1 History and Natural History

The scientific name of the African wild dog (*Lycaon pictus*) means painted wolf, a reference to their patchwork coats of brown, black, and white, which Angier (1996) aptly called "a furred version of combat fatigues." Their shape follows the general canid body plan, with modifications accumulated over 3 million years of divergence from the rest of the dog family. For example, wild dogs have only four toes, having lost the fifth toe that persists as a vestigial dewclaw in most canids. Compared to wolves or coyotes, they are lean and tall, with outsized ears that complement their quiet vocalizations. Altogether, the wild dog is a unique and beautiful animal (Figure 1.1).

Wild dogs stand 65 to 75 cm at the shoulder, and weigh from 18 to 28 kilograms (Smithers 1983). Though they have been described as sexually monomorphic (Malcolm 1979; Girman et al. 1993), males are from 3–7 percent larger than females in linear measures of body size (Table 2.3). The original suggestion that wild dogs are monomorphic was probably based on measurements of body mass, which is extremely variable, because a hungry wild dog can consume 8–9 kg of meat (about ⅓ of its own weight).

Wild dogs have sparse hair, though there is variation among individuals. Part of this variation is related to age—yearlings have more hair than adult dogs, and old dogs can become almost hairless. Hair is particularly lost on the head, which begins to appear gray as the skin shows through. Captive wild dogs in cold climates also tend to have more hair. The color patterns of wild dogs are extraordinarily variable, and they appear to recognize one another individually at distances of 50 to 100 meters, suggesting that they make use of the information that coat variation provides. For example, when two packs encounter one another, dogs chase members of the other pack. The scene rapidly becomes chaotic, but we never saw dogs pursuing members of their own pack. Chases are often initiated from distances of 50 to 100 meters, so it seems likely that individuals are recognized by sight, though olfaction may also be involved.

Most of the variation in color is on the trunk and legs. Patterns on the face are relatively invariant, with a black muzzle shading to brown on the cheeks and forehead, a black line extending up the forehead, and blackish-brown on the backs of the ears. Some dogs have a brown teardrop on the muzzle below the eyes. There is never white on the head, and the posterior part of the head and the dorsal surface of the neck are consistently brown or yellow. Colors on the body and legs are unpredictable. There is often a white patch

Figure 1.1 African wild dogs are unusual canids, with a variegated coat, long legs, and large rounded ears.

just behind the forelegs, and dogs with little or no white elsewhere may have white on their forelegs or on the ventral surface of their neck or chest. The tail is almost always tricolored, with brown at the root, a black band, and a white tip. Some dogs have two black tail-bands, or black dots, or a black tip below the white, and a few have no white at all. Coat patterns are not bilaterally symmetrical. The asymmetry is great enough that photographs of a

dog's right side cannot be matched to photographs of its left side without additional information.

Wild dogs have only four toes on their forelegs, while members of the genus *Canis* have a vestigial fifth toe. The pads of the middle two toes are usually fused at the posterior edge, although in Selous we observed several individuals with unfused toes. The dental formula is 3 1 3 3 (upper), 3 1 4 3 (lower). The last lower molar is vestigial. The canine teeth are narrow for their length, in comparison to other carnivores (Van Valkenburgh 1989). In a set of 23 canids, felids, and hyenids, wild dogs had the largest premolars (relative to body mass) of all carnivores other than hyenas (Van Valkenburgh 1989). This suggests that wild dogs eat bone regularly, although they have a reputation for eating meat almost exclusively. In Selous, wild dogs often eat leg bones, ribs, vertebrae, and skulls. The droppings of wild dogs sometimes turn white with age due to a high proportion of digested bone, similar to the droppings of spotted hyenas.

