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Abstract: By the end of 1994, 14 adult and three juvenile cheetahs (*Acinonyx jubatus*) had been successfully released into Matusadona National Park (MNP), Zimbabwe. These cheetahs had been captured in the southern part of the country where they had been reported to be causing stock losses. Four years after the translocation 13 adult and four juvenile cheetahs were present in the park. Eight records of cheetah litters during these four years gave an average litter size of 2.8 cubs and juvenile mortality between 3 and 24 months was recorded as 60%, much lower than was previously predicted. Adult mortality was estimated as 20.5%. The cheetahs used the tree-line habitat more than would be expected. They utilized the foreshore for hunting and eating and the woodland for resting and moving through the park. Prey selection had not altered significantly since the cheetahs were first released, impala (*Aepyceros melampus*) being the main prey species killed. There was no evidence that the cheetahs would over-utilize the available prey. Home range areas measured were smaller than those measured shortly after the cheetahs were released (53.8 km² compared to 135.5 km² for males, and 23.6 km² compared to 257 km² for females). All home range areas appeared to include an area of productive habitat (foreshore) and cover (treeline and woodland). A very high density of lions (*Panthera leo*) was recorded, 0.317 lions/ km² and hyaena (*Crocuta crocuta*) density was recorded as 0.13 hyaenas/ km². When compared to other conservation areas in Africa, MNP has very few hyaenas for the number of lions present. MNP also has a very low predator biomass for the available prey biomass. After correcting for prey biomass, a negative relationship was found between lion and hyaena biomass, and cheetah biomass for eight conservation areas in Africa, although the relationship was only significant for lion biomass compared to cheetah biomass. The overlap between cheetahs and lions in terms of prey selection is very small, lions preferring buffalo, *Syncerus caffra* (PSR = 9.25) and cheetahs preferring waterbuck, *Kobus ellipsiprymnus* (PSR = 4.67). The overlap in prey selection between hyaenas and cheetahs is considerable, both preferring waterbuck (Hyaena PSR == 1.00) and killing impala predominantly. Habitat preferences of lions and cheetahs were similar with both species using the tree-line and the foreshore more than would be expected and the woodland less than would be expected. Population Viability Analysis concluded that the population of cheetahs was viable and had a 100% chance of persisting for a 100 years. The translocation up to the present date appears to have been a success. However, the PVA used estimates of carrying capacities of MNP for cheetahs based on available area and prey. There is evidence that the amount of productive habitat (foreshore), the high density of lions or a combination of both factors will restrict the maximum number of cheetahs that will be able to utilise the park. If this maximum number is less than 25 cheetahs the population will no longer be viable.

**AN ASSESSMENT OF THE SUCCESS OF A CHEETAH RE-INTRODUCTION
PROJECT IN MATUSADONA NATIONAL PARK**

By

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**A thesis submitted in partial fulfillment of the requirements for the degree of
Master of Science in Tropical Resource Ecology**

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ABSTRACT

By the end of 1994, 14 adult and three juvenile cheetahs (*Acinonyx jubatus*) had been successfully released into Matusadona National Park (MNP), Zimbabwe. These cheetahs had been captured in the southern part of the country where they had been reported to be causing stock losses. Four years after the translocation 13 adult and four juvenile cheetahs were present in the park. Eight records of cheetah litters during these four years gave an average litter size of 2.8 cubs and juvenile mortality between 3 and 24 months was recorded as 60%, much lower than was previously predicted. Adult mortality was estimated as 20.5%. The cheetahs used the treeline habitat more than would be expected. They utilised the foreshore for hunting and eating and the woodland for resting and moving through the park. Prey selection had not altered significantly since the cheetahs were first released, impala (*Aepyceros melampus*) being the main prey species killed. There was no evidence that the cheetahs would overutilise the available prey. Home range areas measured were smaller than those measured shortly after the cheetahs were released (53.8 km² compared to 135.5 km² for males, and 23.6 km² compared to 257 km² for females). All home range areas appeared to include an area of productive habitat (foreshore) and cover (treeline and woodland). A very high density of lions (*Panthera leo*) was recorded, 0.317 lions/ km² and hyaena (*Crocuta crocuta*) density was recorded as 0.13 hyaenas/ km². When compared to other conservation areas in Africa, MNP has very few hyaenas for the number of lions present. MNP also has a very low predator biomass for the available prey biomass. After correcting for prey biomass, a negative relationship was found between lion and hyaena biomass, and cheetah biomass for eight conservation areas in Africa, although the relationship was only significant for lion biomass compared to cheetah biomass. The overlap between cheetahs and lions in terms of prey selection is very small, lions preferring buffalo, *Syncerus caffra* (PSR = 9.25) and cheetahs preferring waterbuck, *Kobus ellipsiprymnus* (PSR = 4.67). The overlap in prey selection between hyaenas and cheetahs is considerable, both preferring waterbuck (Hyaena PSR = 1.00) and killing impala predominantly. Habitat preferences of lions and cheetahs were similar with both species using the treeline and the foreshore more than would be expected and the woodland less than would be expected. Population Viability Analysis concluded that the population of cheetahs was viable and had a 100% chance of persisting for a 100 years. The translocation up to the present date appears to have been a success. However, the PVA used estimates of carrying capacities of MNP for cheetahs based on available area and prey. There is evidence that the amount of productive habitat (foreshore), the high density of lions or a combination of both factors will restrict the maximum number of cheetahs that will be able to utilise the park. If this maximum number is less than 25 cheetahs the population will no longer be viable.

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CHAPTER ONE: Introduction

Between January 1993 and November 1994, the Department of National Parks and Wildlife Management of Zimbabwe, with assistance from local conservation organisations, translocated a total of 21 cheetahs (*Acinonyx jubatus*) to Matusadona National Park (MNP). The project was undertaken in an attempt to find a solution to the increasing conflict between commercial farmers and cheetahs, the latter reported to be taking large number of stock animals. It was an experiment to determine whether the removal of cheetahs from commercial ranches to protected areas of Zimbabwe would be an effective strategy to reduce the conflict without jeopardising the future of cheetahs in the country as a whole. The translocation took place over a period of two years, 14 adults and three cubs survived to be released. Six of the cheetahs released were fitted with radio collars that have never been removed. In order to ascertain whether this strategy has been effective there is a need to study the introduced population of cheetahs in MNP to determine if they have successfully established themselves. MNP has a large population of lions (*Panthera leo*), and hyaenas (*Crocuta crocuta*) are also present. Most protected areas in Zimbabwe have populations of both these large predators and it is necessary to find out if cheetahs can successfully establish themselves in such places.

1.1 Status of cheetahs in Zimbabwe

The cheetah population in Zimbabwe is currently greater now than any time in recorded history (Heath, 1997). The number of cheetahs in the National Parks estate of Zimbabwe is very low, however, on commercial ranches and private land the number of cheetahs is

estimated to be much higher (Zambezi Society, 1994). This increase in numbers is thought to be due to the drastic reduction in the numbers of lions, *Panthera leo*, and spotted hyaenas, *Crocuta crocuta*, in these areas because of hunting, snaring and poisoning. Cheetahs have escaped such persecution because they are very shy of humans and because they do not scavenge they cannot be baited to be shot or poisoned. The reduction in the numbers of the other large predators has benefited the cheetahs because they are known to suffer from adverse interactions with these larger carnivores (Caro, 1994). The cattle and goats on farmland provide a readily available source of food for the cheetahs. In Namibia a similar situation exists where a population of 2500 cheetahs (95% of the total population) occurs in unprotected land (Marker-Kraus and Kraus, 1993). A drastic reduction in the populations of wildlife on commercial ranches in Namibia has resulted in an increase in the number of stock animals taken by cheetahs (Marker-Kraus and Kraus, 1993).

These large numbers of “problem” cheetahs on private land are an anomaly as it is generally accepted that cheetahs are endangered and in need of special protection. Prior to 1992, no cheetahs could be hunted in Zimbabwe because they were on Appendix I of CITES. At the 1992 CITES meeting Zimbabwe was granted permission to hunt 50 cheetahs a year because it was recognised that in some areas of the country cheetahs were creating problems for landowners (Schouten, 1992) but the species remained on Appendix I (World Conservation Monitoring Centre, 1996). This quota has never been fully utilised because of the problems in obtaining a permit to shoot cheetahs from the Department of National Parks and Wildlife Management (DNPWM) of Zimbabwe. To

obtain a permit the individual farmer must prove that his stock losses are due to cheetahs and this is very difficult. A “tag” is then issued to the farmer giving him permission to shoot a specified number of cheetahs, the number being determined by the size of the property. Many farmers are illegally shooting and snaring cheetahs because of the difficulties in getting permission to do it legally. This makes it difficult to monitor the number of animals that are being killed every year and to determine the size of the problem.

Recognising that there is a problem the DNPWM has drafted a new management plan for cheetah conservation in Zimbabwe (Heath and Muchena, 1998). The overall objective of this plan is to have a “secure, free-ranging population of 5 000 individuals” (Heath and Muchena, 1998). This will not be possible within the National Parks estate. The draft plan recognises that unless cheetahs have an economic value many landholders will not be persuaded to maintain cheetahs on their properties. Many farmers have stated that they would be prepared to have cheetahs on their land if they could recognise some economic benefit. The new draft management plan states that there is a need to make permits to shoot cheetahs “readily available” (Heath and Muchena, 1998). If a farmer cannot be persuaded to maintain a population of cheetahs on his property then the plan states that the means to “translocate problem cheetahs need to be readily available” as an alternative. The DNPWM is in the process of identifying protected areas in Zimbabwe that will be suitable areas to attempt to establish viable populations of cheetahs.

1.2 Background to the translocation of cheetahs into MNP

1.2.1 *Translocation of carnivores in general*

The number of carnivore re-introductions is increasing as humans encroach more of carnivore species' habitat. Although there are some guidelines as to what techniques increase the success of carnivore translocations and re-introductions (Griffiths *et al*, 1989) many projects are carried out without consideration of these techniques and strategies (Hein, 1997). Many translocations are not monitored after the animals have been released (Linnell, Aanes, Swenson, Odden and Smith, 1997). This means that a considerable amount of the valuable information concerning factors which affect the success of the re-introduction is lost, a point emphasised by the IUCN Re-introduction Specialist Group (1998). This group stresses that there must be post release monitoring of all, or at least a representative sample, individuals released to further the understanding of the demographic, ecological and behavioural characteristics of such populations. What little information has been collected so far has concluded that the following factors increase the chances of success;

- Translocations of wild caught animals are more likely to succeed than those using exclusively captive reared animals (Griffiths *et al* , 1989);
- Success is correlated with the status of the source population. If the source population is increasing a translocation has a higher chance of success than if the source population is declining, as is the case with most endangered species (Griffiths *et al* , 1989);

- In the case of a re-introduction, the source population should show similar ecological characteristics to the original sub- population (IUCN Re-introduction Specialist Group, 1998).
- Translocations of animals into areas with potential competitors of similar life form are less successful than translocations into areas without competitors (Griffiths *et al* , 1989);
- When the number of animals released is plotted against the success of the operation, the graph reaches an asymptote at about 20 – 40 animals for large mammalian species (Griffiths *et al* , 1989);
- Translocated individuals have been shown to make very large post-release movements increasing the chances of conflict in the re-introduction area. The magnitude of these movements appears to be reduced if the animals are kept in a enclosure in the new area for a period of time – referred to as a “soft release” (Linnell *et al*, 1997). If the re-introduction area is very small the chances of the translocated animals moving out of the protected boundaries is very high and this must be taken into account (Linnell *et al* , 1997).

The IUCN Re-introduction Specialist Group (1998) stresses the fact that re-introduction is a very lengthy, complex and expensive process. The principal aim should be to establish a viable breeding population and the project should involve minimal long term management (IUCN Re-introduction Specialist Group, 1998).

Reviews of the success of translocations come to the same conclusion (Griffiths *et al* , 1989; Linnell *et al* , 1997; Hein, 1997) and argue that it should not be used as a solution

for problem animals (where the reasons for conflict should be addressed and rectified) and in the case of endangered species it should only be used as a last resort because of the low success rate of such projects. However, because of the large amount of information necessary to make a project successful it should be explored long before it is seen to be the last resort for an endangered species (Griffiths *et al* , 1989).

All the above authors agree that the available information on translocations is very small. Hein, (1997) argues that future translocations should be designed more scientifically and experimentally to enable hypotheses about translocations to be tested.

1.2.2 The re-introduction of cheetahs into Matusadona National Park

This project was part of an overall programme of the DNPWM to increase the number of cheetahs in certain National Parks and other suitable protected areas while reducing the number of “problem” cheetahs on private land (Zambezi Society, 1994). The relocation was experimental in nature, as there was little previous experience to draw upon (Zambezi Society, 1994). It was not known if cheetahs had been present in Matusadona National Park (MNP) and had become extinct, or whether they had never been present in that environment at all (Pitman, 1994). The only information that was available at the time of the translocation, because no feasibility study had been carried out, was that there was a large resident impala population and suitable habitat available (Anon, 1994). It was also known that MNP had high densities of lions and that hyaenas were present. The aim of the project was to establish a viable breeding population of cheetahs (Anon, 1987) but the number of cheetahs required to achieve this aim could not be determined.

The cheetahs used in the translocation had been captured opportunistically in the Lowveld area of Zimbabwe where there had been reports from landholders of “problem” cheetahs. On arrival in MNP the animals were kept in a fenced enclosure, known as a boma, for six weeks and fed adult impala. This was in an attempt to habituate the cheetahs to their new surroundings and to the presence of lions and hyaenas (Anon, 1994). The animals were reported to kill impala very soon after release from the boma (Zank, 1995). A female gave birth to three cubs which must have been conceived after release into the area (Zank, 1995). However, a retrospective Population Viability Analysis (PVA) concluded that the population would not be viable because of potentially high juvenile mortality rates due to the large numbers of lions present (Zank, 1995).

1.4 Conservation of cheetahs

Cheetahs are popularly believed to be threatened with extinction – a belief reflected in the fact that it is on Appendix I of CITES. The reasons for this belief are now being questioned and whether rather than declining as a species, “scarcity is the norm” (Hamilton, 1981).

In the early 1980’s a study was carried out on 50 cheetahs in South Africa and it was found that they exhibited very low levels of heterozygosity, the males have large numbers of abnormal sperm and that they displayed low variability at the major histocompatibility complex (MHC) (O’Brien, Wildt and Bush, 1986). These results along

with reports of the difficulties in breeding cheetahs in captivity were used to explain the low densities of cheetahs in the wild. The species was obviously suffering from inbreeding depression, which had resulted in low breeding success, high juvenile mortality and increased susceptibility to disease. It was heralded as a classic example of the problems facing a species with a small population (Caughley, 1994). The cheetah was upheld as a species facing extinction because of its small population size (Caughley, 1994).

