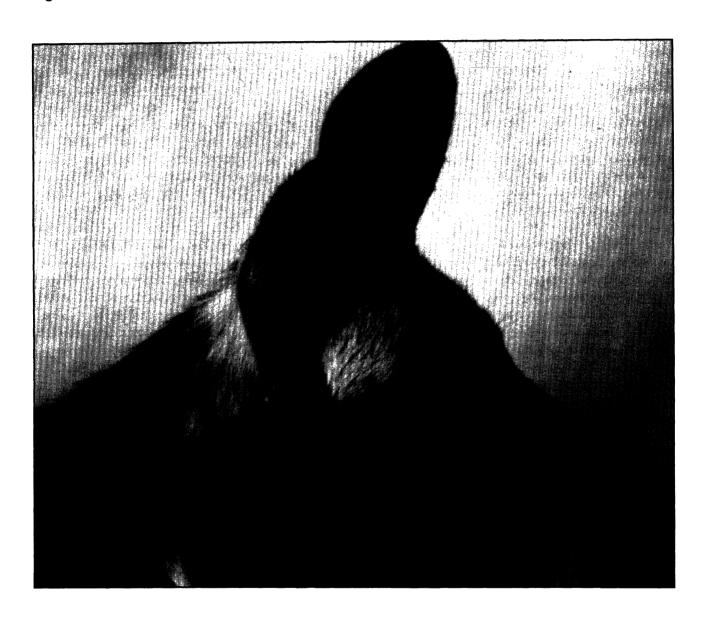
Endangered Species UPDATE Including a Reprint of the latest USFWS Endangered Species Technical Bulletin

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Conservation Biology and Status of the African wild dog, Lycaon pictus

by

Joshua R. Ginsberg

The African wild dog (Lycaon pictus) was once found from Senegal to South Africa. Inhabiting a wide range of ecosystems, from deserts to the alpine meadows of Mount Kilimanjaro (reviewed in Fanshawe et al. 1991; Ginsberg and Macdonald 1990), Lycaon was probably found in all environments except true rainforests. Well over a hundred thousand wild dogs, or five times that many, may have lived in Africa at the turn of the century. By the 1970's, however, many field biologists began to suspect that the species was in rapid decline.

Worried about the decline in wild dog numbers, two scientists who have studied wild dogs in the Serengeti, John Fanshawe and Lory Frame, conducted a postal survey of researchers and managers working in Africa in an attempt to find out how many wild dogs remained in each range state. Their survey (summarized by Ginsberg and Macdonald 1990) showed that wild dogs have disappeared, or have been reduced to relict populations of fewer than 50 individuals, in 19 of 34 countries where they once lived. Frame and Fanshawe suggested that fewer than 5000 wild dogs remain in Africa, and of those individuals, fewer than 3000 are found in protected areas. A significant decline in numbers has even been evidenced in countries where wild dog populations are relatively large. For example, populations in Zimbabwe (Childes 1988) and Namibia (Hines 1990), have halved in a decade. In response to these declines, the wild dog was listed as endangered by the USFWS in 1984. In 1990 the IUCN revised its assessment of the status of the wild dog from Vulnerable to Endangered, reflecting an increased threat (Ginsberg and Macdonald 1990).

Causes of Decline

A number of explanations and hypotheses have been invoked to explain the pan-African decline in Lycaon numbers (Fanshawe et al. 1991). Wild dogs occur at low densities relative to other large predators. For example, while lions frequently occur at densities of one lion per five square kilometers (Schaller 1972), wild dog densities average one dog per 70 to 100 square kilometers (Fuller et al. 1992a). In addition, because wild dogs are highly social animals that hunt and breed in extended family packs of up to 50 individuals, each pack encompasses an extremely large home range (150 to 2000 square kilometers, Fuller et al. 1992). As a result, wild dogs are probably particularly sensitive to habitat fragmentation and habitat loss (East 1981).

