

CHAPTER 7

EVOLUTIONARY ASPECTS, ECOSYSTEM PROCESSES, AND IMPLICATIONS

INTRODUCTION

Up to this point this thesis has been concerned with the description of the methods and results of various investigations into the community of species co-existing in the northeastern Tuli Block of Botswana. The results have been discussed within the constraints of the particular fields of investigation, and Ockham's Razor has determined that only limited conclusions could be drawn from the results obtained.

What the thesis has thus achieved is a description of a particular pattern, or a particular group of patterns, within a specific temporal and spatial framework. After all, every study refers only to a minute sample of the real world. However, the patterns we see are merely a reflection of the disparate and innumerable processes that underly the functioning of every living system. To ignore these processes and to describe only the patterns is to deny the fundamental reality of the biological world. Yet to speculate about processes that have not been specifically studied and identified would be to ignore the constraints of scientific discipline. Yet again, as a Doctorate in Philosophy, this investigation requires a thorough consideration of the philosophical implications of its findings in a manner not permitted by the precise world of published scientific literature.

In order to fulfil the philosophical obligations of this thesis, this chapter is devoted to discussing the implications of the findings of the earlier chapters with unfettered abandon. Once thus recorded, these thoughts may provide the spark for future fires. Unspoken, they would certainly fade, falter and perish with the passage of time. Though I can never pretend to understand the intricacies of the system I have studied, I hope that this holistic discussion will provide some insights into how the different aspects of the study became intertwined to the point where the whole became much greater than the sum of its parts.

EVOLUTIONARY ASPECTS

Jackals and co-operative hunting

Black-backed jackals have been a component of the African ecosystem for over two million years (Wayne, van Valkenburgh, Kat, Fuller, Johnson & O'Brien 1989). The facets of jackal ecology highlighted by the present study are thus a reflection of the evolutionary processes acting on and within the diverse community of African fauna throughout this period.

As a group, the Canidae are particularly well suited to the development of co-operative hunting for the capture of large prey. This can be ascribed to:

1. The absence of morphological adaptations for the efficient killing of large prey by a single animal (such as is commonly evident in the Felidae;

However, as is typical of the medium-sized canids (Kleiman & Eisenberg 1973),

2. Long legs and a cursorial habit facilitating a prolonged chase and elimination of alternative method of close approach - concealment in trees; and

3. A social system wherein strong social bonds exist between the adults and their offspring.

It is the latter trait which facilitates the mutual tolerance between canids at clumped resources and may have facilitated the development of the larger social groups characteristic of the wolf *Canis lupus*, the dhole *Cuon alpinus*, the wild dog *Lycaon pictus* and the bush dog *Speothos venaticus* (Kleiman & Eisenberg 1973). In jackals, the increased family group size and the phenomenon of helping by young from the preceding season are also associated with a well developed social structure (Moehlman 1983).

Wayne *et al.* (1989) have suggested that the similarity in size and morphology between the three sympatric African jackal species, *C. adustus*, *C. aureus* and *C. mesomelas*, is a reflection of the evolutionary processes operating within the rich assemblage of African carnivores. The constraints imposed by the presence of a diverse array of both larger and smaller carnivores in the African environment has resulted in an almost complete absence of morphological divergence between these three species during a period of co-existence spanning over two million years. This is in stark contrast to the marked morphological divergence within less than 250 000 years in South American canids which were not subjected to such restrictions (Wayne *et al.* 1989). If the morphological traits of black-backed jackals reflect these evolutionary constraints, then there can be little doubt that the social and ecological parameters of this species have been similarly shaped. However, as is typical of the medium-sized canids (Kleiman & Eisenberg 1973), jackals are generalized feeders, and their diet at any particular place and time reflects their adaptability on an immediate day-to-day time scale.

Furthermore, the ability of the medium-sized canids to adjust their social system within a short time is also reflected in their ability to utilize clumped resources or large prey through increased co-operation (MacDonald 1979, Bekoff & Wells 1980, Bowen 1981).

In considering the results of the present study, the evolutionary background of the jackal is of significance. As demonstrated in Chapter 3, the harassment and killing of impala in the NTGR is undertaken by groups of jackals considerably larger than the average social group. The question that remains is: Why are these aggregations only temporary? Why have the jackals not resorted to living in packs on a permanent basis? Coyotes have been recorded to resort to pack-living when utilizing larger prey (see Chapter 3). Even the golden jackal, under conditions where a reliable source of food is available, has been recorded to resort to pack living (MacDonald 1979). Is the absence of pack living in the presence of an abundant source of food therefore an indication that the jackal differs from other canids in being unable or unwilling to resort to group living?

Lamprecht (1978b) discussed the possibilities of group hunting in jackals. He speculated that the formation of packs by jackals would depend on: 1. The need for two or more individuals to capture and kill the prey; and 2. The absence or scarcity of scavengers stronger than the jackals themselves. The latter was supported by the findings of MacDonald (1979) which were published shortly thereafter wherein golden jackals were recorded to form packs in the absence of any larger carnivores. Pack formation by coyotes is related to the hunting of large ungulates and the defendability of the carcasses against other groups of coyotes. This condition is not met under normal conditions in the the African savanna where predators far larger than

the jackal abound, which would make defence of a carcass by jackals a dangerous and futile exercise.

Lions and leopards and even occasional hyaenas remain active members of the community of the south-central NTGR. Their presence is thus likely to explain why, even in the presence of a superabundant resource in the form of old, weak impala, the jackals of the Reserve do not display any inclination towards entrenched group living. This deduction is reinforced by the observation, made on many occasions, that the jackals on impala kills were extremely nervous - far more so than when otherwise observed - a reflection, as suggested by Lamprecht (1978a), of their awareness of the potential danger from larger predators. The formation of the packs remains an opportunistic, stochastic event which in this form does not attract undue attention by the larger predators. Jackals in this region have thus escaped the constraints suggested by Lamprecht by a system not previously considered - i.e. the advantages of group living are exploited, while at the same time the disadvantage of attracting attention is avoided by the temporary nature of the group formation.

Competition, therefore, remains a process of considerable importance in the maintenance of the predation pattern recorded during the present study. The presence of the larger predators is likely to be a major factor limiting the emergence of group living in the jackals of the NTGR. However, modification of the large predator community in any way could alter the dynamics of this process, and the observed pattern could, given the potential flexibility of jackal social organization, change substantially from that recorded here.

It is interesting to note that a feature of the well-developed social structure of the wolf is the diverse array of visual, auditory and olfactory communication signals typical of this species; asocial small canids exhibit only a limited communicative ability (Kleiman & Eisenberg 1973). The jackal, while not normally a pack-living canid, utilizes a large number of well developed communication signals (Ferguson 1980, Moehlman 1983). The existence of this entrenched communicative repertoire could represent a pre-adaptation, or exaptation (Gould & Vrba 1982) facilitating the formation of larger cooperative groups under appropriate circumstances while at the same time facilitating a communal response to changing predation pressures, for example the frustratingly ineffective persecution by man. Through this social flexibility the jackal as a predator cannot be classified as a searcher, pursuer or subduer (Griffiths 1980); it is in reality each of these or all of these, depending on the immediate environmental constraints and opportunities. The development of the hunting, harassment, immobilization and killing sequence recorded in the present study is thus no more than a testament to the jackals' ability to respond and adapt on an immediate, rather than on an evolutionary time-scale - an extension of its evolved ability to co-exist in small family groups.