1.1 Taxonomy and Phylogeny

Fossil evidence does not resolve the origin of African wild dogs. Undisputed *Lycaon* fossils come from the mid-Pleistocene (about 1 million years ago), and are very similar to modern wild dogs (Savage 1978). There is some debate over the geographic range for fossils of *Lycaon*. Kurten (1968) suggests that skull fragments from the genus are found in late Pleistocene sites in Europe, but Thenius (1972) and Malcolm (1979) believe that these fragments came from wolves (*Canis*). If so, *Lycaon* may always have been restricted to Africa. Within Africa, identification of the oldest *Lycaon* is complicated by the difficulty of distinguishing *Lycaon* fossils from those of an early Pleistocene wolf, *Canis africanus*. The current view of fossil evidence is that wild dogs arose 2–3 million years ago, in Africa (Savage & Russell 1983).

The first taxonomic description of a wild dog was by Temminck (1820), who considered it to be a type of hyena (and named it *Hyena picta*). Matthew (1930) placed wild dogs in a subfamily of the Canidae, the Simocyoninae, together with the dhole (*Cuon alpinus*) and the bush dog (*Speothos venaticus*). This group was proposed on the basis of the shape of the lower carnassial molar, which in these three species has a short blade and no basined cusp (Van Valkenburgh 1989). *Lycaon*, *Cuon*, and *Speothos* are not particularly similar in other respects. Bush dogs look nothing like dholes and wild dogs. Wild dogs and dholes are similar in morphology, behavior, and ecology (Johnsingh 1982; Venkataraman 1995), but Thenius (1954) described an Asian fossil lineage that leads from a jackal of the early Pleistocene to the dhole. Today, similar carnassial molars within the Simocyoninae are considered analogous rather than homologous, and the subfamily is no longer recognized (Wozencraft 1989).

The wild dog has the same number of chromosomes as the domestic dog (*Canis familiaris*) and similar neuroanatomy (Radinsky 1973). The myoglobins of wild and domestic dogs differ by one amino acid, compatible with a single-point mutation (Romero-Herrera et al. 1976). Girman et al. (1993) sequenced 736 base-pairs of the cytochrome *b* gene in wild dogs and other canids. These sequence data suggest that wild dogs are phylogenetically distinct from the other wolflike canids (wolves, jackals, and coyotes), justifying their current placement in a monotypic genus. Wild dogs showed 11.3–13.7% sequence divergence from the other species, and the single most parsimonious phylogenetic tree placed the divergence of the wild dog just basal to the radiation of the *Canis* clade.

Girman et al. (1993) also noted 1% sequence divergence within the species, and proposed that two geographically isolated subspecies occupy eastern and southern Africa. This suggestion was based on samples from three widely separated locations (Kruger, Hwange, and Serengeti National Parks, respectively located in South Africa, Zimbabwe, and Tanzania). With samples from more locations, and with the addition of data on nuclear microsatellite genotypes and mtDNA control region sequences, the picture has changed (Girman et al. 1997). There are no geographically distinct subspecies, though there is substantial genetic variation among populations. Parsimony analysis of mtDNA control region haplotypes suggests that there are two clades of wild dogs, but the clades are geographically mingled. Unique mtDNA haplotypes are found at the northern and southern extremes of the sampled range (Serengeti and Kruger), but the genetic affinities of intervening populations are not clearly related to geography. In Selous, for example, the predominant mtDNA haplotype is most similar to a haplotype found only in Kruger, but not in the intervening populations of Zimbabwe and Botswana (Figure 1.2). Nuclear microsatellites also reveal gene flow among populations, but the patterns from nuclear and mitochondrial DNA do not match. For example, dogs from the Selous and Serengeti ecosystems share microsatellite alleles that are not found elsewhere, but mtDNA places these populations in different clades (Girman & Wayne 1997). The data, though extensive, leave open some questions about genetic divergence among wild dog populations. In general, continentwide genetic patterns are consistent with a history of radiations north and south from the miombo woodland belt (extending from the latitude of southern Tanzania in the north, to the latitude of northern Zimbabwe and northern Botswana in the south).