Wild dogs naturally have high rates of mortality and natality and appear to have significant intra- and interpopulation variation in demographic measures (Burrows 1994; Fuller et al. 1992). Because of their large litter sizes (up to 16 pups per pack), populations can grow rapidly in years of low adult mortality and high juvenile survivorship. If, however, high adult death rates and low juvenile survivorship coincide, populations can plummet. Computer modeling of Lycaon populations (Ginsberg and Mace, in prep) suggests that even wild dog populations as large as 300 individuals have a distinct probability of going extinct in under 200 years. However, if several populations of up to 300 animals are linked, the probability of extinction drops dramatically. Political initiatives to keep corridors open, such as those found between northern Botswana, western Zimbabwe, eastern Namibia, and southern Zambia are critical, although not necessarily sufficient, if this species is to survive.

Loss of habitat and direct persecution by humans were probably responsible for initial declines and local extinctions. More recently, other factors which may have led to local or regional declines in numbers include competition with other carnivores (Frame 1986; Sinclair, in press); direct conflict with humans (Childes 1988; Hines 1990; Malcolm 1979); disease (Creel et al., in press; Burrows et al. 1994; Gascoyne et al. 1993; Alexander et al. 1993; Schaller 1972; Pienaar 1969); intervention by scientists (Burrows et al. 1994; Burrows 1992, but see Creel 1992 and Macdonald et al. 1992); and road kills (Ginsberg and Cole, in press). A comparison of data on causes of mortality in five different ecosystems indicated that at any time in an ecosystem, and through time in different ecosystems, causes and patterns of mortality differ (Ginsberg et al., in press; Burrows, in press). Studies in Botswana and in Kruger National Park suggest that inter- and intraspecific interactions are responsible for most adult mortality. In Zimbabwe's Hwange National Park, mortality associated with human activity (road kills, snaring) dominates. In the Serengeti/Mara over the past two decades, both interspecific competition (Sinclair in press; Frame 1986; Malcolm 1979) and disease appear to have been responsible for a large proportion of adult mortality (Burrows et al. 1994; Malcolm 1979; Schaller 1972).

While disease may have been responsible for the local disappearance of wild dogs in the Serengeti plains, epidemic disease does not always have catastrophic effects. In the Selous Game Reserve in Tanzania, a closely monitored outbreak of infectious anthrax had minor effects. In a pack of 42 individuals, all adults and yearlings survived and only four of 24 puppies succumbed to the disease (Creel et al., in press). In fact, automobiles had a greater effect

than disease on wild dog population numbers in the Selous Reserve. In Mikumi National Park, located in a small section of the Reserve, 11 wild dogs were killed by automobiles in one year alone (Creel and Creel 1994).

Effects of Intervention

The need for intensive management of fragmented populations is a reality facing not just wild dogs but many species of endangered animals. As populations become increasingly fragmented, intensive management, and thus intervention, will become more common (see papers in Olney et al. 1994). Furthermore, many of the data required for conservation planning and management can only be collected with some level of intervention — translocation, disease screening and genetic studies, for instance, require anesthesia and/or collection of tissue samples. For many species — from large, highly mobile ones to those that are small, cryptic and nocturnal — fitting radio transmitters to study ecology and mortality of animals may be the only way in which accurate longterm data can be collected (Kenward 1987). Intervention, however, has potential costs to survivorship, reproduction, or persistence of a population (e.g., Berger and Cunningham 1994; Pietz et al. 1993; Cuthill 1991; Hall and Harwood 1990). Inevitably, costs of intervention must be balanced against measured benefits.

In studies of wild dogs, intervention has been demonstrably beneficial. Study of wild dog ecology in all but open plains habitats would be impossible without the use of radio telemetry (Ginsberg et al., in press). Use of telemetry has allowed scientists to gain a better understanding of demography, feeding ecology, range use, recruitment, and causes of mortality. Sample collection and long-term monitoring also has shown that disease appears to be relatively common in wild dogs: distemper, parvo-virus, Babesia, and canine ehrlichiosis have been isolated or observed in sera screening in captive and reintroduced animals (Van Heerden 1979, 1980, et al. 1989; Alexander et al. 1993). Anthrax has been diagnosed in

both the Selous Reserve in Tanzania (Creel et al., in press) and the Luangwa Valley in Zambia (Ginsberg and Macdonald 1990).

