Mills MGL. 1991. Conservation management of large carnivores in Africa. Koedoe 34:81-90.

Keywords: 1Afr/Acinonyx jubatus/cheetah/conservation/human-wildlife conflict/management/ pastoralism/predator-prey relationship/protected area/re-introduction/strategy/translocation

Abstract: The conservation management of large carnivores in Africa is reviewed. In large protected areas the complexity of the relations between predators and prey, and between competing predators, indicate that these relationships should not be disturbed, even though, superficially, there may seem to be sound reasons to do so. Management action, however, may have to be taken against carnivores which break out of reserves. The related questions of translocation and re-introduction are also complex. Guidelines for considering whether to and how to implement these strategies are presented. It is stressed that adequate follow-up observation should be made after translocation or re-introducing carnivores, so that more information on the success of these strategies can be obtained. Much of Africa comprises rural areas inhabited by pastoralists. It may be possible to manage some large carnivore species in these areas to the mutual benefit of man and beast, but for this type of program to be successful, a well planned public relations campaign is essential.

Conservation management of large carnivores in Africa

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Mills, M.G.L. 1991. Conservation management of large carnivores in Africa. *Koedoe* 34(1): 81-90. Pretoria. ISSN 0075-6458.

The conservation management of large carnivores in Africa is reviewed. In large protected areas the complexity of the relations between predators and prey, and between competing predators, indicate that these relationships should not be disturbed, even though, superficially, there may seem to be sound reasons to do so. Management action, however, may have to be taken against carnivores that break out of reserves. The related questions of translocation and re-introduction are also complex. Guidelines for considering whether to and how to implement these strategies are presented. It is stressed that adequate follow-up observations should be made after translocating or re-introducing carnivores, so that more information on the success of these strategies can be obtained. Much of Africa comprises rural areas inhabited by pastoralists. It may be possible to manage some large carnivore species in these areas to the mutual benefit of man and beast, but for this type of program to be successful, a well planned public relations campaign is essential.

Key words: conservation, management, carnivores, predator-prey relations, competition, translocation, re-introduction, rural areas, public relations.

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Introduction

Carnivores have received a disproportionate share of the attentions of wildlife scientists and managers. This is because of the position they occupy in ecosystems; being at the top of the food chain makes them vulnerable to perturbations in an ecosystem at almost any level. Furthermore, they frequently clash with man's interests and are persecuted when they are considered a nuisance. Partly because of this persecution several species and sub-species are now endangered. Even in protected areas their role as predators may mean that they affect populations of other animals, which may cause concern for wild life managers. In spite of a great deal of effort and study, our knowledge of the roles of carnivores in ecosystems, both protected and unprotected, is often inadequate and controversial when it comes to making management decisions.

In this paper the conservation management of large carnivores (i.e. those over 20 kg) in Africa is discussed. Firstly, I look at them in some of the pristine areas of Africa, in particular the large national parks. Next I examine the questions of translocation and re-introduction. Finally, I examine conservation strategies for some large carnivores outside of protected areas.

Conservation of carnivores in large protected areas

The conservation management of large carnivores in pristine areas centres around two key aspects: the impact they have on their prey and the impact they have on other carnivores. In addition the question of what action to take when large carnivores leave the confines of protected areas is sometimes difficult for wildlife managers to answer.

Predator-prey relationships

The impact that predators have on their prey is a controversial aspect of predator ecology, but may be important in the management of herbivore populations. It is also extremely

difficult to measure accurately. Information is needed on how many predators and prey there are in an area, the structure of the prey population, how often the predators kill, how they select for species, sex, age and condition, and the contribution of mortality other than predation in the population dynamics of the prey. Additionally, the fact that ecosystems are dynamic means that these processes are also dynamic; what applies today, may not do so tomorrow. For the same reasons it is unwise to extrapolate results from this type of study from one area to another, even if they are ecologically similar. If a 30-year study of a simple predator-prey system, such as that of wolves *Canis lupus* and moose *Alces alces* on Isle Royale in North America, is only now beginning to reveal important characteristics of this system (Peterson 1988), it stands to reason that it will take many more years of intensive research before a multi-species predator-prey system in Africa is fully understood.