1.2 Social Organization

Wild dogs live in permanent packs of 2 to 27 adults and yearlings, though packs of 5 to 15 adults and yearlings are most common. Excluding yearlings, packs held 6.6 ± 0.8 adults, taking the average for six populations (Table

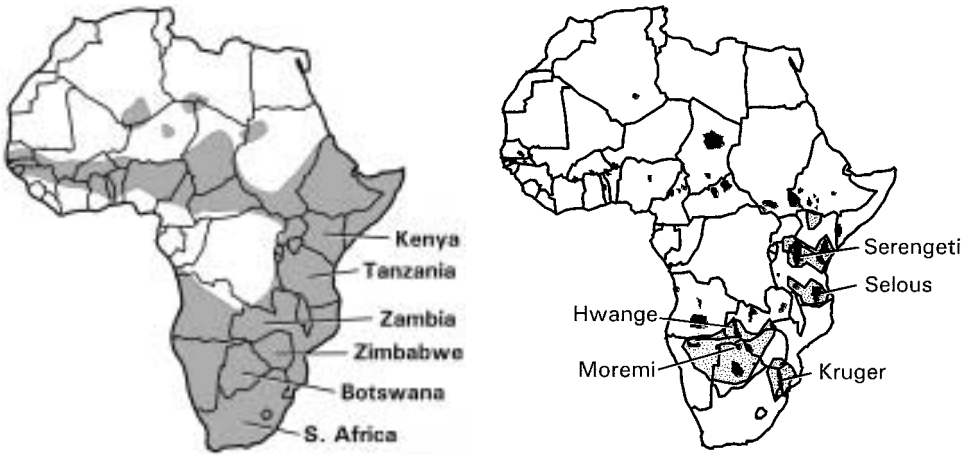

Figure 1.2 Geographic range of the wild dog. (a) Distribution based on sightings in the past 15 years with major populations noted. Dark shading indicates populations within protected areas, stippling indicates populations outside of protected areas. Based on data from Fanshawe et al. (1991) and Ginsberg (1994). (b) Historical distribution. based on data from Smithers (1983), Fanshawe et al. (1991), and Ginsberg (1993).

3.9). Mean pack size varies from 4–5 adults in Kruger N. P. and Masai Mara N.R. to 8–9 adults in Moremi and Selous (Reich 1981; Fuller et al. 1992a; McNutt 1996; Mills & Gorman 1997).

Within a pack, there is a clear dominance hierarchy among males, and another among females. The dominant female is usually the oldest in the pack, but old males often lose their rank to prime-aged males, so many packs include one or more old, formerly dominant males (Chapter 7). Only the dominant female is assured of breeding, though subordinate females do occasionally become pregnant. Reproduction is also largely monopolized by the alpha male, but the pups of a single litter can have more than one father, as in most carnivores (Girman et al. 1997; Chapter 8).

The simplest pack structure is a set of related males and a set of related females, with no genetic relationship (or a distant relationship) between the males and females (Frame et al. 1979; Malcolm & Marten 1982; Girman et al. 1997). This structure becomes more complicated if offspring born within the pack are recruited. Individuals of either sex may stay in their natal pack well beyond the age of maturity. When this occurs, some individuals are related to pack members of the opposite sex. Pack structure can also be complicated by immigration. Generally, successful immigrants evict same-sexed residents. These pack takeovers replace the lineage of one sex, but do not alter the basic structure of unrelated male and female lineages. Occasionally, unrelated immigrants join a pack without evicting all of the same-sexed residents, and this dilutes relatedness within that sex. In Selous, unfa-

miliar and apparently unrelated individuals of both sexes have immigrated successfully without evicting residents. In short, variations in the patterns of immigration, emigration, and breeder turnover may produce a complex web of genetic relatedness within packs. The coefficient of relatedness between packmates averages 0.25–0.35, but for a specific pair of individuals can range from 0 to 0.5 or above in the case of mild inbreeding (Frame et al. 1979; Reich 1981; Girman & Wayne 1997; Chapters 8, 10). Short-distance dispersal can also create genetic ties between neighboring packs (McNutt 1996; Girman et al. 1997).

Females are more likely than males to disperse in some populations, including Selous (Frame & Frame 1976; Chapter 8). In other populations, dispersal is not sex-biased, or is male-biased (Reich 1981; McNutt 1996). Emigrants of both sexes are likely to disperse as yearlings or two-year-olds, and usually disperse as a single-sex group of littermates, or as a group composed of two cohorts born one year apart (McNutt 1996; Chapter 8).

