Abstract: The management of large predators remains a controversial and highly emotional issue all over the world. This can largely be ascribed to a lack of knowledge of the basic factors influencing predators and prey populations. Since about 1903, predator control - principally that of the larger carnivores such as lions, leopards, cheetahs, wild dogs, spotted hyenas, and crocodiles - was routinely practiced in Kruger National Park, South Africa. The possible influence of large predators on prey populations became recently a controversial issue, when wildebeest and zebra populations started declining in the Central District of Kruger Park. Although it was realized that these declines were linked to cropping operations, the drought, and marked habitat changes, there was some evidence that large predators, principally the lion, were the proximate cause of the declines.
Interrelations Between Predators, Prey, and Their Environment

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The management of large predators remains a controversial and highly emotional issue all over the world. This can largely be ascribed to a lack of knowledge of the basic factors influencing predator and prey populations. Scientists today realize that the dynamics of specific animal populations cannot be divorced from those of associated populations or from the environment as a whole. The laboratory predator-prey models of Lotka (1925) and Volterra (1926) simply are not representative of most field situations, because predators no longer determine exclusively the abundance of their prey. The intricate and at times subtle relationships between predators and their environment remain one of the most stimulating, yet involved, aspects of biological research and require an increasing amount of cooperation between field biologists and mathematicians.

Since about 1903, predator control—principally that of the larger carnivores such as lions (Panthera leo), leopards (Panthera pardus), cheetahs (Acinonyx jubatus), wild dogs (Lycaon pictus), spotted hyenas (Crocuta crocuta), and crocodiles (Crocodylus niloticus)—was routinely practiced in Kruger National Park, South Africa. These programs were continued in selected areas up to 1960 with the hope that they would promote healthy predator-prey relationships. However, because of the size of the area (almost 20,000 km²), the limited ranger staff, and the absence of research personnel until 1950, it was impossible to evaluate, with certainty, to what extent carnivore control had succeeded in stimulating the growth of herbivore populations, or even whether the carnivore populations had been significantly reduced in size through being controlled.

The possible influence of large predators on prey populations, however, recently again became a controversial issue (Smuts 1975a) when wildebeest (Connochaetes taurinus) and zebra (Equus burchelli) populations started declining in the Central District of Kruger Park. Although it was realized that these declines (Fig. 1) were linked to cropping operations (1965 to 1972), the drought of 1970/71 (Fig. 1), and marked habitat changes (Fig. 2 & 3) associated with five years of above-average rainfall (1972 to 1977), there was some evidence that large predators, principally the lion, were the proximate cause of the declines (Smuts 1976a).

Computer simulations, which took the annual cropping rates of wildebeest (Starfield et al. 1976) and zebra (Smuts 1974a) into account, indicated that cropping merely served to accelerate natural population declines. These declines are still persisting today (Fig. 1), despite the termination of all wildebeest and zebra cropping. During no year was mortality through disease found to be significant; instead, the vulnerability of wildebeest and zebra to lion predation had increased, both during the drought of 1970/71 and during the ensuing wet period. By contrast, the vulnerability of associated-cover and/or tall-grass-loving species such as buffalo (Syncerus caffer), waterbuck (Kobus ellipsiprymnus), and kudu (Tragelaphus strepsiceros) showed the opposite trend during the wet period (Smuts 1975b, 1976b).

METHODS

Predation could have a marked depressant influence on certain prey species when these are confined to a fenced area such as Kruger Park, where artificial water has been provided. Thus, it was decided to undertake a series of ex-

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Fig. 2. Part of a large herd of zebra in the Central District of the Kruger National Park. Open areas with short grass are preferred by both wildebeest and zebra and foster the formation of large mobile aggregations. With these conditions the populations also achieve their maximum rates of growth. (Lindanda, February 1968.)

experiments to measure the reactions of both predators and their prey to various predator-cropping strategies. Experiments were, however, also designed in terms of certain rare prey species—sable antelope (Hippotragus niger) and sas-saby (Damaliscus lunatus)—which, because of small and isolated distribution patterns, were giving cause for concern.

