to protect their stock also eradicated lions and hyaenas. Thus private land has the potential to provide ideal habitat – combining abundant prey with very low densities of competitors – if persecution could be curbed. Similar reasoning has led to suggestions that private land might play an important rôle in the conservation of cheetahs (Laurenson 1995).

An attempt is underway in South Africa to use private land for wild dog conservation: staff from the Natal Parks Board are negotiating with farmers to allow the wild dog population in the Hluhluwe/Umfolozi Park to use game farms surrounding the park (A. Maddock pers. comm.). The success of this programme will depend upon the goodwill of the farmers, and should greatly increase the possibilities for long-term persistence of this small population. Elsewhere in South Africa, however, farmers are less accommodating: when a pack of wild dogs appeared on private land along the Limpopo, local farmers immediately attempted to shoot them (M.G.L. Mills pers. comm.).

It is also possible to protect wild dogs on communal lands. For example, an innovative new programme of carnivore conservation, with extensive involvement of local people, has recently been set up in north-eastern Namibia (P. Stander pers. comm.). Outside of protected areas, persecution and disease will represent the greatest threats to wild dogs. Effective wild dog conservation will therefore depend upon minimizing these threats. We discuss the measures necessary in the next sections.

Controlling Human-induced Mortality

Persecution

Persecution is a major threat to wild dogs, especially those living outside protected areas. Most persecution is carried out by livestock and game farmers who consider wild dogs a serious threat to their stock. As discussed in Chapter 4, wild dogs may be blamed for more livestock losses than they actually cause. Where this is the case, local education will help to limit persecution – but it must be recognized that wild dogs do occasionally cause substantial losses, especially in areas where small stock (sheep and goats) are kept. Experience with wild dogs and other predators indicates that several measures can help to mitigate the problem.

Legal Protection and Zoning

Although wild dogs are classified as 'endangered' according to the IUCN threat criteria (Baillie & Groombridge 1996), the degree of protection conferred by local legislation varies among different range states. In several countries, wild dogs are only partially protected (Table 6.1); this means that, under certain circumstances, legal persecution of wild dogs can continue. For example, the government of Cameroun licensed professional hunters to shoot 65 wild dogs in the season December 1994–May 1995 (H. Planton pers. comm.). We are not aware of the numbers of wild dogs actually shot by hunters in that season – but it is extremely unlikely that Cameroun's small wild dog population could sustain the degree of persecution permitted by law. In circumstances of this kind, better legal protection represents a crucial first step towards effective wild dog conservation. We must emphasize, however, that legal protection represents only a small part of wild dog conservation: total protection failed to prevent the extinction of wild dogs in the Republic of Congo, Nigeria and Rwanda (Table 6.1).

Despite the need for better legal protection in some areas, efforts to limit persecution must take a realistic view of the threat to farmers' livelihoods. Even in livestock areas, wild dogs usually feed on wild ungulates, but they can occasionally cause substantial livestock losses (Chapter 4). Local governments may decide that large predators simply cannot be tolerated in some areas used for raising livestock, and designate such regions as predator control zones. Such 'zoning' has been an important component of wolf recovery plans in North America (Fritts *et al.* 1992; Mech 1995). As an example, wild dogs are sighted occasionally in agricultural areas of east-central Zimbabwe and northern South Africa, where wild prey have been depleted. It is unlikely that viable wild dog populations could persist in such areas – intensive legal protection of wild dogs might therefore alienate farmers from local conservation authorities, and could even interfere with the smooth running of other local conservation programmes (Stander 1991).

Designation of predator control zones must, however, take into account the conservation value of 'vagrant' wild dogs. As discussed in Chapter 5, movement of animals between populations – even if it occurs only occasionally – can dramatically reduce the probability that small populations will become extinct. Vagrant animals may, therefore, contribute to the long-term persistence of local wild dog populations. For this

Table 6.1
The status of wild dog populations, and their degree of protection, across range states. The columns marked 'date' give, respectively, the date of the most recent information on which the population estimate is based, and the date of the protective legislation. The sources of information about population status are given in the text of Chapter 3. Most of the information about the protected status of wild dogs was provided by the IUCN Environmental Law Centre. Other sources are given in the text of Chapter 3.

Country	Status of wild dogs	Date	Degree of protection	Date
Algeria	rare?	1989	?	–
Angola	rare?	1987	total?	1957
Benin	extinct?	1987	?	–
Botswana	present	1996	partial	1979
Burkina Faso	extinct?	1987	partial	1989
Cameroun	present	1992	partial?	?
Central African Republic	present	1987	total	1984
Dem. Republic of Congo	extinct?	1987	partial	1982
Republic of Congo	extinct	1992	total	1984
Côte d'Ivoire	rare?	1987	noxious	1965
Eritrea	extinct?	1992	?	–
Ethiopia	present	1995	total	1972
Gabon	extinct	1987	?	–
Ghana	extinct?	1987	partial	1971
Guinea	rare	1996	total	1990
Kenya	present	1996	partial	1976
Malawi	rare	1991	partial	?
Mali	extinct?	1989	?	–
Moçambique	rare	1996	total	1978
Namibia	present	1996	total	?
Niger	extinct?	1987	total?	?
Nigeria	extinct?	1991	total	1985
Rwanda	extinct	1987	total	1974
Sénégal	present	1996	partial	1986
Sierra Leone	rare?	1996	?	–
Somalia	rare?	1994	total	1969
South Africa	present	1996	specially protected	?
Sudan	rare	1995	total?	?
Swaziland	extinct?	1992	?	–
Tanzania	present	1996	total	1974
Tchad	rare	1987	?	–
Togo	rare?	1987	partial	1968
Uganda	rare?	1996	?	–
Zambia	present	1994	total	1970
Zimbabwe	present	1992	partial	1990

reason, farmers should not be given carte blanche to persecute wild dogs, even inside areas designated as predator control zones. Wild dogs entering such areas should be removed only if they cause serious livestock losses, and then only by local conservation authorities. Strategies for dealing with such 'problem animals' are discussed below.

Livestock Husbandry

While governments may designate some areas as predator control zones, elsewhere local conservation policy will aim to allow wild dogs to persist in areas also inhabited by livestock. Such circumstances are likely to occur on the borders of reserves inhabited by wild dogs, and in communal and private lands supporting a mixture of wildlife and livestock. In these areas, a number of measures will help to reconcile the requirements of wild dog conservation with the needs of local livestock farmers.

Better livestock husbandry may help to protect livestock from wild dogs, as well as from other predators. Maasai herdsmen interviewed at 20 manyattas in a group ranch near the Masai Mara, Kenya, had no recollection of losing sheep, goats, cattle or donkeys to wild dogs, although a large pack was using the area at the time (Fuller & Kat 1990). In this area, livestock were tended continually by people and guard dogs during the day, and kept in bomas at night. Similar husbandry techniques are used traditionally to protect livestock from wolves in Italy – studies have shown that wolves often approach the bomas but rarely attack (Boitani 1992).

Wild dog predation is likely to be a more serious problem when stock are kept in large herds and poorly tended – this is certainly true of wolf predation (Boitani 1992). However, little is known about the circumstances when wild dogs kill livestock, and more research is needed before better husbandry techniques can be devised. In particular, the value of guard dogs in protecting livestock must be traded off against their role as reservoir hosts for diseases which threaten wild dogs (see below). Any programme which encouraged the use of domestic dogs as guards would also have to involve provision for disease control in the domestic dog population. Such disease control could also benefit local people since rabies, the most serious threat to wild dogs, is also a threat to people and their livestock.

Altering the type of livestock kept may also ease coexistence of wild dogs and people. Cattle are less vulnerable than sheep and goats, and there is speculation that 'traditional' cattle breeds might be better equipped than more modern breeds to deal with attacks from predators – when threatened they tend to show defensive behaviour like that of wild cattle species, protecting vulnerable calves inside of a ring of adults (G. Rasmussen pers. comm.).

Compensation Schemes

Compensation schemes have helped to resolve some conflicts between livestock farmers and wolves in North America and in Italy (Fritts *et al.* 1992; Mech 1995). Such schemes could be useful in wild dog conservation, especially on the borders of reserves holding important wild dog populations. The viability of compensation schemes would, however, depend upon:

1) The availability of funds to provide compensation for livestock lost to wild dogs. On some reserve borders, profits derived from tourism within the reserve could be used to fund such compensation schemes. However, many wild dog populations occur in remote reserves which generate rather little tourist revenue. In such circumstances other funds would be needed to finance compensation schemes.
2) Establishment of local standards of good husbandry to ensure that compensation does not become a substitute for adequate care for livestock (Fritts *et al.* 1992).
3) The availability of skilled staff to investigate alleged attacks as soon as they occur, to determine whether wild dogs were indeed responsible, and whether local standards of good husbandry had been practised (Fritts *et al.* 1992).
4) Adequate supervision of staff carrying out the investigation.

If all of these conditions were met, compensation schemes might form a useful component of wild dog management in some areas where they take livestock occasionally. Such schemes would, however, be expensive and should only be implemented as part of integrated management programmes including local education, work on husbandry practices and, perhaps, disease control in domestic dogs. Programmes of this kind need not, however, be aimed purely at wild dogs – several carnivore species could certainly be managed simultaneously as part of the same scheme.

Control of Poisons

Local education and compensation should help to mitigate persecution where this is directed at wild dogs specifically – for example where livestock farmers shoot them. In some areas, however, persecution is applied indiscriminately to predators in general, by laying out poison baits or adding poison to water holes. Better legal control of poisons in such countries would help to protect wild dogs – this was an important component of successful wolf conservation measures in Italy (Boitani 1992).

Problem Animals

Although wild dogs usually ignore livestock, they can occasionally cause severe problems: for example, a group of wild dogs in Laikipia, Kenya killed 66 merino ewes and 67 lambs in a nineteen-week period in 1996 (M. Dyer pers. comm.), forcing the Kenya Wildlife Service to capture the animals responsible (R. Kock pers. comm.). The circumstances under which wild dogs start to take large numbers of livestock are not clear. However, such attacks may lead to substantial economic losses which farmers cannot be expected to tolerate.

If (as in Laikipia) investigation by local conservation authorities shows that wild dogs are indeed causing losses which are both serious and sustained, and if no compensation scheme is in place or if the losses are too great to be sustained by a compensation scheme, the only solution may be to remove the 'problem animals' from the area. The first possibility is to translocate the problem dogs elsewhere. Translocation would be the best solution if suitable release sites were available. Such sites would have to:

1) Have suitable habitat for wild dogs, but no resident wild dog population
2) Have adequate protection for the translocated wild dogs
3) Be largely free of livestock. Some lions are known to develop a 'taste' for killing livestock (Stander 1990). If the same pattern occurs in wild dogs, then translocated animals might continue to present problems if they were moved to areas where they still came into contact with livestock.

Translocation is discussed in detail in Chapter 7 – however, in practice suitable reintroduction sites are very uncommon, especially outside of southern Africa. Alternatively, problem animals might be taken into captivity, where they could play a very important rôle in public education, and in conservation-related research, such as the testing of vaccines. Again, this possibility is discussed in the Chapter 7.

If no suitable sites were available for translocation, and if no captive facilities had any use for additional wild dogs, then the very last resort for dealing with problem animals would be to shoot them. This is to be avoided wherever possible. However, conservation authorities must make occasional compromises: past efforts to force people to tolerate large carnivores on their land have led to bad relations between conservation authorities and local people (Stander 1991), and a willingness to shoot wolves where they cause genuine problems has been an important component of effective wolf conservation (Mech 1995). By dealing with problem animals, wildlife authorities establish credibility with local citizens, thus improving their ability to effect conservation.

Snaring

Snares are rarely set to catch wild dogs – in most cases they are caught by accident in snares set for wild ungulates. Thus, the best way of protecting wild dogs is to invest in better control of illegal snaring inside protected areas and on their borders– this is a priority for the conservation of other wildlife in virtually all of Africa's protected areas. To be effective, however, enforcement of laws which prohibit snaring should be complemented by programmes which offer people alternative ways to secure protein, such as managed game cropping, better animal husbandry or construction of fish ponds.

Some wild dogs fitted with radio-collars have 'worn' snares unharmed, since the collar prevents the snare from strangling them (J.R.G. Unpublished data). This led to the design of an anti-snare collar which helps wild dogs to remove snares without harming themselves (G. Rasmussen pers. comm.). However, the threat posed by snares rarely warrants immobilizing animals solely in order to fit them with such collars. Investing in better anti-poaching patrols to control snaring is a more appropriate strategy, since it will provide better protection for both wild dogs and their prey.

Road Traffic Accidents

Road traffic accidents are a major cause of wild dog mortality in some areas, especially where tarmac roads pass through areas of relatively high wild dog density (*e.g.* Hwange National Park, Zimbabwe, Kafue National Park, Zambia, and Mikumi National Park, Tanzania). New high-speed roads should not, therefore, be routed through protected areas or along their borders – this is also a priority for the protection of other wildlife. Where such roads are already in use it might be possible to negotiate with highways departments to reduce speed limits. Road signs may also be erected along these roads, asking motorists to slow down to avoid wildlife – this has already been done near Hwange National Park. One wild dog project has built reflective tape into the collars fitted to study animals to make them more visible to motorists (G. Rasmussen pers. comm.) – however, the value of such collars in protecting wild dogs from road traffic accidents has not yet been established. At this stage it does not seem reasonable to immobilize wild dogs solely in order to fit them with reflective collars.

Managing the Threat of Disease

As discussed in Chapters 4 and 5, canid diseases represent a very serious threat to wild dog populations. In the long term, the success of wild dog conservation programmes will depend in part upon their ability to control the diseases to which wild dogs are susceptible.

Wild dogs' vulnerability to disease – and thus the need for disease control – will vary depending upon the population and disease concerned. For example, rabies causes very high mortality and represents a serious threat to all but the largest wild dog populations (Chapters 4 & 5). In contrast, since parvovirus is believed to threaten only small populations (Chapter 5), control of this disease might be inappropriate in larger populations. The threat posed by canine distemper is more difficult to assess – wild dogs have died from canine distemper in Botswana, but survived contact with the virus elsewhere (Chapter 4). Anthrax has little effect upon wild dogs in most areas (Chapter 4). It would be unrealistic, therefore, to invest large amounts of money in protecting wild dogs from anthrax unless an epidemic was believed to be threatening a particularly important population.

Since wild dogs live at such low densities, diseases which cause substantial mortality are unlikely to persist in their populations (Mills 1993). Instead, wild dogs are believed to contract diseases from reservoir hosts living at higher densities. There is good evidence to suggest that domestic dogs provide this reservoir for canid diseases in several areas. Elsewhere, wildlife species such as jackals and bat-eared foxes may act as reservoirs (see Chapter 4).

This information points to several strategies that could be adopted to protect wild dogs from disease. Attempts could be made:

1) to minimize contact between wild dogs and reservoir hosts.
2) to eradicate disease from reservoir host populations.
3) To vaccinate wild dogs directly.

Each strategy has advantages and disadvantages, depending upon both the disease concerned, and the local circumstances. We shall discuss them in order.

Minimizing Contact between Wild Dogs and Disease Reservoirs

It is rarely possible to prevent all contact between wild dogs and reservoir hosts carrying diseases that threaten them. Indeed, for anthrax, which is carried by wild dogs' ungulate prey, this would be entirely impossible. However, it would be possible to reduce contact between wild dogs and domestic dogs, mitigating the threat of disease transmission. Below, we discuss several measures which would be needed. As well as minimizing contact between wild and domestic dogs, all of these measures would also help to increase the efficacy of concurrent vaccination programmes for domestic dogs.

1) Neither tourists nor park staff should be permitted to bring domestic dogs into protected areas where wild dogs occur. If such a total ban were impossible, then owners should, at the very least, be required to prove that their dog has up-to-date vaccinations against rabies, canine distemper and parvovirus. Such dogs should, ideally, have been neutered.
2) Domestic dogs' numbers and movements could be controlled. Where wild dogs use areas also inhabited by people, domestic dogs may play an important social rôle – guard dogs might even be important in reducing livestock losses to wild dogs. Under such circumstances it may be unacceptable – or even undesirable – to completely remove domestic dogs from wild dog areas. Nevertheless, several measures that are often used in public health campaigns to control rabies could be implemented to reduce contact between wild dogs and domestic dogs. Domestic dogs should be tied up whenever possible – this would not interfere with their activities as guard dogs if their principal rôle is to raise the alarm by barking. Owners of domestic dogs should be required to put collars on them, and all dogs without collars (and thus, presumably, without owners) should then be destroyed. Unaccompanied dogs should be shot on sight.
3) Wild dogs can be protected from domestic dogs by secure fencing. This may be appropriate for small reserves, but would be prohibitively expensive across most of Africa, and for larger reserves.

Eradicating Diseases from their Reservoir Hosts

If diseases that threaten wild dogs could be eradicated in the reservoir hosts that maintain them, then wild dogs would also be protected. Where the same diseases also threaten people (*e.g.* rabies, Cleaveland & Dye 1995), or wildlife species other than wild dogs (*e.g.* canine distemper, Roelke-Parker *et al.* 1996), protection could form part of larger-scale public health or wildlife disease control programmes. While the principal of eliminating diseases from their reservoir hosts may be a good one, a number of practical problems arise:

1) The reservoir host is not always known. For example, while domestic dogs appear to be the reservoir host for canine distemper in most areas, no reservoir has so far been identified in Selous (Chapter 4). Efforts to control disease in reservoir hosts are doomed to failure if the wrong host is targeted. More research is urgently needed on the persistence of disease in wild carnivores, and the effect of between-species transmission on their epidemiology.
2) We currently have little information about the efficacy of attempts to protect wildlife by controlling disease in reservoir hosts – even where those hosts are domestic dogs. Both mathematical models and empirical studies have established the proportion of urban domestic dog populations that must be vaccinated in order to eradicate rabies (Coleman & Dye 1996). However, if domestic dogs coexist with wildlife species such as jackals and foxes, which live at high densities, then the wildlife may infect the domestic dogs, as well as vice versa. Whether the same level of vaccination cover will still protect the dogs – let alone both dogs and wildlife – is still unknown.
3) The epidemiology of rabies is relatively well understood, but few quantitative data are available on diseases such as canine distemper. This makes it very difficult to devise strategies for control of such diseases.

Despite these caveats, disease control in reservoir hosts could be a very effective way of protecting wild dogs from disease in the long term. More research is needed in this area to devise effective strategies for disease control. Such strategies would be likely, however, to combine controlling host population size and, ideally, mobility, with programmes of vaccination.

Controlling the Numbers of Reservoir Hosts

Perhaps the best way of managing disease in reservoir hosts will be to control their numbers. This would have two effects. First, it would reduce the rate of contact between wild dogs and reservoir hosts, lowering the probability that disease would enter the wild dog population. Second, it might reduce host population density below the threshold needed to maintain endemic disease. This point is well-illustrated by data collected on rabies in domestic dogs living on the borders of the Serengeti National Park: the infection persisted in one district where domestic dog density exceeded 5 dogs/km², but not in two districts where there were < 1 dogs/km² (Cleaveland & Dye 1995). Thus, reducing domestic dog density could, in principal, eradicate endemic rabies.

The feasibility of controlling the numbers of reservoir hosts depends upon the species involved: culling of wildlife reservoirs would almost certainly be unacceptable inside protected areas. However, where domestic dogs act as reservoirs, it might well be possible to control their population density. In protected areas that are inhabited only by park staff and tourists, there is no excuse for keeping domestic dogs. However, in other areas domestic dogs may play important rôles as guards and hunters. The possibilities for domestic dog control under these conditions would depend upon the opinions of local people, but a reduction in dog density – either by culling or contraception – might well be acceptable if approached with sensitivity. Such a reduction, especially when combined with vaccination and better control of dogs' movements, would greatly reduce the probability of disease transmission between domestic dogs and wildlife. Additional benefits of such a strategy include improved health of the remaining domestic dogs and reduced public health risks associated with rabies.

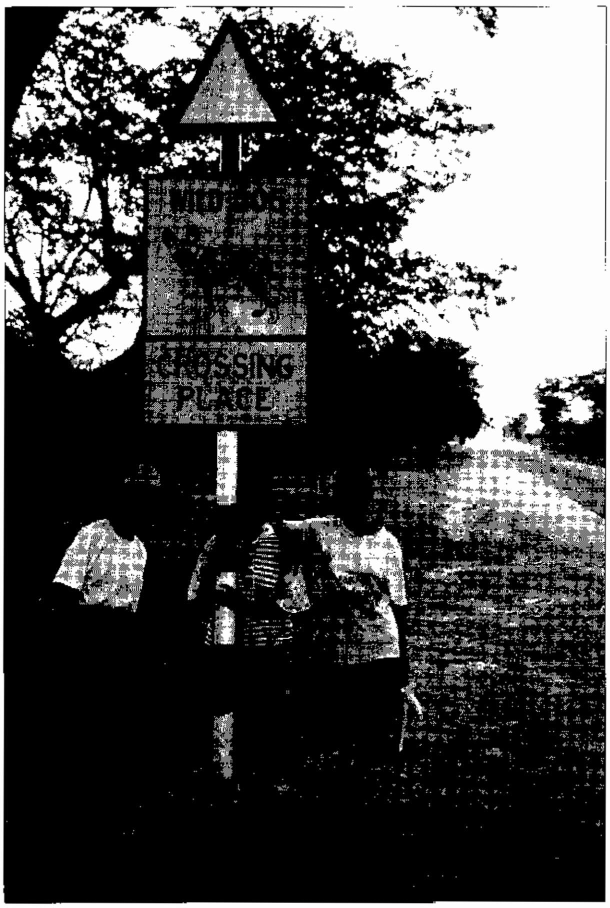
Vaccinating Reservoir Hosts

Contact between susceptible wild dogs and infectious reservoir hosts can also be reduced by vaccinating the reservoirs. Vaccination could be combined with control of host population size and mobility, but could also represent an alternative measure where local people value their domestic dogs very highly, or where the reservoir host is a wildlife species.

It is not necessary to vaccinate all the members of a population in order to eradicate a disease. Vaccination reduces the proportion of hosts in the population that are susceptible to infection. If this proportion falls below a certain critical threshold, hosts die from the disease, or cease to be infectious, before they can transmit the disease to new hosts, and the pathogen is driven to local extinction (Anderson & May 1985). For urban domestic dogs, both empirical studies and epidemiological modelling have established that rabies can be eradicated by vaccinating 70% of the population (Coleman & Dye 1996). The epidemiology of canine distemper is not so well understood, but preliminary modelling suggests that the critical vaccination cover might be as low as 50% (S. Cleaveland pers. comm.). This contrasts with related morbilliviruses such as rinderpest and measles, for which the critical vaccination threshold is much higher (M. Woodford, pers. comm., Dobson & Hudson 1995). Since most domestic dogs are concentrated around human settlements, these levels of vaccination cover can be attained realistically, if at a substantial cost (S. Cleaveland, pers. comm., R. Kock, pers. comm., Laurenson 1996).

Despite these predictions, the effect of a secondary wildlife host upon the epidemiology of rabies and distemper is unknown. It is possible, therefore, that a higher proportion of domestic dogs must be vaccinated to achieve eradication from the whole system. In the meantime, pilot vaccination programmes aimed at controlling rabies and canine distemper in the Masai Mara have managed to vaccinate 80% of domestic dogs (R. Kock pers. comm.). Empirical studies are urgently needed to determine whether such programmes can eradicate disease from wildlife populations.

Vaccination programmes planned for domestic dogs in the Serengeti ecosystem aim to create a disease-free belt on the borders of the protected area (S. Cleaveland pers. comm.; R. Kock, pers. comm.). The width of the belt in which domestic dogs must be vaccinated to protect wild dogs depends upon the mobility of both species. Since wild dogs are known to range over large areas, they could pass through the belt and encounter canid diseases outside. Trial vaccinations around the Masai Mara have produced a belt 15 km wide, but this is much less than the distance that wild dogs may cover in the course of a single day. Furthermore, little is known about the mobility of domestic dogs – if migration in and out of the vaccination zone is commonplace, then the area will not remain free of disease for long. More research is needed to determine the width of cordon sanitaire needed to protect reserves from invasion by canid diseases.



Road signs were erected to try to limit road kills on the Bulawayo to Victoria Falls road outside Hwange National Park.