To illustrate the complexity of predator-prey relationships I examine the roles predators are believed to play in the population dynamics of their prey in four more or less intact ecosystems. The four areas are the Serengeti, the Ngorongoro Crater, the southern Kalahari, and the Kruger National Park.

Table 1 shows the ungulate species that made up more than 10 % of the kills of the large carnivores in some of the studies conducted in each of these four areas. In an attempt to make the observations from each area comparable I have included the studies which covered the largest part of each area and those which relied mainly on direct observations, the exception being spotted hyaenas *Crocuta crocuta* in Kruger National Park, where the most accurate widespread data come from faecal analysis (Henschel & Skinner (1990)). Notable studies that have been excluded from Table 1 are those of Kruuk & Turner (1967) from the Serengeti; Pienaar (1969) from the Kruger National Park, which relied mainly on the location of carcasses after they had been killed; Eloff (1973, 1984); and Bothma & Le Riche (1984) from the Kalahari, which were confined to a particular habitat of the area.

The data in Table 1 show that in each area most of the ungulates eaten by the large carnivores are from only three, or at the most four species; mainly the most abundant ones. Although the impact of predators on low density prey species may be significant, it has not been studied in any detail, and most attempts to measure the influence of predators on prey have involved the more common species.

The two major predation studies in the Serengeti concluded that predation had little impact on the size of the major prey populations (Schaller 1972; Kruuk 1972). It was shown that predators tended to select the most expendable segments of the prey population, by killing mainly old animals, or those in poor condition, as well as a preponderance of males. Also, some 80 % of the prey-population is migratory, whereas the predators are in the main sedentary. This means that for extended periods there are few prey animals in a predator's territory, which limits the number of predators. In almost all cases regulation of prey populations was believed to take place through the food supply.

Some of these conclusions have subsequently been challenged by workers looking at the prey rather than the predators. Sinclair & Norton-Griffiths (1982) suggested that zebras *Equus burchellii* might be limited by predation, and in a later paper Sinclair (1985) presented some data to support this hypothesis. Borner *et al.* (1987) believed that a decline in the Thomson's gazelle *Gazella thomsonii* population was, at least partly due to predation, and that predation could also prevent the population from increasing.

In the southern Kalahari the mainly nomadic prey populations were seen not to be regulated by predation for the same reasons as in

Table 1
The most important ungulate prey of large carnivores in four African ecosystems, giving the percentage each species contributed to the kill sample

Carnivore	Serengeti		Ngorongoro		Kalahari		Kruger	
	Species	Source	Species	Source	Species	Source	Species	Source
Lion	Wildebeest (35 %) Thomson's gazelle (28 %) Zebra (22 %)	Schaller 1972	Wildebeest (61 %) Thomson's gazelle (17 %) Zebra (15 %)	Elliot & Cowan 1978	Wildebeest (37 %) Gemsbok (32 %) Springbok (13 %)	Mills 1990	Impala (30 %) Zebra (15 %) Wildebeest (13 %)	Mills *in prep*
Spotted hyaena	Wildebeest (53 %) Thomson's gazelle (28 %) Zebra (10 %)	Kruuk 1972	Wildebeest (73 %) Zebra 19 %)	Kruuk 1972	Gemsbok (50 %) Wildebeest (18 %)	Mills 1990	Impala (33 %) Buffalo (22 %)	Henschel & Skinner 1990*
Leopard	Thomson's gazelle (63 %) Reedbuck (12 %)	Schaller 1972	—	—	Springbok (65 %)	Mills 1990	Impala (82 %)	Mills *in prep*
Cheetah	Thomson's gazelle (91 %)	Schaller 1972	—	—	Springbok (87 %)	Mills 1990	Impala (73 %)	Mills *in prep*
Wild dog	Thomson's gazelle (42 %) Wildebeest (38 %)	Schaller 1972	Thomson's gazelle (54 %) Wildebeest (36 %)	Estes & Goddard 1967	—	—	Impala (72 %)	Mills *in prep*

* Per cent occurrence in faeces.