Fieldwork, initiated during 1974, consisted of the following:

- A census of the lion population in the 5,560 km² Central District of Kruger Park (Smuts 1976c), which included an attempt to capture and mark a sample of lions from all groups in the area (Smuts et al. 1977, 1978c).
- An annual aerial census of all the larger herbivores in the Central District (Joubert and Pienaar 1977, Smuts 1975b, 1976b).
- The controlled cropping of specific numbers of lions, spotted hyenas, or both, from areas selected for study purposes (Smuts 1976b, 1978a). Depending on the area, either supplementary cropping operations were undertaken or the lion population was resurveyed at intervals to study the details of its short- and long-term recovery.
- Additional aerial surveys of each study area designed so as to register seasonal fluctuations in herbivore numbers and distribution (Smuts 1976b).
- Gross and histological examination of the reproductive tract of each lion (Smuts et al. 1978b), age estimation (Smuts et al. 1978a), and an analysis of stomach contents (Smuts 1976b, 1978b).
- The routine collection of information on all predator kills and, where possible, analysis into age and sex classes (Smuts 1975b, 1976a, b).
- Counts from vehicles undertaken at intervals to register the age structure: sex ratio and female: young ratio of wildebeest and zebra in each study area (Smuts 1975b, 1978b).
- A monitor system for recording changes in vegetation structure in terms of frequency of different height classes of individuals (Coetsee et al. 1973) and surveys during which the crown cover of grasses was allocated to four subjectively estimated categories (Gertenbach 1975).

Finally, data were available from the formal experimental burning plots. Twelve different burning treatments are applied to 48 6-ha plots and a variety of vegetation surveys (Gertenbach and Potgieter 1975, Van Wyk 1971) are undertaken at intervals.

RESULTS AND DISCUSSION

Rather than describe details of results obtained during the study (see references), this paper will discuss their implications and attempt to relate cause and effect in as rational a way possible. In time, and as more projects are completed, it should be possible to fill in some of the gaps with more concrete results. Also, although plants and animals in Kruger are continuously reacting and adapting to changing environmental conditions, these reactions are further influenced by management strategies such as fences, the burning program (Brynard 1971, Van Wyk 1971), the provision of artificial water (Pienaar 1970), the routine cropping of elephant (Loxodonta africana) and buffalo, the current experimental predator-cropping experiments, and finally the influence of roads, rest camps, and any other man-made structures.

Since the initiation of the predator-

Fig. 3. With the above-average rainfall of recent years, tall climax grasses have been favored, and large aggregations of zebra and wildebeest have disintegrated to use remaining islands of short grass or have been forced to enter the taller communities. The situation has been aggravated since small herds do not have the "grazing pressure" to open large areas of tall grass. (Near Mananga in the Central District, August 1977.)

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PREDACTION IMPACT

Although numerous field studies of predator ecology have been undertaken all over the world, the subject is still very much in its infancy. Published works on predator-prey interactions show such variable results that generalizations cannot be made. In one area, for example, predation may limit the growth of a particular prey population, whereas in another its effects may be almost negligible. In the Serengeti, Schaller (1972) found that predation alone had little impact on the wildebeest population and that most individuals were probably dying from a combination of malnutrition and disease. In the Ngorgoro Crater, on the other hand, spotted hyenas, and to a lesser extent lions, have a marked impact on the wildebeest population (Kruuk 1970).

A similar situation was apparently responsible for a dramatic decline in the wildebeest population in Nakaobi Park between 1961 and 1966 (Foster and Kearney 1967). Here, however, lions were the major predators, even managing to maintain a high level of predation on the declining wildebeest population (Rudnai 1974). Evidently, predation needs to be analyzed individually for each particular situation, and its influence may vary not only spatially, but also temporally within a certain area.
In Serengeti, with a population of some 2,000 lions (Schaller 1972) and popula-
tions of over 2,000,000 prey animals (wildebeest, zebra, gazelle, etc.), the li-
ons make little impact on the prey popu-
lation. The Serengeti figure of roughly 1 
lion to 1,000 prey animals contrasts with 
that of the Central District of Kruger 
Park, where the ratio is 1 lion to 110 prey 
animals (wildebeest, zebra, buffalo, gir-
raffe [Giraffa camelopardalis], impala 
[Aepyceros melampus], warthog [Phaco-
choerus aethiopicus], waterbuck, and 
kudu). Other things being equal, one 
would, therefore, expect predation by li-
ons in Kruger to have a far greater im-
 pact on prey populations than it does in 
Serengeti. It has, for example, been cal-
culated that the lion population of some 
700 in the Central District of Kruger 
(Smuts 1976c) required about 2,500 wil-
debeest (adults and calves) as part of 
their minimum diet in 1975 (excluding 
other species which are also eaten). 
Since the potential recruitment to the 
wildebeest population was only about 
3,300 calves, this left an excess of only 
800 calves if lions were the only preda-
 tors. Spotted hyenas (≤ 1,800) (Smuts 
1975b), leopards, cheetahs, and wild 
dogs, however, also take a percentage, 
as do other natural mortality factors such 
as accidents and disease. An otherwise 
healthy population faced with such odds 
could hardly be expected to increase and, 
if in fact, did decline as predicted. 
Computer simulations presently indicate 
that these declines will continue (Star-
field et al. 1976). Recently Mech and 
Karns (1977) provided the first conclu-
sive evidence that intensive wolf (Canis 
lupus) predation can cause deer (Odoco-
ileus virginianus) populations to decline 
dramatically, when such predation is com-
bined with declining habitat conditions 
and inclement weather for several con-
secutive years. 