Ungulates and host-parasite coevolution

Janzen (1980:611) has defined coevolution as "an evolutionary change in a trait of the individuals of one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first". In the field of host-parasite relationships selective pressure exerted by the host is often evident in the parasite, but the converse effect on the host is less often

demonstrated, particularly in the case of animal parasites (Kim 1985, Timm & Clauson 1985).

Mammalian ectoparasites, such as ticks and lice, exhibit an array of adaptations to their parasitic mode of life. Among these are those adaptations - long, barbed mouthparts, claws, a strong cuticle, and dorsoventrally or laterally flattened bodies - which afford physical protection and facilitate firm attachment to the host. If the primary function of grooming behaviour is accepted as the maintenance of the appearance and integrity of the pelage (Timm & Clauson 1985), then these adaptations can logically be ascribed to the evolutionary pressures eliciting a response to the threat of physical removal during this non-specific activity. If, on the other hand, the grooming behaviour is directed at the removal of parasites from the pelage, then one may expect a coevolutionary response in the host animal to the well-developed holdfast abilities of their respective parasites.

Many mammals possess specialized morphological adaptations which are used for grooming: claws on the hind feet of prosimians and kangaroos (DuBost 1970, Croft 1980) and the tooth-comb of lemurs (Cuvier & St. Hilaire 1825, Rose, Walker & Jacobs 1981). The present study demonstrated that small to medium-sized browsing and mixed-feeding ruminants utilize the lateral components of their incisor-canine complexes for grooming purposes. Does the latter constitute a coevolutionary response to parasitic infestation?

The gene-for-gene concept is used to detect coevolutionary relationships in host-parasite systems (Kim 1985). "A gene-for-gene relationship exists when the presence of a gene in a population is contingent on the continued presence of a gene in another population, and where the interaction between

the two genes leads to a single phenotypic expression by which the presence and absence of the relevant gene in either organism may be recognized" (Person, Samborski & Rohringer 1962:562). The present study has provided evidence that the phenotypic absence of the dental comb (in animals with completely worn IC complexes) is accompanied by dramatically increased numbers of ectoparasites on the host, particularly in the well-haired parts of the pelage. The ineffectiveness of the grooming behaviour in the absence of the dental comb thus negates the threat of physical removal to the parasites. If these conditions persisted through true genotypic absence of the dental comb, the frequencies of the genes for the holdfast characteristics of the parasites could conceivably be subject to diminution.

3. That pattern observed in an ecosystem is subject to chaotic forces, and that While the present study thus does not provide robust proof of a coevolutionary origin for the ruminant dental comb, current ecological relationships indicate that, whether by adaptation or exaptation, this structure is intricately involved in the host-ectoparasite relationships of impala and other mixed feeding and browsing ruminants. If not its origin then its persistence, in many diverse species, is suggestive of a strong coevolutionary relationship.

5. That meaningful conservation of any system depends not on the conservation of the components of the system but on the conservation of the processes operating within and upon the system (Ricklefs, Naveh & Turner 1984).

Most of the processes operating within the ecosystem represented by the NTR are not reflected in the findings of the present study. Others are represented but remain unidentified due to the limitations of the human mind. The following process complexes were identified as playing an important role in the development of the emergent pattern referred to as the Northern Tuli

ECOSYSTEM PROCESSES

For the purposes of this discussion, the following are taken as axiomatic:

1. That change is the only constant in the natural world;
 2. That patterns observed in ecosystems reflect the underlying processes within those systems, but that identification of a pattern does not imply identification of the responsible process (Cale *et al.* 1989);
 3. That a pattern observed in an ecosystem is subject to chaotic forces, and that the development of a particular pattern is highly dependent on the original state of the system (Jensen 1987, May 1989);
 4. That the driving force behind all ecosystem processes is the Second Law of Thermodynamics - implying that disruption of any one process within a system has a domino effect on other processes within the system; and
 5. That meaningful conservation of any system depends not on the conservation of the components of the system but on the conservation of the processes operating within and upon the system (Ricklefs, Naveh & Turner 1984).
- Most of the processes operating within the ecosystem represented by the NTGR are not reflected in the findings of the present study. Others are represented but remain unidentified due to the limitations of the human mind. The following process complexes were identified as playing an important role in the development of the emergent pattern referred to as the Northern Tuli

Game Reserve.

Selective Predation by Jackals

Chapter 3 described and recorded the co-operative, selective predation by jackals on adult impala in the south-central region of the NTGR. As a recorded pattern, these results were very interesting in themselves. But what are the underlying processes which have resulted in the emergence of a pattern not previously recorded in Africa?

As indicated at the end of Chapter 3, one of the possible reasons for this may be the paucity of information on jackal predation derived from direct observation. While this is certainly a factor to be considered, it does not account for everything. The high percentage of old impala in the south-central region, as identified in Chapter 4, and the predominance of these old impala in the jackal prey data suggest that other underlying processes have given rise to a situation peculiar to the NTGR.

Predators have long been accredited with maintaining the health and fleetness of their prey populations by removing the old, the weak and the sick (Errington 1946, Curio 1976) - in effect selectively removing "physiologically" old animals from the system. This was termed the "sanitation effect" by Mech (1970). This "sanitation" effect implies, of course, a process of selective predation. Not all predators are selective all of the time, however, and this broad generalization of the beneficial effect of predators has been the cause of extensive debate and dissension. Temple (1987) has recently suggested that predators are only selective when preying on animals which are relatively difficult to capture, subdue and/or kill. His

conclusions were supported by the results of his study on the predatory habits of raptors. Reference to data on large mammalian carnivores from many sources revealed a similar trend (Temple 1987).

In considering the impala as a potential prey animal in relation to the pristine community of the eastern parts of Botswana it is apparent that predation on this species, as a medium sized antelope, was originally of several types. All the large African carnivores, including the jackal, prey on newborn and young impala. Once past the vulnerable early months, the predation threat by the different predators becomes unequal. Lions and leopards cannot hope to outrun a startled adult impala, and their tactics for concealment confirm a need to gain adequate proximity before launching an attack. Under these circumstances it is not surprising that no selectivity for old or weak medium sized antelope by these species has ever been demonstrated. Conversely, spotted hyaenas and wild dogs openly approach and "test" herds of medium sized antelope, and demonstrably select the compromised animals from the population (Pienaar 1969, van Lawick-Goodall 1970b, Kruuk 1972) although this ability seems to depend to some extent on the openness of the habitat (Reich 1981). The cheetah may or may not be selective for vulnerability. Jackals would, under these pristine conditions, be obliged to compete with the wild dogs and spotted hyaenas for the few available old impala and, being a generalist carnivore, would most likely make use of alternative resources - partly accounting for the scarcity of reported predation by jackals on adult antelope.