Rabies was confirmed from analysis of samples taken from a single wild dog carcass in the Serengeti (Gascoyne et al. 1993) and two carcasses in the Masai Mara (Richardson et al., in review). Individuals in each population were vaccinated in an attempt to provide protection against the disease. However, by 1992 all wild dogs in the study areas in the Serengeti and Masai Mara had died or disappeared (Gascoyne et al. 1993; Burrows et al. 1994). Disappearance of the plains subpopulation of wild dogs in the Serengeti ended a 20 year decline in which populations dropped from 77 adults and yearlings in 1970 to 26 adults and yearlings in 1977, and then fluctuated between 12 and 31 individuals from 1976 to 1991 (Burrows, in press, et al. 1994).

Burrows (1992) suggested that handling of the wild dogs to fit radio collars and vaccinating the animals with projectile darts stressed the dogs, activated latent disease infections (probably rabies), and caused the early death of dogs in these packs. This hypothesis has been questioned on theoretical grounds by Creel (1992), who questioned the evidence that handling induced long-term stress, and on epidemiological and virological grounds by Macdonald et al. (1992). In a recently published paper, however, data confirm that patterns of wild dog mortality in the Serengeti are correlated with changes in research practice. The link between correlation and causation, however, is uncertain. While changes in mortality are correlated with changes in research practices, the data are also consistent with the explanation that a disease, either rabies or distemper, could have wiped out the study population even if there had been no handling or vaccination (Burrows et al. 1994). In the Serengeti during the period in question (1985 to 1992) available data are insufficient for determining whether disease induced by handling was responsible for the decline in population num-

Analysis of data from five ecosystems comparing the annual survival of

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Cover: African wild dog (Lycaon pictus) Photo by Joshua R. Ginsberg.

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135 animals that had been handled with the survival of 305 dogs that had not been handled found no difference in survival between the two groups (Ginsberg et al., in press). In the Kruger National Park, where over 55% of the adults and yearlings studied were handled, population numbers have doubled since handling began. Disease prevalence was not investigated in all ecosystems, but the study in the Selous coincided with an outbreak of anthrax in that population of wild dogs (Creel et al., in press). If an interaction between handling and latent disease is responsible for early mortality of wild dogs in the Serengeti, a complex interaction of factors such as nutrition, disease prevalence and virulence, and handling must have existed in the Serengeti but not in other ecosystems.

Trends in Recent Research

Until the late 1980s, our knowledge of African wild dog biology was primarily derived from a study conducted from 1967 to 1978 in the open plains of the Serengeti National Park, Tanzania, and a 1975-1978 study conducted in the Kruger National Park, South Africa (Reich 1981). Much of the Kruger study and the majority of the early work in the Serengeti focused on the wild dog's complex social organization. From the point of view of conservation planning, these studies collected insufficient information on ecological and demographic aspects of the dog's biology.

Beginning in the late 1980s, many Lycaon research and conservation projects were initiated. These research efforts have resulted in numerous collaborative studies of the genetics, behavior and ecology of wild dogs in several ecosystems (e.g., Fuller et al. 1992a, b; Girman et al. 1993; Ginsberg et al., in press). Of particular interest has been an expansion of research in woodland and bushland habitats. The Serengeti-Masai Mara ecosystem, in particular the Serengeti shortgrass plains, is not representative of African ecosystems. Much of Africa, and the majority of African protected areas, is made up of a mosaic of closed woodlands, bushlands and thickets (White 1983). While studies on the treeless plains of the Serengeti might be applicable to conservation and research efforts elsewhere, evidence is accumulating that wild dogs living and hunting in closed habitats (bushland, woodland) behave differently from those living in the open plains.

Comparison of hunting techniques employed by wild dogs in open and closed environments provides a good illustration of these behavioral differences. Early research on the open plains of the Serengeti/Mara (Kruuk and Turner 1967; Estes and Goddard 1967; Malcolm and Van Lawick 1975) showed that wild dogs often chase their prey at high speed for long distances, while in the relatively dense bush of Kruger National Park, South Africa (Reich 1981), wild dogs chased their prey for shorter distances. Furthermore, while wild dogs can approach prey from any direction in open habitats, dogs in denser vegetation will use roads and elephant paths to hunt. Recent studies have yielded similar differences in hunting techniques in the two habitats.