PREDATION IMPACT: KRUGER PARK

Why have lions continued to have 
such a marked impact on the wildebeest and zebra populations in the Central 
District after the initial declines (1969 to 
1971) due to the drought and cropping 
operations? Some of the answers to this 
question can be found elsewhere (Smuts 
1975a, b, 1976a, b) but, as mentioned, 
are basically related to physiognomic 
changes in the vegetation (Fig. 2 and 3) 
caused by the unusually high rainfall of 
the period 1972 to 1977. During this time, 
wildebeest and zebra were compelled to 
use mature and medium-height or tall 
grassland more frequently and for longer 
periods than would have been the case 
during years of normal rainfall when 
grass growth was much slower. This 
could result in a poorer nutritional in-
take, and consequently higher parasite 
loads—both influencing vulnerability to 
predation or disease.

In addition, the abundance of natural 
and artificial water supplies, together 
with a greater increase in cover (Coetze-
et al. 1978), has facilitated predation by 
lions; not only are wildebeest and zebra 
now easier to catch, but the large aggre-
gations common during drier years have 
broken up and become dispersed among 
a much larger percentage of the lion pop-
ulation than would otherwise have been 
the case. Wildebeest are currently de-
clining more rapidly than are the number 
of lion kills recorded per year, and this 
could only be due to a relative increase 
in the level of predation. Direct mortality 
of wildebeest and zebra through disease 
is currently believed to be of little signifi-
cance in the Central District (few to no 
carcasses are located per year). This 
may be due partially to the smothering 
effect of heavy predation and/or to the 
action of scavengers such as spotted 
yenas and vultures.

Recently, the lion population has 
increased considerably (up to 58%—2 ½ 
years) in certain areas favored by wilde-
beest and zebra (Smuts 1978b). In these 
areas, the number of adult lions has 
remained unchanged, but large numbers of 
cubs have reached sub adulthood. The 
fact that there are now four times as 
many subadult lions in certain areas than 
there were 2 ½ years ago is due to the 
segregated distribution patterns of wilde-
beest and zebra, i.e., small groups dis-
tributed over a large area (Smuts 1978b). 
This allows subadult lions, which have 
left their prides of origin, to hunt almost 
anywhere, thereby avoiding contact and 
competition with adults—a situation 
which will most probably end when veldt 
water starts drying up and game start 
concentrating around permanent water-
holes and on shorter grassland.

MAN’S IMPACT: KRUGER PARK

As far as the wildebeest and zebra de-
clines are concerned, there are two pos-
sibilities: either do something to curb 
the decline or ignore the decline and allow

1V. de Vos, veterinary ecologist, National Parks 
Board of Trustees, South Africa, personal communi-
cation, January 1978.

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and identify newborn calves in these small groups. In the migratory aggregations, newborn calves can hide among conspecifics that are a few days older and are thus less likely to be noticed by a hyena (Estes 1976). Accidents due to herd disturbance or crowding at waterholes (Talbot and Talbot 1963) are not significant in Kruger where herds of wildebeest seldom exceed 500 animals.

Another advantage of the large migratory aggregation is that they are able to "mow" grassland down more effectively and hence reduce the cover so essential for a successful lion kill (Bryden 1976, Schaller 1972). Thus, water provision and stabilization can have both positive and negative effects in terms of animal numbers. New species can be enticed into areas that previously lacked permanent water, and the less water-dependent resident animals may eventually be forced into competition with the new immigrants. In the Northern District of Kruger Park, for example, water-influenced increases in animals such as zebra, wildebeest, impala, and buffalo are presently causing concern with regard to their impact on the habitat of rare animals such as roan antelope and sable antelope (Joubert 1976).