Where diseases that threaten wild dogs are maintained in wildlife reservoirs, vaccination is more problematic. Oral vaccination programmes have been used routinely to control rabies in wild carnivores in Europe and North America (Wandeler 1993). Research is underway to devise similar strategies to control rabies in jackals in Zimbabwe, but has not yet reached the stage where oral vaccination could be carried out in protected areas: though effective for jackals, the virus strains used have proven highly pathogenic to some other wildlife species (Bingham *et al.* 1995). Other vaccine strains are available but have not yet been tested – thus, at present it would not be possible to protect wild dogs from rabies by oral vaccination of other wildlife species. Nevertheless, it is highly likely that this will be possible in the future. No such programme could be devised for canine distemper at present: the wildlife species in which the infection persists are not known, and live vaccines against canine distemper are pathogenic to several wild carnivore species (including wild dogs themselves).

Finally, it is possible that controlling the diseases to which reservoir hosts are susceptible might lead to an increase in their numbers. Endemic canine distemper caused 3–5% of domestic dog mortality in Copenhagen in the 1950s (Gorham 1966). If removing this mortality led to population growth, each annual vaccination round would become more difficult and more expensive. Furthermore, if vaccination were halted – perhaps due to lack of funds – the population of susceptible reservoir hosts would be larger, making any subsequent epidemic more severe and increasing the threat posed to wild dogs. Ongoing research on domestic dogs in the Serengeti and the Masai Mara, as well as in Ethiopia, will help to determine whether vaccination programmes do lead to such an increase in domestic dog numbers. Wherever possible, vaccination of domestic dogs is best combined with control of their numbers.

Vaccinating Wild Dogs Themselves

The most direct way of protecting wild dogs from disease is to vaccinate them. Such vaccination does, however, entail a number of problems:

The Availability of Suitable Vaccines

The safety and efficacy of vaccines against the diseases that threaten wild dogs are often unsatisfactory. Inactivated rabies vaccines have caused seroconversion in some free-ranging and captive wild dogs (Gascoyne *et al.* 1993), but others have failed to seroconvert (Visee 1996), or failed to establish sustained immunity (G.R. Thomson, pers. comm.; P.W. Kat, pers. comm.). At least some free-ranging wild dogs which have been vaccinated against rabies have subsequently died of rabies (Kat *et al.* 1995; Scheepers & Venzke 1995). The failure of rabies vaccinations to prevent rabies deaths in wild dogs has led to substantial controversy in both the scientific and popular press (see, for example, Burrows 1992; Dye 1996; Heinsohn 1992; Macdonald *et al.* 1992; Morell 1995) – it has been suggested that, far from protecting wild dogs, vaccination might have hastened wild dogs' deaths. This issue is discussed in detail in Appendix 1; in summary, while inactivated rabies vaccines are unlikely to have caused the deaths of the wild dogs from rabies, they also failed to prevent those deaths. The most likely explanation is that the single dose of vaccine given to each dog was not sufficient to trigger a fully protective immune response: two or more doses have been shown to provoke a better response in both wild dogs (G.R. Thomson, pers. comm.), and domestic dogs (Sage *et al.* 1993). More research, on captive animals, is needed to assess the efficacy of various rabies vaccination protocols for wild dogs (Chapter 8).

Problems also arise with vaccines against canine distemper. While modified live vaccines have brought about seroconversion in some cases (Spencer & Burroughs 1992), in others they have either failed to produce protective antibody levels (van Heerden *et al.* 1980) or have induced distemper and death (Durchfeld *et al.* 1990; McCormick 1983; van Heerden *et al.* 1989). Vaccine-induced distemper can be avoided by using killed vaccines, but studies on captive maned wolves, bush dogs, fennec, kit and crab-eating foxes indicate that such vaccines rarely cause seroconversion (Montali *et al.* 1983). Thus, at present there are no vaccines against canine distemper suitable for use in free-ranging wild dogs.

Modified live vaccines against parvovirus have brought about seroconversion in captive wild dogs (Spencer & Burroughs 1990).

Locating Wild Dog Packs

In order to vaccinate wild dogs in the field, one must first find them – and this is extremely difficult without the aid of radio-collars. In Selous, where wild dogs occur at high density, researchers spent the first five months of the project just looking for wild dogs (Creel 1996). Thus, vaccination would be extremely labour-intensive in areas where wild dogs had not been radio-collared, especially in thick bush. Furthermore, vaccination would have to be repeated annually to maintain immunity in adults, and to protect each new litter of pups. For this reason vaccination of wild dogs would not just be a question of paying for vaccines: vehicles, petrol and skilled manpower would also be necessary.

Halting Selection for Disease Resistance

Since a vaccination programme prevents most animals from being exposed to disease, it will weaken natural selection for disease resistance. Thus if vaccination were to be discontinued, the population would, on average, be more susceptible to infection than it had been before the programme was started. For this reason, once a vaccination programme is commenced, it may be necessary to continue it indefinitely (Hall & Harwood 1990). While there is little evidence of natural resistance to rabies, a fairly high proportion of wild dogs may survive exposure to canine distemper virus perhaps indicating some natural resistance to the disease (Chapter 4). More research is needed on the pathogenicity of canine distemper virus in wild dogs.

Choosing the Best Strategy for Disease Control

None of the options that we have discussed provides a completely satisfactory solution to the problem of disease control in wild dogs. In every case, our knowledge is limited and further research is urgently needed. Nevertheless, it is possible to suggest some circumstances in which each management strategy – or no action at all – would be most appropriate. The questions that must be answered before designing local strategies for disease control are summarized in Figure 6.1.

1) If a particular disease threatens people, livestock or wildlife species in addition to wild dogs, then controlling the disease in its reservoir host will be more appropriate politically, socially, and economically than vaccinating wild dogs directly.
2) If a wild dog population was known to be be facing an acute disease risk – for example, if the wave front of a rabies epidemic was approaching – then

vaccinating wild dogs themselves might represent the most appropriate action providing the epidemic had not yet reached the wild dogs. Far from providing protection, rabies vaccination of animals immediately before they contact rabies virus may hasten the course of the disease (the 'early death' phenomenon, Clark *et al.* 1981). Thus the appropriate response to an acute disease risk requires very accurate information about the threats involved.

3) Smaller populations – including those re-established by reintroduction – will be more

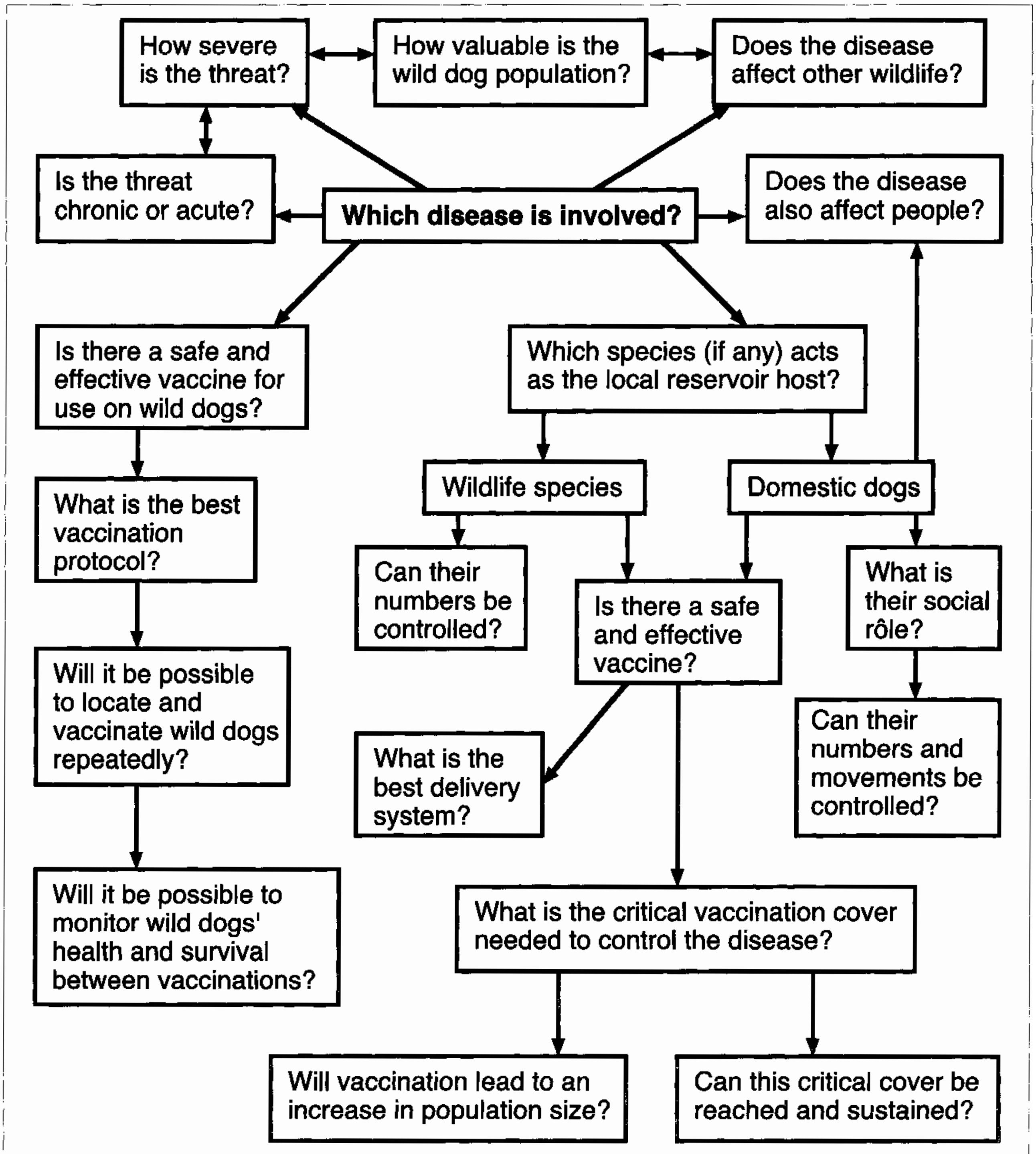


Figure 6.1. Factors that must be taken into account when designing local strategies for disease control in free-ranging wild dog populations.

vulnerable to disease and will therefore require more active management. Disease control programmes will also be more effective if implemented over smaller areas.

4) Larger populations should be sufficiently resilient to recover from periodic disease outbreaks and may require no active management beyond monitoring of disease threats.

Conclusions

The considerations discussed above indicate that different wild dog populations face different threats, and that the appropriate management strategies will vary accordingly. In summary, though, we envisage three paradigms for wild dog management:

1) ***Large populations***

The maintenance of large populations in extensive (> 10,000 km²) protected area networks remains the highest priority for Africa-wide wild dog conservation. The value of populations such as those in Selous and Kruger cannot be stated too highly. Such populations are likely to be large enough to persist in the face of even fairly dramatic perturbations, and should not require intensive management. This is fortunate, since intensive management over such large areas would be logistically difficult and extremely expensive. Protecting such populations is essentially a question of protecting their habitat: maintaining reserve integrity, controlling poaching of prey species, and avoiding the building of high-speed roads – all of these are routine components of reserve management in Africa. Given such protection, there is no reason why wild dog populations should not persist for many centuries in large reserves.

2) ***Smaller protected areas, reserve borders and landscape management***

Where wild dogs use areas inhabited by people on reserve borders, in buffer zones connecting smaller reserves, or in areas which are not close to a protected area, their populations are likely to be under threat from persecution and disease. Managing these landscapes for wild dogs (or for wildlife in general) may be difficult, but in many areas such management is critical: in Kenya, for example, there is not a single population of wild dogs thought to be restricted to protected areas, and, while much of Kenya's wildlife exists outside protected areas, it is uncertain how long this pattern will persist with increasing population and economic growth.

In regions where management of reserves is combined with wildlife management outside protected areas, integrated carnivore management programmes should be implemented to resolve conflicts between human activity and the conservation of predators. Local conservation bodies should work with farmers to minimize livestock losses to wild dogs and other predators and might provide compensation for stock that are killed. Domestic dog populations could be controlled and vaccinated against diseases which threaten wild dogs, perhaps in collaboration with local public health authorities.

Management of this kind will be costly. On reserve borders it might be funded by tourist revenues derived from the reserve. Alternatively, external funding might be available. Such schemes will be extremely valuable on the borders of reserves holding important wild dog populations – as discussed in Chapter 4, human activities on reserve borders can represent a serious threat to such populations. The value of management schemes of this kind in other unprotected areas will depend upon local conservation policy. Intensive management is unlikely to provide value for money in areas which are intensively farmed, where ungulate prey are depleted and domestic dogs are common. It may be more useful to designate such areas as predator control zones.

3) ***Very small, intensively managed populations***

Plans are being considered in South Africa to maintain a metapopulation of wild dogs held in a network of small fenced reserves, each containing just one or two packs. Such a metapopulation would require intensive management: for example, individuals would have to be translocated between reserves to maintain genetic diversity, and annual vaccination of wild dogs against canid diseases might well be necessary. Management of this kind will be useful, especially for the maintenance of substantial numbers of wild dogs within South Africa itself, and represents the kind of strategy that would be needed in highly fragmented habitats. However, in terms of Africa-wide wild dog conservation such schemes have a much lower priority than the continued protection or expansion of large national parks and reserves, where viable populations can persist without the need for such expensive intensive management.

Chapter 7
The Rôle of Captive Breeding and Reintroduction in Wild Dog Conservation

Rosie Woodroffe & Joshua R. Ginsberg

The reintroduction of animals raised in captivity has played an important rôle in the conservation and recovery of a number of species.

- ***Reintroduction of wild dogs is technically possible*** *provided some of the animals released are wild-caught, and that the newly-established population receives adequate protection from persecution and disease. However:*
- ***Reintroduction has limited value for wild dog conservation*** *since*
  - *Suitable release sites are in short supply: few reserves are sufficiently large and well-protected to sustain viable wild dog populations.*
  - *Reintroduction is most needed in West and central Africa, but there are no wild dogs with appropriate local genotypes held in captivity, and no local populations large enough to provide a source of wild-caught animals.*
  - *Reintroduction could be considered in parts of East Africa, but there are few wild dogs of eastern origin held in captivity.*
- ***In southern Africa, reintroduction could create a metapopulation*** *of tiny wild dog populations held in a network of fenced reserves and managed intensively to maintain genetic diversity. This would increase wild dog numbers locally, but would be extremely expensive.*
- ***Protection of existing populations*** *remains a higher priority for Africa-wide wild dog conservation than any attempt at reintroduction.*
- ***Captive wild dogs may still contribute to field conservation*** *by providing subjects for research, and by increasing public awareness and sympathy for wild dogs, both in Africa and abroad.*

Background

Captive breeding and reintroduction can play a number of rôles in conservation. First, captive animals may provide insurance against the extinction of species that are threatened in the wild, and be used to reinstate or augment wild populations. Second, captive breeding may serve to increase the world population of a species, providing a source of additional genetic variation that may be fed into wild populations. Third, captive animals may raise public awareness of the species' plight in both range states and donor countries, leading to greater sympathy for field conservation programmes and, in some cases, to financial support for them. Finally, animals held in captivity may be used for research aimed at better management of free-ranging populations.

The release of animals born in captivity has been used to reinstate populations of several species that had become extinct in the wild. For example, in North America wild populations of both black-footed ferrets (*Mustela nigripes*) and red wolves (*Canis rufus*) have been restored in this way (Phillips 1995; Seal *et al.* 1989). Reintroduction – using either wild-caught or captive-bred stock – has also allowed the re-establishment of species which have become locally extinct. For example, swift foxes (*Vulpes velox*) from the United States have recently been reintroduced to Canada, where they were extirpated in the 1930s (Carbyn *et al.* 1994). On a larger scale, the reintroduction and translocation of ungulates has formed an extremely important component of the South African National Parks system for many years (Novellie & Knight 1994).

In this chapter, we consider whether reintroduction represents a suitable management option for wild dogs. Although some species have been reintroduced successfully, many programmes fail (Beck *et al.* 1994), and captive breeding is always expensive (Balmford *et al.* 1995). Wildlife managers must therefore weigh up the probability of successfully establishing a viable free-ranging population against the costs involved – in some cases protection of the remaining wild populations may represent better value for money. Nevertheless, the reinstatement of wild dogs in areas where they have been extirpated, especially in West and central Africa, is an important goal in their conservation. We therefore consider whether reintroduction could help to attain this goal, and also discuss additional rôles that captive wild dogs might play in field conservation.

Can Wild Dogs be Reintroduced Successfully?

The suitability of reintroduction as a management option for wild dogs depends upon whether viable free-ranging populations can be established from reintroduced animals. Perhaps the best way of assessing this is to review the successes and failures of previous attempts at reintroduction, using both wild dogs and related species. In total, nine attempts have been made to reintroduce or translocate wild dogs, all of them in southern Africa. These attempts are summarized in Table 7.1, and described below.

Previous Attempts to Reintroduce Wild Dogs

1) Kalahari Gemsbok National Park, South Africa

In 1975, five wild dogs were translocated from the borders of the Kalahari Gemsbok National Park to the interior of the Park, after two members of their pack had been shot by livestock farmers outside (Frame & Fanshawe 1990). Wild dogs have never been common in this park, which is probably marginal habitat. The translocated pack soon split into two groups, and, within a few months, both pack fragments disappeared.

2) Etosha National Park, Namibia

In 1978, six wild dogs were introduced into Etosha National Park. At 22,270 km², Etosha is large enough to sustain a population of wild dogs, and prey densities were considered sufficient (Scheepers & Venzke 1995). The reason for wild dogs' absence from Etosha remains unknown, although some sources suggest that they were never common there (See Chapter 3). The dogs introduced in 1978 had been raised in captivity, and were released as yearlings. All six died within four months of their release, mostly from starvation and predation by lions (Scheepers & Venzke 1995).

In 1989, a second attempt was made to reintroduce wild dogs to Etosha. Five captive-born dogs were used: two adult females, two adult males, and one younger animal fostered to one of the pairs. The adults were fitted with contraceptive implants, so breeding would not have been possible until these were exhausted. On release, all five animals died, and were believed to have been killed by lions (Scheepers 1992).

A third attempt was made to reintroduce wild dogs to Etosha in 1990 (Scheepers & Venzke 1995). Eleven animals were involved, all of them bred in captivity from Namibian stock. An attempt was made to teach these animals to hunt before releasing them: live springbok were released into their holding pen. However, the dogs quickly learned to wait until the antelope killed themselves against the pen's perimeter fence. Once the dogs had been released, they were monitored closely and springbok were shot for them every other day if they had not fed. At first, the dogs' hunting attempts were ineffectual and it was five weeks before they made their first kill. When their prey migrated, the dogs did not follow, and had to be lured towards the herds by dragging a carcass ahead of them. By 16 weeks after release, the dogs' hunting skills had improved considerably. Unfortunately, the reintroduction attempt ended in failure. Ultimately, 6 of the 11 dogs were killed by lions, one disappeared, and the last four dogs died of rabies after killing and eating a rabid black-backed jackal (Scheepers & Venzke 1995).

3) Hluhluwe-Umfolozi Park, South Africa

In 1980–1, 22 wild dogs were introduced into the Hluhluwe-Umfolozi Park. Twenty of the dogs (9 females and 11 males) were raised in captivity, but two (one male and one female) were wild-caught adults (Maddock 1992). The 22 dogs were released in four

Table 7.1
A summary of previous attempts at wild dog reintroduction. More details, and sources of data, are given in the text.

Release Site	Year	Source of dogs	Group Composition	No. of releases	Fate of dogs	Final outcome
Kalahari Gemsbok N.P., South Africa	1975	wild	3 adult females 2 adult males	1	Group split and dogs disappeared	Failure?
Etosha National Park, Namibia (1)	1978	captive raised	6 yearlings	1	Starved or killed by lions within 4 months	Failure
Etosha National Park, Namibia (2)	1989	captive raised	2 adult females 2 adult males 1 unknown	1	Killed by lions within 3 months	Failure
Etosha National Park, Namibia (3)	1990	captive raised	2 adult females 2 adult males 5 subadult females 2 subadult males	1	6 killed by lions, 4 died of rabies, 1 diappeared	Failure
Hluhluwe-Umfolozi Park, South Africa	1980–1	2 wild caught 17 captive raised 3 unknown	2 adult females 3 adult males 7 yearling females 5 yearling males 4 males unknown age 1 female unknown age	4	Population still extant, with 13 dogs present in 1994. 8 litters were produced in the period 1982–1993.	Success
Matetsi Safari Area, Zimbabwe	1986	captive raised	4 yearling females 5 yearling males	1	Shot on nearby farm	Failure
Klaserie Game Reserve,	1991	captive raised	2 adult females 6 adult males	1	Moved out of reserve onto neighboroughing farmland and recaptured	Failure
Venetia Limpopo Nature Reserve, South Africa	1992	wild caught	1 adult female 2 adult males 6 yearling females 5 yearling males	1	Pups were born after the release, but the pack left the reserve and were poisoned	Failure
Madikwe Game Reserve, South Africa	1995	3 wild caught 3 captive raised	3 adult females 3 adult males	1	All adults survived, and the pack now contains six yearlings born after the release	Success

groups between September 1980 and September 1981, with the wild pair being caught up again and re-released with the last group of captive-reared animals.

These releases represent the most successful attempt so far to reinstate a free-ranging wild dog population. Fifteen years later, there are still wild dogs in Hluhluwe-Umfolozi, and 8 litters were recorded there between 1982 and 1993 (Figure 7.1, Maddock 1992). However, the success of this introduction is qualified. At just 960 km², Hluhluwe-Umfolozi is a small area that can never sustain a population of wild dogs that will be viable in the long term. Dogs leave the reserve to enter neighbouring ranches and farmland where, fortunately, they are rarely persecuted. Indeed, dogs are welcome on some of the game ranches to the north of Hluhluwe-Umfolozi, and have bred there. Despite this, the wild dog population has not grown and spread into neighbouring areas. While the population has persisted, its numbers have fluctuated considerably (between 3 and 30) and, despite fission and fusion of the existing pack, no new packs have formed. In the long term, extinction seems likely unless intensive management is implemented. Indeed, no pups have been born since 1993. This may be because all members of the population are now close relatives – a plan has therefore been put forward to replace the females with new stock unrelated to the males (Maddock 1996). Alternatively, disease might have contributed to breeding failure (J. van Heerden, pers. comm.). Whether the Hluhluwe-Umfolozi population is viable in the long term or not, the success of this reintroduction will provide extremely useful lessons for future attempts at reintroductions into other areas.

4) Matetsi Safari Area, Zimbabwe

In 1986, nine wild dogs were introduced into the Matetsi Safari Area. Matetsi is contiguous with the Hwange National Park, which sustains a relatively large wild dog population. Thus, this release would have augmented an existing population. The nine dogs – five males and four females – had been raised in captivity and were released at the age of 18 months (Childes 1988). On release, the pack split into two groups, one of four males, and the other of four females and one male. A month after release, the group of four males were starving and injured, apparently, by spotted hyaenas. Two members of the other group disappeared, leaving just three females. These females were in good condition and had been observed hunting successfully on at least two occasions. All of these animals were recap-

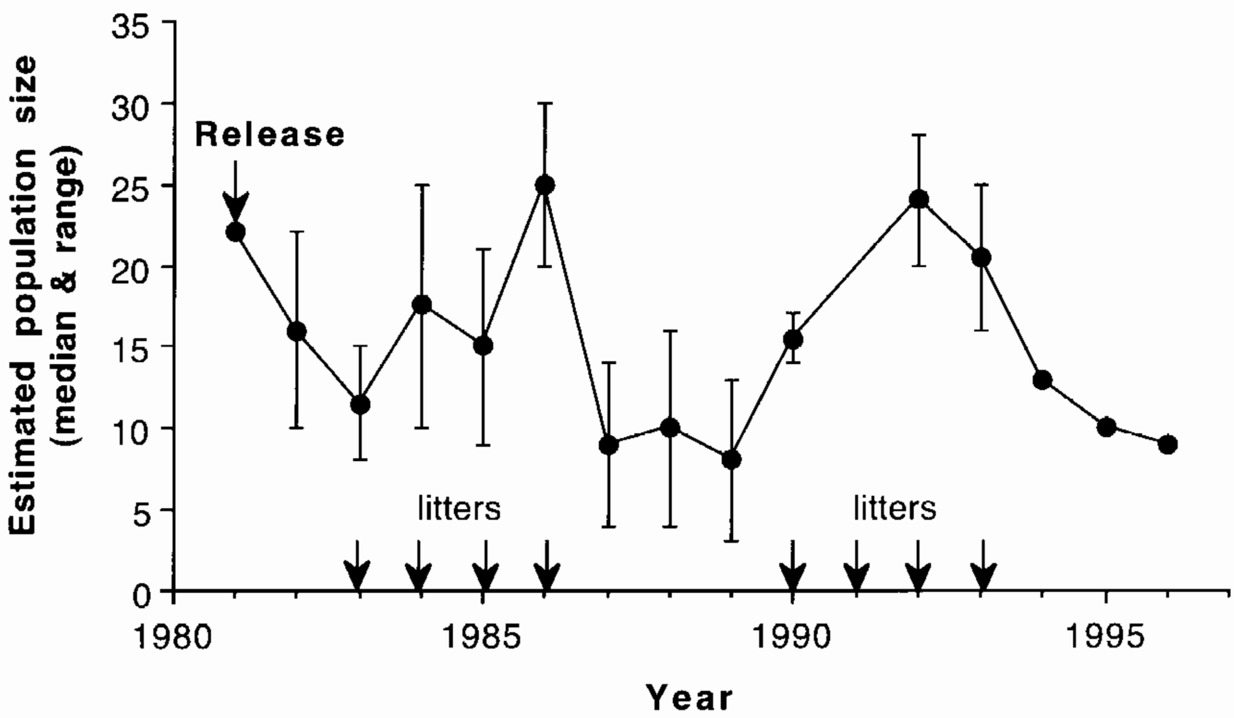


Figure 7.1. Changes in population size since the reintroduction of African wild dogs to the Hluhluwe/Umfolozi Park in KwaZulu-Natal, South Africa, in 1980–1.
For each year, the graph shows the median population estimate, and the known range. Arrows indicate years when litters were born. The data are taken from Maddock, 1996.

tured and translocated to the Kazuma Pans Forestry Area. There, two more males disappeared but the group was seen to kill a young kudu. The following day, however, the remaining five dogs appeared at the butchery of a livestock farm bordering the Matetsi Safari Area, where the owner of the farm shot them all.