Since the results of O'Brien *et al's* (1986) study were published it has been shown that all species belonging to the order Carnivora exhibit relatively low levels of genetic diversity (Merola, 1994). If the cheetah is compared with other species in this group it has relatively high levels of heterozygosity (Merola, 1994). It has been argued that if genetic variability in a species is reduced gradually, many damaging recessive characteristics are selected against and removed without any serious inbreeding effects developing (Merola, 1994). Another suggestion to explain the low genetic diversity of cheetahs is that highly mobile animals are likely to exploit diverse habitats and hence have generalist phenotypes with genomes poorly adapted to local conditions showing little variation (Caro, 1994). Cheetahs mate more or less at random and travel long distances to find mates. It has been suggested that this behaviour reduces overall population heterozygosity (Caro, 1994). Lacy (1992) argues that the few studies of inbreeding in natural populations have produced little evidence that inbreeding is costly under natural conditions. In fact, studies of cheetahs in the wild have shown that they have very high success rates of conception (Merola, 1994), they produce large litters (Caro and

Laurenson, 1994), conceive very quickly after losing a litter (Laurenson, Wielebnowski and Caro, 1995) and mature younger than other felids (Hamilton, 1981). A study carried out to compare juvenile mortality when related cheetahs were mated to that when unrelated cheetahs were mated showed that the latter was much greater than the former. If the cheetah was a highly inbred species there would be no difference in juvenile mortality between the two combinations of mating (Caughley, 1994). In conclusion, although cheetahs do exhibit low levels of genetic variation this does not appear to have any effect on its ability to breed, suggesting that it is not suffering from inbreeding depression. However, Lande (1994) points out that even in highly inbred populations the effects of the fixations of mildly deleterious alleles can be detrimental and result in the extinction of a species.

The currently accepted theory to explain the low densities of cheetahs in the wild argues that ecological factors restrict numbers. As early as 1981, before the genetic argument had begun, a report by Hamilton (1981) argued that cheetah densities in Kenya were low due to ecological factors and had been low long before humans began encroaching on their habitat. Cheetahs are members of the large predator guild of the African savannas and appear to suffer greatly from intra-guild predation (IGP) of cubs and kleptoparasitism (Laurenson and Caro, 1994). 73.6% of cub mortality from birth to independence of cheetahs studied in the Serengeti was due to predation by lions (Laurenson, 1995). Schaller (1972) reported that cheetahs in this area lost 12% of their kills to other predators. In areas where other predators have been eliminated, cheetahs have exhibited very high population growth rates. In Suikersbosrand Nature Reserve in South Africa an

introduced population of eight cheetahs increased to 24 animals in two years (Pettifer, 1981). This reserve has no other large predators. Polis, Myers and Holt (1989) argue that co-existence within a guild is possible because the member which is affected most by the competitive interactions is the most successful at obtaining resources. Cheetahs have been recorded to have a 70% hunting success compared to lions, which were reported as being successful in only 27% of their hunts (Kitchener, 1991). It is thought that IGP acts to decrease the population of the species that is the superior in obtaining resources, thus increasing the supply of resources to other member species (Polis and Holt, 1992). Cheetahs are the most successful hunters in the African large predator guild and have the highest fecundity rates. It could be argued that IGP on cheetah cubs serves to keep the number of cheetahs down in relation to the other less successful predators.

From the arguments above, it appears that the case of low cheetah densities lies within what Caughley (1994) refers to as the “declining population paradigm” of conservation biology. This aspect of conservation biology argues that the species in question is vulnerable either because its range is contracting or there is a tangible cause of decline which can be identified and rectified i.e “there is an agent of decline – small population size is not itself a cause” (Caughley, 1994, P 227). Current research shows that there are two factors that may be causing the decline of cheetahs in Africa. Cheetahs are being increasingly persecuted on private lands because they prey on domestic stock. In protected areas in Africa, high densities of lions and hyaenas result in high levels of juvenile mortality reducing the number of cheetahs present. Laurenson (1995) suggests that cheetah conservation must focus on unprotected areas because the densities of lions

and hyaenas are much lower. However, her conclusions are drawn from studies in the Serengeti and it is not clear yet whether the relationship between lions and cheetahs in this environment is the same elsewhere in Africa. Caughley (1994) points out the difficulties in identifying the causal agent of decline in the number of individuals in a species. Laurenson (1995) reports very high levels of juvenile mortality in the Serengeti but Mills and Hess (1997) suggest that in the Kruger National Park sub-adult cheetahs suffer the highest levels of mortality because they are pushed into sub-optimal habitats by already established adults. It is clear that more research into the demography and behaviour of cheetahs in different environments is necessary before any definite conclusions can be made as to the effect of other predators on the number of cheetahs.

The division of conservation biology into two contrasting paradigms (Caughley, 1994) has been criticised as being too simplistic (Hedrick, Lacy, Allendorf and Soule, 1996). Instead of a division, the two paradigms should operate simultaneously. Many endangered species have small populations as a result of some factor external to their own biology but whatever the cause of decline such populations are still prone to extinction because of random demographic or environmental effects. The case of the cheetah is a good example. Small populations of cheetahs exist which are vulnerable to extinction but there is also a need to try and identify conclusively the factor, or factors, causing a decline in overall numbers.

The challenge for conservation biologists in the case of the cheetah is threefold. The first question that needs to be answered is how the cheetah fits in with and interacts with the

other member species of the large predator guild. This will enable communities of these species to be manipulated in favour of the cheetah. It will also enable conservationists to identify protected areas where the environment would favour cheetahs over the other large predators. The second issue that needs to be addressed is how to reduce the conflict between cheetahs and humans in areas that are not protected. Finally, all current populations of cheetahs should be monitored and managed to prevent extinction as a result of small population sizes.

1.5 Population Viability Analysis (PVA)

The aim of the Matusadona Cheetah Translocation project was to establish a viable breeding population. The minimum number of animals required to achieve this aim can be determined by carrying out a PVA, or conversely, a PVA can determine if the current population size of the cheetahs in MNP is viable. PVA is an attempt by conservationists to determine the likely effects of various threats to small populations (Macdonald, Mace and Rushton, 1998). It is a process which predicts the success or failure of populations to persist after analysing their demographic characteristics (fecundity, age structure, juvenile mortality and so on) and simulating the effects of environmental stochasticity and loss of genetic variation (Caughley and Gunn, 1996). In the early 1980's conservation biology focused on the problems facing small populations, emphasising that the probability that a population will go extinct increases if it loses a certain amount of genetic variation (Caughley and Gunn, 1996). This theory argues that as a population reduces in size, the loss of genetic variation due to genetic drift and inbreeding effects increases. This

reduced genetic variation reduces the “fitness” of individuals within the population and increases the risk of chance extinction (Caughley, 1994). Demographic stochasticity, the variation in r , also increases with decreasing population size. In addition to reduced genetic variation, small populations are not buffered against the adverse effects of chance environmental changes. Once a threshold size has been reached the population enters an extinction vortex where each of the above factors acts to make the effect of the other factors worse (Caughley, 1994).

As a conservation tool, PVA has been criticised as being based on a theory that is too simplistic, that it does not take into account the use of an environment by a species and does not take into account the reasons why populations have reduced in size to the point where they have become vulnerable (Simberloff, 1988; Boyce, 1992; Caughley, 1994; Caughley and Sinclair, 1994). Although these arguments are justified, PVA has been shown to be useful in highlighting the factors that most affect the persistence of a population. These factors can then be manipulated by management to decrease the chance that a population will go extinct (Macdonald *et al*, 1998). It is only when the results of a PVA are taken too literally that the process is harmful. It is necessary to obtain some understanding of the chances of the population of cheetahs persisting in MNP in order to identify, for management purposes, the factors that may affect its long term survival.

1.6 This study

1.6.1 Objective

The objective of this study was to compare the performance of the introduced cheetahs at present in MNP with the performance predicted from previous studies of cheetahs in order to obtain a better understanding of the factors influencing the current and future success of the MNP cheetah re-introduction project. “Success” here is defined as the establishment of a viable breeding population of cheetahs.

1.6.2 Rationale

Translocation of large carnivores is becoming an important tool in the conservation of these large mammals. If it is to be used effectively, the factors affecting the success of such projects must be identified. These are likely to be specific to species and environments but general rules may surface from a comparison of different projects. The translocation of cheetahs into MNP provides an opportunity to identify factors that may increase, or decrease, the success of future translocation projects.

The translocation of cheetahs into MNP was an example of the strategy called “adaptive management” (Bell 1984). MacNab (1983) laments the fact that so few manipulations of natural systems as part of management programs are monitored to gain a better understanding of the underlying ecology. Cheetahs are members of the large predator guild of African savannas. Data on the functional organisation of guilds is derived from

manipulations of natural guilds (Morrison, Marcot and Mannan, 1992). The introduction of cheetahs into MNP is an example of such a manipulation. Knowledge of how guild systems function will aid in making future re-introduction of large carnivores more successful.

1.6.3 Key Questions

The key questions addressed by this study were:

1. What is the current status (total population size, age structure and sex ratio) of the introduced cheetah population in MNP?
2. What are the mortality rates of cubs, subadults and adult cheetahs in MNP?
3. How does the observed population status of the cheetahs compare with that predicted by previous studies?
4. How do the population densities of cheetahs, lions and hyaenas in MNP compare with other conservation areas of Africa?
5. What prey species are taken by cheetahs in MNP?
6. What is the extent of the overlap in prey selection between cheetahs and a) lions and b) spotted hyaenas?
7. How does the predation rate on impala, the main prey species of cheetahs in MNP, compare with the maximum sustained yield of edible impala biomass?
8. What habitats in MNP are preferred by the cheetahs?
9. What is the average home range size of cheetahs in MNP at present?
10. What is the probability of the cheetah population in MNP continuing to be successful given the current situation?

11. Has the MNP cheetah translocation project proved to be a success?

CHAPTER TWO: Study area

2.1 Location:

The study was carried out in Matusadona National Park (MNP) located on the southern shores of Lake Kariba, Zimbabwe (17°00`S, 28°25`E). The park covers an area of 1370km², 980 km² comprises the Zambezi escarpment and 388 km² the valley floor, an area of gently sloping land adjacent to the lake (Figure 2.1). It is bordered on the east by the Sanyati River and on the west by the Ume River. The park is surrounded by communal lands, the Omay to the west and south and Gache-Gache to the east.

2.2 History of the Area:

Lake Kariba was formed in 1958 by the damming of the Zambezi River and at the time of its formation it was the largest man-made lake in the world. MNP was recognised as a wildlife area in 1958 but was not gazetted as a national park until 1963 (Anon, 1993b).

2.3 Climate:

MNP is part of the Zambezi valley and has a semi-arid to arid climate. Annual precipitation ranges from 400mm to 800mm, relative humidity is low (55%) and annual evaporation losses very high, greater than 2 290mm (Taylor, 1985). The years prior to and during the time of the introduction of cheetahs were very dry, the area receiving only

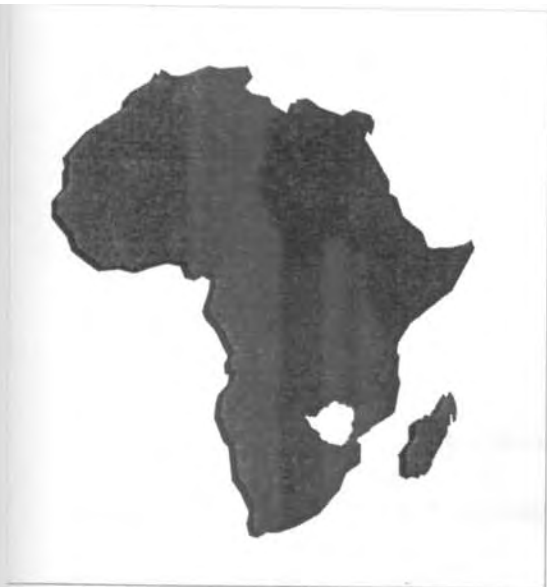


Figure 1: Location of Matusadona National Park
(Adapted from Taylor, 1985)

a third of the average rainfall each year (Zank, 1995). This corresponded to a continuous drop in the level of the Lake exposing a large area of open terrain adjacent to the lake shore. The rains from 1996 to 1998, however, were exceptional and above average. This caused the lake levels to rise to a level close to the highest level ever recorded (487m above sea level) and reduced the area of open terrain near the lake shore considerably.

2.4 Vegetation:

The vegetation of MNP is a complex mosaic of different woodland types. Studies of large carnivores, however, do not require detailed descriptions of the vegetation. For the purposes of this study it was broadly categorised into three main types – foreshore, woodland and escarpment. Foreshore and woodland vegetation comprised an area of approximately 388 km² (the valley floor) and escarpment vegetation covered an area of 980 km². Due to the rugged terrain of the escarpment and the low prey densities it was assumed that the cheetahs would only utilise the valley floor section of the park. The valley floor section of MNP is considered the most productive and is the focus of the current study. This area can be broadly divided into three vegetation types that have significance to the introduced cheetah population – the foreshore, the treeline and the woodland (Zank, 1995).

2.4.1 Foreshore vegetation

The level of Lake Kariba fluctuates annually due to variation in the amount of water entering the lake, increasing for a period immediately after the rains and decreasing

during the dry season. The magnitude of the variation in lake level corresponds to the amount of rainfall received during the season. During dry years the decrease in the water level is greater than the corresponding increase after the rains. The reverse is true during wet years. Prior to 1980 the annual fluctuation was 1.2m (Taylor, 1985). Since then there have been a series of very dry years and the level of the lake dropped to about 476m, compared to 487m, the highest level recorded. In 1998, the lake rose 3.32m between February and July to reach a maximum level of 483.84m

This variation in the level of the lake exposes a strip of open grassland and herbaceous vegetation. The grassland community is dominated by a vigorous and nutritious species of grass, *Panicum repens* (Taylor, 1985) and the herbaceous community is diverse. The foreshore environment is unique as the *Panicum repens* grassland provides an “increasing dry season food source” as the amount of grass exposed increases as the level of the lake drops (Taylor, 1985). This means that it can support a large number of herbivores. In 1995, when the cheetahs were introduced into MNP the foreshore was very extensive (102 km²) as there had been a series of very dry years (Zank, 1995).

The average amount of foreshore exposed was 44 km², less than half that available in 1995 (See Appendix I for calculations). The increase in lake level, due to above average rainfall completely submerged the available grassland and it is unlikely that the drop in the level of the lake during the 1998 dry season will expose the *Panicum repens*. The remaining foreshore exposed consists of sparse herbaceous vegetation. This provides

little cover for the cheetahs to hunt. However, much of the foreshore is undulating terrain with ridges and gullies that could be utilised by the cheetahs to stalk prey.

2.4.2 *Treeline vegetation*

When L. Kariba filled all the trees that were submerged were killed. The highest level the water reached is characterised by a very distinct boundary between the exposed foreshore and the woodland, commonly known as the treeline. This boundary is about 20m wide and comprises predominantly mopane scrub. It covers an area of approximately 5 km².