Many populations, including Selous, have an adult sex ratio biased in favor of males. For populations in which dispersal is female biased, the biased adult sex ratio may result from mortality during dispersal. In captivity, however, the sex ratio of a large sample of pups was also male-biased (Malcolm 1979), and pup sex ratios are male-biased in some wild populations (Fuller et al. 1992a). The sex ratio of pups is 1:1 for some populations, including Selous and Kruger (Maddock & Mills 1994; Chapter 7). Differences among populations in pup sex ratios might be related to rates of alpha female turnover, because primiparous females produce a high proportion of sons, while multiparous females produce a high proportion of daughters (Creel et al. 1998).

No unaided pair of wild dogs has been observed to raise pups, and in Selous no pack smaller than five adults raised pups to independence (Chapters 7, 10). Subordinates of both sexes help to raise the pack's young, which, as we mentioned, are normally produced by the dominant pair. The most important help comes in the form of food. For the first three months after they are born, pups cannot move quickly enough to follow a hunting pack, and are confined to a den. Most of the pack leaves to hunt twice a day, but one or more dogs remain behind as guards (Malcolm & Marten 1982). The alpha female normally guards the pups by herself, but in some cases another dog (usually a female) will remain with her. When the hunters return, both the pups and the mother solicit food, and dogs of both sexes (and all ages) respond by regurgitating meat (Malcolm & Marten 1982). Less often, dogs will carry a portion of a carcass to the den, usually a leg, to gnaw on.

In addition to feeding pups, nonbreeding helpers take part in protecting the pups, from lions, leopards, and spotted hyenas. When the pups begin moving with the pack at about three months of age, they are often bivouacked during a hunt—left behind and later recovered (as with wolves; Mech 1970). One or more dogs of either sex may remain with the pups

under these circumstances. If no adults remain with the bivouacked pups, dogs of either sex may go back to retrieve them and lead them to the kill. Pups are allowed to eat first at carcasses (though adults sometimes eat hastily until the pups arrive), followed by yearlings and then adults (Malcolm 1979; unpublished observations).

1.3 Ecology

Wild dogs rely almost exclusively on mammalian prey that they have killed for themselves. They hunt prey as small as hares (1–2 kg), and as large as adult zebra or juvenile buffalo and eland (about 200 kg), but concentrate on prey between 10 and 120 kg, with larger packs taking larger prey (Chapter 4). Impala and wildebeest are an important part of their diet in most ecosystems. The remainder of the diet is made up of species smaller than wildebeest that are locally abundant, such as greater kudu, warthogs, and duikers.

Wild dogs rarely scavenge, probably to avoid risky encounters with larger carnivores (Kruuk & Turner 1967; Creel & Creel 1996). Where the density of spotted hyenas is high or visibility is good, kleptoparasitism by hyenas at wild dog kills is common (Estes & Goddard 1967; Malcolm 1979; Fanshawe & Fitzgibbon 1993). Predation on wild dogs by lions has been seen in most populations, and lion predation is the most common known cause of death in some populations (Ginsberg et al. 1995; Mills & Gorman 1997). Altogether, interference competition with larger carnivores is an important force shaping the behavior, number, and distribution of wild dogs (Creel & Creel 1996; Mills & Gorman 1997).

1.4 Conservation Issues

Conflict with Humans

Like most large carnivores, the single most important conservation problem for wild dogs is conflict with an expanding human population. Wild dogs formerly had a wide distribution across sub-Saharan Africa, excepting only rainforest (Smithers 1983). Like many species, wild dogs have become patchily distributed as the human population has expanded (Figure 1.2). Wild dogs now live mainly in protected areas, and few areas are known to hold more than a hundred individuals (Fanshawe et al. 1991).