5) Klaserie Game Reserve, South Africa

A group of eight captive-bred wild dogs were released into the Klaserie Game Reserve in 1991 (M. de Villiers, pers. comm.). Since wild dogs from the adjacent Kruger National Park also use Klaserie (Maddock & Mills 1994), this release would have supplemented an existing population. An attempt was made to teach these animals to hunt before their release, by keeping them in an enclosure where they were given gutted and skinned carcasses, then whole carcasses, and, finally, tranquillized impala. The dogs did hunt after their release, although with rather little success (M. de Villiers pers. comm.). In captivity, the two females in the group had competed over breeding and, once released, they split up with some males accompanying each. The pack rejoined within a few days – but after two weeks they moved out of the reserve onto neighbouring farmland. They were then re-captured to avoid conflict with local farmers.

6) Venetia Limpopo Nature Reserve, South Africa

In 1992, a group of 14 wild dogs were released into the Venetia Limpopo Nature Reserve, a private reserve of 350 km² (van Heerden 1993). The animals released were a wild pack which had been captured in the Mthethomusha Game Reserve and translocated to Venetia (English *et al.* 1993). They were held in a large (> 1 km²) enclosure in Venetia, from which two pack members escaped – however, the pack re-formed after the remainder were released (van Heerden 1993). One dog was radio-collared, and subsequent monitoring showed that the pack was hunting successfully. They produced a litter of pups within five months of release. However, because warthogs had damaged the electric fence surrounding the reserve, the dogs were able to cross the boundaries and started to use neighbouring farmland. The pack was last seen ten months after their release and, seven months after that, several wild dog skeletons were found lying close to one another on a neighbouring farm – they had probably been poisoned (van Heerden 1993). The rest of the pack has not been seen since.

7) Madikwe Game Reserve, South Africa

The most recent attempt to reintroduce wild dogs was in Madikwe Game Reserve. Madikwe was chosen as a reintroduction site because, while relatively small (600 km²), it is securely fenced with predator- and warthog-proof fencing, and prey are abundant (M. Hofmeyr pers. comm.). Lions, cheetah and spotted hyaenas were also reintroduced to Madikwe in the period 1994–5. As in Hluhluwe-Umfolozi, a combination of wild and captive-raised dogs were used: 3 adult males from Kruger National Park and 3 adult females (sisters) from De Wildt cheetah centre were introduced to a boma in Madikwe in February 1995. By March 1995, all the pack members were mating, although no pups were produced. In July 1995, the pack was released. Supplementary feeding was needed at first, but the pack made its first kill five days after release. Two weeks after release, one of the captive bred females was first seen to lead a chase, and by two months after release the pack was hunting daily, and the dogs no longer approached vehicles. The pack did, however, learn to chase prey into the fence, and continue to use this as a hunting technique. The pack now has a home range of 180 km², and has made no attempt to escape. At the time of going to press, the pack contained six yearlings born after the release. Since five of these yearlings are females, plans are being considered to release a group of males to try to establish a second pack within the reserve (M. Hofmeyr pers. comm.).

Attempts to Reintroduce other Canid Species

Lessons about wild dog reintroduction can also be learned from attempts to reintroduce related species with similar ecological requirements and social organization. These attempts are summarized in Table 7.2.

Grey Wolves

The grey wolf (*Canis lupus*) is, perhaps, the species most ecologically similar to the African wild dog. Like wild dogs, wolves hunt cooperatively, range over very large areas, and are frequently persecuted when they come into contact with man. As with wild dogs, these characteristics have hampered several attempts at reintroduction.

The first well-monitored attempt at reintroduction involved five captive-bred wolves released in Alaska (Henshaw *et al.* 1979). The wolves were given some access to small live prey before their release, but showed no aptitude for killing it. After release, they followed caribou several times but were hesitant in their hunting attempts and were never seen to catch live prey. Although the group split up, and three of the five were

Table 7.2
A summary of reintroduction attempts carried out with other canid species. Further details, and references, are given in the text.

Species & Release Site	Year	Source of animals	Group Composition	Number of releases	Fate of animals	Final outcome
Grey Wolf; Alaska, U.S.A.	1972	captive reared	3 adult females 2 adult males	1	All 5 approached humans for food. 3 were shot, 1 returned to the captive colony 280km from the release site, and 1 disappeared.	Failure
Grey Wolf; Michigan, U.S.A.	1974	wild caught	2 adult females 2 adult males	1	The group wandered over a very large area but eventually settled. 3 animals were shot, 1 was killed by a vehicle.	Failure
Grey Wolf; Minnesota, U.S.A.	1975–1978	wild caught	30 adult females 32 adult males 24 juvenile females 21 juvenile males	68	Relocated wolves survived at rates similar to those of resident wolves.	Success
Red Wolf; North Carolina, U.S.A.	1987–1995	captive reared	17 adult females 16 adult males 15 juvenile females 16 juvenile males	25	Only 38% of adults and 11% of pups bred after release but by 1994 there was a total of 42 wolves in the wild, 36 of them wild-born.	Success
Swift Fox; Saskatchewan & Alberta, Canada	1983–1991	both wild caught & captive reared	569 total	–	Of 162 radio-collared foxes, 34 (21%) survived 1 year. 47% of wild caught and 11% of captive-raised foxes survived 1 year.	Success

seen in association with wild wolves, all eventually approached humans in search of food. As a result four were shot, and the fifth returned to the breeding colony, some 280 km from the release site, where she was recaptured.

Another reintroduction attempt involved four wolves translocated from Minnesota to Michigan in 1974 (Weise *et al.* 1979). One female – which may not have been a member of the same original pack as the others – left the group immediately upon release but remained within an area of approximately 900 km². The rest of the group wandered over > 4,000 km² before settling in an area some 90 km from the release site. All four wolves died within eight months of release: three were shot and the fourth was killed in a road traffic accident.

Attempts to relocate wolves within Minnesota have met with more success. A total of 107 wolves blamed for depredations upon livestock in Northern Minnesota were translocated to the Superior National Forest and Beltrami Island State Forest in the period 1975–8 (Fritts *et al.* 1985). Although many of the wolves were shot, or trapped and re-released by U.S. Fish & Wildlife Service control teams, overall the mortality of translocated wolves was no higher than that of wolves already resident in the area. Members of the same pack released together did not remain together after release, and all the wolves moved over very large areas. Furthermore, they tended to 'home': 9/32 wolves (28%) returned to within 10 km of their original capture sites (Fritts *et al.* 1984). Wolves settled, on average, 87 km from their sites of release, and animals translocated more than 64 km did not return to their capture sites.

Red Wolves

The red wolf resembles the wild dog in that it has a complex social organization, although it takes slightly smaller prey. As a result of persecution and habitat loss, the red wolf was extirpated from the whole of its former range in the Eastern United States earlier this century. However, in 1987 the U.S. Fish & Wildlife Service started a reintroduction programme in the Alligator River National Wildlife Refuge in North Carolina (Phillips 1995). Between 1987 and 1995, a total of 63 captive-bred red wolves were released into the wild. At the beginning of 1995 the release site contained 42 red wolves, 36 of them born in the wild.

Like grey wolves, the red wolves moved over large areas immediately following their release. The U.S. Fish & Wildlife Service intervened when animals moved outside the intended reintroduction area, although 4 animals were still shot by local people. Eventually, the released wolves settled into home ranges of 50–100 km², feeding upon deer, racoons and rabbits. Although expensive, intensive monitoring and intervention were considered crucial for the success of the reintroduction, since it avoided conflict between reintroduced wolves and local people, maintaining public support for the project. Following this success, local landowners are now allowing red wolves onto their private land (Phillips 1995).

Swift Foxes

Weighing just 2.3 kg, and feeding almost entirely upon rodents, the swift fox might seem to have little in common with the African wild dog. Efforts to reintroduce swift foxes to Canada do, however, provide lessons for wild dog reintroduction. Swift fox releases used a combination of wild-caught and captive-bred stock. As for grey wolves and wild dogs, reintroduction was much more successful when wild-caught animals were used: 32% (6/19) of wild caught foxes bred after release, while 108 foxes reared in captivity produced just 6 breeders after release (6% of those released, Carbyn 1995) This has led to a debate about the usefulness of captive-bred animals in the swift fox reintroduction programme (Carbyn 1995; Smeeton 1995).

The reason for captive-reared foxes' low survival and breeding success is not certain. However, the major cause of mortality in reintroduced swift foxes was predation by coyotes: 34 of 89 foxes (38%) found dead at three release sites in Canada were known or suspected to have been killed by coyotes (Carbyn *et al.* 1994). Coyotes do not eat swift foxes, but they do compete with them for food. Thus the relationship between swift foxes and coyotes parallels that between African wild dogs and lions.

What Lessons can we Learn from Previous Reintroduction Attempts?

A number of patterns emerge from this survey of previous attempts to reintroduce wild dogs and other canids. These patterns point to important lessons for future reintroduction attempts.

1) In all cases, wild-caught animals survived better than captive-reared ones. There are two reasons for this. First, wild dogs and grey wolves reared in captivity lacked skill in hunting – skill which is essential for the capture of large, fast-moving and often well-armed prey. It is extremely difficult to provide animals with experience of live prey under captive conditions, where space may be limited and local laws (not to mention the zoo-going public) may be unsympathetic. Furthermore, since wild dogs quickly learn to use fences to kill their prey, providing live food may still not mimic conditions in the wild.

   The second reason for the high mortality of captive-reared animals involves predation: wild dogs and swift foxes reared in captivity appear unaware of the threats posed by competing predators. It is difficult to imagine a technique whereby captive wild dogs intended for reintroduction could be instilled with a fear of lions and spotted hyaenas.
2) Despite attempts to minimize human contact, captive-bred wolves learned to associate human settlements with food, which brought them into conflict with people and led to their being killed. This may also have contributed to the failure of the attempt to release wild dogs in Zimbabwe.
3) Newly-released grey and red wolves wander over very large areas and may settle some distance from the release site – this may also have occurred with the wild dogs released into the Kalahari Gemsbok National Park. Such long-distance movements may bring newly-released animals into contact with humans, leading either to their persecution (as in Venetia) or to the need for recapture (as in Klaserie). Translocated wolves tend to 'home' to their original capture sites, a problem that has also been encountered in attempts to reintroduce sea otters in California (Estes *et al.* 1993). The behaviour of released wolves resembles that of dispersing 'lone' wolves seeking mates and territories.

   Groups released together tend to split up: this is also characteristic of wild dog releases. Both wandering and group splits may be reduced by keeping the dogs in an enclosure at the reintroduction site for some time before release. For example, at Madikwe wild-caught and captive-raised animals were 'introduced' in an enclosure.
4) Wild dogs released into Etosha died from rabies. This points, once again, to the importance of disease in wild dog conservation: adequate disease control is a crucial consideration for any attempt at reintroduction, especially in areas where disease is believed to have contributed to wild dogs' decline. The measures necessary are discussed in detail in Chapter 6.
5) Even successful release programmes may involve high mortality. Twenty-two wild dogs were introduced to Hluhluwe/Umfolozi Park in 1980–1, but by early 1983 just 8 remained (the birth of a litter of 7 then raised the population to 15; Figure 7.1). Thus, 14/22 (64%) reintroduced wild dogs died before the new pack bred (Maddock 1996). Similarly, 62% of reintroduced red wolves died before breeding (Phillips 1995), and 79% of swift foxes failed to survive a year after release (Carbyn *et al.* 1994). This high mortality is a common phenomenon in reintroduction programmes: for example, only 27/71 (38%) golden lion tamarins (*Leontopithecus rosalia*) and 9/49 (18%) black-footed ferrets survived initial reintroduction (Clark 1994; Kleiman *et al.* 1991). In each of these cases, most or all of the animals released were captive-bred – but even wild born swift foxes suffered 53% mortality in the first year after release (Carbyn *et al.* 1994). In contrast, none of the wild dogs introduced to Madikwe died – perhaps because the predator-proof fence protected them from some of the factors which killed wild dogs released elsewhere. Nevertheless, it seems likely that in most cases some mortality is unavoidable – the only solution may be to release more animals, over a longer period (Beck *et al.* 1994).

All of these considerations indicate that future attempts to release wild dogs must use either wild-caught animals or a combination of wild-caught and captive-raised animals. Holding the animals together in a boma prior to release appears to help newly-introduced animals to form a cohesive pack, and might help to prevent the animals from wandering too far once released. Thus, wild dog reintroduction is technically possible if the animals released can be protected from persecution and disease. The measures needed for such protection are discussed in detail in Chapter 6.

Are there Wild Dogs Available for Reintroduction?

No wild dog reintroduction attempted so far has established a viable population – thus none can be described as an unqualified success. Nevertheless, the discussion above suggests that wild dog reintroduction is technically possible. The success of any reintroduction programme would, however, depend upon the availability of animals for release.

Wild dogs released in an area should be of the appropriate local subspecies or genotype. Wild dogs from eastern and southern Africa are known to be genetically different, and those from West and central Africa may be different again (Chapter 2). Such differences may be a result of random genetic drift, but variation could also be caused by natural selection (Wayne *et al.* 1994). This could create problems for reintroduction programmes: wild dogs of 'foreign' genotypes might not be adapted to local conditions at the release site.

This need to release animals with local genotypes means that very few wild dogs currently held in captivity are suitable for reintroduction. Reintroduction is most needed in West and central Africa, but there are no captive wild dogs representing these genotypes. Almost all of the world's captive wild dogs are of southern African origin; the only east African dogs in captivity at present are 25 animals captured as puppies in 1995 by the George Adamson Wildlife Preservation Trust to set up a captive breeding programme in the Mkomazi Game Reserve, Tanzania (Fitzjohn 1995).

The availability of captive dogs is, however, only one consideration – the examples discussed above indicate that successful reintroduction depends upon some wild-caught animals being used. It is crucial, however, that collecting wild dogs for translocation should not threaten the population from which they are taken. As discussed in Chapter 5, wild dog populations inhabiting small areas are unlikely to be viable in the long term, and any reduction in their numbers could drive them closer to extinction. Thus, reintroduction would depend upon the existence of large, viable populations which could withstand being 'harvested' for animals to be translocated. For example Kruger National Park, together with the reserves that surround it, sustains a population of 350–400 wild dogs which has provided stock for reintroduction attempts elsewhere in South Africa. Selous Game Reserve might provide a source of wild dogs in East Africa. However, there is no obvious source population for wild dogs in West or central Africa. This is a serious barrier to any attempt to reintroduce wild dogs in these areas.

An additional source of wild dogs for translocation would be 'problem' animals in conflict with livestock farmers. As discussed in Chapter 6, wild dogs rarely take livestock. However, genuine problem animals do arise from time to time, and translocation may be one management option for them. For example, the Kenya Wildlife Service captured a group of wild dogs in Laikipia which had killed 137 merino ewes and lambs in a five month period – plans are under consideration to release these animals elsewhere (R. Kock, pers. comm.). However, problem animals should only be introduced to areas where they are unlikely to continue taking livestock: local support is a vital component of successful reintroduction programmes (Beck *et al.* 1994), which would be seriously compromised if reintroduced animals killed livestock on a regular basis. In practice, translocation will only rarely provide the best way of dealing with problem wild dogs (Chapter 6).

Are Suitable Sites Available for Wild Dog Reintroduction?

If wild dogs were available for release, the success of a reintroduction programme would depend upon the availability of suitable reintroduction sites. In particular, the factors which led to the local population's original decline must be removed – otherwise the introduced population is likely to succumb to the same pressures. As discussed in Chapter 3, wild dogs' geographic range has contracted through a combination of habitat fragmentation and persecution. However, the immediate causes of local extinction are rarely known for particular areas.

Reintroduction programmes should proceed with caution if the cause of wild dogs' local decline – or, indeed, whether such a decline has occurred – is not known. For example, plans have been put forward to release wild dogs into the Mkomazi Game Reserve, part of the Tsavo ecosystem which extends into Tanzania (Fitzjohn 1995). Extensive poaching and encroachment of livestock into Mkomazi have now been curbed as part of a well-organized programme of rehabilitation, and reintroduction of wild dogs was planned as part of this process. However, the very low density of wild dogs in Tsavo West, and the fact that dogs are least often seen in the southern part of the park which is contiguous with Mkomazi, raises questions about the suitability of Mkomazi as a reintroduction site. Wild dogs are relatively common in the Maasai steppe, some

100 km from Mkomazi, where existing dens were dug up to obtain stock for the Mkomazi programme (Fitzjohn 1995). With wild dogs breeding so nearby, it is likely that recolonization of Mkomazi would have occurred naturally if the area represented suitable habitat.

Sites must therefore meet several criteria before they can be considered suitable for wild dog reintroduction.

Size of the Reintroduction Site

In Chapter 6 we established that the highest priority for wild dog conservation is to maintain large populations in extensive protected areas, which require little active management. Ideally, then, the best sites for wild dog reintroduction would be large protected areas, where viable populations could be established by reintroduction and then left to persist naturally. In practice, however, such sites are rare, especially in West and central Africa where there is most need for reintroduction.

If the reintroduction site is too small to sustain a wild dog population in the long term, intensive management is crucial. The maintenance of such small populations has a much lower priority for Africa-wide wild dog conservation than does the protection of larger populations more likely to be viable in the long term. Nevertheless, establishing a network of several small populations, managed together as a metapopulation, would be valuable where a need was seen to increase the numbers of wild dogs in a particular range state or area, and where no larger reserve was available as a release site. It must be emphasized, however, that such metapopulations would require intensive management in the form of fencing, disease control and periodic movement of animals between reserves to maintain genetic diversity (Chapter 6). For this reason, it would be extremely expensive to establish and maintain wild dogs in a network of small reserves. Investing in better protection of existing larger populations might well represent better value for money.

People in the Reintroduction Site

Since persecution represents a very serious threat to wild dogs, the release site must either contain very few human inhabitants, or local people must be unlikely to persecute wild dogs. It must be stressed that, in a survey of 145 attempted reintroductions worldwide, Beck *et al.* (1994) found that the one factor which most contributed to the success of any particular reintroduction programme was public support for the programme. With animals as wide-ranging and formerly unpopular as wild dogs, the importance of public support cannot be emphasized too strongly. As discussed in Chapter 6, local peoples' hostility to wild dogs could be mitigated by a combination of local education, compensation, work on husbandry practices and legislation to control the use of poisons. In practice, the threat of persecution may be minimized by releasing wild dogs only inside protected areas.

Disease in the Reintroduction Site

Disease is known to have caused problems in several potential release sites. For example, an attempt to reintroduce wild dogs to Etosha ended in failure when the last few animals contracted rabies from a jackal (Scheepers & Venzke 1995). Plans have been considered to reintroduce wild dogs to the area of the Masai Mara where rabies is known to have killed wild dog packs in the past. In such circumstances, strategies for disease control would have to form an important component of any reintroduction programme. Recent vaccination programmes for domestic dogs may have ameliorated this threat, at least temporarily. Possible alternative strategies are discussed in detail in Chapter 6.

Competitors in the Reintroduction Site

An ideal release site would have abundant prey but low densities of competing predators. Lions killed at least 11 wild dogs released in Etosha, and also represent an important cause of mortality in natural wild dog populations. The presence of lions and hyaenas would be likely to slow the growth of any new wild dog population established by reintroduction (Chapter 5). One option might be to attempt reintroduction on private land where lions and hyaenas have been eliminated (Chapter 6). However, in practice wild dog reintroduction is likely to represent a single component of programmes to rebuild guilds of large carnivores inside reserves – this was certainly the case in Madikwe and in Hluhluwe-Umfolozi. In such circumstances, wild dog reintroduction is more likely to succeed if the wild dogs are released and allowed to establish themselves before lions and hyaenas are introduced to the area.

Suitable Sites for Wild Dog Reintroduction

These observations allow us to suggest a small number of sites which might be suitable for wild dog reintroduction. Etosha National Park, Namibia, would be one possibility. Previous attempts to release wild dogs to Etosha have failed, causing the Namibian government to decide to focus on protecting its existing wild dog population rather than trying to establish another one (Scheepers 1992) – a decision that we strongly support. However, any future attempts might meet with more success. Using a combination of wild-caught and captive-reared animals should avoid the problems of captive-reared dogs' inabilty to hunt or defend themselves against larger predators. In addition, more work on rabies vaccination is likely to establish a safe and effective protocol for use on wild dogs (Chapter 8). At 22,270 km², Etosha should be large enough to sustain a viable wild dog population, particularly if several packs could be released there.

Another possible site for reintroduction might be the Serengeti ecosystem, including the Serengeti National Park, the Masai Mara National Reserve, and surrounding lands. At 25,000 km², the Serengeti ecosystem is large enough to sustain a viable wild dog population. However, unconfirmed sightings suggest that wild dogs are still present in some parts of the ecosystem (Appendix 1). Reintroduction may not, therefore, be necessary. Since disease is known to have contributed to the demise of the study populations in 1989–91, provision for disease control would form a crucial element of any attempt to reintroduce wild dogs to this area.

Another alternative reintroduction site might be the area surrounding Lake Edward on the border between Uganda and the Democratic Republic of Congo (former Zaïre), including the Parc National des Virungas in Congo and the Queen Elizabeth National Park in Uganda. Together, these parks comprise an area of over 9,000 km² – although not all of this is suitable habitat for wild dogs. High densities of Uganda kob (*Kobus kob thomasi*) provide abundant prey, but wild dogs became locally extinct in the 1960s. Most wildlife in Queen Elizabeth was decimated during the civil war in Uganda in the 1970s and 1980s, but, while hippo, elephant and buffalo populations are recovering very successfully, lions remain rare. Two factors argue against this area as a reintroduction site. First, a tarmac road passes through the northern part of Queen Elizabeth, representing a possible threat to wild dogs. Second, it is possible (but by no means certain) that lions' low population density results from persecution by local people living on the park borders. If this were the case, such persecution would also threaten wild dogs. This possibility would need to be investigated thoroughly before wild dog reintroduction could be considered.

Another possible reintroduction site would be the proposed trans-frontier Limpopo National Park. If formed, this park would join parts of the Northern Province of South Africa (including Venetia) with the Tuli Game Reserve in Botswana and conservation areas in Zimbabwe, to protect 6,000 km² of habitat suitable for wild dogs (M.G.L. Mills pers. comm.).

Finally, a plan was formulated in 1989 to reintroduce wild dogs to Akagera National Park, Rwanda (J. Kalpers pers. comm.). At 2,800 km², Akagera is probably too small to support a viable wild dog population and, indeed, its integrity is now under severe threat. Given the current political climate in Rwanda it is unlikely that this programme will be considered again in the near future.

What Rôle can Captive Populations Play in Wild Dog Conservation?

Captive-reared wild dogs are unlikely to survive long if they are released alone. Thus, future attempts at reintroduction must use at least some wild-caught animals. Nevertheless, captive animals can make important contributions to the conservation of wild populations, even if they are never released.