2.4.3 *Woodland vegetation*

The woodland of MNP is very diverse with many different associations of tree species covering an area of approximately 345 km². However, cheetahs probably do not differentiate between different vegetation types and the woodland would be used for its cover. The woodland vegetation in terms of cover can be divided into three main types – jesse thickets (very thick vegetation with a sparse grass layer), open savanna woodland characterised by *Colophospermum* – *Combretum* – *Terminalia* spp. with a dense layer of grass, and Mopane scrub with a sparse layer of grass (adapted from Taylor, 1985).

Within these woodland types are ridges and areas of high ground. The above average rains of 1998 resulted in an abundant production of grass in all areas of woodland.

2.5 Other mammals

A number of large herbivores are present in MNP, the highest densities recorded near the lakeshore during the dry season (Appendix II). The park is known to have a large number of impala (*Aepyceros melampus*) and buffalo (*Syncerus caffer*), the former being an important prey species for cheetahs. Other large carnivores include the spotted hyaena (*Crocuta crocuta*), lion (*Panthera leo*), leopard (*Panthera pardus*), wild dog (*Lycaon pictus*) and side striped jackal (*Canis adustus*).

CHAPTER THREE: The current status of the cheetah population in Matusasdonga National Park (MNP).

3.1 Introduction:

By the end of 1994, 14 adult cheetahs (eight males and six females) and three cubs (two males and one female) had successfully been released into MNP (Zank, 1995). The initial objective had been to release a founder population of 20 adult cheetahs calculated from studies of cheetahs in other areas of Africa. The cheetah re-introduction project in MNP was part of a Department of National Parks and Wildlife Management (DNPWM) programme set up to determine areas which can be used as “sinks” for problem cheetahs from private land. The purpose of the project was to establish a viable population of cheetahs.

A study carried out in 1995 (Zank, 1995) concluded that the cheetahs had settled into MNP, establishing home ranges and killing prey soon after their release from the boma. This is consistent with other observations of translocated populations involving wild animals (Griffiths, Scott, Carpenter and Reed, 1989). A female was observed to give birth to three cubs and the cubs that were brought in as part of the initial exercise were observed to reach 18 months, the age at which they become independent. However, when a population viability analysis (PVA) was carried out on this introduced population the results suggested that the population would not persist, mainly due to the very high density of lions found in MNP (Zank, 1995). Lions are known to prey on cheetah cubs and in the Serengeti National Park account for a large proportion (73.2%) of mortality of

cubs before they reach independence (Laurenson, 1995). Due to time constraints, the parameters used in this PVA were not obtained from the Matusadona population itself, but from studies of cheetahs in other areas of Africa. Simberloff (1988) stresses the importance of basic ecological work when attempting to predict whether a population will persist into the future and laments the fact that many PVAs have to be carried out and used for management purposes before sufficient data is available. The current study produced data that was used to estimate some of the basic population parameters (average litter size, juvenile mortality and adult mortality) for the introduced population. This chapter then compares them with parameters obtained from other studies of cheetahs in Africa.

3.2 **Methods:**

3.2.1 *Sightings of cheetahs*

At the beginning of this study I met with scouts from the DNPWM, Tour Operators and their guides, local fishermen, individual tourists and houseboat captains. I gave them sighting sheets to record any sightings of cheetahs. Using these records it was possible to ascertain the minimum number of cheetahs in MNP by cross-referencing sightings. Observations of cheetahs while working in MNP were recorded with the same information as requested on the public sighting sheets. These were then added to the above records and cross-referenced. The Zambezi Society, along with the Matusadona Tour Operators Association had initiated a continuous monitoring programme for the tour operators in MNP and National Parks scouts when the cheetahs were released into MNP.

This programme provided a valuable source of information on the number of cheetahs in MNP between the release of cheetahs and the current study, especially information concerning the number of cubs born. Where possible cheetahs were identified using the markings on the last 20cm of their tails. These black and white bands are unique to each individual. Any other conspicuous markings were also used in identification.

3.2.2 Calculation of birth rate, juvenile mortality and adult mortality:

The average litter size was calculated as the average number of cubs recorded per female seen with cubs. This gave an underestimate of the true value as it only recorded the number of cubs that were still alive at the time when they began to accompany the mother (called “post-emergence mortality” from now on), and does not take into account the number actually born.

The juvenile mortality rate was calculated from only two records of surviving cubs. It will also be an underestimate because it is calculated using the average litter size. This figure is, therefore, not conclusive but gives an idea of the threat to cheetah cubs in MNP.

The adult mortality rate was calculated mathematically by comparing the number of cheetahs known to be present in MNP to the number that should be present if there was no adult mortality at all. Subadult and adult mortality could not be separated due the lack of data. When calculating the number of cheetahs that should be in MNP it was assumed that females only reproduced when they are two years old and that the sex ratio of cubs was unity. Both these assumptions were based on a study of cheetahs in the Serengeti

(Laurenson, Caro and Borner, 1992). It was also assumed that each adult female would have at least one surviving cub and therefore would only produce once every two years, although in the Serengeti females with cubs were recorded to conceive before their litters became independent (Laurenson *et al*, 1992).

3.3 Results:

3.3.1: Total number of cheetahs in Matusadona in 1998.

There was a total of 28 public sightings of cheetahs between February 1998 and July 1998 (Table 3.1). Of these sightings only four recorded detailed enough information to individually identify the cheetahs. Three of these observations used tail markings (two females and a male) and one used the presence of a collar (a female with three cubs). This last female must have been from the original population of cheetahs introduced as some of these were collared. All four of the above cheetahs were different to the ones identified by me and to any that had been collared during the current field research.

The locations of the sightings of cheetahs within MNP are shown in relation to the position of the main campsites, lodges and National Park's offices (Figure 3.1). It can be seen that all accessible parts of MNP have recorded cheetahs except for the escarpment camp of Kawasiga springs where no sightings have been recorded since cheetahs were introduced into MNP.

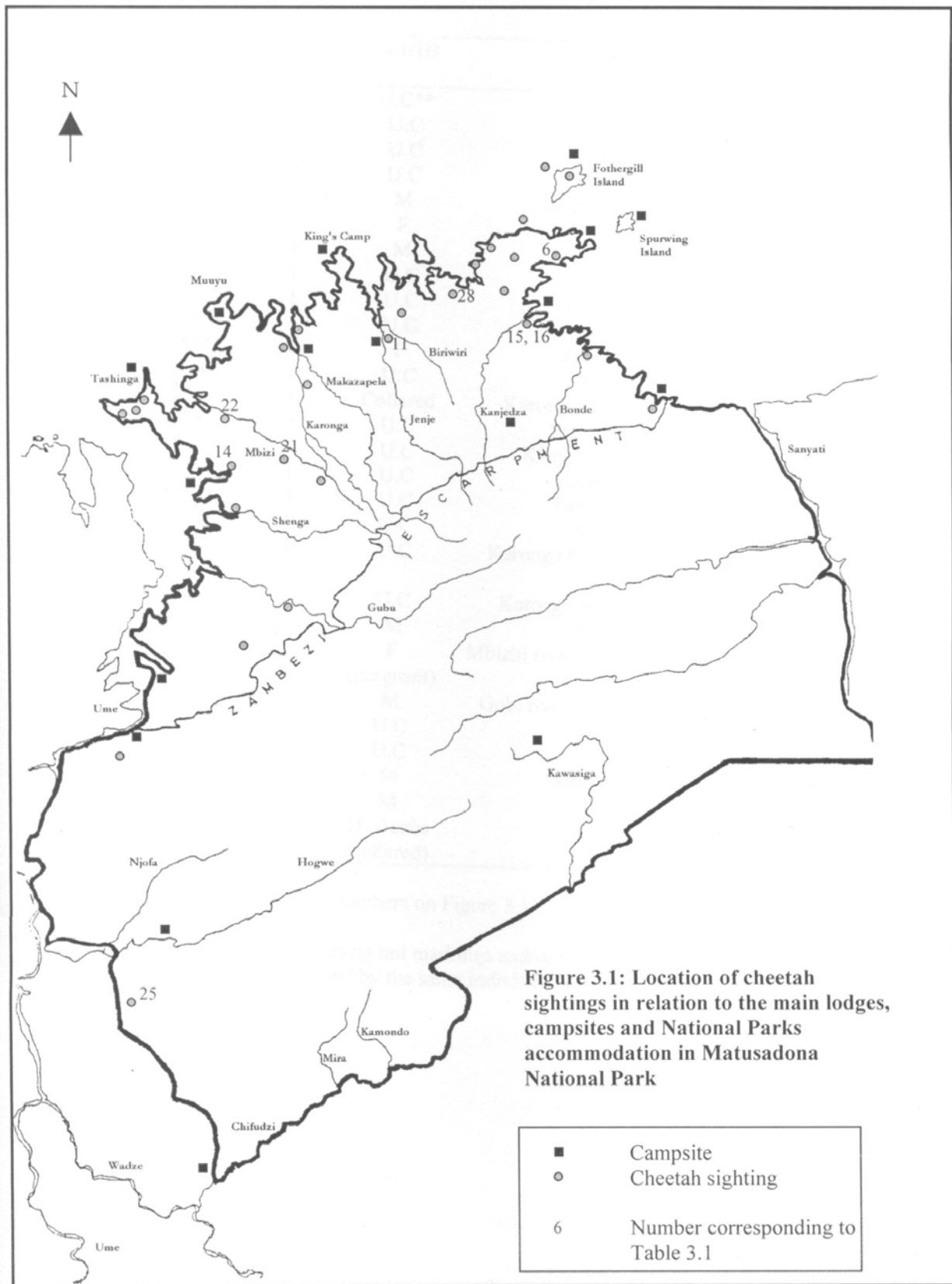


Table 3.1: Summary of the data collected from public sightings of cheetahs during the period February 1998 to July 1998.

| No* | Date | No. of animals | Sex/ID | Location | Time of Day |
|-----|-------------|----------------|-------------------------|---------------------------------------|----------------|
| 1 | 13/02/98 | 1 | U.C** | Gordon's Bay | |
| 2 | 23/02/98 | 1 | U.C | Access road | |
| 3 | 25/03/98 | 2 | U.C | Access road | |
| 4 | 10/04/98 | 1 | U.C | Access road | |
| 5 | 24/04/98 | 1 | M | Shenga river mouth | Mid morning |
| 6 | 14/4/98*** | 1 | F | Duncan's Bay | Early morning |
| 7 | 27/04/98 | 1 | M | Tashinga Bay | Late afternoon |
| 8 | 20/05/98 | 1 | U.C | Access road | |
| 9 | 27/05/98 | 1 | U.C | Kemurara | Early morning |
| 10 | 05/06/98 | 1 | U.C | Access road | |
| 11 | 16/6/98*** | 1 | F | Jenge river bed | Late evening |
| 12 | 16/06/98 | 1 | U.C | Access road | After dark |
| 13 | 16/06/98 | 1 | Collared | Karonga/Makazapela mouth | Early morning |
| 14 | 20/06/98 | 2 | U.C | Water Wilderness | |
| 15 | 20/6/98**** | 1 | U.C | Kanjedza river crossing | Early morning |
| 16 | 20/6/98**** | 1 | U.C | Kanjedza camp | Late evening |
| 17 | 20/06/98 | 3 | U.C | Tashinga airstrip | |
| 18 | 19/06/98 | 1 | U.C | Access road | |
| 19 | 24/06/98 | 1 | U.C | Karonga river crossing/circular drive | Mid afternoon |
| 20 | 25/06/98 | 1 | U.C | Karonga/Makazapela mouth | |
| 21 | 30/6/98*** | 1 | M | Boma pan | Mid morning |
| 22 | 02/07/98 | 1 | F (pregnant) | Mbizha river crossing/circular drive | |
| 23 | 07/07/98 | 1 | M | Gubu river crassing/Access road | After dark |
| 24 | 08/07/98 | 1 | U.C | Access road | Early morning |
| 25 | 11/07/98 | 1 | U.C | Tsetse camp | |
| 26 | 15/07/98 | 1 | M | Kemurara Bay | Early morning |
| 27 | 16/07/98 | 1 | M | Umbabala | |
| 28 | 18/07/98 | 4 | 1F, 3cubs (collared) | Access road | Mid morning |

* This number corresponds to the numbers on Figure 3.1

** U.C = unclassified

*** These cheetahs were identified using tail markings and/or the presence of collars

**** These two cheetahs were observed by the same individual and are recorded as being different

In addition to the above sightings four cheetahs were identified by me, using tail markings. Three of these cheetahs, two males and a female with a cub, were subsequently radio-collared. A total of 12 cheetahs were individually identified (Table 3.2). Two of these cheetahs, a male and a female are from the founder population introduced four years ago.

Of the cheetahs that were not identified by tail markings or collars, there appears to be a total of five different adults. One day three cheetahs were seen at Tashinga and two were seen at Kanjedza, a distance of approximately 60 apart (numbers 15,16 and 17 in Table 3.1). Of the cheetahs seen at Tashinga that day one of them is likely to be the male that was identified from tail markings at Boma pan (number 21 in Table 3.1). This gives four adult cheetahs. However, of these four, one of the cheetahs seen near Kanjedza (number 15 or 16 in Table 3.1) is likely to be the female that was seen and identified at an impala kill in Duncan's bay (number 6 in Table 3.1). This leaves a total of three separate adults. Another adult recorded is the pregnant female seen at Mbizhi river crossing (number 22 in Table 3.1). This gives a total of four adult cheetahs that were not identified using tail markings and the presence of collars. Finally, a fifth individual is the cheetah seen at the tsetse camp just outside the boundary of MNP (number 25 in Table I). There were three reports of a cheetah in this same area during the research period, but unfortunately the details were not specific enough to include in this analysis. However, it would seem that these reports would be of the same cheetah. The total number of cheetahs in MNP as of July 1998, is 13 adults (four males, five females and four unclassified) and four juveniles (one female and three unclassified).

Table 3.2: Characteristics of the cheetah that were positively identified.

| Sex | Age (yrs) | No. in Figure 1 | Collared Y/N | Founder individual or new |
|------------|------------------|------------------------|---------------------|----------------------------------|
| M | 4.5 | - | Y | One of the cubs introduced |
| M | 8 | - | Y | Founder |
| M | 2.5 | - | N | New |
| F | 8 | 28 | Y | Founder |
| F | - | 6 | | - |
| F | - | 11 | | - |
| M | - | 21 | | - |
| F | - | | Y | - |
| F | <1 | | | New (13 months) |
| U.C | <1 | 28 | | New (6 months) |
| U.C | <1 | 28 | | New (6 months) |
| U.C | <1 | 28 | | New (6 months) |

Table 3.3: Sightings of clubs during the period July 1995 to July 1998.

| Date | Number of cubs | Location |
|-------------|--|-----------------|
| April 1995 | 3 cubs seen with uncollared female | Kemurara |
| 28/6/96 | 3 cubs seen without adult | Chifudze |
| 1/8/96 | 4 cubs seen with adult female | Fothergill |
| 10/8/96 | 3 larger cubs seen with different female | Kemurara |
| 22/8/97 | 2 subadults and 1 adult * | Kemurara |
| 16/11/97 | 1 cub seen with female | Fothergill |
| 18/12/97 | 3 cubs seen with female | Kemurara |
| 14/2/98 | 1 cub seen with female | Fothergill |

* Reported as adult in September 1997. In January 1998 two young adults seen on their own in the Jenge area. These may be the surviving cubs of the litter observed in August 1996

3.3.1. Average litter size (post-emergence).

A total of eight sightings of cheetah cubs were reported between July 1995 and July 1998 (Table 3.3). These sightings were of six separate litters. Dividing the total number of cubs in these litters (17) by the number of litters (six) gives an estimate of 2.8 cubs per litter.