Habitat differences also affect the levels of competition kleptoparasitism (the stealing of food by other predators) experienced by wild dogs in different environments. In open plains of the Serengeti, hyenas were present at over 85% of all wild dog kills, with parasitism rates a function of the relative ratio of hyena and wild dog group sizes (Fanshawe and FitzGibbon 1993). In the Masai Mara, where studies were conducted in a mosaic of grasslands, open woodland, and open bushland, hyenas only parasitized 41% of all kills (Fuller and Kat 1990). In habitats with denser bush such as Kruger and Hwange National Parks and Selous Game Reserve, hyenas parasitize a very small percentage (10-16%) of wild dog kills and appear to have no effect on consumption of prey (Mills and Biggs 1993; Creel and Creel 1994; Ginsberg unpublished).

These behavioral and ecological differences illustrate the need for wild dog studies to be conducted in a variety of habitats. Information obtained from such studies will better enable researchers and managers to successfully conserve and protect the African wild dog.

Genetics, Taxonomy, and Captive Breeding

Decline in population numbers, reduction of the species range, and fragmentation of remaining populations should all take their toll on Lycaon genetic variability. Yet effects of habitat loss and fragmentation on wild dog genetic variability appear to have been small. In a collaborative study of genetic samples collected from wild dogs across eastern and southern Africa, and from wild dogs housed in zoos, Girman et al. (1993) found no significant differences in variability between eastern and southern African wild dogs, or between wild dogs and other large canid species. Because wild dogs have not been studied in West Africa, we still know nothing about the genetic/evolutionary history of Lycaon in this region. Southern and eastern African wild dog populations show approximately 1% divergence in mtDNA sequence and each population has three distinct mtDNA genotypes. Physically, southern wild dogs are 30% larger than East African wild dogs; cranial morphological measures also show a separation between the two subpopulations. While these data indicate that the two populations are distinct subspecies, recent data (Girman, pers com.) show that wild dogs in the Selous Game Preserve in southern Tanzania have both east and southern African mtDNA genotypes.

The greatest potential need for wild dog reintroduction is in East and, if habitat exists, West Africa. In these areas, Lycaon populations were either actively exterminated (e.g., Uganda) or fragmented to the point of disappearance. Logically, one should attempt reintroduction of wild dogs in large national parks of more than 5,000 square kilometers where they have gone extinct because of past persecution. Only in these vast areas of wilderness can a reintroduced population have any hope of long-term survival. Potential locations for wild dog reintroduction in eastern Africa include Virunga and Garamba National Parks in Zaire, Akagera National Park in Rwanda, and Murchison Falls National Park in Uganda. The question of what will be used as a source

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population for reintroduction attempts remains. Outside the Selous and Rungwa-Ruaha Game Reserves in Tanzania, few likely source populations exist in eastern Africa. Furthermore, Girman et al.'s 1993 study confirmed, with one exception, studbook data suggesting that all wild dogs in captivity are of southern Africa origin. The mesh of need and availability could not be worse.

The history of reestablishing wild dog populations is not encouraging. A reintroduction program in South Africa's Umfolozi/Hluhluwe Game Reserve, sponsored by the Natal Parks Board, has used mainly captive-bred animals to attempt to establish a population in Natal where wild dogs were pushed to extinction by the turn of the century (Skinner and Smithers 1990). This project has met with limited success in establishing a small population of wild dogs. In contrast, two attempts to reintroduce wild dogs to Etosha National Park in Namibia failed. The first attempt was thwarted before it began when the captive-bred animals contracted a vaccineinduced distemper. The second attempt failed because the dogs did not successfully avoid other predators — each reintroduced wild dog was killed by lions (L. Sheepers, pers com.).