The pristine complement of predation processes no longer occurs in the south-central parts of the NTGR. The total absence of wild dogs and the relative absence of spotted hyaenas (Chapter 5) means that selective predation

definitely does not occur in this area at a rate comparable to the pristine condition. The northern areas, with a higher population of hyaenas, retain at least a component of selective predation by large predators on prey animals of the size of the impala. While the population of cheetahs has noticeably increased in the NTGR in recent years, the population of this species was so low prior to 1984 (Lind 1974, pers. obs.) that its role in the development of the observed pattern is negligible.

Elimination of any ecosystem process imposes a perturbation on the system which induces ecosystem stress (Odum 1985). Such ecosystem stress is responded to first by an alarm reaction and then by the coping reaction (Rapport *et al.* 1985).

In the case of the south-central region of the NTGR the ecosystem stress is represented by the preponderance of old animals in the impala population (Chapter 4, Section 1). A measure of the degree of this ecosystem stress is evidenced by the fact that during the course of the study two kudu and one impala were discovered which had died of old age. In a system which originally provided for removal of weak animals by selective predation, these incidents indicated early on in the study that pristine processes were inoperative or compromised. The coping reaction of the ecosystem in this case is represented by the replacement of the selective predation process by an alternative species not normally a participant - the black-backed jackal. However, total replacement is not achieved as the jackal turns to easier prey - insects - during the wet months of the year (Chapter 3).

Predation by the black-backed jackal does to some extent compensate for the absence of the natural selective predators. The method whereby this

replacement is achieved is uncannily reminiscent of the true process - recall the "testing" behaviour during the selection phase and the fact that large groups are formed during predation (Chapter 3)- the norm for wild dogs and hyaenas when hunting such prey. However, despite the established existence of a stereotyped, successful selective predation sequence, a large proportion of the impala in the south-central region remain old, have no incisors, and lose condition severely during winter, confirming that this resource is not utilized to the extent where the pristine age-structure of the prey population is maintained.

The absence of the natural selective predators of impala from the south-central region of the NTGR has therefore resulted in the pattern observed today - a preponderance of old, weak animals in the impala population and the existence of the observed selective predation by the jackals on these same old impala.

The results of the present study could be used to justify even greater efforts to remove jackals from farming areas and even private "conservation" areas. Prejudice against predators is an emotive issue that can easily become inflamed. Yet if the full implications of the highly selective nature of the jackal predation recorded here are considered, it will be realized that jackals may be a most valuable asset in an agricultural system which cannot hope to regain the original predator community. In hunting old antelope, and even in hunting sheep, jackals are expressing a profound instinct to prey upon those animals which are the least well adapted to exist in the environment in which they find themselves. While wanton destruction may seem unacceptable, the final, permanent removal of the jackal from the ecosystem may have even more serious long-term repercussions. Every effort should be made to reduce

the conflict between stock-farmer and jackal to the point where persecution is no longer necessary. Surely this is the only long-term solution.

Seasonality in jackal predation

Predation on adult impala was demonstrated to be closely linked to rainfall. When available, following good rains, insects were the major source of food and impala were ignored as a resource - even as scavengeable items. Again this pattern is a reflection of underlying processes. Four processes were perceived to potentially make a contribution to the seasonal pattern:

First, the jackal, as a demonstrably opportunistic predator, is predictably predisposed towards eating whatever is most readily available. The limitations of optimal foraging theory aside, the jackal appears to follow the coyote pattern of foraging for that which can be optimally utilized (MacCracken & Hansen 1987). The superabundance of insects after good rainfall may make these the most profitable resource at that time of the year.

Second, the fact that, at least while the vegetation is green, insects can be found in open areas may be of importance in the selection of insects as prey items. Travelling over large distances and/or penetrating dense vegetation definitely exposes a foraging jackal to a greater predation risk than does foraging over a limited area of open plains.

Third, the risk associated with predation on larger prey, both from exposure to injury by the prey itself and from competitive interaction with larger carnivores is considerably higher than that associated with predation on insects.

Fourth, improved summer grazing conditions may make the older impala more difficult to subdue because they would be in better condition.

The seasonality of the jackal predation is an established fact. Whether it is explained by some, all or none of the above processes is insignificant. It is the seasonality itself, whatever the cause, which is an important component of the dynamics of the observed pattern. The abundance of old impala in the southern areas is demonstrably higher than in the northern areas of the Reserve. A component of this old section of the population will always be more susceptible to predation than the average of the population. If, therefore, predation by jackals on these impala was continuous, a greater proportion would be removed on an annual basis. The fact that the old impala are not reduced to a minimal level is therefore a reflection of the seasonality of the predation pattern. This implies that even though the selective predation by the jackals mimics the pristine process fulfilled by wild dogs and hyaenas, it does not replace it completely. In particular, as shown by the comparison between 1987 and 1988 predation levels, a series of years of good rainfall could mean that this process would be only minimally replaced. The jackals do not, therefore, effectively fill the ecological role vacated by the larger selective predators.

Jackal population regulation

Population density is regulated by a complex array of processes (Caughley 1977). Under conditions where food supply is not limiting, jackals have been recorded to reach a population density of 22 km^{-2} (Hiscocks & Perrin 1987).

The density of 4-6 jackals km^{-2} recorded during the present study is

extremely high in relation to other areas which do not have an artificially abundant food supply. However, as demonstrated in Chapters 3 and 4, the impala in the south-central region of the Reserve represent an abundant source of food for the jackals. This source of food is artificially created by the absence of other selective predators. Furthermore, the availability of this abundant food supply actually increases (through loss of condition and thereby increased vulnerability) at that time of the year (late/winter spring) when the jackals could conceivably experience a lack of food in the form of insects, rodents and young antelope. Significantly, this time of the year coincides with the period most closely associated with potential recruitment into the population - i.e. the whelping season.

The absence of a process of selective predation by wild dogs and hyaenas (and possibly the absence of more direct competition between these predators and the jackals) is thus responsible for a density of jackals far higher than that which is normally expected in a savanna ecosystem. The root cause of this situation is, of course, the process of predation by man on the wild dogs and hyaenas prior to the formation of the Reserve (Chapter 5).

Man induced process changes may have created the high jackal population in the south-central NTGR via yet another mechanism. Jackals were demonstrated to prefer open habitats both during foraging and during resting (Chapter 3). The extensive *Boscia foetida* savanna of the south central region of the NTGR is a result of intensive human settlement (Chapters 2 and 5). *Boscias* are not utilized for firewood by the Batswana people but are conserved for use in times of drought (Coates Palgrave 1977), and thus almost all of the remaining trees in this habitat are *Boscia foetida* or *Boscia albitrunca*. The overgrazing and selective wood collection - associated with the settlements

fringing the lower Majale River - have yielded the open, pioneer dominated short-grass plains with sparse woody vegetation which is in stark contrast to the adjacent riverine and hilly areas. The artificially increased availability of a preferred habitat type - through the processes of overgrazing and wood collection - is undoubtedly reflected in the sustained high jackal population of the region.