As a landscape is settled and moves into agricultural use, prey populations are depleted so that carnivore populations cannot maintain themselves. If carnivores persist, they are often killed to remove threats to livestock and people. It is occasionally suggested that wild dogs kill people (Leakey 1983), but we know of no documented cases. Wild dogs are wary of people

unless they have been habituated to tourism, and, in our experience, villagers near protected areas do not fear them. Wild dogs will kill unattended sheep and goats (Rasmussen 1996), but do not attack livestock that are attended by a shepherd. Wild dogs in our study area often moved out of the reserve through areas with scattered rice farms and small dirt tracks. In these areas, they skirted around people, and we never saw a direct interaction other than the dogs running from a person who had approached them without being detected.

Like some other carnivores, notably spotted hyenas, wild dogs were actively persecuted by wildlife managers for much of the 20th century. In general, wildlife managers shot them whenever possible. In Zimbabwe, 3,404 wild dogs were shot for "vermin control" between 1956 and 1975 (Childes 1988). In Namibia, 156 wild dogs were killed over 19 months in 1965–1966 (Anonymous 1967). Most game scouts in Selous recall shooting wild dogs up to the mid 1980s, and it is likely that hundreds were shot, though there are no accurate records. In 1977, the South African Red Data Book stated "[wild dogs are] still considered vermin and are shot on sight even on nature reserves. . . . [They are] likely to get little sympathy from farmers" (Skinner et al. 1977, p. 11).

Dislike of wild dogs can easily be seen in writings from the 1900s through the 1970s. Some examples:

> It will be an excellent day for African game and its preservation when means can be devised for [wild dogs'] complete extermination.—Maugham (1914)

> Although wild dogs, when present in large numbers, are a scourge to the game, killing, terrifying, and scattering it all over the country, they still find a useful place in Nature's economy, and the Kruger National Park would certainly be the better for a considerably larger number than exists.—Stevenson-Hamilton (1947)

> The wild dog is the only animal of the veldt that is always feared. The lion is not. Many a hunter has watched a full-fed lion walk in plain sight of a herd of antelopes.—Hubbard (1954)

> Wild dogs hunt in packs, killing wantonly far more than they need for food, and by methods of the utmost cruelty.—Bere (1956)
> In a later annotation, Bere noted, "This is now known to be nonsense."

> The rapacious appetite of these foul creatures is staggering.—Hunter (1960)

Though some of these authors had a grudging respect for the dogs (Stevenson-Hamilton's 1947 book is a good example), there were two broad reasons for their persecution. The major problem was with the dogs' method of killing prey. Because they are small relative to their prey, and do not have a

specialized killing bite, wild dogs kill their prey by pulling it to a halt and disemboweling it. Large prey can take a half-hour to die (though most die in minutes), and empathy for the prey led to antipathy toward the predator.

A second strike against the dogs was the perception that they disrupted prey populations more than other predators. Because wild dogs are cursorial hunters that rely on an open chase to catch their prey, it is certainly true that a wild dog hunt can set a large number of prey in motion, especially in open habitat. However, it is also true that calm returns quickly to an area in which the dogs have hunted. Wildebeest herds often resume grazing in plain sight of wild dogs feeding on a herdmate. Prey show little fear of wild dogs at rest, just as with other predators. Anyone who watches a pack of wild dogs for a day will undoubtedly see prey herds moving past or feeding nearby, aware of the dogs but unbothered. Zebra and wildebeest sometimes approach resting dogs and harass them. Some early naturalists must have known that relations between wild dogs and prey were much like those of other carnivores.

Active persecution decreased as field studies described the wild dogs' ecology and behavior. By the mid 1980s wild dogs were legally protected in the six nations that hold significant numbers (Botswana, Kenya, South Africa, Tanzania, Zambia, and Zimbabwe).

Road accidents kill wild dogs in areas that are transected or bordered by high-speed roads (Fanshawe et al. 1991; Drews 1995). The rain-rutted dirt tracks in Selous do not allow high-speed driving, and we recorded no road kills. By contrast, Hwange National Park borders a high-speed highway between two large cities, Bulawayo and Victoria Falls, and road kills were the most common known cause of death (Ginsberg et al. 1995). In Mikumi National Park (Tanzania), traffic on the Tanzania-Zambia highway is estimated to kill between 3% and 12% of the wild dog population annually (Drews 1995; Creel & Creel 1998).