Reintroductions of captive-bred animals, particularly social carnivores (Yalden 1993), are technically difficult. While translocation may be simpler than reintroductions (Griffith et al. 1989), finding a source population for animals in decline across a subspecies distribution may be impractical. Yet, because extinction of individual populations of wild dogs is likely, linking populations through wildlife corridors or translocation will be the only strategies that will ensure long-term survival.

Conclusion

Unlike many endangered, threatened, and rare species, wild dogs are receiving attention while their population numbers are in the thousands, not hundreds. Nonetheless, in the next 20 years wild dogs will probably be restricted to large areas of relatively undisturbed habitat. As human populations grow and areas of suitable habitat

decline, national parks and protected areas will offer the only refuge for the African wild dog. While a dog may be man's best friend, the wild dog's future survival will depend on the stewardship of its worst enemy - humans.

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Resilience and Resistance: Relevance for Conservation Biology and Management

Resilience and resistance, two measures of ecological stability, have wide applications in conservation biology, yet their relevance for conservation management may differ. Resilience measures the rate of return of an ecological variable in response to a onetime disturbance. Resistance measures the change in an ecological variable in response to a permanent disturbance. Natural communities are often limited in their ability to recover from a single disturbance (e.g., Kuss and Hall 1991), and are even further limited in their ability to recover from repeated disturbances. The applicability of resilience as a working measure of stability is constrained by the long recovery time of many communities and the increasing probability of human-caused disturbance. Studying and managing for long-term ecological change (i.e., resistance) more accurately reflects the realities faced by many disturbed communities.

Two Measures of Ecological Stability

Resilience measures the rate of return of an environmental variable following a disturbance (Pimm 1984). An example of resilience is the rate at which a deer population regains its former numbers after a onetime hunting season. Many natural communities recover slowly from disturbance. Five years after low-level trampling by hikers, the ground flora at the Hubbard Brook Experimental Forest in New Hampshire had still not recovered (Kuss and Hall 1991). Various other communities have similarly low levels of resilience (e.g., Felix et al. 1992).

Resistance, another measure of ecological stability, gauges the effect of a permanent change in one variable on another variable, or variables, in a system (Pimm 1991). An example of resistance is the response of a deer population to permanent hunting pressure. Savidge (1987) measured the resistance of Guam's avifauna to an introduced snake. Within

less than thirty years, seven of twentyfive bird species were either extinct or so rare as to go undetected.

The Effect of Interconnectedness

Species live together as interconnected parts of a complex natural machinery (Ehrlich 1986). Depending on degree of connectivity, the rate at which communities recover from disturbance is limited by the recovery rate of their less resilient species (Pimm 1991). Golladay et al. (1992) found that streams in clearcut forest areas were more susceptible to nutrient loading during storms than streams in intact forest areas. Soil and nutrients continued to enter disturbed streams after undisturbed streams had recovered. The resilience of the streams, and thus that of the forest/stream complex, was limited by the slow recovery rate of the forest.

Areas of interest to conservation biologists are likely to be disturbed repeatedly. Fuls and Bosch (1991) found that, even after grazing had stopped altogether, patches of a semi-arid grassland that were in poor condition due to past periodic grazing expanded during drought. The drought resilience of the overgrazed patches was compromised as a result of the past grazing disturbances. The inability of a population or community to return to equilibrium between successive disturbances recalls another measure of ecological stability: resistance.

Functional Interrelationship and Probability

Resilience and resistance are functionally related. Consider "A" as the variable being disturbed, and "B" as the variable causing the disturbance. Resilience, then, is the rate at which A returns to equilibrium following a *one-time* change in B. Resistance is the

by William Burnside

extent to which A changes in response to a *permanent* change in B. Variable A may take years to recover after disturbance by B (e.g., Felix et al. 1992). This delay increases the probability that B will act again before A has the opportunity to rebound to equilibrium. Indeed, Fuls and Bosch (1991) describe a situation in which A is unable to achieve its prior equilibrium state even though B disturbs it only occasionally. Actual communities are subject to different levels of disturbance, ranging from none to a constant stream.