Jackals and other prey

The concept of the regulation of prey populations by predators is the subject of extensive literature. Early consensus was that predators had a major controlling influence on prey population abundance. Studied prey and associated predator populations demonstrated sequential patterns of increase and decline which suited this conclusion very well (Lotka 1925, Volterra 1926 in Chapman 1931). A later paradigm was that the major changes in prey populations were due to other environmental factors - the predators were concluded to only be responsible for removing the excess animals which would otherwise have died of other causes (Errington 1946). This was taken to imply that predators could not exert a controlling influence on prey populations, but could merely modify the changes induced by major cycles in climate and food and habitat availability. More recent work has demonstrated that both may in fact be true (Erlinge, Goransson, Hogstedt, Jansson, Liberg, Loman, Nilsson, von Schantz & Sylven 1984). In situations where a predator depends on a specific prey animal for its survival, its numbers cannot achieve such proportions as to be the major factor in the fluctuations in abundance of the prey. In contrast, however, when a predator has a reliable supply of food from one source it can exert a considerable influence on the dynamics of the populations of other prey species (Erlinge *et al.* 1984, Paine, Wootton &

Boersma 1990, Woodroffe, Lawton & Davidson 1990). In extreme cases, where the predator, supported by an abundant supply of food, is numerically abundant compared to a certain alternative prey species, that species may be said to be in a "predator trap". Under such circumstances the population of the affected species cannot attain a level at which predation is negligible in relation to other processes (Caughley 1981). Predation therefore limits, or may even eliminate, the trapped population. Attainment of a predator trap situation is likely to follow a sudden reduction in numbers due to some other factor to a level at which predation can become a limiting factor (Pearson 1966, 1971, Fitzgerald 1977, Gasaway *et al.* 1983).

Independently to the identification of the impala population as a reliable food resource, anecdotal evidence indicated that a predator trap situation exists in the south-central region of the NTGR with respect to the following species. In all cases healthy populations of these species existed in the area prior to the drought of 1983/84 (Lind 1974, pers.obs.), with a major reduction in all species accompanying this severe drought.

1. Springhaas *Pedetes capensis*. Springhaas were abundant on the short-grass plains of the south-central region - ideal habitat for this species (Smithers 1983). Following the drought of 1984 springhaas were reduced to one colony within the study area. In the following four years no springhaas were seen anywhere else in the south-central region other than at this colony, despite the fact that numbers at this colony are high. Dispersal of these animals across the open plains in the presence of the high jackal population is likely to be almost impossible. Jackals are adept at capturing springhaas, particularly when hunting in groups (Ferguson 1980).

2. Warthog *Phacocoerus aethiopicus*. Warthogs are now extremely rare in the south-central region. Again, this situation was precipitated by the 1984 drought but, despite the subsequent development of dense stands of perennial grasses, no improvement was noted in the subsequent four years. Attempted predation by jackals on a family of warthogs was once observed (Chapter 3). Jackals are capable of capturing and killing warthogs up to a year old (Read pers. comm.). The well developed pack hunting techniques recorded in the present study may or may not increase the susceptibility of adult warthogs to predation. However, the chances of a sow defending a litter of young piglets against a pack of jackals is likely to be negligible - two jackals are 67% successful at killing young antelope despite the defensive behaviour of their mothers (Wyman 1967). In a recent film made in northern Botswana by Derek Joubert (*Journey to a Forgotten River*, Botswana Films (Pty.) Ltd., 1990) a group of four jackals is shown attacking a warthog sow with four young piglets. The sow's attempts at defending her young are nullified by the teamwork of the jackals. Two young are killed while a third is injured during the attack. The inability of the sow to attend to all her piglets and all the jackals at once made the outcome of the encounter inevitable. The influence of group predation on recruitment in this species in the NTGR is likely to be considerable.

Game count data support the observation that warthog numbers have not increased significantly since the drought (le Roux 1988, 1989). This is despite the fecundity of this species which enables it to increase rapidly following a reduction in numbers (Mason 1982).

3. Bat eared foxes (*Otocyon megalotis*). Bat eared foxes were extremely abundant in the central areas of the Reserve prior to 1984 (Lind 1974, pers.

obs.). Berry (1978) recorded between 2,25 and 9,2 bat-eared foxes km^{-2} in the NTGR. Subsequently none have been seen in the study area despite an abundance of their preferred food - harvester termites *Hodotermes* sp.. One small family group has been reported from the northern parts of the Reserve (Petty pers. comm.). Young bat-eared foxes are susceptible to predation by jackals (Schaller 1972), a fact which may account for the considerable aggression shown by bat-eared foxes towards jackals (Ferguson 1980).

The presence of a generalist predator with a reliable food supply is the classic situation for the development of a predator trap. The anecdotal evidence given above indicates that this is indeed the case, and probably extends to many other species of mammals as well as birds and reptiles which were simply not monitored. The low numbers of the affected species means that the likelihood of finding remains in faeces or of recording predation by direct means is extremely low indeed. In view of the above, the default assumption should be that the populations of at least some of the species - be they insects, reptiles, birds or mammals - in the NTGR are subjected to constraints by the unnaturally high jackal population. While this is likely to be most intense in the south-central region, a spill-over to other areas is likely in view of the contiguous nature of the different parts of the Reserve.

All of the adult female impala shot during the present study between June In the case of the impala population the possibility of a within-species predator-trap is evident in the NTGR. As mentioned above, the high jackal population density can be ascribed to the presence of a high quality, easily available prey - the old impala - at a time of the year when food supply might otherwise be limiting. Jackals are known to be adept at hunting and killing young antelope (Wyman 1967, Pienaar 1969, van Lawick-Goodall 1970a, Lamprecht

1978a, Stander 1987), particularly when hunting in groups (Wyman 1967, Lamprecht 1978a). The impact of such predation is cryptic, as the small carcasses are rapidly consumed and little remains to tell the tale. In addition, impala give birth within a restricted lambing period during summer (Smithers 1983), and the concentration of predation during this time of greatest vulnerability makes it exceedingly difficult to identify processes responsible for a recruitment lower than the theoretical maximum.

The presence of a high population of a generalist predator with a demonstrated propensity towards co-operative hunting is highly suggestive of a potential dampening effect on the impala population of the NTGR. Inspection of available data supports this hypothesis.

A high impala population in the NTGR (est. 22 000, Walker 1983) declined to approximately 6 600 in 1984 (Joubert 1984), much of the decline being due to the 1983/84 drought, with some of the difference possibly being due to the different census methods used by the two authors. Using the same methods as Joubert (1984), subsequent estimations have been 5 474 (1986), 4 617 (1987), 6 959 (1988) and 5 884 (1989) (le Roux 1988, 1989). The high count in 1988 was ascribed to observer inexperience (le Roux 1988, 1989).