3.3.2 Juvenile mortality.

From the six litters recorded since July 1995, only two were observed until the cubs reached adulthood. Using tail photographs one male adult cheetah (the 2.5 year male in Table 3.2) was identified as being the surviving cub from the litter of four seen at Fothergill in August and September 1996. A cub from the litter of one observed in November 1997 was still surviving at the age of 13 months in July 1997. This gives a juvenile mortality rate of 60%.

If the subadults seen in September 1997 and January 1998 are the surviving cubs from the litter of three observed in Kemurara in August 1996 then the estimated juvenile mortality reduces to 50%. However, as these sightings did not positively identify these cheetahs as being the grown up cubs, this study will use the estimate of 60% in all calculations of population viability.

3.3.3 *Adult and subadult mortality:*

The founder population of cheetahs comprised eight males, six females and three cubs (two males and one female). At the end of 1995 all these females had been released. Using the average litter size and assuming that every female bred, had at least one surviving cub and the sex ratio of cubs was unity, it is possible to estimate how many adult cheetahs there should be in MNP if no mortality had occurred. By the end of 1995, six females would be breeding, producing 17 cubs of which seven (four females and three males) would survive to adulthood. By 1997 eleven females would be breeding, producing 31 cubs of which 12 (six females and six males) would survive to adulthood. At the beginning of 1998, there should be 22 adult cheetahs (eleven females and eleven males) and 12 juveniles (six females and six males). The actual number of cheetahs observed was 13 adults and four juveniles. The annual adult and subadult mortality rate is 20.45%.

It is known that one of the original males collared was snared in the Omay communal lands before the end of 1995, and that a male was found dead up a tree in 1997 (Tour operator sighting). Two females released are known to move out of MNP but it is not clear if they have left MNP completely. The estimate of subadult and adult mortality assumes that any adult cheetahs that move out of MNP are effectively “dead”. However, many of these individuals may move back into MNP periodically and still contribute to the MNP population.

3.3 Discussion:

The population parameters for the MNP cheetahs appear to be different from that which would be expected with such a high density of lions (0.32 lions/ km², See section 5.3.2). The average post-emergence litter size, 2.8 cubs, was higher than the Serengeti population, 2.2 cubs (Laurenson, 1995). In the Serengeti ecosystem lions kill about 58% of cubs before they emerge from the lairs (Laurenson, 1995). The density of lions in the Serengeti ecosystem is 0.1 lions/km² (Sinclair, 1995), lower than what has been recorded in MNP. The litter size (post-emergence) of 2.8 cubs as was recorded in this study suggests that the cheetahs are able to avoid predation to a large extent. However, in areas of Africa where cheetahs are the terminal predator, the average litter size appears to be closer to 4 cubs (McVittie, 1979; Pettifer, 1981). This suggests that some cubs are lost in Matusadona but whether this is due to predation or to other mortality factors is not clear.

The post emergence mortality recorded for the Matusadona population is less than what would be expected with the high density of lions and the fact that hyaenas are present. Post emergence mortality in the Serengeti is very high (83.3%) with spotted hyaenas accounting for 41.7% and lions for 33.3% (Laurenson, 1995). The relatively low density of hyaenas in MNP (0.13/km², section 5.3.1), along with the availability of thick bush may be the reason why the mortality recorded in Matusadona is less (60%) than that of the Serengeti ecosystem where the density of hyaenas is 0.4 animals/km² (Sinclair, 1995). The presence of thick vegetation may enable females to effectively hide cubs and allow cubs to disperse and hide themselves if attacked by another predator. During the study

period a female with an eight-month-old cub was observed being chased by two lionesses. She and the cub separated, disappeared into thick bush and the lionesses gave up the chase. Some cubs must be lost to predation or other factors in MNP, as studies of cheetahs where other predators are absent record a 85% success rate in raising cubs to adulthood (Pettifer, 1981; McVittie, 1979) whereas at present only 40% of cubs in MNP appear to reach adulthood.

The viability of the cheetah population in MNP may not be dependent on the mortality rates of cubs but on the mortality rate of young adults. In Kruger National Park the most significant mortality was that of subadults and young adults who were forced to disperse into suboptimal habitat by already established cheetahs (Mills and Hess, 1997). In the Serengeti ecosystem, 50% of adult males are lost due to intraspecific competition over access to territories (Laurenson, 1992). Although territorial systems in cheetahs are not properly understood it is known that they will avoid contact with each other, resulting in a “time-plan” territorial system where scent marking is used to warn other cheetahs (Eaton, as quoted in Pettifer, 1981). This behaviour may limit the number of cheetahs that can use an area thus effectively reducing the carrying capacity of the area for cheetahs. In MNP, subadults and young adults may be being forced out of the park into the surrounding communal lands by the adult cheetahs already established in MNP accounting for the annual adult mortality of 20%. The records of a cheetah on the outskirts of MNP near the Omay communal lands (Number 25 in Table 3.1) provide some evidence that this is happening. In addition to this record, a group of three adult cheetahs was seen on a kill near the entrance to MNP in November 1997 and tourists

reported seeing two adult cheetahs on the road into MNP in April 1998. It was not possible during this study to determine whether cheetahs are being sighted more frequently outside MNP since the translocation. There were records of cheetahs in the surrounding communal lands before the cheetahs were released into MNP (Zank, 1995) but it is important to find out if the numbers of sightings reported has increased since the introduction. There is an urgent need for a survey of the communal lands to be done to test the hypothesis that the cheetahs are acting as a source population for the surrounding areas.

The data collected in this study suggests that the extent of intraguild predation varies with the environment, as the mortality rates of cheetahs cubs in MNP is lower than other areas of Africa where lions and cheetahs co-exist. This is only a point estimate of juvenile mortality and the value will vary over time due to changes in the environment. As it is only five years since the release of the first cheetahs into the park, the full effect of either juvenile or adult mortality cannot yet be measured.

CHAPTER FOUR: The use of space and prey by cheetahs in Matusadona National Park.

4.1 Introduction:

Cheetahs have a wide geographic distribution, occurring over much of Southern and East Africa and utilising open plains, sparsely wooded areas as well as thick bush (Caro, 1994). The species is adapted to reach high speeds over short distances, which earned it the reputation of being a hunter of open plains, such as those found in the Serengeti ecosystem of Africa. Despite these adaptations, it has often been recorded in thick vegetation and areas with small ridges and hills (Hamilton, 1981). It is known to take a wide variety of prey species although it will tend to specialise on one species in any one area; in the Serengeti the main prey species is Thomson's gazelle, *Gazella thomsonii*, in Kruger National Park it takes predominantly impala, *Aepyceros melampus*, and in the Kalahari Gemsbok National Park it specialises on springbok, *Antidorcas marsupalis* (Mills, 1991). Cheetahs usually hunt during the day but there are records of it hunting at night (Stander, 1990). It is hypothesised that this tolerance to a wide range of ecological conditions enables the species to adapt to new conditions relatively quickly (Caro, 1994)

No feasibility study was done prior to the translocation of the cheetahs into Matusadona National Park (MNP) and it is not clear how many animals the area can support. After introducing a species to a new area it is necessary to determine whether the introduced population will reach and overshoot the carrying capacity of the area. Conversely, it is necessary to know whether the use of the available resources will restrict the number of

individuals below that of a minimum viable population. An understanding of how the introduced cheetahs are using the available prey and space in MNP is required before a conclusion can be drawn.

Shortly after the cheetahs were released, a study was carried out to determine the prey use, habitat preferences and home range size of the introduced animals (Zank, 1995).

This chapter addresses the current prey use, habitat preferences and home range size of the cheetahs in MNP with the aim of assessing whether the resource use has altered since the cheetahs were released. This information can then be used to assess whether the cheetah population is at carrying capacity (K) or whether there are factors that are preventing it from reaching K.

4.2 Methods:

4.2.1. Radio tracking

During the study period, three adult cheetahs were fitted with radio collars (two males and one female with a cub). Unfortunately due to logistical constraints it was not possible to collar any cheetahs who utilised the western and escarpment areas of the park. Laurenson and Caro (1994) found no significant difference between hunting success of female cheetahs fitted with radio collars and females without. For the purposes of this study it was assumed that the collars would not adversely affect the animal. The collared animals were located predominantly by ground tracking using a Telonics TR-4 receiver and a two element antenna. The location (using a GARMIN 40 Global positioning

system), activity of the animal, habitat type (see section 2.4) and time of day was recorded each time a collared cheetah was seen. When it was not possible to actually see a collared animal, its position was recorded by triangulation. Aerial tracking was done twice during the study. These location points were then used in home range analysis. Only data points recorded 24 hours apart (Swihart, Slade and Bergstrom, 1988) were used and the minimum convex polygon method was used to estimate home range area (Jennrich and Turner, 1969). This method involves drawing the smallest convex polygon that contains all the location points of the animal. The area of this polygon is then assumed to be the same as the area of the animal's home range. The area of each polygon in this study was estimated by placing a 1km² grid over the area outlined on a map and counting the number of square kilometre blocks that the polygon covered. Areas within the polygon that included the lake were excluded from the estimate.

4.2.2 *Cheetah prey composition:*

When a cheetah was observed at a kill, the habitat type in which the prey animal was killed, the species killed and the sex of the animal killed was recorded. Faeces were collected where possible, most of them from two well-known scent-marking trees and one anthill. Most of the samples are likely, therefore, to be from males (Mills, 1992). The faeces were dried at 80°C and a 5g sample removed. Hair was identified using colour, texture and cuticular scale patterns (Keogh, 1983; Buys and Keogh, 1984). A Prey selection ratio (PSR) for each species recorded in the diet of the cheetahs was calculated as follows:

$$\text{PSR} = \% \text{used} / \% \text{available}$$

Where % used is the percentage of the diet comprising the species and % available is the percentage of the total available prey biomass made up by the species. The latter value was calculated using prey population sizes calculated during this study (See Section 4.2.3).

4.2.3. *Prey availability:*

The availability of impala, the main prey species of cheetahs in MNP, was estimated in the two main habitat types (foreshore and woodland) as well as the total number of other prey animals available to cheetahs in the park. However, it was only possible to estimate the prey population in the valley floor section of the park, an area covering about 388km². Six road transects were set up in the woodland and covered a total of 20.2km. Two of these transects (13km) were located in woodland close to the foreshore and two (7.2km) were in woodland closer to the base of the escarpment (Figure 4.1). Two of these transects were located near Tashinga and two near Fothergill as the vegetation in these two areas is different (Figure 4.1). Six blocks were randomly marked out on the foreshore near Fothergill covering a total area of 0.334 km² in the wet season and 0.115km² in the dry season because of changes in the level of the lake (Figure 4.1; see Appendix II for calculation of areas). The lake level peaks at the end of June and only begins to drop in August. The dry season for the purposes of this study was May to July hence the fact that the dry season block area is smaller than the wet season.

The road transects were counted 51 times from February to July, either between 06:00 and 08:30 (morning transects) or between 16:00 and 19:00 (evening transects). They

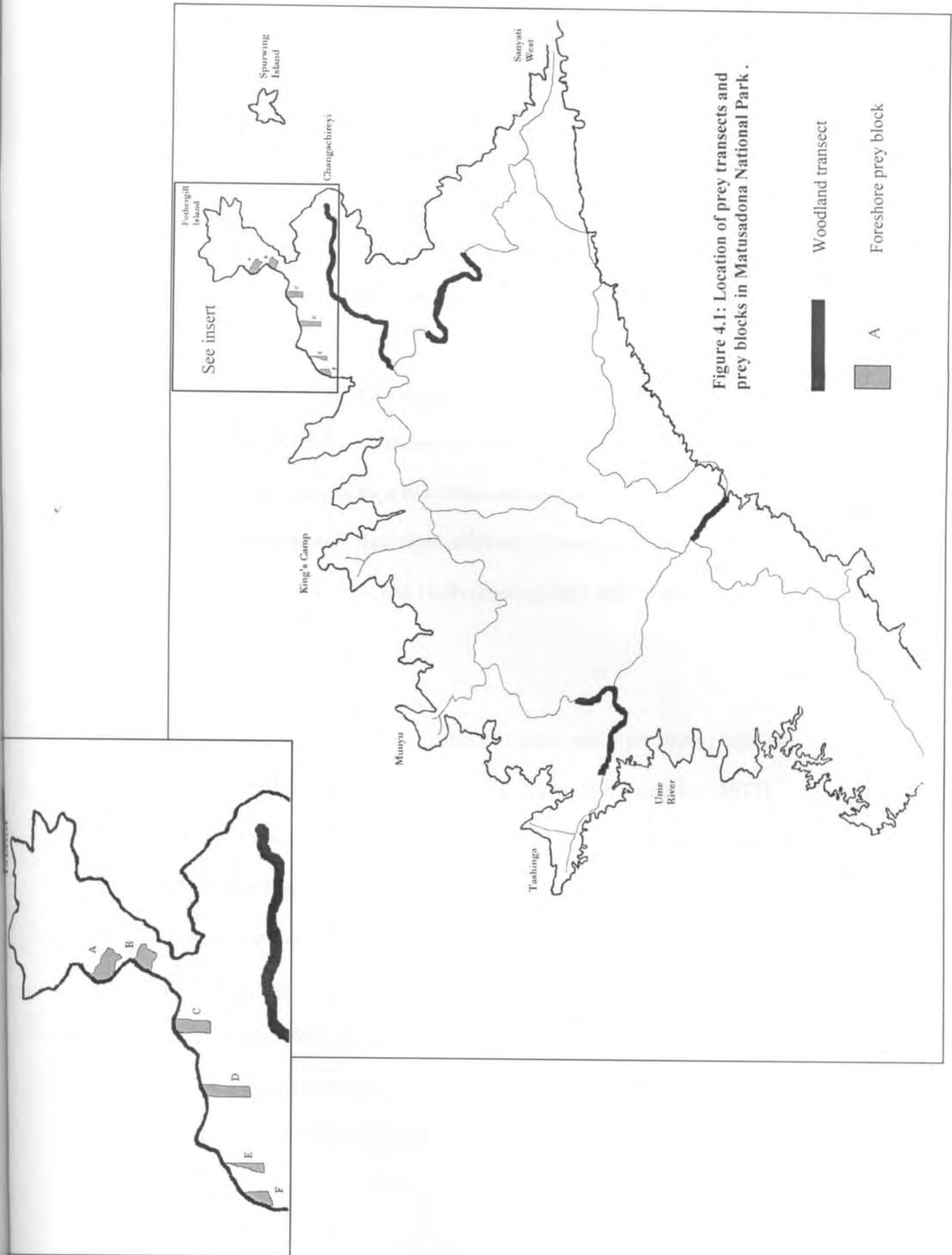


Figure 4.1: Location of prey transects and prey blocks in Matusadona National Park.

were driven at a speed of between 15-20 km/hr and there were two observers each time. All the animals seen within 20m of the road and on the road itself were recorded. Transects were run not less than 24 hours apart to ensure that the distribution of animals being sampled was independent of previous transect counts.