Perhaps the most important rôle that captive wild dogs can play is as the focus for research. Many possible management strategies for wild dogs are hampered by the need for better information. For example, research is urgently needed into the safety and efficacy of vaccines against diseases such as rabies and canine distemper (Chapter 8), and this research can only be carried out in captivity. Captive animals can also be used to perfect techniques for use on free-ranging animals, allowing protocols for immobilization and designs for equipment such as radio-collars to be tested in captivity before they are used in the field. Captive animals can also be used to refine techniques already in use: for example, the belly scores used to estimate food intake (Appendix 2) could be calibrated using feeding experiments with captive dogs.

Captive wild dogs can also play an extremely important rôle in raising public awareness – and even funds – in both range states and donor countries. For example, several zoos in the United States have 'adopted' reserves in developing countries, formulating education programmes aimed both at people living in and around the reserves, and at people in the U.S., as well as sponsoring technology transfer and raising funds for field conservation (Hutchins & Conway

1995). Captive animals form an integral part of such programmes. The rôle played by zoos in conservation education is a very important one which is often undervalued.

In some cases animals held in captivity have been used to increase genetic variation in wild populations by transferring individuals or gametes from captive populations into the wild (Olney *et al.* 1994). However, such interactive management would have limited value in wild dog conservation. Population viability analyses (Chapter 5) suggest that loss of genetic variability is unlikely to be an important cause of local extinctions in wild dogs. Furthermore, almost all of the wild dogs currently in captivity are of southern African origin, while the populations in West and central Africa are most in need of augmentation. In addition, genetic studies indicate that wild dogs usually avoid close inbreeding (Chapter 2). It has been suggested that the dogs in Hluhluwe-Umfolozi stopped breeding altogether when the only mates available were relatives (Maddock 1996). If this is the case, artificial insemination of females living in groups at risk of inbreeding would be unlikely to produce litters which would be raised by all group members.

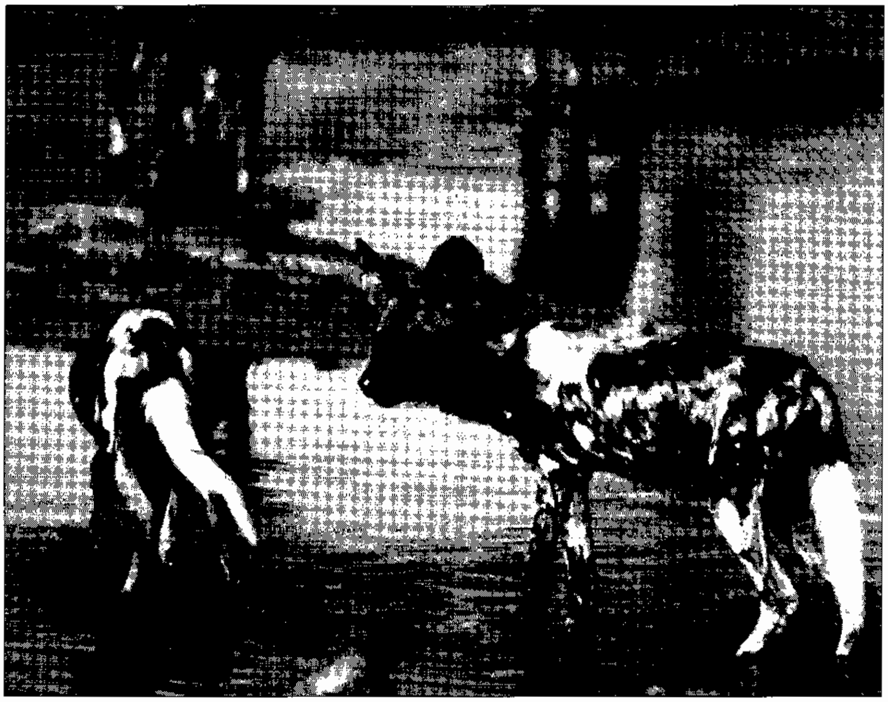
Conclusions

Wild dogs held in captivity are useful to field conservation since they provide subjects for crucial research, and may contribute to public education and fund-raising. However, captive-bred wild dogs lack skills needed to survive in the wild, and can never be released without wild-caught animals to accompany them. Nevertheless, experience in South Africa indicates that wild dogs can survive release if at least some of the pack members are wild-caught. It should, therefore, be technically possible to re-establish wild dog populations by reintroduction if the animals could be protected from persecution and disease after their release.

In practice, however, successful reintroduction would be very difficult where it is most needed, in West and central Africa. Wild dogs of the appropriate local genotypes are not available for release, since there are no captive stocks and no wild populations large enough to provide a source. Furthermore, there are no suitable release sites known to us in these areas. In West and central Africa, then, the protection of the few remaining populations remains a much higher priority for wild dog conservation than any attempt to establish additional populations.

Elsewhere in Africa, reintroduction of wild dogs is also hampered by the availability of suitable release sites. There are very few reserves large enough to sustain viable wild dog populations although Etosha, Serengeti and the proposed cross-border Limpopo National Park are candidates. Reintroduction could, however, be used to establish a network of small sub-populations containing just one or two packs in fenced reserves and private land in southern Africa. While no such sub-population would be viable alone, as discussed in Chapter 6 each could be managed as part of a metapopulation. Such intensive management would be expensive – although, funds permitting, it would be valuable for bringing about local increases in wild dog numbers in highly fragmented landscapes.

To conclude, much of the technical knowledge needed to establish and manage wild dog populations by reintroduction has now been assembled. The usefulness of reintroduction is, however, limited by the availability of wild dogs with the appropriate local genotypes, and by the availability of suitable release sites. Overall, then, the protection of existing populations has a much higher priority for Africa-wide wild dog conservation than does any programme of captive breeding and reintroduction.



Chapter 8
Research and Monitoring: Information for Wild Dog Conservation

Joshua R. Ginsberg & Rosie Woodroffe

While a great deal of information about wild dog ecology has become available recently, further research will allow more effective wild dog management.

- ***Surveys are needed, especially in central Africa,*** *to give a better picture of wild dog distribution.*
- ***Simple, effective monitoring techniques are needed*** *to track the status of known populations.*
- ***Long term studies of larger populations should be continued;*** *such studies will identify new threats as they arise, and will also determine wild dog populations' ability to recover from natural perturbations, a crucial component of their viability which has not yet been quantified in the field.*
- ***Research to help resolve conflicts between wild dogs and farmers*** *is urgently needed, since persecution represents an extremely serious threat. This must involve work on:*
    - *The true economic losses caused by wild dog predation on livestock.*
    - *The circumstances under which wild dogs take livestock.*
    - *The degree to which public attitudes reflect a real or perceived assessment of the damage caused.*

  Such information will help to determine the combination of husbandry practices, local legislation, compensation and education needed to allow wild dogs and people to coexist.
- ***Research to design strategies for disease control in wild dogs*** *is also urgently needed. In particular:*
    - *Can vaccines against rabies and canine distemper be delivered to wild dogs in a manner that is safe and effective?*
    - *Can these diseases be eradicated from their reservoir hosts, protecting wild dogs without vaccinating them directly?*
- ***Additional genetic work*** *will help to set priorities for the conservation of populations which may be genetically unique.*

Background

In previous chapters, we have formulated plans for wild dog conservation using the best information available to us. However, in several cases we have found that more research would enhance the creation and implementation of effective management strategies. A great deal of research has been carried out on wild dogs recently (See Appendix 3), so that wildlife managers are now much better equipped to conserve wild dogs than they were ten, or even five years ago. Nevertheless, there are still areas where more information would be extremely valuable. In this chapter, we summarize the research we feel would facilitate wild dog conservation. Techniques for carrying out some of these projects are described in Appendix 2.

This chapter is divided into sections, dealing with broad research topics. We have arranged these in an order which reflects the structure of the Action Plan, rather than any priority. However, within each section we have highlighted the topics that we consider need most urgent attention.

Taxonomy

Despite extensive research, some questions remain about the taxonomic status of wild dogs and what, if anything, constitutes a wild dog sub-species. Resolution of this question is important for two reasons. First, the maintenance of genetic diversity is an important component of biodiversity conservation. Genetic analyses indicate that some populations – such as the one in Kruger National Park – may contain genotypes not found elsewhere (Chapter 2). Analysis of DNA taken from a museum skin suggests that wild dogs in West Africa might also be genetically distinct from those in East and southern Africa (Chapter 2, Roy *et al.* 1994). Such distinctiveness may place a high conservation value on certain populations, and yet no research has been carried out on the genetics of several wild dog populations, especially those in West and central Africa.

While we question the universal value of reintroduction as a conservation tool for wild dogs (Chapter 7), wherever possible, wild dogs released into a given area should be as similar as possible, genetically and morphologically, to those dogs which originally occured at the release site. In practice, it may be difficult to determine the genotypes or phenotypes appropriate for specific release sites without better information. For example, in Chapter 7 we suggested that Selous might represent a source of wild-caught animals for translocation to other parts of East Africa, but recent work suggests that this population is genetically closer to those in southern Africa than to others in East Africa (Chapter 2). Similarly, re-establishment of populations in West Africa is a priority, but we know little about the genetic and phenotypic characteristics of West African wild dogs.

The importance of such genetic considerations to reintroduction programmes must be considered in this and other species – if no animals of the appropriate genotype are available to reintroduction programmes, is the release of animals with 'foreign' genotypes an acceptable alternative? The answer to this question depends, in part, upon the adaptive basis of genotypic variation. Since animals with foreign genotypes might not be adapted to local ecological conditions, reintroduction programmes which used them could, theoretically, end in failure. It would be very difficult, however, for field projects to determine whether populations which differed in their genetic makeup also differed in their behaviour and physiology. Further morphological work on museum specimens might go some way to solving this problem.

Distribution

Wild dogs' status in East and southern Africa is fairly well known, but basic surveys are still needed in several other areas, especially central Africa. There is an accepted protocol for the use of photographic surveys to census wild dog numbers (*e.g.* Maddock & Mills 1994) but we lack simple, inexpensive, but effective mechanisms with which to carry out preliminary censuses or long-term monitoring of wild dog populations. Postal surveys, such as those presented in Chapter 3, are effective tools for assessing status, but they cannot substitute for sustainable local efforts administered either by government departments or a local non-governmental organizations.

In Chapter 9, we list country-by-country priorities for action, many of which include census and survey activities. Some of the highest priority activites are:

1) Is there really a relict population of wild dogs in the Teffedest Mountains, Algeria? If this isolated population really exists, it is likely to be genetically (and perhaps ecologically) distinct from other populations, and would have a very high conservation value.
2) What is the status of the wild dog populations in Cameroun and the Central African Republic? Very little is known about these populations, which may represent a reservoir of wild dogs in central Africa.
3) What is the status of the wild dog population in southern Sudan? Little is known about this population, but it may be the source of wild dogs sighted recently in northern Uganda. If so, it could link the populations in southern Ethiopia and northern Kenya with those in central Africa.
4) What is the status of the wild dog population in southern Ethiopia?
5) Where wild dogs are sighted fairly regularly, more intensive surveys would be useful. Photographic surveys based (in part) upon pictures taken by tourists have been set up in a number of countries, including South Africa (Maddock & Mills 1994), Tanzania (Burrows 1995; Creel & Creel 1993) and Zimbabwe (J.R.G., Unpublished data). Countries such as Kenya and Zimbabwe have a fairly large volume of tourists visiting networks of protected areas. In these countries, nationwide photographic surveys could help to give a better estimate of wild dog numbers, and to assess the degree to which animals move between protected areas.
6) Even where such surveys are already in place, better coordination between projects in neighbouring countries, more involvement of local people, and better advertising of such projects in both the range states and the tourists' home countries would all contribute to the accumulation of more useful data.

Ecological Monitoring

Wild dogs' conservation requirements are now much better known than they were 10 years ago, principally as a result of ecological research on populations in several parts of Africa. Such work has identified the main threats to wild dog populations, and therefore forms the basis of this Action Plan. Continued study of these populations will contribute to wild dog conservation biology by monitoring exisiting threats and, perhaps, by identifying new ones. They will also help to determine the factors which cause wild dog populations to rise and fall in different areas.

Disease is one threat which requires continued monitoring. Not only will this will allow the identification of new disease risks that emerge, but repeated samples taken from the same population – or, better still, from the same individual – will provide extremely important data upon disease dynamics within wild dog populations. For example, the pattern of seroprevalence in different age classes can help to determine whether animals are facing a chronic disease threat, or whether seropositive animals simply represent a record of past epidemics (Thrusfield 1986). No wild dog should ever be immobilized without being screened for disease. Any wild dog found dead should be necropsied and screened for disease – even if disease is not suspected as a cause of death. Such monitoring will help to determine the threats posed by diseases such as parvovirus, adenovirus, coronavirus and herpesvirus, whose impact on wild dog populations is not yet clear (Chapter 4). Wherever possible, domestic dogs and wild carnivores living in wild dog areas should also be screened for disease.

Long-term ecological monitoring will also help to determine the resilience of wild dog populations. Ecological studies have established that competition with larger predators is likely to limit wild dog numbers over the long term (Creel & Creel 1996; Fuller *et al.* 1992; Mills & Biggs 1993), but they have not yet determined how wild dog populations recover from episodes of high mortality. Our simulations of wild dog populations suggest that their large litter sizes should equip them to recover rapidly from perturbation (Chapter 5), but empirical studies have not yet documented any such recoveries. Empirical evidence would help to test the reliability of our simulations and, therefore, the validity of our conclusions. The recent loss of several whole packs in Northern Botswana may provide an opportunity to monitor the recovery of a study population.

Conflicts between Wild Dogs and People

Despite the fact that persecution remains one of the most important threats faced by wild dog populations, little is known about the precise circumstances under which people come into conflict with wild dogs.

1) When do wild dogs stop ignoring livestock (as they did in the area of the Masai Mara, Fanshawe 1989; Fuller & Kat 1990) and start to kill them? Are livestock taken only when wild ungulate prey have been depleted? Are more livestock taken during the denning period, when the dogs' movements are restricted?
2) What tactics do wild dogs use to hunt livestock? This would help with the development of techniques to protect livestock from wild dogs.
3) How serious are the economic losses caused by wild dog predation? Are there persistent losses in some areas (*e.g.* on the borders of reserves with substantial wild dog populations), or are losses sporadic?
4) What is the public attitude to wild dogs in areas that they use regularly? Does the local attitude reflect the real losses that wild dogs cause?
5) Can husbandry techniques be modified to mitigate losses to wild dogs in areas where predation on livestock is a serious problem? Would confining livestock to bomas at night, or better-designed bomas, help to reduce losses? Would the use of guard dogs help (if disease could be controlled adequately)?
6) Would compensation schemes help to reduce local peoples' hostility to wild dogs? Would funds be available, and could such schemes be implemented realistically?
7) Where communal and private lands have been converted to wildlife use, wild dogs' prey species become a valuable commodity both for consumption and for game viewing. Some of these uses, such as photo-tourism, may benefit wild dogs but others, such as game ranching and hunting, may place wild dogs in real or perceived competition with humans for wild ungulates. Can we develop land-use zoning plans which provide a clear definition of where predators will, and will not, be tolerated?

Further research to answer these questions is a high priority for wild dog conservation, especially for populations that use livestock areas on the borders of reserves, and for those that persist outside protected areas.

Strategies for Disease Control

Disease represents a serious threat to several wild dog populations, but in no case are wildlife managers fully equipped to deal with the problem. Research is needed in several areas to help devise better strategies for disease control in wild dogs.

Protocols for Rabies Vaccination in Wild Dogs

Rabies has spilled over into wild dog populations in the past, and it is likely that this will happen again. For example, rabies is endemic in jackals and domestic dogs in many parts of Zimbabwe, with no immediate prospect of a control programme (Bingham 1995; Bingham *et al.* 1995). It may be just a question of time before wild dogs in Zimbabwe become infected. In the past, some researchers faced with proven risks of rabies infection have vaccinated wild dogs (Appendix 1). However, the death from rabies of some of the vaccinated animals has led several authors to question the value of rabies vaccination as a tool in wild dog management (Burrows 1992; Burrows *et al.* 1994).

The rabies vaccination programmes that have been carried out on free-ranging wild dogs are discussed in detail in Appendix 1. In summary, however, the most likely cause of the vaccine failures lies in the vaccination protocols used. Each wild dog was given only a single dose of vaccine. However, administration of single doses of inactivated rabies vaccine to wild dogs held in captivity in Tanzania failed to bring about seroconversion (Visee 1996), and preliminary vaccine trials in South Africa suggest that two doses must be given in order to achieve and maintain protective antibody levels (G. Thomson, pers. comm.). Further vaccine trials are urgently needed to determine the best protocol. In particular, they need to ask:

i) Are two or more doses of vaccine, given 2–8 weeks apart, needed to establish high circulating levels of rabies neutralizing antibodies? How often must boosters be given thereafter?
ii) Does vaccination by dart produce as strong an immune response as vaccination of immobilized animals by hand?
iii) It has been suggested that handling stress could have compromised wild dogs' cell-mediated immune response to rabies infection (Burrows *et al.* 1994) – does vaccination induce a cell-mediated immune response? Cell-mediated immunity can be assayed in the laboratory from blood samples (Gerber *et al.* 1985; Jayakumar & Ramadass 1990).

The ultimate test of vaccine efficacy is challenge with a dose and strain of rabies virus known to be lethal to unvaccinated animals. However, establishing the necessary challenge conditions, followed by carrying out the challenge experiments themselves, would necessitate killing at least 20–30 captive wild dogs. The consensus of vets and biologists involved in research on rabies in wild dogs and other carnivores is that challenges would be both unnecessary and unethical – for this reason, applications for government licences to carry out such experiments would probably be unobtainable (M. Artois pers. comm.; S. Cleaveland, pers. comm.; G. Thomson, pers. comm.). Nevertheless, the experiments suggested above would answer most of the questions that have been raised concerning the efficacy of inactivated rabies vaccines, without the need for carrying out challenge experiments.

Vaccination of Wild Dogs against Canine Distemper Virus

Canine distemper may represent a serious threat to wild dog populations. However, experimental administration of live CDV vaccines to captive wild dogs has, on occasion, found them to be ineffective or even dangerous. More research is needed to answer the following questions:

1) How serious is the risk of vaccine-induced distemper? While live CDV vaccines have induced distemper in several cases (Durchfeld *et al.* 1990; McCormick 1983; van Heerden *et al.* 1989), some captive facilities vaccinate their wild dogs routinely without reporting any ill effects (van Heerden 1986). No informed decision about further use of live CDV vaccines can be taken without detailed knowledge of how often they cause distemper, and the circumstances under which this occurs. For example, are adults as vulnerable as pups (all recorded cases of vaccine-induced distemper have involved pups, Durchfeld *et al.* 1990; McCormick 1983; van Heerden *et al.* 1989)? A postal survey of zoos holding wild dogs might easily answer this question.
2) Does the administration of live CDV vaccines bring about seroconversion? One study, of three litters of pups, found no evidence of seroconversion (van Heerden *et al.* 1980), while another found that adults given booster vaccinations did seroconvert (Spencer & Burroughs 1992). These results provide circumstantial evidence that, as suspected for rabies vaccination, more than one dose of vaccine might be needed to achieve and maintain protective antibody levels. In zoos that vaccinate wild dogs against CDV routinely, more studies could be carried out to assess the efficacy of different protocols. As for rabies, it would be useful to know whether multiple doses of vaccine are more effective than a single dose, whether dart-vaccination is as effective as vaccination by hand, and how often boosters must be given.
3) Do inactivated vaccines represent a viable alternative to live CDV vaccines? Inactivated CDV

vaccines do not trigger seroconversion in several other wild canid species (Montali *et al.* 1983), and caused seroconversion in only 3/12 (25%) captive wild dogs in Tanzania (Visee 1996). Nevertheless, further experiments, perhaps involving the administration of multiple doses, are needed to determine whether inactivated vaccines have any value for CDV control in wild dogs.

Possibilities for Disease Control in Reservoir Hosts

In some circumstances, controlling disease in its reservoir hosts could be a better long-term solution than vaccinating wild dogs themselves (Chapter 6). For example, rabies control in domestic dogs would protect people and their livestock as well as wild dogs. In other cases, however, it is not always clear that attempts to control disease in other species will provide effective protection for wild dogs. This highlights the need for more research, to address the following questions:

1) How does interaction with wildlife affect the epidemiology and control of rabies in domestic dogs? As far as we are aware, all mathematical models of rabies control in domestic dogs have considered the dog population in isolation (*e.g.* Coleman & Dye 1996). For the wild dog–domestic dog interaction, this may be a reasonable approximation: domestic dogs encounter one another far more often than they encounter wild dogs, and it is unlikely that transmission from wild dogs to domestic dogs would be an important component of rabies epidemiology. However, where rabies affects wild dogs, it also affects other wild carnivores such as bat-eared foxes (Cleaveland & Dye 1995) which live at much higher densities than do wild dogs. Interactions with such species might contribute to the persistence of the disease in domestic dogs, making it more difficult to eradicate. Empirical and theoretical research is needed to establish whether vaccination of domestic dogs can protect wildlife, and whether a higher proportion of dogs must be vaccinated than is necessary when domestic dogs are considered in isolation.
2) In areas where rabies occurs in domestic dog populations, why does the infection appear not to affect wild canids in some areas (as, for example, in Kruger and Hluhluwe-Umfolozi, M.G.L. Mills pers. comm.), but spill over into bat-eared foxes and jackals elsewhere (as, for example, in Serengeti and Etosha, Cleaveland & Dye 1995; Scheepers & Venzke 1995)?
3) If vaccination programmes aim to establish a cordon sanitaire around wild dog areas, how wide must the cordon be? A pilot scheme in the Masai Mara vaccinated domestic dogs in a belt 15 km wide (R. Kock, pers. comm.), but this might not be wide enough if domestic dogs and wildlife range over longer distances.
4) Can rabies be controlled in wildlife reservoirs? Domestic dogs are important rabies reservoirs in East Africa, but in southern Africa wild species such as bat-eared foxes and jackals may be more important. Achieving anything approaching adequate vaccination cover in these species would be impossible if vaccines had to be delivered by hand, but oral vaccination is a possible alternative. This method of vaccine delivery has successfully eradicated rabies from red foxes in some parts of Europe and North America (Wandeler 1993). However, although experimental administration of live oral vaccines to black-backed and side-stripe jackals has been shown to confer protection from rabies, the strain used proved highly pathogenic to baboons (Bingham *et al.* 1995). Thus, more (ongoing) research, using other strains, is needed to perfect a method for vaccinating wild canids safely and effectively.
5) What is the reservoir host for CDV? Although domestic dogs seem to be the reservoir in the Serengeti ecosystem (Alexander & Appel 1994;

Roelke-Parker *et al.* 1996), in Selous the disease appears to persist in wildlife in the absence of domestic dogs (Creel *et al.* in prep.). Research is needed to identify the wildlife reservoir(s) in systems of this kind.

6) What is the critical vaccination cover needed to eradicate CDV from domestic dog populations? Very little is known about the epidemiology of CDV in domestic dogs, and there are no published mathematical models. This makes it very difficult to formulate targets for vaccination cover. The possibility that the disease might also persist in wildlife species adds another complication to the epidemiological picture that needs addressing. More work is needed to formulate epidemiological models of CDV in domestic dog populations.
7) Can the population density of reservoir hosts be reduced? In principal, reducing the density of reservoir hosts could lead to lower transmission rates and prevent disease from persisting in the population. The practical possibilities of doing this depend upon a number of factors. If the reservoir host was a wildlife species, controlling population size would rarely be possible. For domestic dogs, the possibilities would depend upon local peoples' requirement for those dogs.
8) Can contact between wild dogs and domestic dogs be minimized? Again, this would depend upon local peoples' need for domestic dogs. More research is needed to determine whether domestic dogs' movements could be restricted by, for example, requiring that owned dogs be collared, that dogs be tied up at night, and shooting unaccompanied dogs.
9) Could eradicating disease affect mortality in domestic dog populations? The mortality caused by CDV is poorly known, but it is conceivable that the disease is important in limiting the numbers of domestic dogs. If this were the case, then eradicating CDV could bring about an increase in the domestic dog population. This could present two further problems for wild dogs. First, if the domestic dog population was larger, other diseases might be able to persist when this was previously impossible. Second, if vaccination had to be stopped – perhaps due to lack of funds – a high proportion of domestic dogs would soon become susceptible. This would set the stage for a severe epidemic with an increased probability of transmission to wildlife.