All of the adult female impala shot during the present study between June and November were pregnant - even the oldest individuals with no incisor teeth. Skinner (1969) reported that a single female impala in the northern Transvaal produced lambs every year of her 13 year productive lifespan, and Fairall (1983) recorded a fecundity of 95% in mature impala females in the Kruger National Park, with no indication of reproductive senility even in the oldest animals. Both these authors recorded the fact that drought has little

or no influence on the high fecundity of impala. animals are being born but are not being recruited into the population it can be deduced that a significant

Taking: factor is operating within the population. Furthermore, the fact that the population in the south-central region is skewed towards the older

1. A minimum fecundity of 95% in adult impala (Skinner 1969, Fairall 1983, present study);

2. Attainment of female sexual maturity at 18 months - i.e. production of the first lamb at 2 years (Fairall 1983);

3. A potential longevity of 15 years (Skinner 1969);

4. A sex ratio at birth of 1:1 (Fairall 1973);

5. An adult sex ratio in the NTGR of 70% females to 30% males (unpubl. data); and

6. A mortality rate of 36% in the first year under natural circumstances, including predation (Fairall 1983, Kruger National Park data), and assuming:

1. An even rate of mortality of 4,6% p.a. from the second year (64% of mortality after 1st year (Fairall 1983));

2. That a population of 6 600 was present at the beginning of 1984; and

3. That 25% of the population at the beginning of 1988 consisted of lambs from the 1987/88 lambing season,

then: the impala population could, even under mortality conditions such as those prevailing in the Kruger National Park, including years of drought, have reached a total of 24 200 animals by the beginning of 1989. However, not only has the impala population of the NTGR not increased but, in fact, shows a

decline of 11% over this period. Because the animals are being born but are not being recruited into the population it can be deduced that a significant mortality factor is operating within the population. Furthermore, the fact that the population in the south-central region is skewed towards the older age-classes (Chapter 4, Section 1) indicates that it is the younger components of the population which are most affected by this mortality factor. With the ideal theoretical conditions for a predator trap in existence in the NTGR, and the established fact that group-hunting jackals are highly successful predators of young antelope, at least some of this negative growth can be ascribed to jackal predation. The interesting corollary of this situation is that it is the impala population itself - via the high proportion of old animals, which are primary prey for the jackals during winter - which is responsible for its own demise.

Jackals and the epizootiology of rabies

Jackals are accused of being a major vector of rabies in Africa (Meredith 1982). Rabies was not incorporated as a part of the present study, and therefore no substantive discussion on this topic will be attempted. Nevertheless, some recorded observations, combined with the general conclusions of the present study, indicate a possible avenue of future investigation.

Rabies was positively diagnosed in jackals on two occasions during the study, and one further case was suspected but not confirmed. All cases were diagnosed using the Fluorescent Antibody Technique by the Veterinary Services Laboratory, Gaborone. In one case distemper was specifically excluded as a

differential diagnosis after it was suspected from clinical signs.

What is thus recorded by the present study is two cases of confirmed rabies within an area where the jackal population density was determined to be between 4 and 7 km⁻². What is remarkable is not what was recorded but what was not recorded. If indeed the jackal is the ideal vector for rabies as it is claimed to be, then the dense population recorded here combined with the confirmed positive cases could, according to a classical interpretation of the mode of spread of rabies in wild carnivore populations (MacDonald 1980), have led to a large scale rabies epizootic amongst the jackals of the Reserve.

The fact that rabies is relatively scarce in natural ecosystems represented by National Parks has been known for some time (Cumming 1982, de Vos pers. comm.). Cases of rabies in the Kruger National Park, South Africa have been diagnosed in dogs entering the park from neighboring areas, but not in wild carnivores resident in the Park. This situation has been closely monitored by resident veterinarians since 1961. The conclusion drawn from these observations is that the healthy natural system of the KNP does not allow the development of a cycle of rabies (de Vos pers. comm.).

The cases of rabies recorded during the course of the present study may have originated in adjacent areas, as affected animals can move over considerable distances, and rabies in jackals in the adjacent northern Transvaal is commonplace (Meredith 1982). Even if the recorded cases originated from within the Reserve, the present study has demonstrated that even in an artificially high population of jackals the presence of the disease does not manifest itself as an explosive or even a mild epizootic.

Springer (1982) suggested that limited aggression within a population of coyotes could be explained by acquaintance with animals in adjacent home ranges. This phenomenon was used to explain the absence of territorial aggression, the high level of tolerance, and the advanced level of co-operation recorded in the present study (Chapter 3).

The spread of rabies within a carnivore population depends on close physical contact (MacDonald 1980). This may be expected to occur as part of the normal social interactions within a group of jackals, or as an aggressive encounter between jackals from different social groups. Under the situation prevailing in the NTGR the former is a possible scenario, but the latter, due to minimal levels of aggression, can be concluded to be of minimal likelihood: An aggressive interaction requires motivation from both participants, and the elevated aggression of a jackal exhibiting symptoms of "furious rabies" may not be matched by a conspecific which is accustomed to mutual tolerance. A potential mechanism for the spread of rabies through the population is thus reduced by the stable, established social structure of the NTGR jackal population.

In contrast to the above, jackals from farming areas are heavily persecuted. The resultant disruption of the social system is certain to result in a situation with less acquaintance between individuals, less tolerance and elevated aggression, as reported in coyotes by Springer (1982). Under such circumstances, the opportunity for the spread of rabies amongst the few remaining jackals is likely to be enhanced - a consequence of the vacuum effect caused by the removal of established adult animals (MacDonald 1980, 1982).

The fact that the above scenario accords well with observed trends in rabies epizootiology indicates that there may well be reason to suspect that the stable, undisrupted ecosystem is resilient to rabies epizootics. The results of the present study suggest that the key to the enigmatically low incidence of rabies in a normal or even a high jackal population may be the nature and stability of the population. Specific investigations into the processes of spread of rabies epizootics could benefit from further investigations into jackal sociology, particularly the relatedness between individuals within high-risk and low-risk areas.

Grooming and ectoparasite ecology

Grooming has been identified by the present study as an important process for the maintenance of acceptable ectoparasite burdens on impala and possibly many other ruminants (McKenzie 1990). In the context of the results of the present study, grooming is also an important process at the ecosystem level.

As has been shown by the present study, grooming, as a natural bodily function, results in attrition of the incisor-canine complex of antelope. Such attrition, if allowed to proceed for long enough, eventually leads to total absence of any dental elements in the anterior mandible (Chapter 4, Section 1). As indicated in Chapter 6, this condition is characterized by a high parasite load, particularly of engorged adult ticks, poor condition and, through repeated grooming efforts, the baldness here dubbed autogenous alopecia.