The foreshore blocks were counted 61 times between February and July. The vehicle would be stopped at one end of the block and the total number of animals seen within the block was recorded. There were always two observers and an average would be taken if the numbers counted by each individual were different. Counts were carried out between 06:00 and 09:00 (morning) and 16:00 and 19:00 (evening) and were at least 24 hours apart.

The maximum sustainable offtake of prey biomass (impala) was estimated as follows:

$$MSY = r_m K / 4 * 30.7\text{kg} * 85\% \quad (\text{adapted from Caughley , 1977})$$

Where $r_m = 1.5M^{-0.36}$ (Western, 1979), K = the population size at carrying capacity and 30.7kg is the unit mass of an impala (75% the mass of an adult female). During the study, cheetahs were observed to eat the viscera so the amount of biomass available to the cheetahs per individual prey animal was taken to be 85% of the unit mass of an impala (Blumenschine and Caro, 1986). Hence, the sustained yield of edible biomass is 85% of the maximum sustainable biomass. Impala was the only species that MSY was calculated for, as it was by far the most numerous prey species available.

4.2 Results:

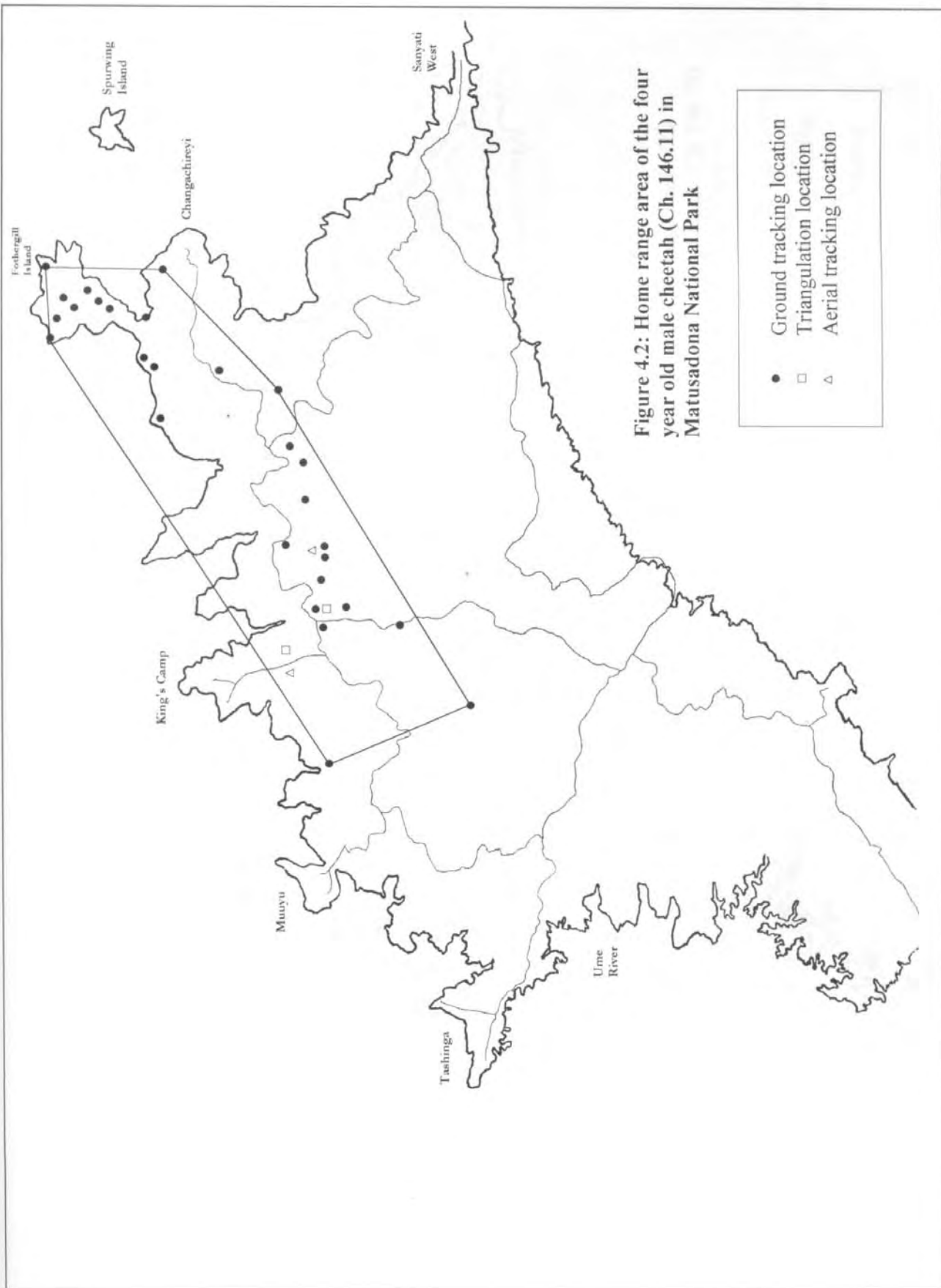
4.3.1 Home range analysis

The home ranges of the two males overlap with each other and with the female range (Figures 4.2, 4.3, and 4.4). The young male's home range (Figure 4.2) was concentrated around the Fothergill area of MNP until this almost became an island in the middle of May due to the rising lake levels (Figure 4.2). After this happened he was not seen around the Fothergill area again and began moving large distances. His home range was the largest of all the three cheetahs, 53.8km² as compared to 11.3km² (older male) and 23.6 km² (female and cub) (Table 4.1). All three cheetahs concentrated their movements near the foreshore.

4.3.2 Habitat preference:

The data used to determine the habitat preferences of the cheetahs of MNP were collected using the radio-collared cheetahs. The cheetahs were found in the treeline habitat significantly more often than was expected (Chisquare test, n = 62, $\chi^2 = 70.505$, df = 1, P < 0.005) (Table 4. 2). The woodland and the foreshore habitats were used as frequently as would be expected from habitat availability by area

The use of the available habitats for different activities was also non-random (Chisquare test of association; n = 62, $\chi^2 = 15.433$, df = 6, 0.025 > P > 0.01)(Table 4.3). Cheetahs used the foreshore predominantly for eating and hunting, and the treeline for resting.



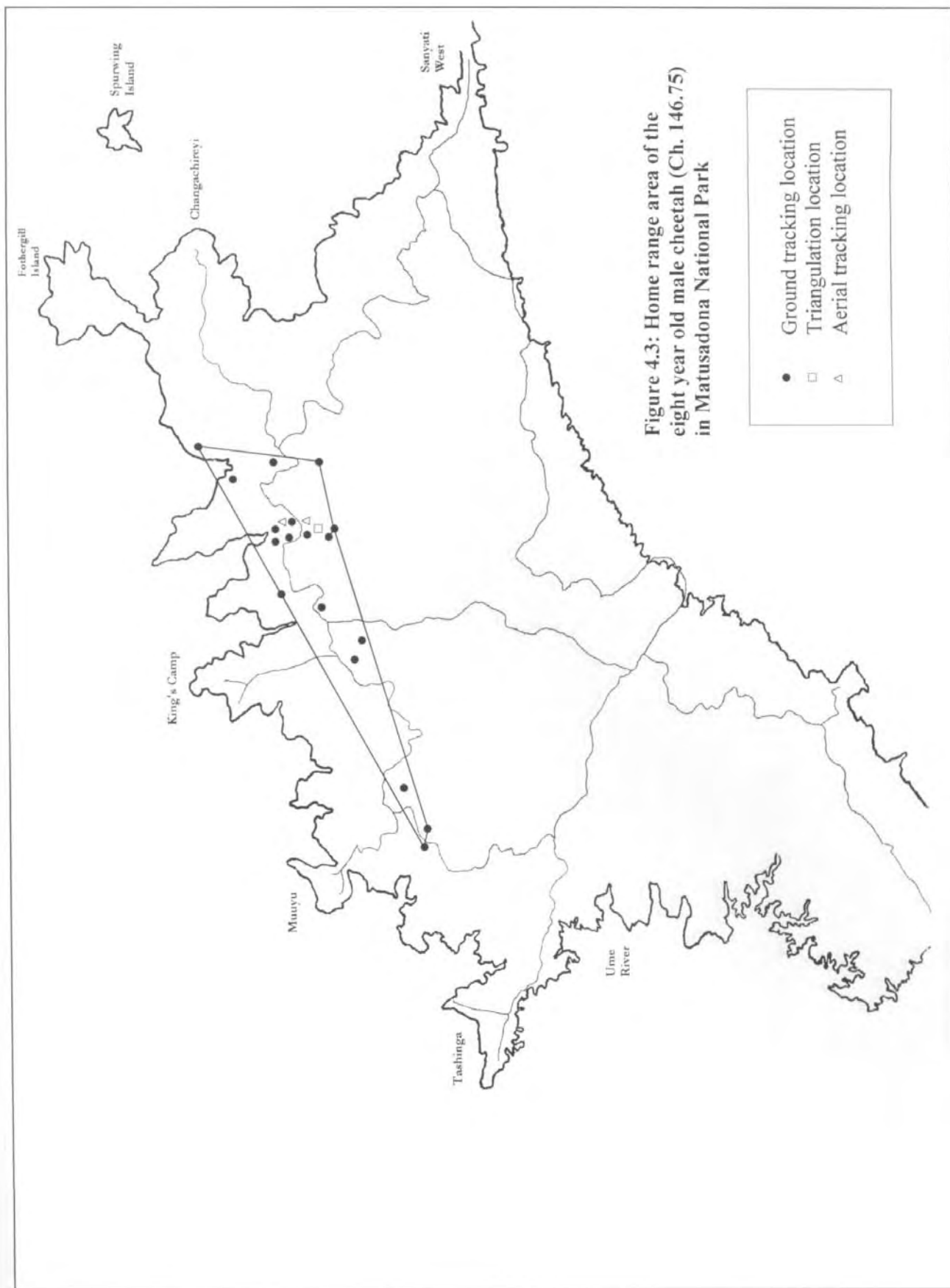


Figure 4.3: Home range area of the eight year old male cheetah (Ch. 146.75) in Matusadona National Park

- Ground tracking location
- Triangulation location
- △ Aerial tracking location

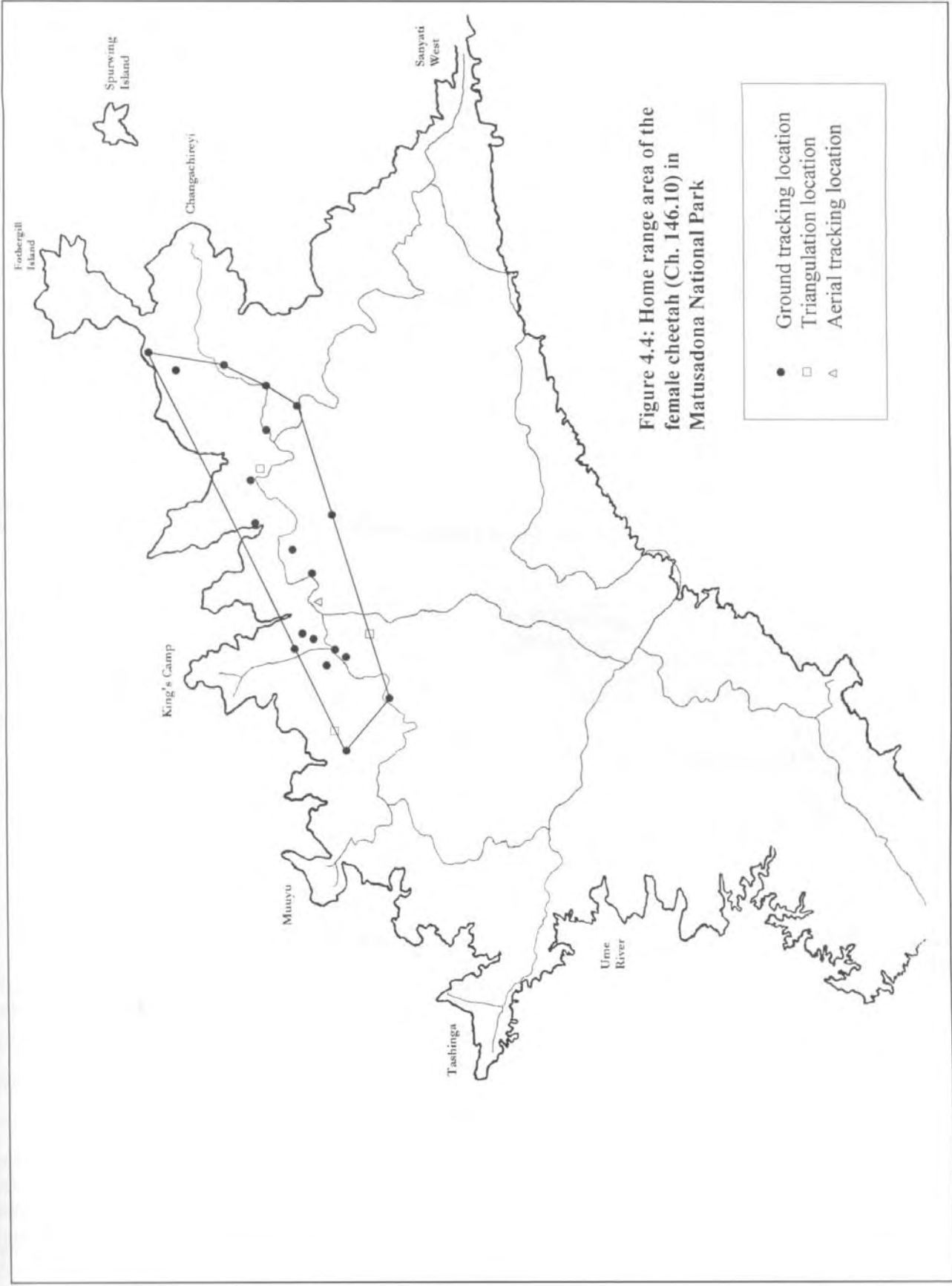


Figure 4.4: Home range area of the female cheetah (Ch. 146.10) in Matusadona National Park