Wire snares set for game species can unintentionally catch carnivores, and this is a surprisingly common cause of death in some places (Hofer et al. 1993). In Selous, snaring and poisoning by illegal game hunters caused 11% of 45 known-cause deaths. Snaring and shooting accounted for 18% of 57 deaths in Kruger (van Heerden et al. 1995), and 29% of 31 deaths in Hwange (Ginsberg et al. 1995). Though its force varies among populations, human impacts on wild dogs are substantial even in large protected areas.

Low Density within Protected Areas and Interspecific Competition with Larger Carnivores

If conflict with humans was the only problem that wild dogs faced, they would not be endangered. Many African nations have set aside large areas for wildlife, and these parks hold a great many lions, leopards, and hyenas. All three of these species pose a greater threat to livestock (and people) than

Table 1.1
Densities of wild dog populations throughout Africa (adults/1,000 km^2)

Population	*Density*	*Source*
Selous, Tanzania	38	Creel & Creel 1996
Moremi, Botswana	40	McNutt 1996
Hluhluwe, South Africa	33	Maddock 1993
Kruger, South Africa	16.7	Mills & Gorman 1997
Hwange, Zimbabwe	15	Childes 1988; Ginsberg 1993
Ngorongoro, Tanzania	0–26	Estes & Goddard 1967
Serengeti, Tanzania	0–15	Malcolm 1979; Burrows et al. 1994
Botswana/Namibia/Zambia	2–3[a]	Ginsberg 1993
Northern Kenya	2–3[a]	Ginsberg 1993

[a] Populations largely outside of protected areas.

wild dogs do, but they remain abundant and widespread. Although their ecological needs are similar, a fundamental difference between wild dogs and these larger carnivores is that wild dogs remain at low population density under all conditions. It seems likely that competition between wild dogs and larger carnivores explains this pattern (Creel & Creel 1996; Mills & Gorman 1997; Gorman et al. 1998). Frame (1985) described wild dog-hyena interactions in Serengeti: "Hyenas typically assembled behind wild dog packs as they hunted, and we recorded periods of weeks at a time in which hyenas stole almost all kills made by the dogs before the latter finished eating" (p. 3). Mills & Gorman (1997) showed that lions account for 43% of natural wild dog deaths in Kruger. Interference competition with lions and spotted hyenas also has a strong impact on cheetahs (Laurenson 1995; Durant 1998; cf. Crooks et al. 1998), and considerable data suggest that interspecific competition has strong effects on many carnivore populations (Palomares & Caro 1999; Creel et al. in press). We discuss interspecific competition in Chapter 11.

Analyses of carnivores' distributions (within ecosystems and among ecosystems) suggest that interspecific competition limits wild dogs in number and distribution (Creel & Creel 1996; Mills & Gorman 1997). Regardless of the cause, wild dog densities are spectacularly low (Table 1.1). The highest population density on record is from the northern Selous, with an average of 1 adult/26.0 km^2 over six years. A more typical density is 1 adult per 60–100 km^2. Even at maximal density, an area of 1,000 km^2 holds a population of only 40 adults, which is unlikely to be viable in the long run. As a result, small parks will play a small role in wild dog conservation, unless they are actively managed. In the end, conservation of wild dogs comes down to understanding the causes and consequences of their invariably low population densities.

Infectious Diseases

The literature on wild dogs often states that they are "particularly sensitive to disease" (Fanshawe et al. 1991, p. 140), or that infectious diseases have played "a main role in the numerical and distributional decline of African wild dogs" (Kat et al. 1995, p. 229). This idea is based almost exclusively on data from the Serengeti ecosystem. There, wild dogs declined to local extinction while experiencing recurrent outbreaks of rabies and possibly canine distemper (Schaller 1972; Malcolm 1979; Gascoyne et al. 1993; Alexander & Appel 1994). The data from Serengeti clearly shows that viral diseases can cause substantial mortality in wild dogs, and can contribute to a local extinction.