As demonstrated in Chapter 4, old impala constitute a high proportion of the adult population of the south-central region of the Reserve. The presence

of this high proportion of old animals has profound implications for tick population dynamics. As compromised hosts, the old impala are unable to remove the parasites which infest their bodies. The high numbers of engorged female ticks on these impala means that, per unit time, these animals are producing a significantly greater number of ticks to infest the environment than would normally be the case. Development and engorgement of *Boophilus decoloratus* on the host takes approximately 21-30 days. An adult *B. decoloratus* female lays approximately 2 500 eggs after engorgement (Soulsby 1968). Old, toothless female impala carried a mean of 130 adult ticks (Chapter 4, section 4)). This amounts to the production of approximately 65 engorged female ticks per month per old female. At a density of 15,6 impala km^{-2} there are approximately 700 impala in the south-central region of the Reserve, 5-30% (35 - 200) of which are old animals (Chapter 4, Section 5). This means that the presence of the old animals results in the production of between 5,5 and 32,5 million ticks per annum in the south-central region of the NTGR. These figures are approximate, but as adult tick numbers are at a minimum in winter (Short & Norval 1981), they are likely to represent a minimum value. Even if the true numbers are an order of magnitude less than those calculated the impact of the presence of these old animals remains considerable.

The role of the above scenario in the tick population dynamics of the Reserve is indicated by two related phenomena:

1. Impala generally carry few adult ticks even when larval and nymphal tick burdens exceed 600 (Horak 1982). This is confirmed by the observations on 61 impala shot in the northern parts of the Reserve and by the absence of adult ticks on the two impala from the northern areas processed during the

quantitative study (Chapter 4, Section 4). The presence of relatively high adult tick burdens on the southern control animals (mean = 30 ± 17 , n = 6) indicates that some environmental factor has resulted in a higher infestation rate in the south-central parts of the Reserve.

2. Total attrition of incisors naturally represents the oldest age group as can be determined from incisor wear (Roettcher & Hofmann 1970). The oldest age group that can be discerned by attrition of mandibular cheek teeth corresponds to a relative age of 8,5 years (Spinage 1971, Murray 1980), and is distinguished by extreme wear of the first molar tooth (Spinage 1971). Skinner (1969) has recorded a lifespan of 15 years for an impala living under natural conditions in the nearby northern Transvaal. By comparing incisor and molar ages, it can be seen that many of the "old" animals in Tables 11 and 12 and Appendix A8 are not of the oldest age category when molar wear is used as the criterion. Animals with totally worn incisors may be from 6,5 to 8,5 years old as determined by molar attrition, i.e. approximately half the potential lifespan recorded by Skinner (1969). In other words, animals can become "incisor" old before they are "molar" old, implying that incisor attrition, of the type which can be exclusively ascribed to grooming, is proceeding at a relatively rapid rate in this population. No vertical attrition of incisors was recorded by Roettcher & Hoffmann (1970), Spinage (1971) or Murray (1980) even in their oldest age groups. This implies that the animals in the population under consideration in the present study are required to groom themselves at a far greater rate than the populations considered in these three independent studies. And a high rate of grooming supports the above scenario - i.e. the greater rate of infestation by parasites from the old animals necessitates excessive grooming by the younger animals resulting in early incisor attrition. Because of the ecosystem

implications of the grooming process, these animals could be said to become "ecologically" old before they are chronologically old.

A single specimen of an impala mandible exhibiting total vertical attrition has been obtained from Pilanesberg National Park, Boputhatswana. This animal also exhibited the extreme molar attrition described by Spinage (1971). None of the old animals from the NTGR exhibited such extreme molar attrition. In other words, this animal was both ecologically and chronologically old - implying that the above scenario does not exist in the Pilanesberg National Park at the present time, but also confirming that incisor attrition due to grooming is not unique to the NTGR.

The presence of susceptible hosts is known to be a major factor in the build-up of high numbers of ticks in the environment (Patrick & Hair 1978, Lightfoot & Norval 1981, Norval & Lightfoot 1982). What the present study has demonstrated is that susceptibility of antelope to ticks may be strongly linked to grooming ability. This varies not only between species but also between individuals within a species. The presence of animals which are unable to groom, even if only a few individuals, is possibly the single most important factor in the build-up of ticks in the African environment.

The cyclical annual appearance and disappearance of autogenous alopecia is possibly a reflection of tick ecology in mixed habitats. It is known that woodland areas are often the most heavily infested with ticks (Norval 1977, Patrick & Hair 1978, Hair & Bowman 1986). As the open areas of the NTGR are almost totally devoid of vegetation during the winter dry season due to the predominance of annual herbaceous plants (Chapter 2), impala must, of necessity, utilize more densely vegetated habitats in order to obtain

sufficient food - those utilizeable trees that are available in the open areas are exceptionally heavily browsed (Joubert 1984, pers. obs.). Following the appearance of fresh shoots of grass and *Tribulis terrestris* following the first summer rains, the impala no longer need to penetrate the dense vegetation in search of food. It appears, therefore, that the sudden disappearance of autogenous alopecia is related to the equally sudden change in habitat following the first substantial summer rains. Certainly both phenomena occur at the same time (Chapter 4). The change to open habitats would result in an immediate decrease in the rate of tick infestation, and thereby a decrease in the necessity to groom. While absolute tick numbers may be higher in summer, risk of exposure to infestation may thus be lower due to changes in habitat choice. Reduced grooming would then allow the pelage to regenerate. The velvety appearance of the old animals at this time (Fig. 35) is evidence of a sudden, synchronised regrowth of the hair, and suggests that this may be the process underlying the cyclical nature of the occurrence of autogenous alopecia. Further investigation may yield interesting results in this regard.

Grooming, autogenous alopecia and disease

Grooming itself is a natural process. Its consequence may be the general maintenance of the appearance and alignment of the pelage, or it may be the more specific process of the control of the number of ectoparasites within the pelage (Snowball 1956, Riek 1962, Bell *et al.* 1962, Bell & Clifford 1964, Bennett 1969, present study).

The consequence of excessive oral grooming in antelope extended by unnatural longevity as recorded in the present study is the attrition and

eventual destruction of the organ responsible for this function. Thus the extension of the natural process beyond its natural limitation results in its elimination. The result of the elimination of the process is, in turn, the accumulation of the products (parasites) normally subjected to a degree of homeostasis by this process. These results reflect the usual consequence of the elimination of any natural process. In addition to the loss of homeostasis, the continuation of the process in a non-functional manner results in the syndrome of autogenous alopecia. This pathological syndrome is thus the result of a perfectly natural process - grooming.

The question that arises is "Is autogenous alopecia a disease?". At the level of the individual antelope autogenous alopecia does not constitute a disease. The animals exhibiting this syndrome are merely old - a natural consequence of life. At the level of the population autogenous alopecia also does not constitute a disease. A population must normally be comprised of individuals from each age-class, and the existence of old animals in the population certainly does not constitute a pathological syndrome with respect to the population itself. At the level of the ecosystem, however, autogenous alopecia does indeed constitute a disease. The disease is the consequence of the disruption of the natural process which regulates the number of old animals in the ecosystem. The autogenous alopecia is merely a symptom in the ecosystem indicating that this disruption has occurred. The existence of a positive feedback loop whereby the autogenous alopecia, via the production of excessive numbers of parasites, accelerates its own development is typical of the terminal stages of disease. The transition from a natural to a pathological process following disruption is thus as much a feature of ecosystems as it is of physiological systems.