Table 4.1: Home range sizes of the Matusadona cheetah

| Sex | Age | Size of home range (km²) | No. of ground tracking points | No. of aerial tracking points | No. of triangulation points | Total |
|------------|------------|--|--------------------------------------|--------------------------------------|------------------------------------|--------------|
| Male | 8 | 11.3 | 18 | 2 | 1 | 21 |
| Male | 4 | 53.8 | 28 | 2 | 2 | 32 |
| Female | UK | 23.6 | 20 | 1 | 4 | 25 |

Table 4.2: Number of observations of collared cheetah in four different habitat types (foreshore, treeline and woodland)

| Habitat Type | % of Total area | % of sightings (observed) | No. of sightings (observed) |
|---------------------|------------------------|----------------------------------|------------------------------------|
| Foreshore | 11 | 16.1 | 10 |
| Treeline | 1 | 11.3 | 7 |
| Woodland | 88 | 72.6 | 45 |
| Total | 100 | 100 | 62 |

Table 4.3: Number of times four different cheetah activities (resting, walking, hunting and eating) were observed in the three main habitat types of MNP (foreshore, treeline and woodland)

| Habitat Type | Activity | | | | | | | | Total |
|---------------------|-----------------|------------|----------------|------------|----------------|------------|---------------|------------|--------------|
| | Walking | | Resting | | Hunting | | Eating | | |
| | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | |
| Foreshore | 2 | 5.32 | 2 | 2.58 | 2 | 0.81 | 4 | 1.29 | 10 |
| Treeline | 6 | 3.73 | 0 | 1.81 | 0 | 0.56 | 1 | 0.9 | 7 |
| Woodland | 25 | 24 | 14 | 11.6 | 3 | 3.63 | 3 | 5.81 | 45 |
| Total | 33 | | 16 | | 5 | | 8 | | 62 |

Cheetahs were observed using the foreshore mostly during the early morning and the late evening (Figure 4.5). The woodland was used predominantly during the middle of the day (Figure 4.5). The treeline was used during the time of day where hunting was most often observed (compare Figure 4.5 and 4.6). Although all activities were observed in the woodland, it appears that it is used by the cheetahs mainly to rest up during the day and to move around the park (Figures 4.5 and 4.6; Table 4.3)

4.3.3 Prey composition:

A total of 15 kills were observed during the study period, 13 (86.6%) of them were impala, one (6.7%) waterbuck (*Kobus ellipsiprymnus*) and one (6.7%) guineafowl (*Numida meleagris*). 14 scats were collected all together and five prey species were recorded; impala, waterbuck, kudu (*Tragelaphus imberbis*), bushbuck (*Tragelaphus scriptus*) and duiker (*Sylvicapra grimmia*). There was no significant difference in the percentage of prey species recorded in the two data sets (Chi-square test of heterogeneity) and they were pooled for analysis. Impala was the main prey species recorded (Figure 4.7) but selection for waterbuck (PSR = 4.67) and kudu (PSR = 4.00) was stronger than for impala (PSR = 0.85).

4.3.4 Prey availability:

The foreshore and the woodland had approximately the same number of animals available. The average density in the foreshore during the wet season was 306 impala/km² and in the dry season was 234 impala/km² whereas the average density in the woodland during the wet season was 6.9 impala/km² and during the dry season was 33.2

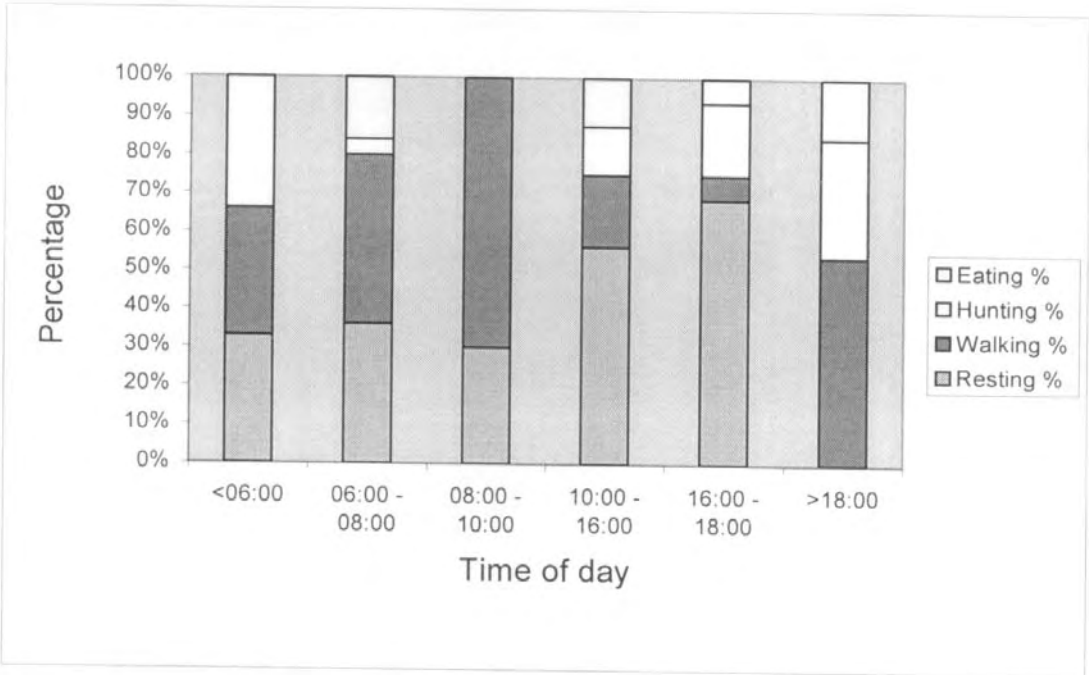
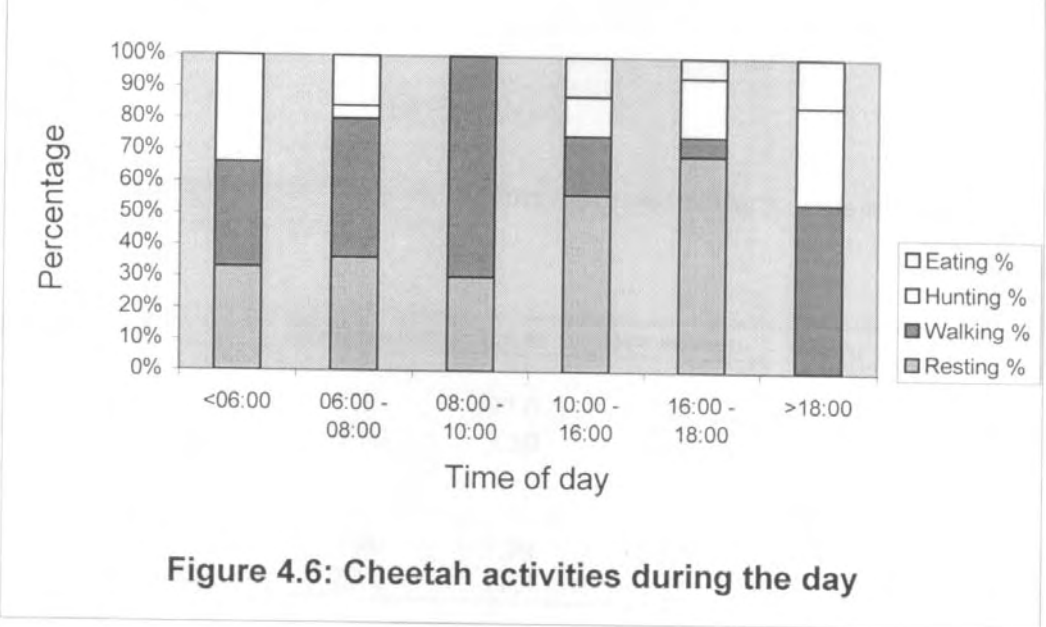


Table 4.4: Density of impala (animals/km²) on the foreshore and in the woodland in the wet (February - April) and dry season (May - July).

| Habitat Type | Wet season | s.e.m | Dry season | s.e.m | Total | s.e.m |
|----------------------------|-------------------|--------------|-------------------|--------------|--------------|--------------|
| Foreshore | 306.00 | 97.00 | 234.00 | 61.00 | | |
| Woodland | 6.90 | 3.80 | 33.20 | 11.00 | | |
| Woodland (near foreshore) | | | | | 27.60 | 9.60 |
| Woodland (near escarpment) | | | | | 28.90 | 16.00 |
| Woodland (near Fothergill) | 3.90 | 3.90 | 55.00 | 22.00 | | |
| Woodland (near Tashinga) | 22.20 | 11.00 | 12.60 | 6.80 | | |

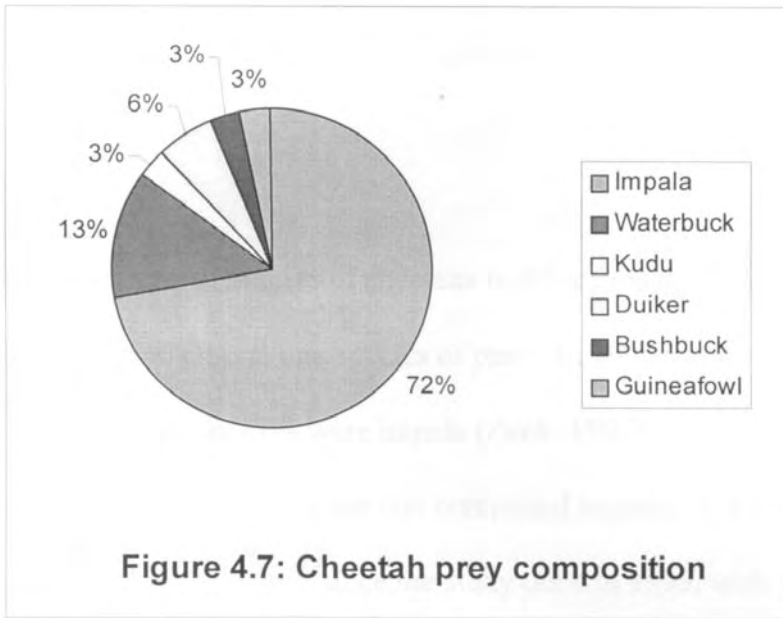
impala/km². The foreshore density of impala was significantly greater both in the wet season (two sample *t*-test, *n* = 57, *t* = 3.07, *P* = 0.0047) and the dry season (two sample *t*-test, *n* = 81, *t* = 3.23, *P* = 0.0026) (Table 4.4). There was no difference between the density of impala in the woodland near the foreshore and the woodland near the escarpment and the density of impala at Fothergill and Tashinga did not differ in either the wet season or dry season (Table 4.4).

The total number of waterbuck and kudu in the valley floor section of MNP was estimated at 521 and 235 respectively. No kudu were seen on the foreshore during the study period. Waterbuck were counted once in the foreshore blocks and three times in the woodland during the study period. It was not possible to compare densities between the two habitats. The total density of waterbuck in the MNP is 1.34/km² and kudu is 0.61/km². The smaller prey species population could not be estimated.

The amount of prey biomass required by 13 adult cheetahs in one year is 18980kg (calculated by assuming that each cheetah requires 4kg/day (Schaller, 1972). The maximum sustained yeild of impala biomass produced is 67 141 kg calculated as follows:

$$MSY = (0.44(20\ 000)/4) * 30.7$$

Assuming that the carrying capacity (*K*)of the impala population is 20 000 animals. This is based on observation that the size of the impala population has not changed significantly between 1995 (19531 animals, Zank, (1995)) and 1998 (19184 animals) and



is thus likely to be an underestimate of K as the population is harvested by the resident predator population. The sustained yield of edible biomass is 57 070kg per year, 85% of the maximum sustained yield of impala biomass (Section 4.2.3).

4.4 Discussion:

As has been observed in other studies of cheetahs in Africa (Mills, 1991), the cheetahs of MNP appear to be specialising on one species of prey. In 1995 soon after the release of the cheetahs, 75.7% of cheetah kills were impala (Zank, 1995). In this study 86.6% of cheetah kills were impala and 72% of the diet comprised impala. The prey choice of the cheetahs has not altered significantly since the study done in 1995, with waterbuck, bushbuck, duiker, kudu and guineafowl recorded this time compared to waterbuck, grysbok (*Raphicerus sharpei*), scrubhare (*Lepus saxatilis*), duiker and bushbuck recorded in the previous study (Zank, 1995). The cheetahs in MNP appear to feed predominantly on adult impala, 53.3% of impala kills in this study and 51.2% in 1995 (Zank, 1995). This behaviour is similar to that of observed in cheetahs in Kruger National Park where impala were the preferred prey species and adults were killed ten times more than juveniles (Mills and Biggs, 1993). Similarly, cheetahs introduced into the Suikerbosrand Reserve specialised on killing blesbok (*Damaliscus dorcas*) with adults making up 57.7% of kills (Pettifer, 1981). In the Kalahari Gemsbok National Park, springbok made up 86.9% of cheetah kills and more adults (78%) were killed than juveniles (22%)(Mills, 1990).

The cheetahs in MNP are selecting for waterbuck and kudu as was recorded in the 1995 study (Zank, 1995). The data for this analysis comes from scats, hence it was not possible to determine if the hair in the scats came from adults or juveniles (Mills, 1992). Cheetahs are known to select for juveniles of these species unless they are hunting in a group (Zank, 1995; Mills, 1990; Caro, 1994) and it is likely that the cheetahs in MNP were killing juveniles of these two species. The strong preference for waterbuck does not appear to have a adverse effect on the waterbuck population which has increased from 99 animals to 521 animals between 1995 and 1996. This could be due to above average rainfall during this period. The pattern of use of smaller ungulates by cheetahs may simply be a result of their abundance and the fact that they are easily killed. Where possible cheetahs may kill larger animals that provide a greater amount of biomass.

When cheetahs were introduced into the Suikerbosrand Reserve they caused a drastic reduction in the blesbok and springbok populations and prey availability became the limiting factor of the introduced population (Pettifer, 1981). The initial population viability analysis of the MNP cheetahs concluded that prey was unlikely to become a limiting factor for the cheetahs, although it was suggested that they might overutilise the waterbuck population (Zank, 1995). The number of impala in MNP in 1998 was approximately the same as was present in 1995, 19184 animals compared to 19531 animals. Despite the predictions of the 1995 study the number of waterbuck present in the park is greater than it was before. The calculated sustained yield of edible biomass from the impala population suggests that it is unlikely that prey will be the limiting factor for the introduced population of cheetahs as it is more than twice the amount required by

the cheetahs. This amount of biomass will only be realised when the impala population is reduced to half the carrying capacity. Therefore, not only is the sustained yield of edible biomass well in excess of what is needed by cheetahs, but a large amount of impala biomass could be removed from the population before this sustained yield is affected. This biomass could support a population of 40 adults. Despite the fact that these calculations are based on the assumption that cheetahs are the only predators removing prey from the prey population, lions, hyaenas and leopards have been present in MNP for a while and do not seem to have reduced the impala population below the carrying capacity.