ISSN 0075-6458

the Serengeti. Good evidence for the blue wildebeest *Connochaetes taurinus* population being regulated by drought conditions was obtained (Mills 1990). However, the density of an important prey species, gemsbok *Oryx gazella*, was found to be higher in an area devoid of predators outside the Kalahari Gemsbok National Park than it was in an equal sized area of similar habitat, but containing predators, within the park. Predation on springbok *Antidorcas marsupialis* may not have influenced their numbers, but may have been responsible for the distorted sex ratio of adults (Mills 1990).

The Ngorongoro Crater has an extremely high density of prey animals throughout the year, which in turn supports a high density of predators. Here predators tend to select more evenly from the prey population than in the neighbouring Serengeti. Kruuk (1972) concluded that the blue wildebeest population was under considerable predation pressure. The population showed a high rate of turnover, but it appeared that the blue wildebeest population density was limited by the amount of herbage available, not by the numbers of predators.

In the Kruger National Park impala *Aepyceros melampus* was found to be the most important prey species for all five large carnivores (Table 1), but, because of the difficulty in obtaining accurate counts of impala, it was not possible to establish the impact this predation had on their population. The high incidence of buffalo *Syncerus caffer* in the spotted hyaena's diet was mainly a result of them scavenging from carcasses of animals that died during a drought (Henschel & Skinner 1990).

In the south east of the Kruger National Park where there is a small sedentary population of blue wildebeest and a larger nomadic population of zebra, lions *Panthera leo* were found to be the only significant predators of these two species. The large number of spotted hyaenas do not appear to hunt them to any great extent. Lion predation was the largest mortality factor for blue wildebeest and, like the Ngorongoro predators, these lions took blue wildebeest in proportion to their occurrence in the population. With zebra the lions showed a strong selection for foals, which coupled with their nomadic behaviour, significantly lessened the impact of predation on this population, even though zebra were taken in more or less the same proportions as wildebeest (Mills *in prep*).

Previous to the above-mentioned study in the south-east of the Kruger National Park, considerable attention had been given to predator-prey relationships in the central district (Smuts 1978). Zebra, and particularly blue wildebeest populations, declined between 1969 and 1977 due to a combination of factors, of which cropping operations of these prey species, followed by five years of high rainfall were identified as being the most important. There was also some evidence that lion predation was the proximate cause of the declines. Accordingly a number of experiments to measure the reactions of both predator and prey to various lion and spotted hyaena cropping strategies were conducted. The results of these experiments showed that the removal of these predators had little impact on the decline in the prey populations, mainly because lion losses were rapidly replaced.

Relations between carnivores

Competition between carnivores is of two types; **exploitation competition**, where two species compete for the same resources, and **interference competition**, where they interact with each other directly. The nature and amount of competition between carnivores may play an important role in determining the distribution and numbers of certain species.

As is the case with predator-prey relationships, relationships between carnivores are complex and dynamic. This is illustrated in Table 2 which summarises the nature of the relationships between large carnivores in the southern Kalahari. Some relationships benefit species, whereas others have a detrimental effect. Cheetahs *Acinonyx jubatus* and brown hyaenas *Hyaena brunnea* seem to be most sensitive to the activities of other carnivores in the area.

Management practices may disturb the balance between competing carnivores. For example, the provision of artificial water may lead to a more even and wider distribution of large herbivores in an area. With a more predictable prey base an increase in the numbers of lions and spotted hyaenas is likely. This in turn may have a detrimental effect on the rarer and less aggressive competing species.