Conclusions

A great deal of information about wild dog ecology has become available in recent years. Many of the research questions raised at the IUCN/SSC Canid Specialist Group's 'Workshop on the Conservation & Recovery of the African Wild Dog' (Ginsberg 1992) have now been answered, and generated a new set of research priorities. Persecution remains a serious threat, and work is urgently needed to devise ways of resolving conflict between the interests of wild dogs and those of livestock farmers. A substantial volume of research is also needed into disease control – it was not until the wild dog study populations disappeared from the Serengeti ecosystem that it became clear just how severe a threat disease could pose to wild dogs. We still cannot determine the best strategy for controlling disease – and at present we are not fully equipped to carry out any of them.

Chapter 9
Country-by-country Action Plans for Wild Dog Conservation

Rosie Woodroffe & Joshua R. Ginsberg

This section presents options for wild dog conservation in each range state. These recommendations represent the opinions of the authors, but we hope they may serve as a basis for actions initiated by local conservation authorities and NGOs. While we have endeavoured to collect the most current information, some of the measures that we have suggested may already have been implemented.

For each country, we have briefly summarized wild dogs' status (see Chapter 3 for greater detail) and made recommendations for further actions including surveys and monitoring of wild dog distribution and abundance. In some countries such surveys may be needed to confirm wild dogs' presence or absence in particular areas – elsewhere we have recommended long-term monitoring to track increases or decreases in wild dog numbers, or photographic surveys to determine population sizes and connectivity with other populations.

Where wild dogs are known to be present, we have made recommendations for their conservation and management. We have not given specific recommendations for wild dog management in countries where the status of local populations is unclear. Nevertheless some such countries (*e.g.* Algeria, Sudan) might contain very valuable wild dog populations in need of active management.

For some countries, we have also proposed research projects which would contribute to local or pan-African wild dog conservation.

Algeria

Status: Unknown, but if a population remains it would have an extremely high conservation value.

Actions: Survey of the Teffedest mountains to determine whether any wild dogs remain there.

Angola

Status: Uncertain, but possibly extinct.

Actions: Confirm the status of wild dogs in the Cuando-Cubango region.

Benin

Status: Possibly extinct

Actions: Confirm the status of wild dogs in Pendjari and 'W' National Parks.

Botswana

Status: Good – northern Botswana contains a relatively large population of wild dogs contiguous with those in eastern Namibia and western Zimbabwe. Long-term survival of this population is of the highest priority.

Actions: Ensure links with wildlife areas in eastern Namibia and western Zimbabwe – consider establishing a formal cross-border reserve complex in this area.

Maintain the areas between the Moremi Wildlife Reserve and Chobe and Nxai Pan National Parks as wildlife lands, encouraging the contiguity of areas available to wild dogs in northern Botswana.

Establish collaborative photographic surveys across Northern Botswana, eastern Namibia and western Zimbabwe to assess the contiguity of the populations.

Assess the status of wild dogs in the Central Kalahari and Khutse Game Reserves and, depending upon the results, establish a predator management programme to mitigate persecution of wild dogs in this area.

Develop a public education programme to raise the profile of wild dogs in Botswana.

Research: Monitor disease in wild dogs and other carnivores in Northern Botswana – several packs have been lost to disease in recent years.

Burkina Faso

Status: Probably extinct
Actions: Confirm status of wild dogs in Arli National Park.

Burundi

Status: Extinct

Cameroun

Status: Uncertain but extremely valuable – Cameroun probably contains one of the largest, if not the largest, wild dog population in central Africa.
Actions: Confirm the status of the populations in and around Faro, Bénoué and Bouba-Ndija National Parks.
Maximize contiguity of Faro and Bénoué National Parks by encouraging land use favouring wildlife in the intervening lands.
Ban hunting of wild dogs.
Develop local education programmes to raise the profile of this valuable population.
Research: Facilitate studies to assess the genetic distinctiveness of Central African wild dogs.

Central African Republic

Status: Uncertain – but the population would be extremely valuable if still present.
Actions: Confirm the status of the populations in Manovo-Gounda-St Floris and Bamingui-Bangoran National Parks.

Democratic Republic of Congo

Status: Extinct

Republic of Congo

Status: Extinct

Côte d'Ivoire

Status: Probably extinct

Eritrea

Status: Extinct

Ethiopia

Status: Uncertain but very valuable – Ethiopia probably contains the largest wild dog population in North-East Africa.
Actions: Assess the status of the populations in Omo and Mago National Parks, and in Gambela National Park.
Survey the area between Ganale and Wabe Shabelle rivers where local people report wild dogs' presence.
Consider establishing predator management programmes in the environs of the Omo-Mago National Park complex, working with local pastoralists to try to mitigate persecution of wild dogs.
Establish public education programmes to raise the profile of wild dogs in Ethiopia.

Gabon

Status: Extinct

Gambia

Status: Vagrant

Ghana

Status: Possibly extinct
Actions: Confirm the status of wild dog populations in the Bui, Digya and proposed Kyabobo Range National Parks.

Guinea

Status: Very vulnerable, but extremely valuable – Guinea's wild dog population is contiguous with the one in Sénégal, and together they represent the only potentially viable population in West Africa.
Actions: The linking of Badiar National Park with Niokolo-Koba National Park in Sénégal will have substantial benefits for Guinea's few remaining wild dogs. If possible, the area available to wild dogs should be expanded still further by encouraging land use favourable to wildlife in the areas bordering Badiar.
Set up a predator management programme in the areas surrounding Badiar. Local conservation authorities should work with livestock farmers to protect wild dogs

from persecution. It might also be appropriate to control domestic dog numbers and movements in these border areas.

Establish a programme of local education to raise the profile of wild dogs in northern Guinea.

Kenya

Status: Still present but apparently declining. There are no protected areas or other lands which support large populations. Conserving wild dogs in Kenya presents a tremendous challenge and opportunity. If appropriate actions are taken, Kenya could serve as a model for management in other increasingly fragmented African landscapes.

Actions: Assess wild dogs' status in Kenya. Kenya supports sufficient number of tourists, amateur naturalists and professional biologists to establish a nationwide photographic survey. This would help to assess the degree to which animals move within and between wildlife areas. Developing a systematized, simplified reporting system for sightings of wild dogs by KWS staff, county council rangers, and local communities would also be helpful.

Encourage the use of private and communal lands for wildlife, to maximize the contiguity of small, isolated protected areas. Establish a nationwide programme of predator management, in which some areas are designated predator conservation zones, and others predator control zones. In protection zones, work with livestock and game farmers to minimize persecution of wild dogs through local education, changes in livestock husbandry and, perhaps, compensation schemes.

Public education to raise the profile of wild dogs in Kenya.

Malawi

Status: Uncertain – wild dogs sighted may be resident or could be vagrants from Zambia.

Actions: Consider establishing photographic surveys in collaboration with neighbouring Zambia. Track sightings and demography of wild dogs sighted to determine whether they are vagrants or breeding residents.

Consider establishing cross-border reserves with Zambia.

Mali

Status: Possibly extinct

Actions: Confirm the status of wild dogs in south-western Mali, where there have been a few recent sightings.

Moçambique

Status: Uncertain

Actions: Assess the status of wild dogs in northern Moçambique.

The establishment of a cross-border park which links south-western Moçambique with Kruger National Park, South Africa, and Gona re Zhou National Park, Zimbabwe, will have substantial benefits for wildlife in general and wild dogs in particular.

Mauritania

Status: Probably extinct

Namibia

Status: Good – there is a reasonably large population of wild dogs in north-eastern Namibia which is probably contiguous with those in northern Botswana and western Zimbabwe.

Actions: Continue and expand predator management programmes already established in north-eastern Namibia.

Consider vaccinating domestic dogs, and controlling their numbers, to minimize disease risks to wild dogs in north-eastern Namibia.

Consider photographic surveys in collaboration with those in northern Botswana to assess the contiguity of the two populations.

Public education to raise the profile of wild dogs in Namibia.

Niger

Status: Probably extinct

Actions: Assess the status of wild dogs in 'W' National Park.

Nigeria

Status: Possibly extinct

Actions: Confirm the status of wild dogs in the far north-east of Nigeria, where there have been a few recent sightings.

Rwanda

Status: Extinct

Sénégal

Status: Vulnerable, but extremely valuable – Sénégal's wild dog population is contiguous with the one in Guinea, and together they represent the only potentially viable population in West Africa.

Actions: The linking of Niokolo-Koba National Park with Badiar National Park in Guinea will benefit Sénégal's remaining wild dogs. If possible, the area available to wild dogs should be expanded still further by encouraging land use favourable to wildlife in the areas bordering Niokolo-Koba and the Falémé Hunting Area.

Set up a predator management programme in the areas surrounding Niokolo-Koba and Falémé. Local conservation authorities should work with livestock farmers to protect wild dogs from persecution. It might also be appropriate to control domestic dog numbers and movements in these border areas.

Establish a programme of local education to raise the profile of wild dogs in and around Niokolo-Koba and Falémé.

Research: Continue monitoring of threats to the Niokolo-Koba population.

Sierra Leone

Status: Possibly extinct

Actions: Confirm the status of wild dogs in Outamba-Kilimi National Park.

Somalia

Status: Very rare

Actions: Confirm the status of wild dogs in the southern Somalia, including Bush Bush National Park.

South Africa

Status: Good – Kruger National Park supports one of the largest wild dog populations remaining in Africa.

Actions: Maintain and, wherever possible, expand the area available to wildlife in Kruger National Park and the reserves that border it. Plans to link Kruger with Gona re Zhou through neighbouring Moçambique will have substantial benefits for wild dogs.

Establish photographic surveys in collaboration with Zimbabwe to assess the contiguity of wild dog populations in Kruger and Gona re Zhou National Parks.

Maintain links with game and livestock farmers in the areas surrounding Hluhluwe-Umfolozi Park to expand the area available to this population.

Capitalize on reintroductions carried out in Madikwe and proposed in Pilanesberg by establishing a network of tiny populations in fenced reserves across South Africa, managed together as a metapopulation.

Consider reintroduction of wild dogs to the proposed cross-border Limpopo National Park if it is established.

Sudan

Status: Uncertain, but Sudan might support an important wild dog population.

Actions: Confirm the status of wild dogs across southern Sudan, including Dinder and Southern National Parks and the Bengagai Game Reserve, and throughout the eastern Nile floodplain.

Swaziland

Status: Vagrant

Tanzania

Status: Good – Tanzania has more wild dogs than any other country in Africa.

Actions: Maintain the contiguity of the Selous Game Reserve and surrounding wildlife areas – this is the most important wild dog population in Africa and its value cannot be stated too highly.

Assess the status of the wild dog population in Ruaha National Park.

Assess the status of wild dogs in the Maasai Steppe in northern Tanzania.

Coordinate photographic surveys across Tanzania to assess movement of animals between wildlife areas.

Avoid routing of high speed roads though Selous or along its borders.

Encourage wildlife use of communal and private lands in southern Tanzania to maximize the contiguity of Selous and Ruaha.

Establish predator management programmes on the borders of Selous and Ruaha – and also, if appropriate, on the Maasai Steppe – to minimize persecution of wild dogs.

Establish a nationwide programme of public education to raise the profile of wild dogs in Tanzania.

Research: Support continued long-term monitoring and research of the Selous population: long term studies of wild dog ecology are critical to management.

Tchad

Status: Uncertain – but the population would be extremely valuable if still present.

Actions: Confirm the status of wild dog populations in Ouadi-Rimé-Ouadi-Achim and Siniaka-Minim Game Reserves.

Uganda

Togo

Status: Possibly extinct

Actions: Confirm the status of wild dogs in the Fazao Malfacassa Game Reserve, and on the Mazala, Kpeya and Kibidi mountain-sides.

Status: Vagrant

Western Sahara

Status: Probably extinct

Zambia

Status: Fair at present but declining.

Actions: Focus efforts at conservation of wild dogs in the Luangwa Valley and Kafue complexes. These two areas, while discontinuous, each represent potentially important sites for wild dog conservation.

Wild dogs on a kill in Hwange National Park.

Improve control of poaching across Zambia's reserve network to maintain wild dogs' prey base and protect them from snaring.

Establish a nationwide programme of predator management, defining zones where large carnivores are to be conserved. In these zones, encourage land use which favours wildlife and establish predator conservation programmes to minimize the threats posed to wild dogs by persecution and disease.

Consider establishing cross-border reserves with Malawi to increase the area available to wild dogs and other wildlife.

Establish public education programmes to raise the profile of wild dogs in areas surrounding reserves in Zambia and to mitigate persecution.

Erect road signs along the road passing through Kafue National Park to limit wild dog deaths due to road accidents.

Research: Compare anthrax strains isolated from Zambia with those from other parts of southern Africa, to determine why anthrax appears to have decimated wild dogs in the Luangwa valley while having little effect upon them in South Africa and Namibia.

Zimbabwe

Status: Good – Zimbabwe's wild dog population has expanded in recent years.

Actions: Continue to maximize the contiguity of areas available to wild dogs by encouraging land use favourable to wildlife on private and communal lands bordering parks and reserves.

Establish a nationwide programme of carnivore management, defining zones where predators are to be conserved, and zones where they may be controlled.

Inside predator conservation zones, work in collaboration with local game and livestock farmers to protect wild dogs from persecution, and livestock from predation, and control the numbers and mobility of domestic dogs. Where appropriate, domestic dog vaccination programmes might also be implemented.

Implement public education to raise the profile of wild dogs in Zimbabwe, particularly along the borders of protected areas.

Continue photographic surveys to assess the contiguity of populations within Zimbabwe.

Collaborate with photographic surveys in northern Botswana to determine the contiguity of wild dog populations in these countries.

Research: Carry out research on the economic losses caused by wild dog predation on livestock, and analysis of the circumstances under which such predation occurs.

Assess disease risks to wild dogs in Zimbabwe.

Appendix 1
The Conservation Implications of Immobilizing, Radio-collaring and Vaccinating Free-ranging Wild Dogs

Rosie Woodroffe

Many of the data compiled in this Action Plan have been collected from radio-collared wild dogs. However, it has been suggested that immobilizing wild dogs to fit radio-collars may lead to high mortality. Likewise rabies vaccination, one of a suite of measures considered for rabies control, has been blamed for wild dog deaths. The handling-immunosuppression hypothesis proposes that handling – defined as immobilization, radio-collaring and/or rabies vaccination – killed wild dogs in the Serengeti-Mara ecosystem by compromising their immune response to rabies virus. In the light of this hypothesis, it is important to assess the risks associated with handling before making recommendations for future wild dog management and research. In this Appendix, I review the available evidence and conclude that:

- *Rabies killed wild dogs under study in the Serengeti-Mara ecosystem.*
- *Handling was associated with reduced longevity in Serengeti, although this association may be explained without assuming a causal relationship.*
- *Data are not available to determine whether handling was associated with mortality in the Mara study.*
- *Immobilization is not associated with mortality in other wild dog populations.*
- *Mortality was not confined to vaccinated packs in the Serengeti-Mara ecosystem, and may not have been confined to study packs.*
- *It is extremely unlikely that a significant proportion of wild dogs were harbouring rabies virus at the time of handling.*
- *It is very unlikely that immobilization or vaccination would have reactivated a nonfatal rabies infection.*
- *Rabies vaccination has failed to protect some wild dogs from rabies.*

A scenario in which vaccination failed to protect wild dogs from exposure to rabies in the Serengeti-Mara ecosystem is much more plausible, therefore, than one which hypothesizes a causal link between handling and mortality. Since radio-collaring plays an important rôle in wild dog research, I conclude that the benefits of immobilization outweigh the risks, provided:

- *Research is oriented towards wild dog conservation*
- *Radio-collaring is followed up by efficient monitoring*
- *The number of animals immobilized is kept to a minimum*
- *Maximum use is made of the opportunities presented by immobilization to collect data on disease, genetics etc.*

The rabies vaccination protocols used so far on free-ranging wild dogs seem to confer few benefits. Further research, on captive animals, is needed to establish more effective protocols. However, only rarely will direct vaccination of wild dogs represent the most appropriate strategy for disease control.

Background

Much of the information collated in this Action Plan derives from research carried out on wild dogs in the field. Almost all intensive ecological studies of wild dogs have fitted some animals with radio-collars: these are crucial for locating packs that range very widely, often in fairly thick bush. Radio-collaring involves immobilizing animals with anaesthetic darts; this also allow the collection of samples for disease screening, genetic profiling and hormone analysis. Over the past 10 years, immobilizing wild dogs has formed a central part of research aimed at their conservation.

Two projects have administered rabies vaccines to free-ranging wild dogs. In the Masai Mara-Loita area, in Kenya, wild dogs that had been immobilized for radio-collaring were routinely vaccinated in 1988 and 1989, since rabies was known to occur in the local domestic dog population (P. Kat pers. comm.). This project also vaccinated some wild dogs without immobilizing them, delivering the vaccine by dart (P. Kat pers. comm.). In the Serengeti National Park, Tanzania, contiguous with the Masai Mara, wild dogs from two packs were vaccinated in 1990, after rabies had killed one Serengeti and one Mara pack in the previous 13 months (Gascoyne *et al.* 1993a; Gascoyne *et al.* 1993b). Vaccine was delivered by dart to 30 wild dogs, and by hand to four immobilized animals (Gascoyne *et al.* 1993a).

These vaccination programmes failed in their attempt to protect the wild dog population in the Serengeti-Mara ecosystem: all of the study animals eventually disappeared and today there are no wild dog packs known to be resident in either the Serengeti or the Mara study sites. Disease was implicated in the deaths of three study packs in the Mara and one in Serengeti following vaccination, and at least one of the animals vaccinated in the Mara area definitely died from rabies (L. Munson pers. comm., P. Kat pers. comm., Alexander & Appel 1994).

Following the disappearance of the Serengeti-Mara study packs, it was suggested that handling – defined as immobilization, radio-collaring and/or rabies vaccination – might be extremely harmful to wild dogs. A handling-immunosuppression hypothesis proposed that handling, perhaps in combination with some form of social stress, compromised wild dogs' immune systems leading to the reactivation of latent rabies infections (Burrows 1992; Burrows *et al.* 1994). Burrows and his co-authors argued that such reactivation would be followed by transmission of the virus to pack members that had not been handled, leading to rapid death of the whole pack.

This handling-immunosuppression hypothesis provoked a spirited debate in both the academic and popular press, which sometimes ranged beyond the scope of the data available (reviewed and discussed by Heinsohn 1992; Gates 1993; Morell 1995; Harper 1995; Dye 1996). If correct, the hypothesis has extremely serious implications, not only for wild dog research and conservation, but also for research carried out on other wild animals.

In this context, it is not my aim to consider all of the various arguments brought forward to explain the disappearance of wild dogs from the Serengeti-Mara study sites. However, it is the aim of this Action Plan to develop recommendations for the conservation and management of free-ranging wild dogs. It is important, therefore, to consider the risks associated with immobilization and vaccination, and to determine whether these risks might outweigh the benefits of such handling. For this reason, in this Appendix I discuss the handling-immunosuppression hypothesis, and use this discussion to evaluate the future rôle of immobilization and vaccination in wild dog management and research.

Recent History of the Serengeti-Mara Wild Dog Population

Although there were separate research projects established around the Masai Mara National Reserve (in Kenya), and in Serengeti National Park (in Tanzania), the Serengeti ecosystem spans the international border and the wild dogs inhabiting the area formed a single contiguous population (Burrows 1995). Individuals first identified in Tanzania dispersed into Kenya and formed packs with Kenyan wild dogs, and *vice versa* (P. Kat pers. comm., Burrows 1995; Fuller *et al.* 1992b), and wild dogs sampled by the two studies shared a unique mitochondrial haplotype (Chapter 2).

Rabies was confirmed in wildlife in the Serengeti ecosystem for the first time in 1986, in bat-eared foxes

The open plains habitat of the Serengeti made it just possible to study wild dogs without radio-collaring in the past (left), whereas in denser bush like in Hwange National Park (right) wild dog research would be impossible without radio collars.

(*Otocyon megalotis*) in Serengeti National Park (Maas 1993). In the same year, all the wild dogs in one of the Serengeti study packs, the Pedallers pack, died of disease (Table A1.1; J.H. Fanshawe pers. comm.). One carcass was recovered but necropsy was inconclusive; rabies was suspected but not confirmed. One pack member had been blood-sampled prior to death and found to be seronegative for canine distemper (J.H. Fanshawe pers. comm.).

The first confirmed case of rabies in the Serengeti-Mara wild dog population was recorded in August-September 1989, when 21 of 23 members of the Aitong pack, north of the Masai Mara, died within a six-week period (Kat *et al.* 1995). Two of the animals that died had been vaccinated against rabies in June-July 1989 using Imrab (Rhône-Merieux), an inactivated rabies vaccine (P. Kat pers. comm., Kat *et al.* 1995). Despite this, necropsy of the carcasses of four pack members revealed that all were rabies-positive (Kat *et al.* 1995), and one of the rabies-positive carcasses was that of a vaccinated animal (L. Munson pers. comm.). Viruses were extracted from three of these carcasses, and molecular genetic analysis showed that the rabies viral variant was one common in sympatric domestic dogs (Kat *et al.* 1995).

In August 1990, most members of the Mountain pack, a Serengeti study pack, disappeared. One animal was found still alive, showing symptoms suggestive of rabies, and rabies was confirmed in the carcass of another pack member found dead nearby (Gascoyne *et al.* 1993b). As in the Aitong pack, the virus isolated from this carcass was found to be a viral variant common in local domestic dogs (Kat *et al.* 1995).

In 1990, Tanzania National Parks decided to implement a rabies vaccination programme in Serengeti. In September 1990 an inactivated vaccine (Madivak, Hoescht) was administered to members of the two remaining study packs, the Salei pack and the Ndoha pack (Table A1.1, Gascoyne *et al.* 1993a; Gascoyne *et al.* 1993b).

Carcass of one of the Serengeti animals subsequently found to have died of rabies. Note that the carcass has been partially eaten by scavengers; few carcasses were found due to their activities [photo © K. Laurenson].

Subsequent to the confirmation of rabies in wild dogs in the Serengeti-Mara ecosystem, all of the study packs disappeared – their histories are summarized in Table A1.1. The Ndoha pack was last sighted in January 1991, then disappeared (Gascoyne *et al.* 1993a). The Salei pack split in late 1990, and three new packs were formed: the New Barafu, Trail Blazers and M&S packs. All of these packs had disappeared by July 1991 (Gascoyne *et al.* 1993a). The Trail Blazers pack was last sighted in May 1991, when two animals had disappeared and other pack members appeared lethargic; the radio-collars were found subsequently, but there were no signs of carcasses (Gascoyne *et al.* 1993a). A photograph showing members of the Salei pack was passed to Frankfurt Zoological Society by a tour driver, but the date on which it was taken could not be confirmed and, despite extensive searching, the tourist who took the photograph could not be traced (S. Cleaveland* pers. comm.). The radio-collar of a member of the Salei pack was retrieved by July 1991, but the carcass was not recovered. Thus, there were no confirmed sightings of any of the Serengeti study animals after June 1991 (Gascoyne *et al.* 1993a).

Another pack which was not part of the Serengeti study population, the Moru Track pack, was identified in 1990 and may also have disappeared in 1991 (Table A1.1, Burrows 1995).

By 1990, only two wild dog study packs remained in the Mara study site (Table A1.1). Members of one, the Intrepids pack, were seen dead and dying in December 1990 (Alexander & Appel 1994), although eleven members of this pack had been vaccinated against rabies during the previous 13 months (P. Kat pers. comm.). A radio-collar was recovered, but no carcasses were found and the pack was not sighted again (Alexander & Appel 1994). The other study pack, the Ole Sere pack, contained a radio-collared male which had been vaccinated as a member of the Intrepids pack in January 1990 (P. Kat pers. comm.). This animal was found dead in early January 1991, and tested positive for rabies, although the sample was badly decomposed and the rabies diagnosis was not confirmed by a second laboratory (P. Kat pers. comm., Alexander & Appel 1994).