The preference for the treeline shown by the cheetahs in MNP is similar to the behaviour shown by the cheetahs in the previous study conducted soon after they were released (Zank, 1995). This supports the argument that cheetahs quickly adapt to a new environment (Caro, 1994). However, cheetahs in the western and escarpment parts of MNP may well have very different habitat preferences because of the difference in the availability of the three habitat types. There is little available foreshore habitat in these areas. In the Serengeti, although cheetahs do use the open plains, they are often observed hunting from the plains-woodland boundary (Caro and Collins, 1987). In Suikerbosrand, the cheetahs were observed to hunt predominantly in the gullies and the ravines rather on the open plains (Pettifer, 1981). Cheetahs are the top predators in Suikerbosrand and it is unlikely that this use of the gullies and ravines reflects an attempt to escape harassment from other predators, but rather a need to hunt more effectively. The use of the treeline in MNP may simply be for hunting purposes rather than an attempt to hide from

competing predators as cheetahs were observed most often in this habitat at the time of day that most hunting occurred (Figures 4.4 and 4.5). It is known that cheetahs usually require cover to stalk their prey (Caro, 1994). There are open grassland areas within the woodland of MNP that cheetahs would use to the same extent as they utilise the treeline and open foreshore. More information about habitat use by the cheetahs in MNP found in areas where there is no foreshore need to be obtained to compare habitat use to determine if the same pattern emerges. However, in Kruger National Park (KNP) cheetahs preferred the open plains and hunted during the middle of the day (Mills and Biggs, 1993). Hyenas took 14% of cheetah kills in KNP and the habitat preference shown by the cheetahs in KNP is probably a response to this threat of kleptoparasitism.

The home range sizes observed were much smaller than was recorded soon after the animals were released into the park (Zank, 1995). In 1995, the cheetahs were moving long distances and home ranges for males averaged 135.5km^2 and for females 267 km^2 (Zank, 1995). In this study the largest home range was that of a young male cheetah (53.75 km^2). This is less than half that recorded for males in 1995. The home range of the female and cub was 23.6 km^2 and was concentrated along the foreshore part of the valley floor but included all three habitat types (Figure 4.8). A study of the Blanford's fox, *Vulpes cana*, provided evidence that home ranges have to be large enough to include a productive area that can support the individual animal during periods of low food production (Geffen, Hefner, MacDonald and Ucko, 1992). This same study also concluded that productive areas where the risk of predation is high did not influence the size of the home range (Geffen *et al*, 1992). In MNP the home range of an individual

female may have to include a minimum length of treeline rather than a minimum area of productive foreshore. Home range sizes may be primarily determined by the need to include an area with suitable amounts of prey as cheetahs in areas where prey is migratory have very large home range sizes, average 833 km² for female cheetahs in the Serengeti (Caro, 1994). If this is the case it might explain why home range sizes of the cheetahs in MNP are much smaller than recorded for any other area of Africa as the available prey is concentrated into a small area. If prey density is the primary factor determining home range size then the hypothesis would be that the cheetahs utilising the western and escarpment areas of the park would have larger home range areas than those observed during this study.

Male home range sizes are usually smaller than those of females (Caro, 1994; Pettifer, 1981). Caro and Collins (1987) argue that male cheetahs adopt two strategies to obtain females to mate with; one strategy involves setting up a territory that includes areas that females use, the other involves moving over large distances to increase the chances of encountering females. One female's home range would include many male territories but as females' home ranges overlap to a very large extent each male would have a high chance of encountering at least one female while utilising a smaller area than the average used by females. If male territories are defined by females' use of an area this could explain the patterns observed in MNP. Both males in MNP would have had a chance of encountering females as their home range areas included productive and safe habitat. The older male appeared to have an established territory that included both foreshore and woodland (Figure 4.3). The younger male appeared to have an established a territory of

similar size until the core area was almost cut off by the rising lake levels (Figure 4.2). He then seemed to abandon his territory and started to move large distances. A similar occurrence was recorded for a cheetah in the Serengeti that abandoned his territory after losing his coalition partner. He then moved over an area 14.7 times as great as his initial territory (Caro, 1994).

The use of MNP by the cheetahs observed during this study has not altered significantly since they were introduced, except that the average home range size is much smaller. The use of the treeline may be in response to the threat of harassment by other predators but could also be to enable them to hunt more successfully. Burt (1943), in one of the earliest papers on the concept of home range states that “it is only after [an animal] has established itself, normally for the remainder of their lives, unless disturbed, that one can rightfully speak of a home range”. The large areas that the cheetahs were recorded using soon after their release were not strictly home ranges. The small home ranges recorded in this study suggest that prey distribution is the primary determinant of home range size, although there may be a need to include a minimum amount of safe, productive habitat (the treeline). This hypothesis could be tested by comparing home range sizes and habitat preferences of cheetahs in MNP that are using the less productive areas of the park. If there is evidence to support the hypothesis then the number of cheetahs that will be able to utilise MNP will be determined by the distribution certain habitats and prey, rather than the total amount of prey *per se*. The fact that there are approximately the same number of cheetahs in the park in 1998 as there were in 1995 suggests that this may be the maximum number that are able to use the area.

CHAPTER FIVE: Population sizes, use of habitats and prey selection by lions and hyaenas in Matusadona National Park (MNP)

5.1 Introduction

A number of large predators including lions, *Panthera leo*, spotted hyaenas, *Crocuta crocuta*, leopard, *Panthera pardus*, wild dog, *Lycaon pictus* and side striped jackals, *Canis adustus* are present in MNP (Taylor, 1985). Only lions occur in large numbers. By the end of 1994, 14 adult cheetahs, *Acinonyx jubatus*, had been introduced into this community as part of a re-introduction project (Zank, 1995). Studies in other areas with similar communities of large predators have indicated that there is a certain amount of ecological separation between the large predators in terms of prey choice, habitat preferences and preferred time of day for hunting (Schaller, 1972 – Serengeti; Mills and Biggs, 1993 – Kruger National Park; Mills, 1990 – Southern Kalahari).

However, there is also evidence that there are areas of overlap in the use of available resources between the large predator species. These areas of overlap may result in adverse competitive interactions (Polis, Myers and Holt, 1989). Lions are known to prey on cheetah cubs resulting in significant mortality (Laurenson, 1995), lions and cheetahs are known to suffer from kleptoparasitism by hyaenas (Schaller, 1972; Mills and Biggs, 1993; Stander, 1990) and lions have been reported stealing carcasses from cheetahs (Stander, 1990). Such adverse interactions can limit the number of the smaller, more specialised predators such as cheetahs and wild dog (Creel, 1998).

The current and continued success of the introduced cheetah population in MNP will depend to a certain extent on the interactions between the cheetahs and the other predators of MNP. A population viability study conducted in 1995 predicted that the possibility of adverse interactions with lions and hyaenas would limit the success of the cheetah re-introduction, especially through intraguild predation of cheetah cubs (Zank, 1995). To determine the extent of this threat of intraguild interactions to the long term survival of the cheetahs, there is a need to know the number of lions and hyaenas in MNP, their prey selection and their habitat type preferences. This chapter addresses two questions: how does the use of the available resources by lions and hyaenas compare to cheetahs and how do the observed patterns of population size, prey use and habitat preferences of lions, hyaenas and cheetahs compare with other areas of Africa which have all three predators.

Methods

5.2.1 Estimation of hyaena numbers.

Broadcasts of hyaena vocalisations were used to attract hyaenas to determine the number of hyaenas in MNP. This method is known to be very accurate (Ogutu and Dublin, 1998) and has been used in many different parks (Bowler, 1991; Zank, 1995; Pole, unpubl). A total of thirteen call-up sites were chosen randomly within the limits of road access. Nine were located in the valley floor section and four in the escarpment section of MNP (Figure 5.1). Altogether, using the minimum area covered, these sites broadcast over

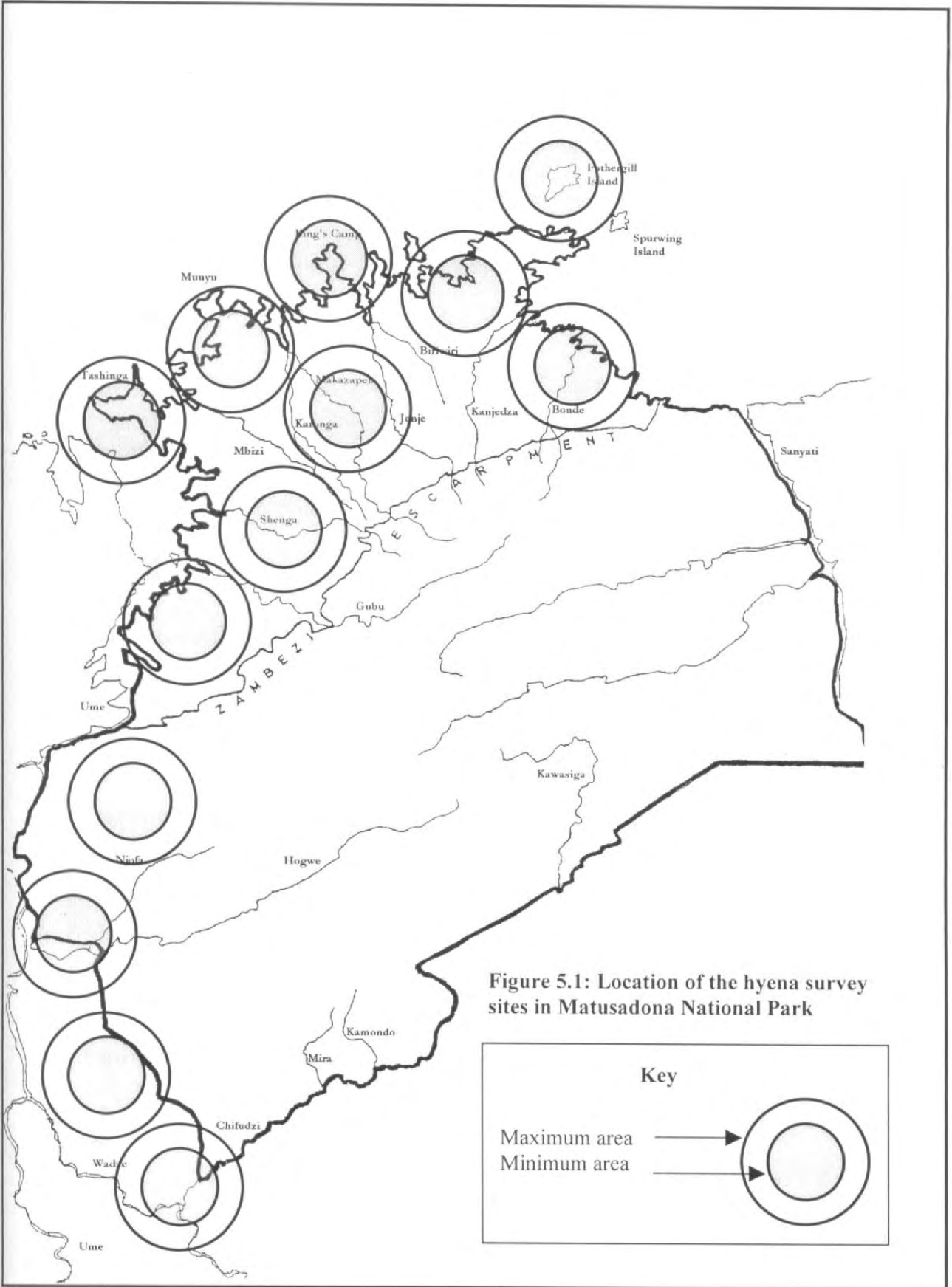


Figure 5.1: Location of the hyena survey sites in Matusadona National Park

17% of the total area of MNP, and 46% of the valley floor. Ogotu and Dublin (1998), in an assessment of the method, concluded that only 20% of the total area needs to be surveyed to obtain an accurate estimate of the population.

At each call-up site, two 100W speakers were placed on the roof of the vehicle, approximately 2.3m above the ground. These had been calibrated already and were known to broadcast over a maximum distance of 3.5km and a minimum distance of 2km (Pole, unpubl). A tape with recorded hyaena vocalisations was played three times for six minutes, followed each time by four minutes of silence. The speakers were rotated 90° after three minutes of playing the tape. A spotlight was used to locate any predators who had responded to the hyaena vocalisations. During the first six minutes of play it was not shone at all, during the second play it was shone periodically and during the last six minutes of play it was shone continuously. The presence of any predators and their time of arrival after the tape was first played were recorded using a portable tape recorder.

Each site was only surveyed once as hyaenas are known to habituate to the sounds from the tape and a period of six months between surveys is necessary to ensure that this habituation does not influence the response of hyaenas (Mills, pers comm). Where possible sites close to each other were surveyed on the same night to avoid counting the same animals twice. The sites in the valley floor were surveyed from 20–22nd May and the sites in the escarpment were surveyed on the 15th July.

5.2.2 Estimation of lion numbers

Although Ogutu and Dublin (1998) have shown that the above method can be used to estimate lion numbers it has not been tested whether this is true in all habitat types. Lion numbers during this study were estimated from tour guides' and scouts' knowledge of pride sizes. The resident lion prides have been observed by tour guides for a number of years and the number of animals in each pride is known. After a patrol, scouts report where they have seen lions and how many they saw. This information was then used to confirm the numbers given by the tour guides.

5.2.3 Comparison of predator biomass in MNP with other conservation areas of Africa.

Lion, hyaena, cheetah and prey biomass data was available for seven other conservation areas in Africa where cheetahs occur. Parks without cheetahs were excluded from the analysis. Cheetah densities are known to be positively correlated with prey biomass in the 15 – 60kg range (Gros, Kelly and Caro, 1997) so all the data was corrected for this range of prey biomass before comparisons were made. This correction was done by dividing the highest prey biomass recorded by each of the other values of prey biomass to obtain a correction factor for each park. This correction factor was then used to standardise the cheetah biomass density value recorded for each park from the literature. Lion and hyena biomass densities were not corrected for as they are not specifically affected by the availability of prey in the 15 – 60kg range.

5.2.4 *Lion and hyaena prey composition*

Lion and hyaena scats were collected throughout the study period, the former opportunistically and the latter from known midden sites. Each scat was dried at 80% and then crushed. A five gram sample was removed and all the hair within this sample was identified using colour, texture and cuticular scale patterns (Keogh, 1983; Buys and Keogh, 1984).

When a lion or group of lions were observed at a kill, the species killed, its age and sex and the habitat type that the lions were in were recorded. It was not possible to do this for hyaenas as work at night was not feasible. Preferences for prey species was calculated as shown below:

$$\text{Prey selection ratio (PSR)} = \frac{\% \text{used}}{\% \text{available}}$$

Where % used is the frequency of occurrence of a prey species in the diet and % available is the percentage of the total available prey biomass made up by that prey species. The latter value was calculated using prey population sizes calculated during this study (See Section 4.2.3) except for buffalo where the PSR was calculated using a population size estimated from an aerial survey conducted in 1996 (Mackie, 1996).