However, the Serengeti population was probably vulnerable to extinction for other reasons. First, the population was small enough (less than 30 dogs) to be vulnerable to a knockout blow, regardless of the cause (Ginsberg et al. 1995). Second, the Serengeti dogs faced intense competition from larger carnivores (Frame & Frame 1981). Finally, Serengeti held a diverse suite of carnivores, many at high densities, that were known to carry rabies virus and/or canine distemper virus (Maas 1993; Alexander & Appel 1994; Alexander et al. 1994, 1995; Roelke-Parker et al. 1996). Under these conditions, it is expected that spillover transmission from high-density species will endanger species living at lower density (Grenfell & Dobson 1995).

For these reasons, it might not be justified to generalize the conclusion that wild dogs are especially vulnerable to diseases. Little is known about the regulatory role of diseases in other wild dog populations, but current data suggest that disease is not a major factor for all populations. Several dogs have died of infection with the bacterium *Bacillus anthracis*, in the Luangwa valley, Kruger N. P. and Selous (Turnbull et al. 1991; Creel et al. 1995; van Heerden et al. 1995). In Kruger and Selous there have not been detectable disease-related population declines over periods of 22 and 6 years, respectively (Reich 1981; van Heerden et al. 1995; Creel et al. 1997c). Combining demography, serology, post-mortems and veterinary examinations, van Heerden et al. (1995) concluded that "disease could not be incriminated as an important cause of death" (p. 18) in Kruger. In summary, current data are compatible with a wide range of views on the role of infectious disease in wild dog population dynamics. We discuss infectious diseases in Chapter 12.

1.5 Issues Addressed by the Research and Organization of the Book

This book moves between results that are relevant to conservation and results that are relevant to behavioral ecology. Most chapters are more closely aligned to one of these fields than the other, but some data are relevant to

both fields. For example, we use data on hunting success to address the evolution of cooperative hunting, but also test whether hunting success is a limiting factor for some populations. For this reason, some results appear in different forms in more than one chapter, with discussions aimed at different goals.

Chapter 2 gives a description of the Selous Game Reserve, the study site and population, and our general methods. We give narrower descriptions of some specific methods in other chapters for the sake of coherence. In Chapter 3 we discuss habitat selection, determinants of home range size, and overlap of home ranges. These analyses are relevant to conservation, because (all else equal) large home ranges lead to low population density. Wild dogs can have home ranges larger than 1,000 km^2, among the largest reported for carnivores (Frame et al. 1979; Mills & Gorman 1997). Understanding why wild dog packs require large ranges is central to understanding why they are endangered.

Chapters 4–6 deal with hunting. In Chapter 4 we present basic data from wild dog hunts in Selous and analyze the energetic costs and benefits of hunting in different pack sizes. A prominent question in behavioral ecology has been whether cooperative hunting favors life in groups or is simply an unselected consequence of life in groups. Among carnivores, this question has been addressed by studies of lions (Schaller 1972; Packer et al. 1990; Stander 1992), spotted hyenas (Kruuk 1972; Mills 1990; Holekamp et al. 1997), cheetahs (Caro 1994), wolves (Schmidt & Mech 1997), and wild dogs (Estes & Goddard 1967; Fanshawe & Fitzgibbon 1993; Fuller et al. 1995; Creel & Creel 1995b; Creel 2001). The question has also been studied in other taxa, notably chimpanzees (Boesch 1994), Harris's hawk (Bednarz 1988), and killer whales (Baird & Dill 1996). Conclusions have varied, depending on the species studied and on the currency used to measure foraging success (Packer & Caro 1997; Creel 1997). Some authors argue that cooperative hunting has not been an important force in the evolution of sociality in carnivores (Packer et al. 1990; Caro 1994), but for wild dogs, it is clear that foraging success depends on group size. We feel that this important issue remains unresolved for carnivores in general (Creel 2001).

In Chapter 5 we focus on prey selection. We use our hunting data to measure the profitability of each prey species, then test whether the proportion of each prey species in wild dogs' diet is correlated to its profitability. The diet might also be determined by the availability of prey types, rather than their profitability alone. Because we have data on the abundance of each prey species, encounter rates between dogs and prey, and measures of profitability, we consider availability and profitability together.