Although the recent declines in wildebeest and zebra populations in the Central District have been accentuated through having been cropped and by vegetational changes, no one knows to what extent the decline in the impala population over the same period may have been responsible. Impala comprise an important part of the lion's diet in the Central District, and in a sample of 252 lion stomachs examined (12I or 48% were empty), 40 contained impala remains. Of the eight prey species so identified, impala remains were the most common (31.3%), followed by wildebeest (28.2%), giraffe (15.6%), zebra (10.9%), warthog (7.8%), water buck (5.5%), kudu (2.3%), and buffalo (2.3%) (Smuts 1978b). Therefore, should impala numbers decline drastically, lions would have to find an alternate source of food; hence, the impala would be an important buffer animal with regard to lion predation on wildebeest and zebra. Spotted hyenas also prey extensively on impala, and 68.7% of all hyena stomachs examined (n = 144) contained impala remains (Smuts 1978b). Impala were cropped between 1968 and 1975 (n = 7500), and more recently high postnatal mortality and even deaths among pregnant ewes (e.g. 1975) have caused further population declines.

Finally, the cropping of some 3,500 buffalo in the Central District since 1969 (present population = 8,350) has not only reduced their possible buffer effect in terms of lion predation but also their grazing pressure in terms of opening up areas of tall grass for other animals (zebra and wildebeest) in the grazing sequence.

MANAGEMENT CONSIDERATIONS

Wildebeest and zebra need to be encouraged to form mobile aggregations rather than to become sedentary and dispersed into small groups or herds. Factors influencing their movements and distribution need to be monitored over long periods of time so that the necessary steps can be taken to alleviate some of the problems. Management considerations here would include, primarily, the use of fire as well as water manipulation and the relaxation of buffalo and elephant cropping during years of good rainfall.

Periodic resurveys of lions in the experimental cropping areas and surrounding zones have indicated that they react rapidly to the reduced density both by infiltrating from surrounding areas and by showing increased reproductive success (Smuts 1978a). Subadults (two to four years old), particularly males, entered the cropping areas in greater numbers than expected on the basis of their relative abundance in the population, whereas the opposite was true for adults where the sex-specific response difference also appeared to be minimal. Further indications are that heavy cropping of lions, undertaken over a large area, will attract many foreign lions, which interact with one another to suppress reproduction and/or to reduce cub survival. By contrast, more gradual cropping operations, during which only a few individuals are lost from neighboring prides at a time, or when only one pride is removed at a time, lead to a lower influx of new lions with the result that reproduction appears to be more successful. By both methods, nevertheless, losses are rapidly replaced, since lions show a number of effective traits that allow them to recognize and exploit potential sources of food (Smuts 1978a). Spotted hyenas, by contrast, are slow to recolonize areas where their numbers have been reduced (this phenomenon is currently being investigated).

The results of the experimental cropping operations of 1974 to 1976 are that, since only about 134 lions were removed, the lion population for the whole Central District has remained almost unaltered, i.e., the cropping operations were basically taking off excess lions, many of which would normally have died. At the same time the populations settling in the cropping areas were reacting to the lowered density by either breeding more and/or by having an increased rate of survival. These facts partly explain why wildebeest and zebra populations in the Central District have not reacted by increasing over the same period. The cropping of an additional 201 lions mainly during the latter half of 1977 will, however, have reduced the lion population to the extent that prey survival will be influenced.

If, however, the aim is to curb the present decline in the wildebeest population by predator cropping, a similarly large number of lions and, possibly, spotted hyenas will have to be killed each year. Such a strategy would require that careful thought be given to the delicate relationship between predators and their prey. Intensive removal of one predator may influence the dynamics of other predators that are not cropped. Similarly, the dynamics of the predator(s) being cropped may be influenced more than just by the net loss to cropping, e.g., spotted hyenas might be reduced below their level of social security. These changes would be reflected in the dynamics of certain prey populations. Here various self-limiting stress factors, which include competition for food or mates, territoriality, weather, or disease, can be expected to maintain lower densities of prey animals since these forces app:enently operate more severely as population controls than does predation (Howard 1974).

Although management strategies such as burning, water provision, and elephant and buffalo cropping are indispensable to the now confined plant and animal communities of Kruger, these practices have altered the upper and lower density limits of all animals. Despite this, however, most, if not all, animal populations have an innate tenacity to survive and, given adequate habitat conditions, can retain healthy densities within a reasonable period of time, depending on their sensitivity to habitat changes.

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