Selective predation, grooming and man

"Premeditated control of animals is a prerogative that only man can exercise. If man takes this responsibility lightly, he may alter the natural order and indirectly threaten his own place in the unnatural world thus created" (McCabe & Kozicky 1972: 393,394).

Old animals breed more parasites. Young animals become old when they groom more often than usual. Old animals, in the absence of selective predators, remain active producers of parasites within the system until removed by eventual old age or opportunistic selective predation.

Given a pristine scenario in the African savanna, a certain percentage of impala in any population will belong to the oldest age category within the population. On approaching natural senescence these old animals would become more prone to selective predation than the average members of that population. This susceptibility would, in the normal course of events, be enhanced by factors which would stress the already compromised physiological responses of these animals - eg. starvation, pregnancy, lactation, disease, high parasite load etc.. If, however, predation as the final mortality factor is removed, these old animals may persist for many more years in the system.

As a result of the presence of man, wild dogs and hyaenas are absent from most of Africa today. It is possible, therefore, that the scenario which has developed in the south-central region of the NTGR could be the forerunner of similar situations in the many unnatural islands created throughout the continent as nature reserves and game farms where the predator community is no longer intact. The development of the situation described in the NTGR has

taken over 25 years to reach current proportions, and may be as a result of processes peculiar to the NTGR itself. The fundamental nature of the processes of grooming and selective predation are, however, likely to result in the development of the same scenario on a large scale in other man-modified ecosystems in Africa in the future. The fact that autogenous alopecia was also recorded in steenbok and kudu in the present study (Chapter 6) highlights the potential of the syndrome described here to involve other components of the ecosystem.

The only other case of a high incidence of autogenous alopecia in Africa known to me at the time of writing was recorded in the north-eastern sector of the Kruger National Park in South Africa in the mid-1960s. Many old impala along the Levubu River in this area exhibited the classic signs of autogenous alopecia as described in the present study (Fairall, *in litt.*) At first the presence of a presumably intact predator population in the KNP appeared to contradict the conclusions of the present study. Significantly, however, Fairall (*in litt.*) who investigated the presence of these "mangy" impala, reports that predators in this area, particularly wild dogs and hyaenas, were attracted over the Reserve boundary, which at that time was unfenced, into neighboring Mocambique where they were destroyed by occupants of an agricultural settlement. The two areas, remarkably similar in other ways, thus are case studies of what may happen to systems when predation processes are removed or compromised. Factors such as dustiness (greater than normal abrasiveness), high impala populations, and the long-standing *status quo* in the two areas may explain why they are the first to exhibit the results of such interference.

Outside of Africa a remarkably similar scenario is evident from Isle

Royale in Canada - coincidentally the site of a long-term study of predation by wolves. Moose on this 544 km² island are preyed upon by wolves (Mech 1970, Peterson 1977). Mech (1970) reported that bare areas of skin on the moose were related to tick infestation. This was disputed by Peterson (1977), but later Peterson agreed with this observation (Peterson 1989). Moose first populated this island in the early 1900's. In the absence of any predators moose numbers increased dramatically and crashed several times due to habitat over-utilization (Peterson 1977). Large numbers of old moose in this population were found to carry large numbers of ticks and to have areas of bare skin (Mech 1970) in contrast to Alaskan moose populations (Franzemann in Peterson 1977). Wolves only populated the island in the late 1940's, and subsequent to their establishment were shown to prey selectively on the older component of the moose population. Subsequent to the arrival of the wolves the moose population did not reach such extremely high numbers until the unexplained decline in wolf numbers in the early 1980s. With the increased population and the reduced predation, tick infestation has again become a severe problem (Peterson 1989). The occurrence of alopecia in moose has been found to be correlated to the severity of tick infestation, and has been found to be due to grooming behaviour in response to this infestation (Glines & Samuel 1984). While the parallels between the two studies may be only superficial, the implications from both these areas of the absence of natural processes is readily apparent.

At the time of writing I am aware of increasingly severe tick problems on many small game reserves and game farms throughout southern Africa. Many cases of severe infestation, particularly of the ears of animals (which cannot be groomed!) have been reported in conversation with farmers and conservation officials. Cases of deaths amongst kudu due to tick induced abscesses of the

ears represent the most extreme cases. Ferrar & Kerr (1971) reported a crash in a population of reedbuck *Redunca arundinum*; a high tick population associated with an artificially high ungulate population was considered to have played an important role in this crash. In view of these increasingly severe problems in areas where the natural predator community has vanished, the likelihood that autogenous alopecia and its associated ecosystem ramifications will become of increasing importance is potentially high - time being the factor required for the perturbation to become fully apparent, as is usually the case with disruptions at the ecosystem level (Odum 1985).

IMPLICATIONS

The overall implications of the findings of the present study will be discussed at two levels - first at the academic/heuristic level and second at the management level.

Academic/heuristic implications

Specific implications of the findings of the present study have already been discussed where appropriate. What remains is to briefly discuss the holistic implications of the study from the point of view of its potential contribution to the understanding and conservation of ecosystems in general.

It became apparent to me during the course of the study that I was dealing with a disturbed ecosystem. The disturbance had been created by man, and was manifested in the absence of certain essential processes from the system. My medical background obliged me to conclude that the system was "diseased". Initially this appeared to be a spurious conclusion. Perhaps,

however, there may be profound implications to this "clinical" observation.

Strong parallels exist between the functioning, or physiology, of organisms and the functioning of higher-order systems - i.e. ecosystems (Knight & Swaney 1981). At first glance such parallels may appear superficial, and it certainly appears "unscientific" to make too much of this comparison. However, the definition given by Lindeman (1942) of an ecosystem i.e. "The ecosystem [is any] system comprised of physical-chemical-biological processes active within a space-time unit of any magnitude" certainly indicates that the distinction between organisms and ecosystems may not be all that distinct. Indeed, using this definition, the distinction drawn by us between organisms and ecosystems may be said to be entirely artificial.

A holistic understanding of ecosystem or even of bodily function is an almost superhuman feat, and sufficient knowledge of both systems to draw meaningful comparisons is thus a rare accomplishment. Fortunately, however, functional similarities between these different levels of organization are highlighted by dysfunctional similarities. The stress response at the organism and ecosystem levels are uncannily similar (Odum 1985, Rapport *et al.* 1985), drawing us yet closer to considering ecosystems as mega-organisms. At both levels, disruption is followed by a stress reaction, the stress is followed by a coping reaction, and an insufficient coping reaction is followed by system collapse (Rapport *et al.* 1985).

It could be said that the similarities between organisms and ecosystems are simply due to the fact that both systems are cybernetically regulated, and that the feedback loops result in the same sequence of events at both levels - a predictable consequence of the laws of thermodynamics.

Does this parallelism belong in the realms of academia? Or does it have a greater relevance? After all, James Lovelock tried to portray the world as a single organism - Gaia (Lovelock 1982) - yet he failed to convince the public at large - let alone the scientific community - of the relevance of his hypothesis.