Two unmonitored packs may also have disappeared from the Mara area in 1991 (Kat *et al.* 1995). These packs, the Bardamat and Maji Moto packs, were seen repeatedly by farmers and missionaries to the North of the Mara study site, although they were never photographed (P. Kat pers. comm.). They were last sighted in

* formerly S. Gascoyne

Table A1.1
The fates of individually identified wild dog packs in the Serengeti-Mara ecosystem post-1986. Sources: [a] J. Fanshawe pers. comm.; [b] Lelo (1990); [c] Kat *et al. (1995)*; [d] Fuller & Kat (1990); [e] P. Kat pers. comm.; [f] L. Munson pers. comm.; [g] Burrows (1993); [h] Gascoyne *et al.* (1993a); [i] Gascoyne *et al.* (1993b); [j] Alexander & Appel (1994); [k] Scott (1992) (cited by R. Burrows 1994); [l] Burrows (1994); [m] Burrows *et al.* (1994).

Pack	Last seen alive	Immobilized?	Vaccinated?	Comments	Fate
Pedallers	June 1986[a]	Yes; collar fitted March 1986[a]	No	Four dogs found dying in June 1986. Rabies was suspected although no conclusive diagnosis could be made from the one carcass that was examined[a]	Died
Naabi	September 1988[b]	Yes; last collar fitted May 1988[b]	No	An empty radio-collar and jawbone were recovered; the rest of the pack disappeared[b]	Disappeared
Aitong	September 1989[c]	Yes; last collars fitted July 1989[d]	Yes; three vaccinated in July 1989[c,e]	21 pack members died – the carcasses of four were recovered and tested positive for rabies[c]. One of these had been vaccinated[f]	Died
Ndutu	November 1989[g]	Yes; last collar fitted July 1989[h]	No	Two collars were found. Rabies was suspected but not confirmed	Probably died
Lemuta	February 1990[g]	Yes; collared February 1990[g]	No	Seen only once, at collaring[g]	Disappeared
Mountain	August 1990[i]	Yes; last collar fitted June 1990[i]	No	The last pack members seen alive showed rabies signs; one carcass was recovered which was positive for rabies, and one radio-collar was recovered in August 1990[g]	Probably died
Intrepids	December 1990[j]	Yes; last collar fitted September 1990[e]	Yes; 11 vaccinated, last in 1990[e]	Pack member were seen dead and dying but no carcasses were recovered[j]	Died
Ole Sere	January 1991[j]	Yes; last collar fitted February 1990[e]	Yes; one vaccinated in the Intrepids in December 1989[e]	The carcass of the vaccinated pack member was recovered. This was found positive for rabies with one test, but negative by another[j]	Probably died
Triangle (= Border Rovers)	January 1991[k]	Yes; last collar fitted February 1990[k]	No	The two radio-collared animals were lost in late 1990. Others were seen subsequently	Unknown
Ndoha	January 1991[h]	Yes; last collar fitted January 1991[g]	Yes; 13 vaccinated September 1990[h,l]	One radio-collar was retrieved in July 1991[l]	Probably died
Salei	May 1991[g]	Yes; last collar fitted February 1991[g]	Yes; 21 vaccinated September 1990[h,l]	One radio-collar was found but the carcass was not recovered[h]	Probably died
Trail Blazers	May 1991[i]	Yes; last immobilized November 1990[g]	Yes; vaccinated in the Salei & Ndoha packs in September 1990[i]	Formed in February 1991 by dispersing members of the Salei and Ndoha packs. The last pack member seen alive appeared lethargic. The two radio-collars were found in July 1991, but there was no sign of the carcasses[i]	Probably died
M & S	June 1991[g]	Yes; last immobilized September 1990[g]	Yes; vaccinated in the Salei pack in September 1990[i]	Formed by breakaway of a subordinate pair from the Salei pack[i]. Neither was radio-collared at the time of their disappearance	Disappeared
New Barafu	May 1991[g]	Yes; last collar fitted September 1990[g]	Yes; vaccinated in the Salei pack in September 1990[i]	Formed by dispersal from the Salei pack[h]. Two collars were never recovered	Disappeared
Moru Track	December 1991[m]	No	No[i]	A possibly non-resident, non-study pack first verified in December 1990[m]	Disappeared

April–May 1991, and no further sightings were reported in 1992 (P. Kat pers. comm.).

Evidence for an Association between Handling and Mortality in the Serengeti-Mara Study Population

Analysing data from the Serengeti study population, Burrows *et al.* (1994) found that whole packs and adult individuals both showed decreased longevity in 1985–1991, when routine handling occurred, compared with 1970–77 when little handling took place. Within the 1985–1991 study period, the proportion of adults and yearlings that survived for 12 months after handling was significantly smaller than the proportion of unhandled adults and yearlings that survived for 12 months after the first sighting as an adult or yearling. Animals which were vaccinated by dart survived for shorter periods than did those which were only radio-collared (Burrows *et al.* 1994); this association persisted when non-significant effects of age and sex were excluded from the model (Burrows *et al.* 1995; Ginsberg *et al.* 1995b), and when a later, unconfirmed sighting of the handled New Barafu pack was included (Burrows *et al.* 1994). Animals radio-collared after they had joined a new pack survived for shorter periods than did those collared prior to dispersal (Burrows *et al.* 1994).

A similar analysis of data from the Mara study population, along with four other wild dog populations, was carried out by Ginsberg *et al.* (1995a). This analysis found no association between handling and survivorship. However, the analysis was incomplete since it did not take into account the fact that some of the wild dogs from the Mara which were classified as 'unhandled' had, in fact, been vaccinated by dart (East 1996; Ginsberg 1996). Using published sources, Burrows *et al.* (1995) attempted to reconstruct the Mara dataset, identifying 24 handled and 44 unhandled individuals (*cf* 20 handled and 67 unhandled reported in Ginsberg *et al.* 1995). They hypothesized a 'best-case scenario', in which all dispersing animals were assumed to survive, and a 'worst-case scenario' in which dispersers were assumed to have died. Their calculations showed significantly higher mortality of handled animals under the 'best-case scenario', but no significant effect under the 'worst-case scenario'. They discounted the 'worst-case scenario' because it generated mortality rates they considered unrealistically high, when compared with mean mortality rates for the Mara population published in Fuller *et al.* (1992a), although the exact mortality for the period when handling occurred remains unknown.

As a result of these complications, neither Ginsberg *et al.* (1995a) nor Burrows *et al.* (1995) provides firm evidence for an association (or lack of an association) between handling and mortality in the Mara study population. I attempted to obtain the complete Mara dataset, but, regrettably, was unable to do so. Thus, the question of whether any such association exists remains unresolved.

After considering a whole suite of other ecological factors, Burrows *et al.* (1994; 1995) concluded that the handling-immunosuppression hypothesis was the most likely explanation for the associations between handling and longevity that they found in the Serengeti dataset, and for a similar association postulated for the Mara dataset. In the following sections I therefore discuss the questions I consider critical to the testing of the handling-immunosuppression hypothesis.

Did the Last Wild Dogs in the Serengeti-Mara Die of Rabies?

Burrows' hypothesis concerns the effect of handling-induced immunosuppression on rabies infection (Burrows 1992). However, several authors have suggested that some of the Serengeti-Mara study packs might have died from canine distemper (CDV) rather than rabies.

The exact reasons for the loss of study packs are often lacking – in some cases it is not even certain that pack members died (Table A1.1). No live wild dogs in either study site were ever found to be seropositive for CDV (Chapter 4). Carcasses were available from only four packs that disappeared from the Serengeti-Mara region in 1986-91 (Table A1.1). Carcasses from 3 packs were tested for rabies, and all were found to be positive (although one diagnosis was not confirmed, see above). Tissue samples from the Aitong carcasses were also tested for CDV by immunohistochemistry and found to be negative (L. Munson pers. comm.). Thus, there is no direct evidence that canine distemper played any rôle in the disappearance of wild dogs from the Serengeti-Mara study sites.

Macdonald *et al.* (1992) considered death from CDV a plausible explanation for whole-pack deaths, because they thought it unlikely that rabies would have killed wild dogs which had been rabies-vaccinated. Alexander & Appel (1994) reported a CDV epidemic among domestic dogs in the Mara study site in late 1990/early

Collecting brain tissue from a wild dog carcass in the Serengeti. Rabies was subsequently confirmed for the individual.
[Photograph © K. Laurenson].

1991. Thus, there is circumstantial evidence that wild dogs might have contacted CDV around the time that they disappeared from the two study sites. The next two sections therefore address questions critical to testing the hypothesis that CDV might have played a rôle in the pack disappearances.

Would CDV Have Caused such High Mortality?

The mortality caused by CDV in wild dogs is poorly known. The only documented outbreak involved a pack in Botswana: all pups and four of six adults died, while the remaining adults disappeared (Alexander *et al.* 1996). The carcass of one of the pups was recovered, and CDV infection was confirmed by immunohistochemistry; tests for rabies and parvovirus proved negative (Alexander *et al.* 1996). Thus, in this case CDV appears to have caused mortality on a scale similar to that which occurred in the Serengeti-Mara.

Data from elsewhere indicate that a fairly high proportion of wild dogs may survive contact with CDV: populations may show seroprevalences of 50–100% while remaining stable (Chapter 4). However, none of 28 wild dogs sampled in the Serengeti-Mara was seropositive for CDV (Chapter 4), suggesting that the population may have been naïve to CDV prior to the epidemic postulated for 1990–1. Under such circumstances high mortality would be expected. Thus, the mortality caused by CDV in wild dogs may be lower than that caused by rabies in some populations, but CDV could have caused very high mortality in the apparently naïve Serengeti-Mara population.

Could Wild Dogs Die from rabies if they had been Vaccinated?

At least 48 of the wild dogs that disappeared from the Serengeti-Mara study sites in 1989–91 had been given inactivated rabies vaccines to protect them against rabies (Table A1.1). The vaccines used (Madivak (Hoescht), Rabisin (Rhône-Merieux) and Imrab (Rhône-Merieux), Gascoyne *et al.* 1993b; Kat *et al.* 1995; Macdonald *et al.* 1992) are licensed in Europe to protect domestic dogs from rabies for up to 3 years (Rhône-Merieux, pers. comm., Gascoyne 1992). Death of all of the vaccinated wild dogs, from rabies, within 13 months of vaccination would therefore be unexpected. Several explanations have been put forward, some more convincing than others:

Vaccination Protocol

It is possible that the vaccination protocols used did not induce protective antibody levels in the wild dogs that were treated. Most commercial inactivated rabies vaccines are licensed to give protection after a single inoculation (Rhône-Merieux pers. comm.; Intervet, pers. comm.), but this protocol may not always generate a protective antibody response. Administration of a single dose of the inactivated rabies vaccine Dohyrab (Solvay Duphar) to captive wild dogs held in the Mkomazi Game Reserve failed to generate protective antibody levels (Visee 1996). Five of 12 animals sampled before and after vaccination showed no rise in antibody titre after 10 weeks. Of the 25 that were vaccinated in total, 12 had no detectable rabies antibodies 10 weeks later, and none developed nominally protective antibody levels (rabies serum neutralizing antibody (RSNA) levels > 0.5 International Units/ml are considered likely to be specific and nominally protective). Unpublished studies of captive wild dogs in South Africa suggest that animals must be given more than one dose of inactivated vaccine to establish antibody levels likely to be protective (G.R. Thomson, pers. comm). Some studies of domestic dogs show a similar pattern: for example, in Alaska domestic dogs given several doses of vaccine had higher antibody titres than did those vaccinated just once (Sage *et al.* 1993).

Likewise, the available evidence suggests that the

Researchers in the Serengeti draw blood from an immobilized wild dog. This animal was one of those vaccinated in 1990 [photo © B. Hastings].

single vaccination given to wild dogs in the Serengeti and the Masai Mara might have failed to generate protective antibody levels. One animal that had been vaccinated as a pup in the Intrepids pack in December 1989–January 1990 was found to be seronegative for rabies when he was immobilized for radio-collaring in September 1990 (P. Kat pers. comm.). Two animals that were blood-sampled before and after vaccination in Serengeti showed rises in antibody titres within 28 days (Gascoyne *et al.* 1993a). However, one was considered seropositive before vaccination (RSNA 0.55 IU/ml), and the other, which was vaccinated by dart, seroconverted but developed a low antibody titre only just above that considered likely to be protective (0.55 IU/ml, Gascoyne *et al.* 1993a). Thus there is no strong evidence that wild dogs vaccinated in the field seroconverted to high antibody titres. It is possible, therefore, that at least some of wild dogs vaccinated in the Serengeti-Mara failed to achieve protective antibody levels.

It is also conceivable that antibodies might not have remained at protective levels: 26 domestic dogs given a single dose of an inactivated vaccine licensed to provide protection for 3 years all had nominally protective RSNA levels 30 days post-vaccination, but in 7 (27%) antibody titres had fallen to < 0.5 IU/ml after 60 days (Sage *et al.* 1993).

Taken together, these findings raise the possibility that the single dose of vaccine given to wild dogs in the Serengeti-Mara might have been insufficient to establish and maintain protective antibody levels. This would be especially likely if animals vaccinated by dart did not receive the full dose of vaccine (Burrows 1994). Animals without protective antibody levels would have been vulnerable to infection had they contacted rabies some months later.

Pathogenicity of the Rabies Strain

It is conceivable, but unlikely, that the rabies strain which affected the wild dogs in the Serengeti-Mara was so pathogenic that it overcame the immunity induced by vaccination (Macdonald *et al.* 1992). This does seem to have occurred in the past in domestic dogs; eleven of 26 dogs which died of rabies in Gabon had been vaccinated – some of them repeatedly, using inactivated vaccines including Rabisin (Bourhy *et al.* 1988). Bourhy *et al.* (1988) commented that some African rabies strains are more pathogenic than the European strains usually used to test vaccine efficacy. However, the virus isolated from wild dog carcasses retrieved from the Serengeti-Mara was from a strain common in the local domestic dog population (Kat *et al.* 1995). Thus it seems unlikely that a highly pathogenic rabies strain was responsible for the disappearance of wild dogs from the Serengeti-Mara.

Cold Chain Breakdown

It is extremely unlikely that inappropriate storage of the vaccines used can explain the apparent vaccine failures. Inactivated vaccines require refrigeration, but it is known that the vaccines used in both the Serengeti and the Mara wild dog vaccination programmes were kept cool at all times (S. Cleaveland pers. comm.; P. Kat pers. comm.). Furthermore, trials carried out with Rabisin have shown that it still protects domestic dogs against rabies challenge when it has been stored for a week at 37°C before administration (Chappuis 1995).

Maternal Antibodies

Interference between the vaccine and maternally-derived antibodies in young animals cannot account for the putative vaccine failures, because most of the animals vaccinated were adults and yearlings (Macdonald *et al.* 1992).

Reversion to Virulence

It is impossible that the vaccine itself caused clinical rabies. Modified live vaccines may have this effect, but only inactivated vaccines were used in the Serengeti-Mara (Gascoyne *et al.* 1993b; Kat *et al.* 1995; Macdonald *et al.* 1992). Inactivated vaccine preparations contain only dead virus and cannot be pathogenic (Bunn 1991).

In evaluating the possibility of rabies vaccine failure in the Serengeti-Mara study populations, it is important to bear in mind that, whatever the mechanism involved, there is firm evidence that wild dogs vaccinated against rabies have died of rabies in the past. Two of three wild dogs vaccinated in the Aitong pack died during a disease outbreak in 1989: the carcass of one was recovered, and rabies infection was confirmed from tissue samples (L. Munson, pers. comm., Kat *et al.* 1995). Furthermore, four wild dogs released in the Etosha National Park, Namibia, died from rabies even though they had been vaccinated annually with Rabisin while held in captivity (L. Scheepers, pers. comm., Scheepers & Venzke 1995). Unexplained vaccine failures have also occurred in domestic dogs living under field conditions: 14/176 rabies cases in Texas and 13/247 cases in Mexico involved vaccinated dogs (Clark *et al.* 1981; Eng *et al.* 1994).

On the basis of these data, I conclude that it is entirely possible that rabies was responsible for the disappearance of the last study packs in the Serengeti-Mara area. Attempts to protect them from rabies by vaccination could have failed. Since there is no direct evidence to suggest that CDV killed any of the study animals, rabies remains the most likely cause of their disappearance.

Was it only the Study Packs that Disappeared?

Burrows *et al.* (1994; 1995) suggested that unhandled non-study packs persisted while packs handled by researchers disappeared in 1990–1. They calculated that the number of unknown wild dogs entering the Serengeti study area was no lower after the last study packs disappeared in 1991 than in 1985–1991. This, they claimed, showed that the population of wild dogs outside the study area had persisted (and still persists) even though all of the study packs had disappeared. Other authors have, however, contested this claim (Dye 1996; Gascoyne & Laurenson 1994).

It is difficult to keep track of wild dogs that are not radio-collared (which is the reason researchers use radio-collars to mark study packs). This means that the data on the non-study packs in the Serengeti-Mara ecosystem are extremely poor. One pack – the Moru Track pack – was identified in Serengeti from photographs taken by tourists, although it was never located by researchers (Gascoyne & Laurenson 1994). This pack was seen repeatedly in December 1990, and last sighted in December 1991 (Burrows *et al.* 1994). However, it is not clear whether this pack was ever really resident in the study area.

Two non-study packs, the Bardamat and Maji Moto packs, apparently disappeared from the area of the Mara study site in 1991 (see above). However, these packs were never seen by researchers, and never photographed, so sightings remain unconfirmed.

Another non-study pack, of 12 animals, was sighted from the air in the Loliondo area, to the east of Serengeti National Park, in November 1990 (S. Cleaveland pers. comm.). A pack was sighted again in this area in early 1992 but, although this group was photographed, no animals could be recognized from earlier photographs (Burrows 1993). Thus, it is not known whether a pack had persisted in the Loliondo area while those inside Serengeti study area disappeared, or whether the dogs sighted in 1992 were new arrivals. A den was reported from the Loliondo area in 1993, indicating that a resident pack was using the area at that time (S. Cleaveland pers. comm.).

All of the wild dogs sighted in the Serengeti study site since 1991 have been single-sex groups (Burrows *et al.* 1994). It is difficult to interpret such sightings. Dispersing groups of wild dogs may move over very large areas, and the wild dogs sighted in the Serengeti study site since 1991 may not have came from immediately adjoining areas. The distribution data presented in Chapter 3 indicate that dispersing groups of wild dogs occasionally turn up in countries where they have been locally extirpated, travelling hundreds of kilometres.

I conclude, then, that the available data are not sufficient to substantiate claims that unhandled packs definitely survived when handled packs disappeared (Burrows 1992; Burrows *et al.* 1994; East & Hofer 1996). Disappearance of wild dogs from the Serengeti-Mara ecosystem might not have been confined to the handled study packs. The Moru Track, Bardamat and Maji Moto packs, which were never handled, may have disappeared around the same time as the study packs. At least one pack used the Loliondo area after the study packs had disappeared. The possibility remains that this pack survived the disease outbreak when study packs died. However, even if this pack persisted through the outbreak, it is impossible to assess whether this was because it was outside the area where wild dogs were handled.

Could the Handled Wild Dogs have been Carrying Rabies?

Burrows (1992) argued that handling by researchers reactivated quiescent rabies infections in the Serengeti-Mara wild dogs. Such reactivation would, he suggested, be followed by signs of disease and transmission of the virus to pack members that had not been handled. How likely is it, then, that the wild dogs that were handled were harbouring quiescent rabies infections?

Rabies is not always fatal in domestic dogs – the alternative host responses are illustrated in Figure A1.1. When a domestic dog is infected with rabies, the virus may remain latent close to the site where it entered the host, producing neither disease nor an immune response (Fekadu 1991b). Alternatively, the rabies virus may be resisted by the dog's immune system, so that the infection is aborted without the animal ever showing signs of disease. However, once the virus enters the central nervous system, symptoms of rabies begin (Fishbein & Robinson 1993). Even now, infection may not prove fatal: some domestic dogs may recover without clinical support, and a very small number have continued to excrete the virus in their saliva after recovery (Figure A1.1, Fekadu 1991b).

Data collected in Serengeti raise the possibility that rabies might not always be fatal in wild dogs. Gascoyne *et al.* (1993b) sampled 12 animals from five packs between 1987 and 1990, and found that three of them, from two packs, had positive titres of rabies neutralizing antibodies (5 seropositive animals were initially reported, but this was due to inconsistencies in the calculations of RSNA titres between laboratories, Burrows 1994; Gascoyne & Laurenson 1994). None of 18 wild dogs sampled in the Mara study site was seropositive for rabies (Alexander *et al.* 1993). The results from Serengeti must be interpreted with caution (Gascoyne *et al.* 1993a). It is possible that they represent a non-specific reaction: the assay used was developed for humans and had not been validated for wild dogs (S. Cleaveland* pers. comm.). Domestic dogs may have significant amounts of nonspecific virus-neutralizing antibodies in their sera, which generate low measured RSNA titres (Fekadu 1991b).

Despite these caveats, it is possible that Gascoyne *et al.*'s (1993b) data show that wild dogs from two packs in the Serengeti population had survived contact with rabies in the past. If this were the case, it would have two implications for the handling-immunosuppression hypothesis. First, it raises the possibility that the seropositive wild dogs might have been rabies carriers. Second, it suggests that even seronegative pack members might have had some contact with rabies and might, therefore, be harbouring latent infection. I shall discuss these two possibilities in order.

Aborted Infection and Recovery from Rabies

If Gascoyne *et al.* (1993b) detected rabies-specific serum antibodies, their results would suggest that the seropositive wild dogs had either aborted rabies infection, or contracted the disease and then recovered (Figure A1.1). It is impossible to be sure which of these alternatives is the most likely. Recovery from rabies can only be distinguished from aborted infection by looking for antibodies in the cerebro-spinal fluid (Fekadu 1991b). Cerebro-spinal fluid was not sampled in wild dogs immobilized in Serengeti for obvious ethical reasons. However, experimental studies of domestic dogs indicate that aborted infection is more common than recovery: of 28 dogs given intramuscular inoculations of a (rather avirulent) strain of rabies virus, 7 (25%) aborted

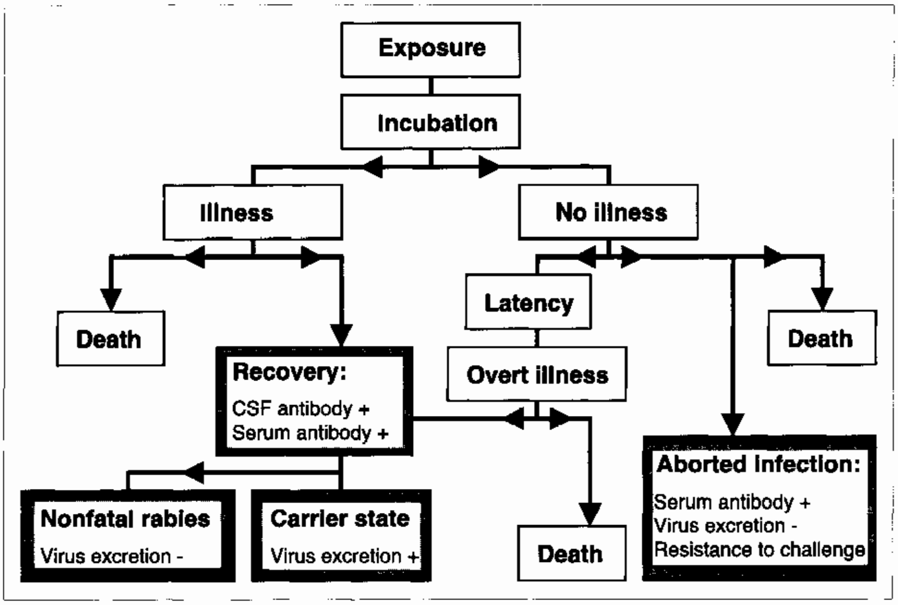


Figure A1.1. Alternative responses to infection with rabies virus in domestic dogs, modified from Fekadu (1991a).
The shaded boxes indicate the responses that might have led some wild dogs in Serengeti to carry antibodies against rabies.

* formerly S. Gascoyne

infection and 2 (7%) recovered; the remaining dogs all died (Fekadu & Shaddock 1984; Fekadu *et al.* 1981).

If the seropositive wild dogs had aborted rabies infection, then handling could not have reactivated the infection, since animals which have aborted rabies no longer carry the virus. Indeed, domestic dogs that have aborted infection subsequently resist challenge with rabies virus (Fekadu & Shaddock 1984). Under this scenario, then, seropositive wild dogs might have had a better chance of surviving subsequent contact with rabies than those which had never been previously exposed. All three seropositive dogs were alive five months after sampling, and one is known to have survived 30 months (Gascoyne *et al.* 1993a).