Table 2

The direction in which large carnivores in the southern Kalahari effect each other through interference and exploitation competition

		On				
		Lion	Leopard	Cheetah	Spotted hyaena	Brown hyaena
By	Lion	-	0	-	-(+)	-(+)
	Leopard	0	-	0	0	0
	Cheetah	-	0	-	+	+
	Spotted hyaena	0(+)	-	-	-	-
	Brown Hyaena	0	0	0	0	-

\- Negative effect
\+ Positive effect
0 No effect
( ) Occasional alternative nature of the relationship

Interactions between species that compete most closely for food are most intense. Perhaps the best example of this is the aggressive and noisy interactions that take place between lions and spotted hyaenas (Kruuk 1972; Mills 1990). An unnatural disturbance to this relationship may have unforseen consequences. For example, after the predator reduction campaigns in the Kruger National Park referred to above, the lion population recovered rapidly (Smuts 1978), but seven years later spotted hyaena numbers had still not fully recovered (Henschel 1986). It was suggested by Henschel (1986), that part of the reason for spotted hyaena numbers not recovering was due to competition from lions. Because hyaena numbers had been reduced, females were apparently not able to synchronize litters and establish a communal den. This appeared to lead to an unusually high cub mortality, and recruitment was inadequate to balance adult mortality, most of which was caused by lions. Henschel (1986) concluded that the unpredictability and irreversibility of events following population reductions underlie the need for caution when considering such conservation measures.

Several studies have shown that when two phylogenetically related species compete for resources the larger species tends to displace the smaller one (Schaller 1967; Kruuk 1976; Seidensticker 1976; Fuller & Keith 1981; Skinner & Van Aarde 1981; Sargeant & Allen 1989). For example, in the arid southern Kalahari, where the brown hyaena is better adapted to the environment and more widely distributed than is the spotted hyaena, the former tends to avoid those areas frequented by spotted hyaenas (Mills 1990). In the Kruger National Park, with a relatively high density and even distribution of spotted

ISSN 0075-6450
ISSN 0075-6450

hyaenas (Mills 1985), brown hyaenas are extremely rare. No breeding record for this species from the area has been obtained for at least 40 years. Yet close by in areas where spotted hyaenas have been eliminated, brown hyaenas are present.

In summary, the large carnivore studies referred to above illustrate how complex predator-prey relationships and relationships between competing carnivores are. With the present state of knowledge it seems that in large pristine areas it is best not to interfere with these relationships, even though superficially it may seem that there are good reasons to do so. The contention of Schaller (1972) that "predators are the best wildlife managers" is as true today as it was then.

Management of predators leaving protected areas

Breakouts of predators from protected areas may cause problems for managers, particularly if the predators take to killing domestic livestock. Not only will this frequently have an adverse effect on public attitudes towards nature conservation, but also the animals which break out may be endangered and, therefore, valuable.

Anderson (1981) attempted to devise a management strategy for the lion population in the 96 000 ha Hluhluwe-Umfolozi Complex, whereby a representative population inside the protected area could be maintained, while reducing livestock killing in the areas densely populated by humans adjoining agricultural areas. This was accomplished by selectively killing sub-adult males and, when their numbers warranted it, sub-adult females as well. Attempts were made to improve on this strategy by Venter & Hopkins (1988) using a simulation model for the lion population. The advantage of this model was that it could simulate many different population control strategies, and measure the effectiveness of each. However, the most effective strategy drastically reduced the lion population inside the protected area. Furthermore, the model was not able to cater for the movements of pride animals out of the protected area, nor to allocate different levels of lion prey availability on a geographic rather than a pride basis (Venter & Hopkins 1988).

Through keeping long-term records of individual lions in northern Namibia, Stander (1990) was able to differentiate between occasional stock raiding lions and habitual problem animals. Occasional raiders were predominantly animals from established prides and short distance (≤ 100 km) translocations of these animals resulted in them ceasing to kill stock and returning to their pride territories. Habitual problem animals could not be successfully translocated and were best eliminated. Stander (1990) stressed the fact that for these strategies to work, co-operation between farmers and conservation authorities is vital.

The highly endangered African wild dog *Lycaon pictus* poses particular problems when leaving protected areas. Because of the large home ranges that wild dog packs occupy, even established packs sometimes leave the safety of a protected area (personal observations). Many people still have an exaggerated opinion of the impact wild dogs have on their prey populations and are intolerant of their presence, even if this is transitory. For example, in 1974 two of eight wild dogs from the only resident pack in the Kalahari Gemsbok National Park were shot by farmers less than 24 hours after leaving the park (Mills 1981). Even more so than with lions, co-operation between farmers and parks authorities is important for wild dog conservation. This is particularly so in arid regions, where wild dog densities are particularly low and their home ranges are very large.