I believe that the parallels need to be taken one step further for their significance to become fully apparent. The outcome of stress at the organism level is disease. This disease is manifested in various symptoms, all of which can be traced, via physiological or pathological processes, to the original stressor. I believe that the same principle applies at the ecosystem level, with ecosystem disease and ecosystem pathology being the outcome of unresolved ecosystem stress. With the exception of traumatic events, this disease is a reflection of processes at work within the system. And resolution of all the pathology depends on the reinstatement of the original processes which were disrupted by the original stressor. Failure to do so will result in failure to restore functional status to the ecosystem. Processes, not components, are the key to restoration.

Ecologists know too well the role that processes play in ecosystems. And the burgeoning branch of this science known as "Restoration Ecology" applies this knowledge to restoring disturbed ecosystems. The hiatus that remains is in passing on this knowledge to the general public which is still marching to the tune of species, or occasionally habitat, conservation. I believe that this hiatus is due in no small measure to the fact that nobody can truthfully claim to fully understand the functioning of any ecosystem. How can anyone therefore teach the lay public - who have even greater difficulty grasping the slippery complexities - about ecosystem function. And if we do manage to

explain the intricacies of ecosystem function, we must now end off by saying that it is all chaos anyway! (May 1989).

Enigmatically, dysfunction is easier to understand than function. Every person on Earth, no matter how "primitive", has an understanding and some personal experience of how their own bodies can, and do, malfunction. Teaching people about disease therefore means teaching them about something which they understand **and can personally relate to.** And using the parallel, as outlined above, between body and ecosystem, an understanding of how ecosystems can go wrong can be almost instantaneously achieved.

The parallel between the body and the ecosystem is not a spurious one. Using this parallel to create increased awareness of the importance of environmental conservation may nevertheless sound simplistic. But if they do not resort to being simplistic when the moment demands it, will ecologists ever transfer their knowledge to where it really matters - the public at large? I believe that the present study illustrates the processes of disease in an ecosystem, and illustrates how this can be ascribed to interference in fundamental processes. The problem, and the solution, illustrate how ecosystems can and should be conserved by conserving the integrity of the ecosystem processes - even if the pristine components (species) have been lost to the system.

Management

The findings of the present study can only be of relevance within a framework of defined management objectives for the NTGR. As I am not aware of any defined objectives for management of the Reserve in existence at the time

of writing, the statements made here are made assuming that any such future statement of objectives will include the principle that "The impact of man-induced changes on the functioning of the ecosystem will be minimized".

The following is a brief synopsis of the management implications of the study.

Continued absence of selective predation by wild dogs and hyaenas in the south-central region of the NTGR will mean that numbers of old impala are likely to remain high or even increase in this part of the Reserve. This means that the jackal population will remain high, that parasite numbers will continue to increase, and that small animals will remain in a predator trap situation unless a series of exceptionally wet years allows population recovery despite the heavy predation losses. The spill-over effect of the high jackal population on the rest of the Reserve should continue or increase, with stochastic events making this an unpredictable process.

The components of the ecosystem stress and the coping reaction have been identified. The fact that the stress remains unresolved due to dysfunctional processes means that the next component - ecosystem collapse (Rapport *et al.* 1985) (probably only partial collapse) - is inevitable if the situation is not resolved. As stated by Odum (1985:421) "When stress is detectable at the ecosystem level, there is real cause for alarm, for it may signal a breakdown in homeostasis"

A process-based management approach is essential to permanent resolution of the disruption of the NTGR ecosystem. Essentially this implies the reinstatement of selective predation on impala in the south-central region of

the Reserve. In taking a process-based management decision it is essential to realize that it is the process, not the components, which is of paramount importance. The following two management possibilities illustrate the priority assigned to the process.

1. Re-introduction of wild dogs. The findings of the present study provide a strong ecological motivation for the re-introduction of the wild dog into the NTGR. The large numbers of susceptible prey are likely to make the chances of successful re-introduction relatively high, and the exercise would prove instructive for similar undertakings in other areas. A single small pack of wild dogs would be sufficient for the purpose of restoring the pristine selective predation process in the south-central region, and the pack may remain in this region while there is an abundant supply of suitable prey. As the stock of old impala becomes depleted and as the pack increases in size the wild dogs could be expected to move over a wider area. Conflict with stock-farmers in surrounding areas could potentially arise if the Reserve is still not fenced at that time. This problem can be approached in one of two ways. The dogs can be re-introduced under semi-wild conditions wherein they are fed a supplementary diet which would contain them within a restricted area where their predation would be concentrated. Alternatively, the movements of the dogs should be closely monitored using radio-telemetry to determine the site, nature and seriousness of any conflict situations, whereupon appropriate preventative and compensatory action could be taken.

2. Process simulation. If, for some reason, wild-dogs cannot be re-introduced into the Reserve, an alternative would be to simulate the selective predation process. As indicated in Chapter 4, old impala can be reliably identified in winter by the appearance of autogenous alopecia at this time of

the year. These animals could be selectively culled from the population, thus simulating selective predation on the oldest age-class. Ideally, if this could happen over a protracted period, the carcasses could be used to encourage the spotted hyaenas from the north to frequent and perhaps eventually settle in the south-central region - a process which could be further encouraged by the provision of suitable, well protected, artificial denning sites. A degree of natural selective predation could thus eventually be established. Practical considerations may, however, dictate that a short intensive culling period be used.

Re-instatement of the selective predation process can be expected to precipitate the following sequence of events:

1. Reduction in the proportion of old impala in the south-central region;
2. Reduction in tick production and infestation. Environmental levels would decline only after several years due to the longevity of ticks;
3. Reduction in the jackal population due to removal of the super-abundant food resource. Initial fluctuations, disruptions and increased predation pressure on scarcer species could be expected;
4. Reduction in recruitment of jackals to areas outside the south-central region, with cessation of spill-over effects;
5. Recovery of scarcer prey species released from the predator trap; and
6. Unforeseen consequences.

Because of the possibility of the latter, monitoring of the changes is recommended.

The temptation to short-circuit events by direct reduction of jackal numbers is strongly discouraged. This symptomatic approach would not provide a permanent solution, would aggravate the imbalance in the impala age-structure, and could have severe stochastic consequences - eg. a rabies epizootic.

A process-based management approach will provide the only solution to what I suggest is a serious environmental problem which does require attention. The alternative - a lack of management action - would provide the opportunity to determine at what point ecosystem collapse will occur, and what ramifications this will have. The management decision rests with the landowners of the NTGR. It is hoped that whatever action is taken, or not taken, the opportunity will be used to learn from the experience in order that other conservation areas may benefit in the future.

1. One or two jackals rush towards a herd of resting impala. This is followed by close observation of the fleeing animals as well as by excited sniffing at the ground in the vicinity of the herd's original position;

2. A selected impala is cornered and harassed, with the aggregation of a larger group of jackals;

3. The prey is immobilized and possibly silenced by one jackal biting the throat;