Several studies have examined the effects of repeated disturbances on communities. Folsier (1986) found the vegetation in a northern Saharan watershed in a highly unstable state partly due to stress from human-set fires. The frequent fire disturbances upset the balance of a system already stressed from drought. Fuls and Bosch (1991) found that long-termpatch overgrazing stressed vegetation "beyond a threshold of drought resilience." Even occasional disturbances can effectively alter a community's "equilibrium."

Pristine systems are subject to occasional, periodic, or even frequent natural disturbances. However, humans are disturbing areas with increasing frequency and intensity, decreasing the probability that many communities will recover between perturbations. Furthermore, conservationists are concerned with the subset of human-affected populations and areas with the highest probability of effectively undergoing permanent ecological change. Long recovery time, together with the increasing probability of disturbance, combine to limit the relevance of resilience as a working measure of ecological stability. Resistance, which measures the response to a permanent change, represents an increasingly accurate measure of stability.

Conclusion

Effectively permanent change is increasingly the rule rather than the exception for natural communities. Unfortunately, conservation management is a triage discipline, whose adherents lack the resources to save all imperiled species and areas. Managers and biologists must therefore concentrate their efforts as efficiently as possible. Their constraints necessitate weighing the relative merit of these different conceptual approaches to ecological stability. While resilience and resistance are important concepts for research, stability as measured by resistance has more immediate relevance for actual conservation and management efforts.

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Bulletin Board

Biodiversity Center Listserver

The Smithsonian Institute, in cooperation with the University of California at Berkely, is pleased to announce the creation of a new listserver to discuss information management for the proposed U.S. National Biodiversity Information Center. The listserver, Biodicen-L, may be of interest to those desiring biodiversity information sources and tools. New subscribers from any sector are welcome. Readers can find a short description of the Center concept in the Smithsonian National Museum of Natural History's gopher (nmnhgoph.si.edu) under Biodiversity Programs.

The draft mission for the Center is to function as a clearinghouse to 1) provide awareness of available biodiversity data and information; 2) enable access to such data and information; and 3) facilitate the use and exchange of, and collaborative discussions about, the information in order to meet the needs of public and private customers for conservation, sustainable use, education, and scientific inquiry.

To subscribe, send: "subscribe biodicen-L < firstname > < lastname > "to "listserv@ucjeps.berkely.edu".

Ecosystem Management Study: call for all nationwide projects

The University of Michigan's School of Natural Resources and Environment is sponsoring an Ecosystem Management Project which will inventory ongoing ecosystem management efforts nationwide. The goal of this project is to assemble a comprehensive source of information on ecosystem management efforts, to be used as a tool for academics, natural resource managers, and decision-makers. This 'catalog' is designed to aid in the development of new ecosystem management applications and the refinement of existing ones. The project is currently identifying efforts which contain at least one of the following two attributes: efforts which extend land management units beyond property or political boundaries to incorporate ecological boundaries, or efforts revealing a shift in management priorities away from a single resource or species emphasis to consideration of ecosystem processes. The project is actively soliciting information on existing or potential ecosystem management efforts for inclusion in the catalog. To help in this effort, please contact the Ecosystem Management Project at (313) 936-3891 (Tel) or (313) 936-2195 (Fax).

Change of Editor

After serving as editor of the UP-DATE for the past year, Lynn Gooch has completed her graduate work and left Ann Arbor. Our loss is The Nature Conservancy's gain, as Lynn accepted a position with TNC's office in Portland, Oregon. Her dedication and expertise will be missed here at the UPDATE and throughout the School of Natural Resources and Environment as well.

Soon after I took over the position of editor, a long time UPDATE reader remarked to me that "the UPDATE keeps getting better and better." That comment is a tribute to Lynn and all the other editors who have come before me. At the same time it presents me with a challenge to keep the UPDATE at its present level of quality while seeking to improve wherever possible. I look forward to that challenge, and I hope to hear from UPDATE readers with suggestions or ideas. Please call or write to the address and phone number given on the second page, or send E-mail to <jfwatson@umich.edu>. I look forward to hearing from you.

Announcements for the Bulletin Board are welcomed. Some items from the Bulletin Board have been provided by Jane Villa-Lobos, Smithsonian Institution.

Endangered SpeciesUPDATE

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