Translocation and re-introduction

In order to offset the reduction of large carnivores over much of their former range, animals have been caught in areas where they are regarded as a nuisance and relocated in conservation areas. Relocated animals are usually released into the new area with little or no attempt at monitoring the success of the operation. Van der Meulen (1977) recorded limited success in the translocation of lions in northern Zimbabwe. However, the best documented study of the effectiveness of translocations in an African carnivore is that of Hamilton (1981) with leopards *Panthera pardus* in Kenya. Twelve stock-raiding leopards were caught, radio-collared and released: ten in the Meru National Park and two in Tsavo-West National Park. Of the ten Meru animals, five left the park within three days and the others all left within two weeks. Although some did return later, only one settled down in the park. Neither of the two Tsavo animals remained in the relocation area. It was concluded that the translocation of leopards was not sufficiently successful to justify its continuation as a rational conservation and management policy.

Another well-documented relocation exercise involved cheetahs which were trapped in livestock areas in the Transvaal and relocated to the Suikerbosrand Nature Reserve, Republic of South Africa (Pettifer 1981a). Eight adults were released in the 13 400 ha reserve over a 15-month period and within two years the cheetah population rose to an estimated twenty four. The absence of other large predators was thought to have contributed significantly to the cheetah's rapid increase. However, this imposed severe ecological problems for the managers of the reserve as the cheetah began to remove unacceptably high proportions of the blesbok *Damaliscus dorcas phillipsi* and springbok populations. Blesbok numbers, in fact, were augmented by excess stock from other reserves, and eventually it was decided to remove the cheetah from the reserve (S. Wolff *pers. comm.*). It is unfortunate that this experiment could not have been allowed to run longer, as it would have been valuable to establish if a successful balance between predator and prey in a small reserve could eventually be achieved.

A related management option to relocation of animals from areas where they are a problem, is the reintroduction of captive-born animals into conservation areas. Pettifer (1981b) reported on the experimental release of three captive-bred male cheetahs into the Klaserie and Timbavati Private Nature Reserves, adjoining the Kruger National Park. Apart from insurmountable problems associated with the fact that these captive-bred cheetahs were habituated to and dependent on man, they encountered and fought with resident cheetahs and also moved right away from the original release site. Eventually one of the cheetahs died and the remaining two were returned to captivity because of their continued attacks on domestic chickens (P. Viljoen *pers. comm.*).

Childes (1988) reported on an attempted introduction of 10 captive-bred African wild dogs in Zimbabwe. Again these animals showed considerable dependence on man, repeatedly staying around butcheries for several days at a time. Some of the dogs were recaught in a starving and badly injured condition and relocated to another area. Eventually, after five of the original ten had probably died from natural causes, the remaining five were shot seven weeks after their initial release.

Translocations and re-introductions of large carnivores are complicated management practices and seem rarely to be successful. Animals released into areas where their species already exists will have to compete with the established residents in the area to the detriment of one of these groups. Those that are released in areas where the species has been exterminated will have to face the same pressures as their counterparts before them did. Only if a species is extinct in an area, the causes of its extinction known and rectified, and the area is judged to be large enough to support a viable population, should a reintro-

duction be attempted. As far as possible wild-caught animals should be reintroduced, as captive-bred carnivores do not adapt well to natural systems. Even low density populations produce excess animals which could be removed before natural mortality takes its toll.

A further important consideration with regard to reintroductions is the question of genetics. It is important to determine the level of genetic differences between surviving populations before mixing animals from different populations because of the possible deleterious long-term genetic consequences of such a strategy (Ashley *et al.* 1990). Before this information is available a conservative policy with regard to mixing populations is recommended.

Whenever a translocation or reintroduction operation is carried out, adequate follow up observations to asses the success of the exercise are essential. Only when an adequate number of studies have been carried out will we be in a position to judge whether, and when, these high profile conservation measures should be embarked upon.