If, rather than having aborted a rabies infection, the seropositive wild dogs had recovered from clinical rabies, then there is a very small possibility that they might have still been carrying the rabies virus. A few domestic dogs have recovered from rabies but continued to excrete the virus in their saliva (Fekadu 1972; Fekadu *et al.* 1981). However, such cases are extremely rare. From a total of 1,083 healthy unvaccinated dogs sampled in Ethiopia just five (0.46%) were rabies carriers (Fekadu 1972). Furthermore, surveys of 791 stray dogs in Buenos Aires, Bangkok, and Cairo failed to find any animals that were carrying rabies, even though rabies was endemic in all three areas (Bell *et al.* 1971; Botros *et al.* 1979; Ratanarapee *et al.* 1982). In the laboratory, the carrier state has been produced only once (Fekadu *et al.* 1981), despite the many domestic dogs experimentally inoculated with rabies virus. In experimental studies one of 28 dogs (3.6%) inoculated with an Ethiopian rabies strain subsequently became a carrier (Fekadu & Shaddock 1984; Fekadu *et al.* 1981). Other experiments using different, more virulent rabies strains, have demonstrated recovery but have never produced rabies carriers (Arko *et al.* 1973; Fekadu *et al.* 1982). These studies of domestic dogs suggest that it is extremely unlikely that the wild dogs found to be seropositive in Serengeti were carrying the rabies virus.

Latent Infection

If Gascoyne *et al.* (1993a) detected rabies-specific antibodies in Serengeti wild dogs, this would indicate that they had been exposed to rabies virus in the past. This raises the possibility that others in the population might have exhibited another form of non-fatal rabies: latent infection. In such cases, the virus remains at or near the site of infection without provoking a humoral immune response. As a result, latent infection is extremely difficult to detect: diagnosis can only be made when the virus reactivates and the animal develops signs of disease. Latent infection cannot be distinguished from protracted incubation. In humans the virus has occasionally remained quiescent for as long as 6 years after infection (Smith *et al.* 1991). Since latent infection cannot be detected *in vivo*, it is extremely difficult to determine whether this is a common phenomenon in naturally infected animals. However, a two-year study of 63 domestic dogs found that incubation periods for experimentally infected animals varied from 7–125 days (Fekadu 1991a). The few survivors of this study subsequently showed resistance to challenge with rabies virus, indicating that they had experienced aborted rabies infection and were not still harbouring latent infections (Fekadu *et al.* 1982). Latent infection has not been shown to occur in wild dogs, but there is no reason to suppose that it might be more common in wild dogs than in domestic dogs.

Since few data are available on rabies pathology in wild dogs, it is impossible to quantify the rôle played by nonfatal infection in wild dog rabies. RSNA titres measured in Serengeti were low, and the assays might have detected non-specific virus-neutralizing antibodies rather than rabies-specific antibodies. Latent infection and the carrier state are extremely rare in domestic dog populations, and neither state has been shown to occur in wild dogs. I conclude, therefore, that it is highly unlikely that a significant proportion of the wild dogs handled in the Serengeti-Mara studies was harbouring the rabies virus.

Could Handling Reactivate Quiescent Rabies Infection in Wild Dogs?

Though highly unlikely, a small possibility remains that a few of the wild dogs in the Serengeti-Mara study populations might have been carrying rabies or supporting latent rabies infection. Could such an infection be reactivated if the animals were handled by researchers?

Burrows *et al.* (1994; 1995) proposed three mechanisms whereby different forms of handling might have reactivated quiescent rabies infection. First, the stress of immobilization for radio-collaring might have reactivated infection. Second, the drugs used for immobilization might have suppressed the wild dogs' immune systems, making them more sensitive to rabies. Third, the vaccines delivered might have had an immunosuppressive effect. Any of these might combine with social stress and contribute to immunosuppression (Burrows *et al.* 1994). I shall deal with the three mechanisms in order.

Could the Stress of Immobilization Reactivate Rabies Infection?

Experimental studies have suggested that rabies infection might be reactivated by chronic stress (McLean 1975; Soave 1964; Soave et al. 1961):

1) Soave *et al.* (1961) infected 11 guinea pigs with rabies virus, five of which developed rabies and died after an average incubation period of 43 days (range 37 – 56). The six survivors were given injections of adrenocorticotropic hormone (a stress hormone) every two days, and within 9 days one animal started to develop symptoms of rabies and died on the 13th day. The other five animals remained healthy until they were killed about two weeks later.
2) Soave (1964) investigated the effect of social stress on rabies infection: ten guinea pigs that had been exposed to rabies were kept in isolation for 7 months and then subjected to intense crowding. One of the ten died of rabies after 6 weeks of chronic stress.
3) Fifteen racoons were experimentally infected with rabies, and eight died after an average incubation period of 44 days (range 27 – 66). Six of the survivors were subjected to daily injections of cortisone, and one died of rabies after 15 days (McLean 1975).

None of these experiments showed conclusively that stress caused reactivation of rabies infection, since none included a control group of individuals which was exposed to rabies but not to the stressor. An alternative explanation for the results is, therefore, that the animals which 'survived' rabies exposure (and thus passed into the experimental treatment groups) simply had longer incubation periods than those which died before they could be exposed to the stressor. Nevertheless, the possibility remains that chronic stress might reactivate latent rabies infection, or hasten death from rabies.

Observational studies have also proposed a relationship between chronic stress and rabies pathology – Maas (1993) suggested that lactation stress might account for the much higher rabies mortality in female bat-eared foxes than in males.

Evidence that acute (rather than chronic) stress might trigger the reactivation of latent rabies infection is scarce, although Fekadu (1991b) suggested that the stress of parturition might have reactivated rabies in a domestic dog which had been a healthy rabies carrier for 10 months.

How Stressful is Immobilization for Wild Dogs?

The available data suggest that chronic stress is more likely than acute stress to play a rôle in rabies pathology. However, immobilization for radio-collaring appears not to impose chronic stress on wild dogs. Creel *et al.* (1996b) found that, in Selous, faecal corticosterone levels were no higher in wild dogs wearing radio-collars than in uncollared dogs. Furthermore, repeated sampling before and after collaring revealed no elevation in corticosterone levels (Creel *et al.* 1996b).

de Villiers *et al.* (1995) attempted to measure the acute stress caused by immobilizing wild dogs. They used plasma cortisol levels immediately after darting as an approximation of baseline levels, and showed a 2.2–fold increase in free-ranging wild dogs that had been anaesthetized. This increase is similar in size to that recorded for immobilized spotted hyaenas, suggesting that the acute stress associated with darting is no greater for wild dogs than for other large carnivores (de Villiers *et al.* 1995).

A wild dog immobilized for radio collaring.

Might Natural Stressors also Play a Rôle?

The stress imposed by immobilization could combine with natural social stressors to bring about rabies reactivation. Burrows *et al.* (1994) showed that wild dogs radio-collared after they had formed a new pack survived for shorter periods than did those collared before they dispersed. Subordinate pack members have lower glucocorticoid levels than do dominants (Creel *et al.*

1996a), but no data are available upon the stress involved in pack formation. Since dominant status seems to impose chronic stress, while immobilization involves only acute stress, it might be expected that social status alone would play a more important rôle than handling in rabies pathology.

Timescales for Rabies Reactivation

In all of the laboratory studies which have claimed to show reactivation of rabies infection, either by acute or by chronic stress, clinical rabies and death have occurred rapidly. Assuming that the stressor triggered reactivation (rather than simply being administered to animals with longer incubation periods, see above), in most cases the incubation period was much shorter than that measured in newly-infected animals (9 days vs. 43 days in Soave *et al.*'s (1961) study; 15 days vs. 44 days in McLean's (1975) study; 42 days vs. 30-66 days in Soave's (1964) study). However, wild dogs immobilized in the Serengeti-Mara ecosystem did not disappear within days of immobilization. Twelve wild dogs radio-collared in Serengeti survived an average of 17 months (510 days) after collaring (Burrows *et al.* 1994), and six radio-collared in the Mara study site survived between 2.2 and 3.7 months (66–111 days Burrows *et al.* 1995). For comparison, the only available data on rabies in wild dogs suggest that the incubation period is normally 8–42 days (Kat *et al.* 1995). It seems unlikely, therefore, that the disappearance of these animals was caused by acute immobilization stress reactivating quiescent rabies infection.

Stress of Immobilization vs Dart-vaccination

One further piece of evidence argues against a rôle for immobilization stress in the disappearance of the Serengeti-Mara study animals. Burrows *et al.* (1994) found that animals which had been radio-collared in Serengeti survived significantly longer those which were vaccinated by dart (Burrows *et al.* 1994). Immobilization stress is believed to result from the disorientation that occurs as the anaesthetics start to take effect (de Villiers *et al.* 1995). If this is the case, one would expect radio-tagging to be more stressful than vaccination by dart gun, and, if anything, to lead to a more rapid death – the opposite of the association found by Burrows *et al.* (1994).

Conclusion

In conclusion, I consider it unlikely that the stress induced by immobilizing wild dogs played any rôle in the course of rabies infection. Immobilization imposes a mild acute stress, but there is little evidence to suggest that rabies infection can be reactivated by acute stress. Chronic stress might reactivate such infection, but there is no evidence that immobilization causes chronic stress in wild dogs. Furthermore, chronic stress would be likely to reactivate rabies infection on a timescale much shorter than the one observed.

Could Anaesthesia itself Reactivate Rabies Infection?

Several studies have shown that general anaesthesia can suppress the immune system. Is it possible that immobilizing agents, rather than immobilization stress, compromised the Serengeti-Mara wild dogs' immune systems?

Felsburg *et al.* (1986) showed that anaesthetizing domestic dogs with methoxyflurane had a marked effect upon their lymphocyte function. Clinical work on humans has suggested that anaesthesia with ketamine (one of the immobilizing agents used in the Serengeti study, Gascoyne *et al.* 1993b) can depress the immune response to rabies infection and cause death (Fescharek *et al.* 1994). However, two pieces of evidence suggest that immunosuppression by immobilizing agents played no rôle in the disappearance of the Serengeti-Mara study packs.

First, Burrows *et al.* (1994) found that wild dogs which had been immobilized and radio-collared appeared to survive significantly longer than those which were vaccinated by dart. This would not be expected if immobilization, rather than vaccination, was involved in reactivating rabies infection.

Second, anaesthetics have only a short-term effect upon the immune system: experimental work has shown that domestic dogs regain their full immune capacity within 1–4 days of anaesthesia (Felsburg *et al.* 1986). In contrast, wild dogs disappeared from the Serengeti-Mara study sites several months after some of them had been immobilized (Burrows *et al.* 1994; Burrows *et al.* 1995).

Could Vaccination Reactivate Rabies Infection?

The effect of rabies vaccination on immune responses to rabies infection depends upon whether vaccination is carried out before or after exposure to the virus.

Vaccination after Exposure to Rabies

It is extremely unlikely that rabies vaccination would cause death in wild dogs that were already carrying latent rabies infection or incubating the virus. Post-exposure vaccination is a routine component of clinical treatment for rabies exposure (Fishbein & Robinson 1993). As the virus incubates at or near the site of infection, there is no immediate humoral immune response, and, once the virus enters the nervous system, it is sequestered from the immune system (Fishbein & Robinson 1993). During the incubation period, however, a programme of intramuscular injections of rabies vaccine exposes the body to rabies antigens and allows it to mount a humoral immune response earlier than would naturally be the case (Fishbein & Robinson 1993). Thus, post-exposure vaccination takes advantage of rabies' relatively long incubation time and confers protection on the host. This means that, far from hastening death, vaccination of wild dogs immediately after exposure to rabies infection might make them more likely to survive the infection.

Vaccination Immediately before Exposure to Rabies

Vaccination immediately before exposure to rabies virus can cause immunosuppression. The immune system is confronted with both the vaccine and the viral infection simultaneously, which means that its ability to respond to the virus is reduced. This may result in the phenomenon of 'early death' from rabies. For example, of 17 domestic dogs that contracted rabies less than 30 days after being given inactivated rabies vaccine, 17 (41%) died within 7 days of exposure (Clark *et al.* 1981) – a shorter incubation period than that seen in unvaccinated dogs (Fekadu 1991a).

It is possible, then, that if wild dogs had been exposed to rabies within a few weeks of vaccination, they might have died from the disease more rapidly than they would had they remained unvaccinated. This scenario is highly unlikely, however: wild dogs in Serengeti disappeared, on average, 7 months after vaccination (Burrows *et al.* 1994).

In conclusion, it appears unlikely that rabies vaccination would have triggered mortality from rabies on the timescale that was observed. Furthermore, several of the study packs that disappeared from Serengeti contained no members that had been vaccinated (Table A1.1).

Why might Longevity be Correlated with Handling?

This discussion has, so far, concluded that neither immobilization nor vaccination is likely to have killed the last members of the Serengeti-Mara wild dog study populations by reactivating rabies infection. Why, then, is there a statistical association between handling and decreased longevity among wild dogs in Serengeti (Burrows *et al.* 1994) and, perhaps, the Mara (Burrows *et al.* 1995; Ginsberg *et al.* 1995a)?

The most likely explanation for the disappearance of the Serengeti-Mara study populations is that they were killed by a disease, from which the rabies vaccination programme failed to protect them. Since most of the packs disappeared in 1990–1 (Table A1.1), the correlations reported by Burrows *et al.* (1994) can also be explained by the timing of handling relative to a disease outbreak (Ginsberg 1996). In the Serengeti study area, 18 wild dogs were radio-collared between 1985 and 1989. Only one or two dogs were collared in each pack, so the majority of study animals were not handled in any way. Four more dogs were radio-collared – and also vaccinated – in 1990. Thus, 18 of the 22 dogs (82%) were radio-collared at least a year before the pack disappearances that occurred in 1990–1.

Also in 1990, an additional 30 dogs were vaccinated by dart in Serengeti. Thus, 34 of the 52 dogs (65%) that were either radio-collared or vaccinated in 1985–90 were handled in 1990. As a result, most of the handling carried out on the study population in 1985–90 was done in 1990, immediately before the putative disease outbreak.

Most of the wild dogs that were assumed to have died in Serengeti in 1985–91 disappeared along with their whole packs (Burrows 1995). Of 11 packs studied in 1985–91, eight disappeared in 1990–1 (Table A1.1, Burrows 1995). Thus, most of the wild dogs that were presumed to have died did so in 1990–1, at the time of the putative disease outbreak. For this reason, Burrows *et al.* (1994) excluded the 1990 data from their calculations of mortality during the period of intensive study in 1985–91 (Burrows *et al.* 1995). The 1990 data were, however, necessarily used in their calculations of the longevity of immobilized and dart-vaccinated animals (Burrows *et al.* 1994).

Given these circumstances, it is not surprising that the data show radio-collared dogs to have survived longer than dart-vaccinated dogs in Serengeti. The majority of animals were collared in 1985–9, but all of the vaccinations were carried out in 1990. Thus, vaccinated animals had less time to live before the 1990–1 disease outbreak than did radio-collared dogs. In the same way, it is not surprising that unhandled dogs survived longer than handled dogs. The majority of handling occurred in 1990, but most of the unhandled animals were identified for the first time in 1985–9. Thus, wild dogs which had been handled survived for a shorter period before the 1990–1 disease outbreak than did unhandled wild dogs.

These results mean that the association between handling and reduced longevity in Serengeti can be explained without assuming any causal relationship. As discussed above, the question of whether a similar association occurs in the Mara data set remains unresolved; likewise, data are not available to assess whether an argument similar to that outlined above might explain the association that has been hypothesized (Burrows *et al.* 1995).

Is the Handling-immunosuppression Hypothesis the Best Explanation for the Disappearance of Serengeti-Mara Study Packs?

Having reviewed the available evidence, I conclude that:

1) Death from rabies is the most likely explanation for the disappearance of most of the wild dogs under study in the Serengeti-Mara ecosystem.
2) Rabies vaccination has definitely failed to protect some wild dogs from exposure to rabies in the past.
3) Mortality was not confined to vaccinated packs, and might not have been confined to study packs.
4) It is extremely unlikely that a significant proportion of wild dogs were harbouring rabies virus at the time of handling.
5) Even if handled wild dogs were harbouring rabies infection, it is very unlikely that either immobilization or vaccination would have reactivated the infection, or that this would have generated the observed pattern of mortality.
6) There is an association between handling and reduced longevity in the Serengeti data set, but this can be explained without assuming a causal relationship.
7) Data are not available to determine whether a similar association occurred in the Mara study.

On the basis of these findings, I conclude that the handling-immunosuppression hypothesis is not the best explanation for the disappearance of the wild dog study packs from the Serengeti-Mara ecosystem. There is no realistic mechanism by which either immobilization or vaccination could have hastened death of study packs by reactivating latent rabies infection. In contrast, rabies vaccination is known to have failed on at least two occasions. A scenario in which vaccination failed to protect wild dogs from exposure to rabies is much more plausible, therefore, than one which hypothesizes a causal link between handling and mortality.

Do the Risks of Immobilizing Wild Dogs Outweigh the Benefits?

The probability that wild dogs died in the Serengeti-Mara study populations as a direct result of immobilization is very small. Nevertheless, it can never be proven that immobilization was entirely harmless. It is important to determine, then, whether the possible risks of immobilizing wild dogs outweigh the benefits.

Additional information about the relationship between immobilization and mortality comes from other studies of wild dogs. Ginsberg *et al.* (1995a) analysed data from 353 wild dogs studied in four areas of East and southern Africa. Data from these populations are not directly comparable with those from the Serengeti-Mara, since none of the study populations had a known history of rabies exposure (East 1996). Nevertheless, these data do provide useful information about the general risks of immobilizing and radio-collaring wild dogs. In these four populations at least, immobilization was not associated with any reduction in wild dogs' probability of survival (Ginsberg *et al.* 1995a).

What, then, are the benefits of immobilization? Chapter 8 of this Action Plan calls for continued research into population processes in wild dogs. The majority of wild dog researchers agree that immobilization to fit radio-collars is an essential part of their work. Locating wild dog study packs without the aid of radio-collars is extremely difficult. While the Serengeti wild dog population occupied areas of open plains habitat, most other studies (and most other wild dog populations) occupy fairly thick bush. At the start of the wild dog project in Selous, researchers took a year to radio-collar just two packs (S.R. & N.M. Creel, pers. comm.), while in Hwange it took over a year to locate and re-collar a pack in which both radio-transmitters had failed (J.R. Ginsberg pers. comm.). Once animals are collared, radio-tracking allows researchers to locate wild dog packs, and thus to collect data on wild dogs' health, causes of mortality, interactions with human activity, contacts with other carnivores, including lions, hyaenas and domestic dogs, and many other topics important to wild dog conservation.

A secondary benefit of immobilizing wild dogs for radio-collaring is that it allows researchers to collect tissue samples. Such samples include blood and tissue taken for disease screening – since disease represents such a serious threat to wild dog populations, knowledge of the diseases to which they are exposed may be crucial in formulating local management plans. Genetic samples can also be collected to study both the effects of inbreeding and the subspecific status of various wild dog populations (See Chapter 2).

I conclude, therefore, that the benefits of immobilization outweigh the risks, provided immobilization is carried out in the course of research aimed at wild dog conservation. It is vital that radio-collaring be followed by an efficient monitoring programme, to check that all handled animals remain healthy, and to ensure that the very best use is made of the opportunities offered by radio-collaring. Monitoring of animals radio-collared in Serengeti was inadequate, and this contributed to the confusion over their ultimate fate. In the light of such considerations, the IUCN/SSC Canid Specialist Group's 'Workshop on the conservation & recovery of the African wild dog', held in Arusha in 1992, resolved that "Research which involves intervention is only justified where the planning and execution of a project give a reasonable expectation that the rewards for wild dog conservation will outweigh the costs. To ensure this fruitful outcome project planning and execution should always involve close liaison with local governmental policy-making agencies, and extensive consultation with appropriate colleagues." As with any endangered species, the number of wild dogs handled should be kept to a minimum, without sacrificing scientific validity. The greatest of care should be taken to minimize stress to immobilized animals. Wherever possible, alternatives to handling should be explored: for example, efforts should be made to use samples that can be collected without immobilization (*e.g.* faeces, Creel *et al.* 1996b). Finally, all animals that are immobilized should be screened for disease.

New projects planned on wild dogs may benefit from contacting the IUCN/SSC Canid Specialist Group for detailed advice on handling protocols – it has established a Lycaon Working Group, chaired by Dr M.G.L. Mills, to assist in such cases.

Immobilization provides an opportunity to collect extensive data in addition to fitting a radio-collar.

Do the risks of vaccination outweigh the benefits?

It is extremely unlikely that rabies vaccination caused the deaths of any of the Serengeti-Mara study animals. Nevertheless, rabies vaccination did not prevent pack extinctions. Although administering inactivated rabies vaccines to wild dogs seems to have no detrimental effects in captivity (de Villiers *et al.* 1995; Gascoyne *et al.* 1993b; Visee 1996), the vaccination protocols used in the field may have failed to stimulate sustained protective antibody levels. So far, then, the possible risks of vaccination appear to outweigh the benefits.

As discussed in Chapter 6, direct vaccination of wild dogs will rarely represent a viable option for protecting free-ranging populations from rabies. In thick bush, and in areas where wild dogs are neither radio-collared nor individually identified, vaccination programmes would be near-impossible or, at best, extraordinarily expensive. Nevertheless, direct rabies vaccination would be an option in small well-monitored populations, such as those re-established by reintroduction. Further vaccine trials are therefore needed to devise rabies vaccination protocols more likely to provide protection in such areas – details of the questions to be addressed are given in Chapter 8. Elsewhere, wildlife managers should consider the alternative strategies for rabies control detailed in Chapter 6.

Diseases other than rabies, notably CDV, also represent threats to wild dogs (Chapter 4). However, live CDV vaccines may induce distemper in wild dogs (Durchfeld *et al.* 1990; McCormick 1983; van Heerden et al. 1989), and inactivated vaccines appear ineffective (Visee 1996). Thus, the risks of vaccination against CDV clearly outweigh the benefits at present.

Appendix 2
Some Techniques for Studying Wild Dogs

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Background

Chapter 8 of this Action Plan outlines the information needed to conserve wild dogs more effectively. However, our knowledge has increased dramatically over the past 10 years. This is partly because researchers studying wild dogs in various parts of Africa have made efforts to use similar techniques, making the data they collect directly comparable across ecosystems (*e.g.* Fuller *et al.* 1992). In this chapter, we describe some of these established techniques, and also discuss some new techniques which wild dog researchers and managers might find useful. Some of the techniques are only appropriate for use in intensive research programmes, but many do not require that information be collected systematically. Almost all wild dog sightings, even those recorded by observers who have never seen wild dogs before, can be useful, especially if sightings are accompanied by photographs. Wild dog research programmes can, therefore, be organized at local, national and international levels. We would be very grateful if anyone collecting data of any kind on wild dogs would make contact with the Canid Specialist Group's Lycaon Working Group, which is chaired by Dr Gus Mills. His address is given at the end of this Appendix.

Surveying Wild Dog Populations

Some of the most important information to be collected about wild dogs continues to concern their distribution and abundance. The Canid Specialist Group would very much appreciate details of any wild dog sightings anywhere in Africa. Where wild dogs occur, their numbers can be estimated using photographic surveys: these take advantage of the fact that every wild dog has a unique colour pattern on its fur. Thus, photographs taken by researchers, tourists and other observers can be used to obtain a direct measure of wild dog numbers. Furthermore, if such surveys are coordinated over larger areas, they can be used to identify movements of individuals between protected areas: for example, a wild dog from the reintroduced population in Hluhluwe/Umfolozi Park in South Africa was photographed in Itala Game Reserve some 150 km away (Maddock 1992).

Photo-surveys

Since photo-surveys rely on individual recognition of animals, they will produce a minimum estimate of population size. However, given enough photographs, such surveys should be less biased than other survey methods, since repeated sightings of the same animals will be recognized.

Photographs and sightings can be requested from field staff and tourists. People are asked to accompany each set of photographs with details of the date and time of sighting, the locality, and the number of adults and pups (animals approximately half adult size) seen. Results from a large-scale survey in Kruger National Park, South Africa, showed that the same individual dogs were seen together repeatedly, within well-defined areas, and that a similar number of individuals were seen on each occasion. Thus, packs could be identified (Maddock & Mills 1994). Left- and right-side photographs of all individuals from each pack were pasted onto large cards and each was given a reference num-

Skilled trackers may use tracks to detect wild dogs.

ber. Wherever possible, the researchers followed up sightings by field staff and tourists and took additional photographs – especially useful in matching left- and right-side photographs. This process allowed a direct count of the total number of individually recognizable dogs seen (Maddock & Mills 1994).