Chapter 6 digresses to take the perspective of the prey. In particular, we examine how herd size affects the vulnerability of impala and wildebeest to wild dogs. Grouping could reduce vulnerability to predation in several ways (Caro & Fitzgibbon 1992; Fitzgibbon & Lazarus 1995; Lima 1995a, 1995b).

Most studies of group size and vulnerability to predation have involved stalking predators, focusing on the benefit of detecting predators before they can come close enough to make a kill (fish: Krause & Godin 1995; birds: Lima & Zollner 1996; mammals: Fitzgibbon 1990). However, stalkers and coursers hunt in very different ways, and our analyses suggest that many mechanisms that reduce vulnerability to stalking predators do not reduce vulnerability to coursing predators.

Chapters 7–10 describe social organization and behavior. In Chapter 7 we present basic data on demography and population dynamics, including the following topics: (1) life tables, (2) the effects of social rank on survival and reproduction, (3) the effectiveness of helpers, (4) sex-ratio evolution, (5) population dynamics, and (6) effective population size (Wright 1969; Nunney & Elam 1994).

Chapter 8 describes patterns of immigration and emigration. Early studies showed that female wild dogs were the primary dispersers in Serengeti (Frame & Frame 1976). Female-biased dispersal is rare among carnivores (Waser 1996) and among mammals in general (Chepko-Sade & Halpin 1987). Even among wild dogs, female-biased dispersal may not be the general rule, as McNutt (1996) found that all dogs of both sexes dispersed in Moremi. In Selous, females are substantially more likely to disperse than males. Chapter 8 describes patterns of dispersal, and discusses the effect of dispersal on genetic relationships within and among packs. We compare predicted patterns of relatedness to data from mitochondrial DNA and microsatellites (Girman et al. 1997).

Dominant wild dogs do not disperse unless evicted by immigrants, but subordinates of both sexes commonly leave their pack. This suggests that escape from reproductive suppression is a driving force behind dispersal (Waser 1996). In Chapter 9, we discuss the behavioral and endocrine mechanisms that prevent reproduction in social subordinates, addressing six questions: (1) What is the effect of social subordination on mating rates? (2) To what degree is reproductive suppression of subordinates due to aggression from dominants? (3) Is reproductive suppression of subordinates strictly a behavioral process, or is it physiologically mediated by depressed sex-steroid levels? (4) Is suppression of subordinates mediated by stress? (5) How do mechanisms of suppression differ between males and females? (6) How do behavioral and endocrine patterns relate to wild dogs' social organization? We then take a comparative perspective, asking how the physiological and behavioral correlates of reproductive suppression differ among social carnivores, and among cooperative breeders in general.

In Chapter 10 we examine reproductive suppression from an evolutionary standpoint, asking why social subordinates tolerate reproductive suppression and help to raise the young of others. A gargantuan literature addresses this question from a theoretical perspective (Hamilton 1964; Brown 1987) or with empirical data from birds (Brown 1987; Stacey & Koenig 1990), in-

sects (Bourke & Franks 1995), and, to a lesser extent, mammals (Solomon & French 1997). Rather than attempting to review this subject (a book in itself), we take a narrow focus and apply a quantitative model for the evolution of reproductive suppression (Vehrencamp 1983). We compare patterns predicted by the model to data on mating rates and reproductive physiology, and to direct data on maternity and paternity.

Chapters 11–13 turn to conservation, addressing the issues discussed earlier in this chapter. In Chapter 11 we examine interspecific competition between wild dogs and larger carnivores. Across ecosystems, the density of wild dogs is negatively correlated with the densities of lions and spotted hyenas, and considerable data suggest that interference competition and predation cause this correlation. In Chapter 12, we discuss the effects of infectious diseases. In Chapter 13, we provide an overview of six factors that may limit wild dogs in number or distribution: intraspecific competition, interspecific competition, prey limitation, disease, genetic problems, and human activities. We then use simulations to model the probability of local extinction in Selous.