Conservation in unprotected areas

Much of Africa consists of rural areas inhabited by pastoralists. Predators, and particularly large carnivores, compete with these people by killing livestock. While it is impractical to implement the total protection of large carnivores in most unprotected areas, there are measures that should be taken in order to reduce the impact of predation. These are particularly applicable in third world areas where large carnivores are present but difficult to control.

Kruuk (1980) researched the impact of carnivores on domestic stock in northern Kenya. He found that negligence of the herdsmen played an important role in most predation incidents. He recommended that loss of stock could be prevented by more vigilance by herdsmen during grazing, by preventing animals straying, and by returning herds to the manyattas before dark. He also recommended that government or international organisations could assist the herdsman by selective removal of problem animals, promoting the use of domestic dogs (as people who did so suffered significantly less predation than people who did not), and by helping the people to build better bomas.

Some species may be both ecologically and economically advantageous to manage as a sustainable resource in certain areas. Most leopards in Africa probably live outside protected areas. Martin & De Meulenaer (1988) projected that the available range of the leopard will decrease by half over the next 20 years. Private citizens, they add, will continue to kill leopards and trade illegally in skins if no legal channels are open to them. In Botswana, by allowing citizens to kill leopards to protect their livestock and to trade legally in skins, the leopard has become a valuable resource. Allowing sport- hunters to remove problem animals, or to harvest a small proportion of the population, would prove even more lucrative. Martin & De Meulenaer (1988) made a strong case for opening up the leopard fur trade with strict controls. Lions, and particularly cheetahs, could also become valuable resources for pastoralists in certain areas.

Stuart *et al.* (1985) proposed a concept of "safezone" or "open sanctuary" for the leopard in the mountain regions of the southern Cape Province, Republic of South Africa. This concept was further developed by Norton (1986) who suggested that attempts should be made to conserve the leopard in this area as one continuous population. This would entail certain "core" areas where little disturbance of the leopard would be allowed to take place, linked by more disturbed, lower density populations. The main objective of the leopard sanctuary would be to reduce mortality of leopards by reducing the leopard-stock farming conflict to the point where farmers had little need or excuse to kill leopards. This, he suggested, can only be achieved by a range of methods (see below), with each situation being evaluated on its own merits.

Even more so than the leopard, the brown hyaena is a species which is able to survive in certain agricultural areas (Skinner 1976). There is an adequate supply of food from human refuse, as well as domestic and wild animals which have died from natural causes, and small wild animals which may be caught. In addition spotted hyaenas and other large competing carnivores are usually absent (Mills 1990). Certain areas of South Africa have been designated as being only suitable for extensive cattle production (Anon 1965). These could be declared brown hyaena conservation areas. In these areas only proven stock-raiding brown hyaenas should be removed as most brown hyaenas would not be a menace to cattle. For such a program to be effective a well-planned public relations campaign aimed at the local residents should be conducted.

The main aim of predator control should be to reduce the damage caused by the predators at the most economical price. In some cases this may entail management of the livestock rather than killing the pests. I have already alluded to measures that could be taken in undeveloped regions. In the more developed regions, synchronising calving, the use of portable electric fences for protecting breeding herds at night, increased vigilance by shepherds during the breeding season, the use of livestock guard dogs, frightening devices such as sirens and strobe lights, and taste averse conditioning could all be of practical use and need to be tested in the African situation (see Mills 1990 and references therein). The conservation of carnivores in non-protected areas is as much a public relations exercise as it is a biological problem. The needs and interests of the local people must take precedence and a rational approach is essential. This is the only way in which the vital co-operation of the local people can be obtained. The eradication of a species may not only be unethical, it may be impossible. By regarding carnivores as a renewable resource, as well as looking at their ecological roles, it should be possible to develop a management policy to the mutual benefit of both man and beast in many unprotected areas.

Acknowledgements

I thank the National Parks Board for facilities provided, Petri Viljoen and Siegfried Wolff for discussions, and Dr Marlya Gorman for reading through the manuscript.

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ISSN 0075-6450

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Paper presented at the conference: Wildlife Management and Utilisation — The African Experience, held at the University of Pretoria, Pretoria, 2-5 July 1990.