In Botswana, J.W.M. (Unpublished data) tried using coloured ear tags to help tourists and field staff to identify individual wild dogs and wild dog packs. However, this proved unhelpful: tourists often failed to see ear tags, and did not report the colour of the tag consistently. Furthermore, the tags caused damage to the ears which did not heal due to licking and further abrasion by other pack members. The tags did not seem to bother the dogs excessively, but they did not prove useful and eventually the researchers removed them.

In Kruger, photographs were collected from tourists by means of a photographic competition run by the Endangered Wildlife Trust. The competition offered worthwhile prizes as incentives to tourists to submit pictures (Maddock & Mills 1994). Other surveys have taken slightly different approaches to attracting tourist photographs: for example, researchers in Selous offer to pay back the costs of sending them copies of photographs (S.R.C. & N.M.C. Unpublished). However, while such reward systems are helpful, they seem not to be essential for the success of surveys. Wild dog researchers carrying out such surveys have found that tourists are usually happy to help, although some tour guides are more reluctant. For this reason, every effort should be made to contact tourists directly. Posters and leaflets requesting wild dog sightings and photographs should be boldly displayed where they will be seen (in lodges and campsites) and should, ideally, be available in several languages. Advertisements in local and international natural history magazines, and through wildlife clubs, may also help to raise awareness of the need for wild dog photographs, and might increase the number of sightings reported from outside protected areas. In all cases, the costs of such surveys – mostly the production of sighting sheets and posters – can be kept down by cooperation among projects. Researchers intending to start such surveys may, therefore, benefit from contacting the C.S.G. to check the current situation of such cooperative efforts.

Sightings by field staff are also crucial to wild dog surveys: rangers represent a body of skilled observers, often travelling in areas which are not frequented by tourists. The efficiency with which such information is collected from field staff can be improved in a number of ways. Game scouts may be given forms to fill in, asking for details of wild dog sightings: motivation may be improved by asking a particular individual in each patrol to take responsibility for recording sightings. A local member of staff – for example, a parks ecologist – should oversee the collection of sightings. In many areas (*e.g.* Kenya, Tanzania) such techniques are already in operation. However, the Canid Specialist Group would be happy to provide advice and assistance with collating results in areas where such surveys are not yet underway.

Surveying Wild Dogs' Predators and Competitors

As discussed in Chapter 4, an important question in wild dog ecology concerns the factors which limit their numbers. Evidence is accumulating that competitors and predators might keep wild dog numbers low (Chapter 4). Surveys of spotted hyaenas and lions are, therefore, of interest both in areas where wild dogs occur, and in areas that are being considered as sites for wild dog reintroduction.

Censusing Spotted Hyaenas

A rapid and reliable technique for censusing spotted hyaenas can be achieved by using sound. A six-minute long tape of sounds known to attract spotted hyaenas – the bleating of a wildebeest calf being killed by hyaenas, as well as sounds of hyaenas feeding at a carcass, mobbing lions and involved in territorial fights – is played over two 8W horn speakers pointing in opposite directions. This attracts hyaenas from distances varying from about 2–3.5 km, depending on conditions. This tape is played at a succession of calling stations, each situated about 10 km apart to prevent double-counting. The tape is played for half an hour at each station, so up to 10 stations can be surveyed on any one night. Copies of the tape and a detailed report of the technique and results obtained can be obtained from Dr Gus Mills, whose address is given at the end of this Appendix.

Censusing Lions

Lions must be censused using individual identification techniques for accurate estimates. Individuals can be identified by the pattern of whisker spots on the muzzle, so the technique is very similar to the one used to survey wild dogs. We urge that photographs of lions also be collected by people engaged in wild dog censusing efforts.

Censusing lion roars using acoustical playbacks is another way to estimate densities. This method will give only a minimum estimate, but can at least be used to obtain an idea of relative lion densities in different habitats.

Studying Food Acquisition in Wild Dogs

Information is accumulating to suggest that wild dogs are not limited by the availability of their prey – although this might not be the case in lower density populations or those inhabiting very arid areas. Testing whether wild dogs are food-limited depends in part upon studying their diet, and, for this reason, we present here a number of techniques currently in use in field studies of wild dogs.

Direct Observations

There are several methods by which food acquisition of wild dogs can be measured. The most frequently used is generally termed direct observation. The observer uses a vehicle to follow packs that are foraging, and then records all the kills made, as well as other features of the animals' hunting behaviour. This method provides the least biased data, and must be the first choice. In open, flat habitats like the Serengeti plains, the method is relatively easy to apply. In areas of thicker bush and broken ground, such as the Kruger National Park and Hwange, it becomes more difficult to follow wild dogs and more damaging to vehicles. This can only be accomplished in certain, more open areas, and then only with the aid of radio-tracking apparatus. Furthermore, it is impossible to record details of hunting behaviour as is possible in open areas.

Although wild dogs are predictable in their hunting

behaviour in that they are normally crepuscular, they do sometimes hunt at night. Then the problems mentioned above become even more difficult to overcome. Direct observations need to be carefully planned, especially when consumption rate is being measured. The time period for which the dogs are going to be followed should be determined before each observation session, to avoid the temptation to continue observations if the dogs have not killed for a while, or to terminate observations when it seems likely that the dogs will not hunt again for some time.

Faecal Analysis

Where direct observations are impossible, several indirect methods may be used. It is important to realize the biases that these indirect methods introduce. Faecal analysis is a useful indirect method. Dogs often defaecate around daily resting sites, along roads and at dens, so it should be possible to collect a large enough sample when dogs are radio-collared. Because dogs from one pack almost always feed from the same carcass, caution must be exercised in sampling. Only one scat per pack per day should be collected.

Observations of passage rate and number of defaecations per meal for different prey species would help to improve the accuracy of faecal analysis. Such experiments, which could be conducted in captivity, would help wild dog researchers to interpret the results of faecal analysis more accurately.

Opportunistic Observations of Kills

In areas where field staff and others patrol regularly, opportunistic observations of wild dog kills can provide some information on food habits. The main problem with this technique is that it is biased towards larger prey and is the least accurate method for documenting food acquisition.

Belly Scores

Information on wild dogs' feeding behaviour can also be collected from short follows, chance sightings and even photographs, by using 'belly scores' to assess how full the stomach is. Such data give no information about the prey species wild dogs are catching, but can give a measure of food intake. By recording belly scores during continuous follows with good simultaneous data on diet, researchers can calibrate such scores with known categories of food intake.

The number of belly score categories should be kept low (three to five) so that categories remain sufficiently distinct to be reliable. We suggest the following four categories:

1 = Belly well above the chest line
2 = Belly level with the chest line
3 = Belly somewhat below the chest line but not distended laterally
4 = Belly well below the chest line and distended laterally (the 'hyaena look')

Belly scores are visual estimates, and are therefore subjective. Because of this subjectivity, it is important to assess consistency of scores among observers, and to minimize variability of scores. A good method is to prepare a card with drawings (or, better, photographs) of dogs with each belly score. This provides a consistent standard against which belly score estimates may be checked, and should improve inter-observer reliability.

Several researchers have noticed one complication: belly scores may differ systematically between the sexes. These researchers noted that after most kills females had consistently lower scores than did males. It is not yet resolved whether differences in belly scores reflect real differences in food intake or sexual dimorphism in the anatomy of the abdomen. If sex differences in belly scores do not reflect real differences in feeding behaviour, the complication could be resolved in one of two ways: (i) separate scales could be prepared for each sex, or (ii) sex differences in score could be accounted for statistically using a single scale. The second method is preferable because it does not complicate the scoring process, and makes no subjective assessment of which belly sizes represent equal feeding access for males and females. If, however, sex differences in belly sizes prove to reflect real differences in the amount of food eaten by males and females, separate scales for the two sexes would be invalid.

Regurgitation

Regurgitation, which occurs at the den, is often easier to record than hunting or feeding. Researchers at the 1992 meeting in Arusha therefore considered the possibility that food limitation of wild dog populations might be quantified from measures of regurgitation rates.

In Serengeti, well over 90% of all regurgitation took place within 12 hours of feeding and any regurgitation therefore provided some measure of food consumption (J.R.M. Unpublished data). In one pack observed in 1985 at a time of food stress, yearlings failed to regurgitate to pups at the den despite their priority at kills. The yearlings stole food regurgitated by the adults to the young pups. This pack eventually abandoned their pups in response to food stress. In this extreme case, regurgitation could have been used to infer food limitation. However, there were many other cues, notably the long absences of the pack from the den, and the poor condition of the pups.

The weight of food available to Serengeti packs correlated with the number of subsequent regurgitations: dogs in packs that had more food available to them regurgitated more often. However, there was a great deal of variation in the rate of regurgitations, both among packs and among different members of the same pack. It appeared that even a small number of adults could easily supply the food needs of pups at least to 10 weeks of age. Even though the packs studied were small, the adults gave only about 10% of the food they ate to the pups at each regurgitation. Dogs on average regurgitated three or four times after a full meal: maybe a third of their intake. That wild dogs can provide more was illustrated by a female that regurgitated 11 times after a meal. The packs in this study did not appear to be food stressed: it was not uncommon to see adults approach the pups as if to regurgitate but leave as no pups begged. Uneaten food often lay around the den. The largest pack, with the highest food availability, gave the smallest proportion of its food to the pups – the pack with least food seemed able to compensate for the lower consumption by increasing the frequency with which each group member regurgitated to the pups.

These results suggest that regurgitation will seldom provide a useful measure of food intake. It is possible that a food-stressed pack, living on comparatively small prey items where a single kill does not provide an immediate glut of food, would regurgitate to pups in proportion to what they ate. Otherwise, the large food items and small food requirements of pups at a den mean that regurgitation rates will rarely provide a measure of the amount that packs are eating.

Disease Screening in Live Wild Dogs

As discussed in Chapter 4, diseases represent an extremely important problem in the conservation and management of wild dog populations. It is very important, then, that wild dogs be screened for infectious diseases whenever the opportunity arises. Screening of live animals usually requires that individuals be immobilized and is only appropriate, therefore, for intensive research projects. Carcasses of dead wild dogs can also be screened for disease, and we describe techniques for collecting such samples in the next section.

Researchers who are capturing wild dogs for any reason should collect blood samples for disease screening. Ideally, collect two blood samples, one into a large (10 ml) vacuum tube without anticoagulant, and another into a small tube (2 ml) containing EDTA or heparin as an anticoagulant. The larger sample is for serological screening and is the more important one. The smaller sample allows full blood counts to be performed, and also allows screening for blood parasites. Make blood smears from it and fix them immediately in methanol. Keep the rest of the sample cool and submit it to a lab for blood counts within a day if possible.

The larger sample – the one without anticoagulant – must be centrifuged. Pipette off the serum, keep it cool and freeze as soon as possible. The sera should be divided into at least two separate samples, and one sample should always stay in the country of origin with the appropriate government agency. Aliquots of the same sample should be stored in two separate freezers to protect against sample loss as a result of freezer failure. Sera can be stored almost indefinitely at –70°C before testing for antibodies, enzymes etc. Do not forget to maintain (and update) a log of all samples, along with information about the animals from which the samples were taken and the places where the samples are stored.

Screening of samples can often be carried out by local veterinary laboratories. However, if anyone needs assistance in organizing the analysis of samples taken from wild dogs, they should contact Nancy Kock, who is Chairman of the African section of the Wildlife Disease Association. Her address is given at the end of this Appendix. The results of disease screening should be reported to the appropriate government agency in the host country, even if screening is carried out elsewhere.

Post-mortem Examination of Dead Wild Dogs

Quantifying the causes of wild dog mortality forms an important part of assessing their local conservation needs. In particular, examining dead wild dogs for evidence of disease may provide a crucial warning that local disease control is necessary. Even animals that are known to have died from other causes (such as road accidents or predation by lions) may be carrying diseases that threaten other population members. *Post-mortem* examinations are best carried out by vets or other qualified personnel, but in some cases this is not possible. Since diagnoses often rely upon the collection of tissue samples as soon after death as possible, it may be more useful for inexperienced observers to collect samples immediately, than to wait hours or days for a vet to be available. For this reason, we outline, here, a protocol for *post mortem* examination of any wild dogs found dead in the field. If at all possible, photographs should be taken throughout the examination – or, better still, the whole process should be recorded on video – this can be very helpful in arriving at a diagnosis. Finally, remember that useful information about wild dog genetics can also be obtained from carcasses – indeed, carcasses which are far too decomposed for disease screening can often yield useful samples for genetic analysis. We describe protocols for collecting genetic samples in the next section.

A Note on Safety

Keeping in mind that over 75% of the infectious diseases that affect animals may also occur in humans, it becomes obvious that in performing necropsies observers must ensure that they are protected from potential pathogens. Gloves and protective clothing should be worn wherever possible, although this may not be possible in the field. Alternatively, one can guard against infectious diseases by washing up thoroughly afterwards. Do not smoke or eat while carrying out a *post mortem* examination. Do not cut towards yourself or others, and if accidental cuts do occur, attend to them immediately with appropriate flushing and antiseptic.

Equipment Needed for the Examination

Use the correct instruments if they are available – only a few are necessary: strong, sharp knives, a sharpening steel or stone, scissors, forceps, scalpel handles and blades, a hacksaw or rib cutters, and possibly a small hatchet. Perhaps the most important samples to take from wild dog carcasses are brain samples, and for these you will need ordinary drinking straws, about 5 mm in diameter.

It is wise to plan ahead for samples that you might submit for bacterial or viral culture. Sterile swabs and transport media are available for bacterial samples, and viral samples can be frozen, preferably in sterile vials. Parasites, along with tissues, can be fixed in 10% buffered formalin. 10% formalin can also be used to store samples of brain tissue. In addition, if possible additional brain samples should be stored in a 50% solution of bidistillated glycerin in phosphate buffered saline mixed with 10^{-4} thimerosal (also called thiomersal or thiomersalate).

General Points about Sampling

Remember that any tissues you preserve will be interpreted to best advantage if they are not damaged at the time of necropsy, so treat them gently. If you need to palpate something, do not do so until a portion has been safely placed in formalin. Although it is often easier to examine tissues after the blood has been washed off them, take samples first, as water will damage the tissues.

Tissue samples should be 5–10 mm thick, and placed in about 10 times their volume of 10% buffered formalin. Hollow organs may be opened and their contents (*e.g.* faeces) removed before fixation. Once the tissue is fixed, you can drain away most of the formalin, leaving just enough to keep them moist, and submit them for examination by post if there are no local experts who can interpret the results.

It is important to select samples carefully for bacterial culture: remember that by about 24 hours after death invading bacteria may obscure results, making culture for pathogens unwarranted.

Carrying out the *Post Mortem*

1) Begin with a visual examination of the animal, and then palpate any abnormalities. Record the nutritional state (body condition) of the animal.
2) Cut into the right axilla (armpit) and coxofemoral (hip) joint, and turn back both right legs. Then make a shallow incision along the ventral midline, cutting through the skin from the chin to the pelvis. Do not cut across hair: instead, roll the skin back after making the first incision, and cut underneath, which preserves the edge of the knife. Peel the skin back from the underside of the dog.
3) Open the abdomen cavity by carefully cutting through the abdominal wall from the xiphoid cartilage along the last rib – avoid cutting into the intestines. Extend the incision so that you can view the abdominal organs in place. Note any abnormal contents in the peritoneal cavity, and take bacterial swabs if appropriate. Determine whether the organs are in their appropriate positions, but leave them in place at this point.
4) Cut through the diaphragm and remove the right half of the ribcage with the rib cutters or hacksaw. Examine the organs of the thorax, but leave them in place at this point, taking bacterial swabs if relevant.
5) Make cuts along the inside of the lower jaw, grasp and pull back the tongue. Cut the hyoid apparatus and draw back the tongue, oesophagus and trachea together to the level of the thoracic cavity. Remove the lungs and heart attached to the tongue, oesophagus and trachea, cutting attachments as you go. Sever the oesophagus and large blood vessels at the diaphragm. This group of organs is called the pluck – you must now examine it.
   i) Examine the tongue and oral cavity.
   ii) Dissect out the thyroid and parathyroids, and take tissue samples.
   iii) Palpate the oesophagus before opening it, looking especially under the mucosa in the part of the oesophagus that passes through the thorax for nodules caused by *Spirocerca lupi*, a nematode worm, which may sometimes grow large enough to obstruct the oesophagus.
   iv) Examine the thymus, and take tissue samples.
   v) There are also lymph nodes in the partition between the lungs, near the thymus: find one by palpation and take a tissue sample.
   vi) Palpate the lungs, and note their colour and texture. Take a sample from the dorsal part of one of the apical lobes.
   vii) Open the trachea and examine the contents. Extend the incision into the lung and through the bronchi.
   viii) Open the pericardium (the fibrous sac that encloses the heart) and look for any abnormalities in the fluid. Take swabs if appropriate.
   ix) Now examine the heart. There are several ways of doing this. The most important points are to examine all of the surfaces for haemorrhages, and all cut surfaces for pale patches. Look for lesions on the valves, and determine whether the size and shape of the heart is normal. Take samples from the septum between the ventricles, and from the papillary muscle (of the left ventricle).
6) Next, examine the organs of the abdomen. It is extremely important that you leave examining the intestines until last, because their contents are topologically outside the body and will, therefore, contaminate other tissues with bacteria from the outside world.
   i) Remove and examine the spleen. Make multiple cuts through the parenchyma and take tissue samples.
   ii) Remove and examine the liver. Make multiple cuts through the parenchyma and take tissue samples. Open up the gall bladder last, as the bile that it contains will damage the tissues. If the gall bladder appears thickened, sample it.
   iii) Locate both kidneys and adrenal glands and remove them together. Cut the kidneys sagitally,

peel off the capsule and examine all of the surfaces. Take tissue samples, ensuring that your samples include both the cortex and the medulla. Cut the adrenal glands in half, examine the cortex and the medulla, and take samples.

iv) Examine the bladder *in situ* before you open it. Have a vial ready to catch any urine, but only keep the sample if it appears abnormal. Take a tissue sample from the bladder.

v) Remove the stomach and the intestines, and cut all the attachments to separate the loops from one another. Take tissue samples from the pancreas and mesenteric lymph nodes. Then open the stomach and continue down the length of the gut to the rectum, taking tissue samples of the gut as you go. Bear in mind that the mucous membranes of the intestines are very easily damaged, so be careful, and never scrape the surfaces.

vi) Examine the reproductive tracts and take samples as necessary. Older domestic dogs often have tumours in the testicles which can be seen with the naked eye if you make repeated cuts through them.

7) It is always a good idea to look at the articulating surfaces of some of the joints. Open up the coxofemoral (hip) joints and look for abnormalities. The knees and the joints of the ankles and toes are also easy to look at.

8) Take samples of bone marrow by cracking one of the femurs near one end, and extracting a bit of the gelatinous marrow along with spicules of bone.

9) Perhaps the most crucial organ to sample in any dead wild dog is the brain, because many of the most important diseases that affect wild dog populations attack the brain.

i) Cut the skin and the neck muscles over the joint between the back of the skull and the first vertebra (the atlas).

ii) Bend the head forward to give access to the occipital foramen (the hole in the back of the skull).

iii) Push a drinking straw into the foramen and towards one of the eyes. In this way the rachidian bulb, the base of the cerebellum, the hippocampus and parts of the cortex are all sampled.

iv) Before drawing back the straw, pinch it between your fingers to ensure that the brain sample does not fall back out of the straw. Then carefully withdraw the straw.

v) If you are storing your brain samples in 10% formalin, squeeze the brain sample out of the straw and into the formalin solution. If you are using glycerin solution, plunge the straw into the solution and cut the straw into pieces as necessary, but do not remove the sample from the straw.

10) Do not forget to collect samples for genetic analysis from the remains of the carcass. We describe protocols for doing this in the next section.

It is usually possible to have samples examined by local veterinary laboratories. If this is not possible, Nancy Kock is willing to examine histological samples fixed in formalin. Her address is given at the end of this Appendix.

Collecting Samples for Genetic Analysis of Wild Dog Populations

As discussed in Chapter 2, the study of wild dog genetics can yield useful information for their conservation. For this reason, Dr Robert Wayne of the Canid Specialist Group is keen to receive tissue samples from wild dogs for genetic analysis. Samples can be collected from living wild dogs in the course of immobilization by researchers carrying out intensive field studies on wild dog populations. In addition, however, useful information can also be obtained from samples taken from wild dog carcasses found anywhere in Africa – road kills are a good source, and even samples from decomposed carcasses can be useful. Dr Wayne is especially keen to receive samples from West and central Africa, but will welcome any samples that are sent to him. His address is given at the end of this Appendix.

Collecting Samples from Anaesthetized Live Wild Dogs

Draw blood samples into vacutainer tubes containing EDTA. You can then follow one of four protocols which are, in order of preference:

1) Wrap whole blood samples in a paper towel, pack them into a styrofoam container with ice packs (the paper towel stops the blood itself from freezing), and send it by next-day air freight. Samples must be received by the lab within a week of collection, and, ideally, within 1–2 days. This is the best method, but is rarely practicable in tropical countries.

2) Centrifuge the blood once, and remove the plasma to just above the buffy coat (white cells). Place the plasma in a freezer vial. Remove the buffy coat, along with several millimetres of the red cell layer below the buffy coat, and place this in a second freezer vial – this sample should be about 1 ml. Finally, remove 1 ml of the red cell layer and place in a third freezer vial. Label all three vials carefully, and store them in a freezer. These samples can then be shipped packed in dry ice.
3) If a centrifuge is not available, keep whole blood samples cool and freeze them as soon as possible. Such samples can also be shipped packed in dry ice.
4) If neither a centrifuge nor refrigeration are available, it may still be possible to store samples using a preservative solution. This solution consists of 100 mm tris pH 8.0, 100 mm EDTA, plus 2% SDS (Sodium Dodecyl Sulphate). Dr Wayne is happy to provide this solution, or the reagents, but any University laboratory will have these reagents. Then mix 5–10 ml of whole blood with an equal volume of preservative solution. The blood can then be stored at room or low temperatures for several months.

Using a straw to take a brain sample for rabies diagnosis. [Photograph © K. Laurenson].

Collecting Samples from Wild Dog Carcasses

Any wild dog carcass can yield useful genetic samples, which are easy to collect. New techniques mean that researchers may be able to extract DNA from almost any tissue that was once living, even materials such as hair, skin and bone, and even if the tissue is several years old and dried or decayed. Please do not throw anything away if it might be important! If you find a wild dog carcass, do please try to collect samples from it. The best tissues are, in order of preference, heart, tongue, skeletal muscle, kidney and liver. Heart and skeletal muscle are the best, but any tissue will do. Collect a sample 1–2 cm across. If at all possible, place the sample in a ziplock bag and freeze it. For liquid nitrogen storage, wrap the samples in foil or place them in cryo-safe freezer vials. These samples can then be shipped packed in dry ice. However, if refrigeration is not available, chop up the sample into 1 mm pieces and place it in a container with the preservative solution described above, or 90% EtOH.

Please contact Dr Wayne before sending samples, to avoid problems with importing them into the U.S. Do not hesitate to contact him should you need supplies for collecting genetic samples from wild dogs.

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Appendix 4
Literature on *Lycaon pictus*

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Background

The following bibliography was started in 1985 and has grown from just over 100 references to well over 300 in that time. Many of these references added since the bibliography began are from before 1985, however there has been an exponential growth in publications concerning wild dogs, with over 140 publications since 1985. This increased scientific interest in the species cuts across scientific fields of study, with an increase in publications on subjects ecological, behavioural, and medical.

The bibliography is maintained in an EndNote2 (Niles Associates 1994) database by J.R. Ginsberg. Copies of the database can be provided in a number of formats (EndNote, REFER, ProCite, TABText). To obtain a copy of the database, please send a disk and return mailing label to Dr. Ginsberg. Alternatively, the database can be sent across the Internet as a text file or as a formatted AppleMacintosh Word 5.0 BinHex file at no cost. Please contact Dr. Ginsberg via the internet for a copy and indicate format reference.

While this bibliography aims to be comprehensive, we suspect that we have missed much, if not most, journalistic and 'grey' literature coverage of *Lycaon* (*e.g.* newspapers, newsletters, local conservation magazines, unpublished departmental reports). As with all sections of this Action Plan, we would be grateful to receive any additional information, or corrections to information published here. To maintain the database we would be grateful if authors of articles on *Lycaon* could send a copy of their papers to Dr. Ginsberg for inclusion in all electronic, and future printed, versions of the bibliography.

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