5.2.5 *Habitat preference of lions*

Public sightings of lions and cheetahs were used in this analysis to enable a comparison to be made. Two guides from two separate safari lodges were given sighting sheets to record the habitat type and time of day when they observed lions. These same guides also recorded the same information when they observed cheetahs to enable a comparison to be made between the two species. It was assumed that the two guides would search the available habitat to the same extent for both species. Habitat preference was then determined using the equation below:

$$PR = U/A$$

Where U is the number of sightings in each habitat divided by the total number of sightings across all habitats and A is the area of a specific habitat divided by the total area (Mills and Biggs, 1993). A Chisquare test of association was used to determine if there was a relation between the time of day and the habitat used. This analysis was restricted to the early morning (5:30 – 8:30) and late evening (16:00 – 19:00) as this was the time of day when the guides used MNP.

5.3 Results

5.3.1 *Hyaena Population size*

For each survey site there was a maximum and minimum density of animals recorded depending on whether the broadcast had been over 3.5km or 2km respectively. There

were no significant differences between the two figures in any of the thirteen survey sites and an average value for each site was used to estimate the total population of hyaenas, the population of the valley floor and the population of the escarpment (Table 5.1).

In addition to the hyaenas called, a total of 29 lions responded to the broadcasts during six surveys. In three of these cases the lions displayed aggressive behaviour. In one case a male lion chased a hyaena for a distance of 200m before giving up the chase.

The previous study of predators conducted in MNP found that there was a very low density of hyaenas, 0.08/km² (Zank, 1995). The density calculated during this study was 0.127 hyaenas/ km² for the whole park, 0.13 hyaenas/ km² for the valley floor section and 0.119 hyaenas/ km² for the escarpment section (Table 5.2). Hyaenas in MNP appear to be concentrated in the western part of the valley floor and the foothills of the escarpment (Figure 5.2).

5.3.2 Lion population size

The guides and scouts in MNP identified a total of seven prides that inhabit the valley floor section of MNP. It was not possible to determine how many prides utilised the escarpment. In addition to the lions in the prides of the valley floor, it was assumed that there was a coalition of two adult male lions for every pride. This gives a total of 123 lions in 388km², a density of 0.317lions/ km² (Table 5.3). The density of lions in the eastern area of the valley floor appears to be greater than the western area (Figure 5.3).

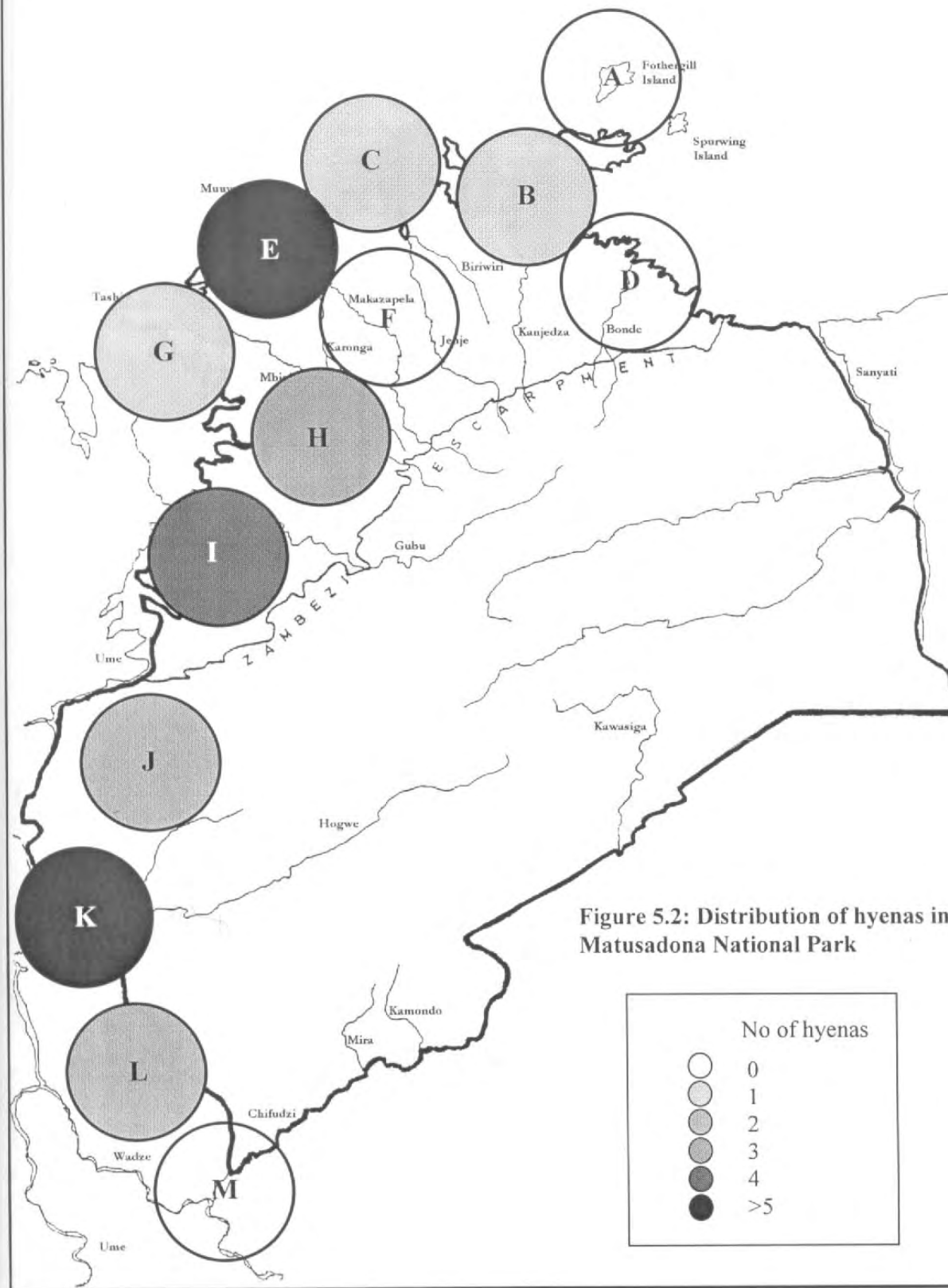


Figure 5.2: Distribution of hyenas in Matusadona National Park

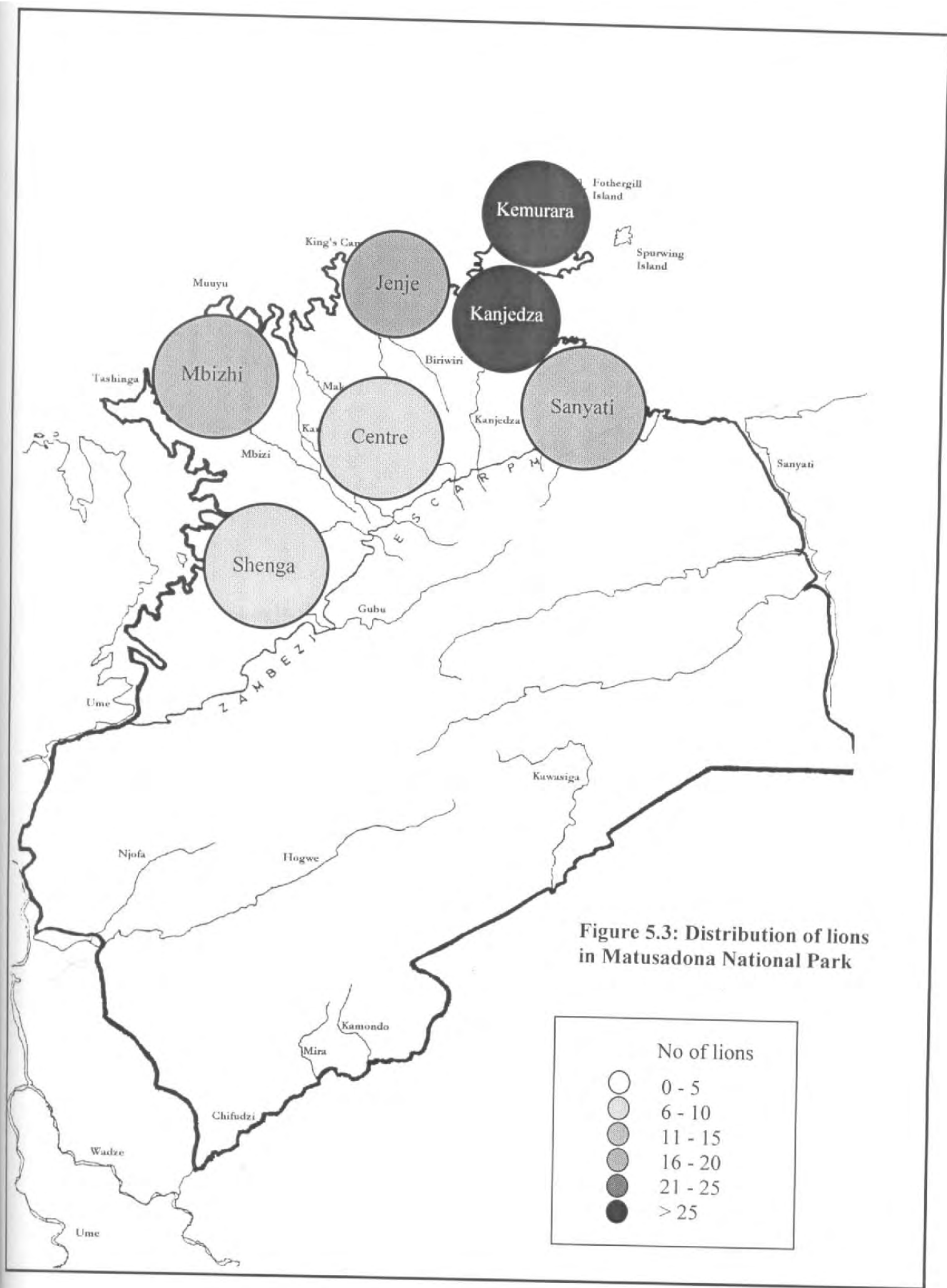


Table 5.1 Summary of data from thirteen hyena survey sites

| Site | No. of hyenas | Max area (km ²) | Min. area (km ²) | Min. density (hyenas/km ²) | Max. density (hyenas/km ²) | Average (hyenas/km ²) |
|--------------|---------------|-----------------------------|------------------------------|--|--|-----------------------------------|
| A | 0 | 15 | 6 | 0 | 0 | 0 |
| B | 1 | 35.26 | 12.4 | 0.028 | 0.081 | 0.055 |
| C | 1 | 15.08 | 5.52 | 0.066 | 0.181 | 0.124 |
| D | 0 | 34.3 | 12.57 | 0 | 0 | 0 |
| E | 9 | 35.74 | 12.57 | 0.252 | 0.714 | 0.483 |
| F | 0 | 38.5 | 12.57 | 0 | 0 | 0 |
| G | 1 | 10.76 | 5.48 | 0.093 | 0.182 | 0.138 |
| H | 3 | 38.5 | 12.57 | 0.078 | 0.238 | 0.158 |
| I | 4 | 37.74 | 12.57 | 0.106 | 0.317 | 0.212 |
| J | 2 | 34.7 | 12.57 | 0.057 | 0.159 | 0.108 |
| K | 5 | 38.5 | 12.57 | 0.13 | 0.397 | 0.264 |
| L | 2 | 38.5 | 12.57 | 0.052 | 0.159 | 0.106 |
| M | 0 | 38.5 | 12.57 | 0 | 0 | 0 |
| Total | 28 | 411.1 | 142.5 | | | 0.127 |

Table 5.2 Density of hyenas in different areas ofMNP

| | Area(km ²) | Density(hyenas/km ²) | s.e.m |
|---------------------|------------------------|----------------------------------|-------|
| Valley Floor | 388 | 0.13 | 0.051 |
| Escarpment | 982 | 0.119 | 0.054 |
| Total | 1370 | 0.127 | 0.038 |

Table 5.3 Number of lions in the valley floor section of MNP

| Pride | Number |
|--------------|------------|
| Sanyati | 14 |
| Kanjedza | 26 |
| Kemurara | 25 |
| Jenje | 18 |
| Centre | 7 |
| Mbizhi | 13 |
| Shenga/Gubu | 6 |
| Total | 109 |

5.3.3 *Comparison of predator biomass of MNP with other conservation areas in Africa*

MNP had the highest prey biomass in the 15 –60kg range, 1517kg/km², of all the conservation areas compared (Table 5.4). This is due to the effect of the density of prey on the foreshore of MNP which is very high (See Section 4.3.4). There were no significant relationships between the biomass densities of the three predator species (Figures 5.4 and 5.5) although there is a suggestion that lion and hyaena biomass has a negative influence on cheetah biomass and that the biomass of hyaenas and lions is positively correlated. If Nairobi National Park (NNP) is removed from the data set (see Discussion) then there is a strong negative relationship between lion and cheetah biomass ($n = 7, r^2 = 64\%, P = 0.056$). In all the conservation areas compared, MNP is the only one where the biomass of lions is greater than that of hyaenas (Table 5.5). MNP also has the lowest predator biomass density for prey biomass density (Table 5.6). If the data from MNP is removed from the comparison of lion and hyaena biomass, there is a significant positive relationship between lion biomass and hyaena biomass ($n = 5, r^2 = 82.8\%, P = 0.03$). There was no correlation between the ratio of lion and hyaena biomass to prey biomass, and cheetah biomass (Spearman's rank co-efficient correlation).

Table 5.4. Densities of lion, hyena, cheetah (corrected for prey biomass in 15-60kg range) and prey biomass, in the 15-60kg range (kg/km²) in eight conservation area of Africa

| Conservation area | Prey biomass ** | Lion | Hyena | Cheetah | Size of area (km ²) | Ref * |
|--------------------------------------|--------------------|-------|-------|---------|---------------------------------|------------|
| Hluhluwe-Umfolozi Park | 700 | | 17.85 | 7.61 | | 1 |
| Hwange National Park | 30 | 3.31 | 8.93 | 13.64 | 14000 | 1 |
| Kruger National Park | 246 | 4.25 | 3.41 | 4.19 | 400*** | 2 |
| Serengeti ecosystem (1986 - present) | 468 | 13.23 | 43.05 | 3.38 | 25000 | 1 |
| Ngorongoro Crater | 490 | 37.8 | 57.23 | 0 | 8288 | 3, 4 |
| Etosha National Park | 16 | 1.89 | 2.63 | 12.78 | 22270 | 5 |
| Nairobi National Park | 461 | 22.68 | | 35.06 | 130 | 6, 7 |
| Matusadona National Park | 1517 | 29.96 | 6.83 | 1.58 | 388 | This study |

* 1, Woodroffe, Ginsberg, Macdonald and IUCN/SSC Canid specialist Group (1997); 2, Mills and Biggs (1993); 3, Hanby, Bygott and Packer (1995); 4, Sinclair (1995); 5, Stander (1990); 6, Rudnai (1973) and 7, Eaton (1974).

** Gros, Kelly and Caro (1997)

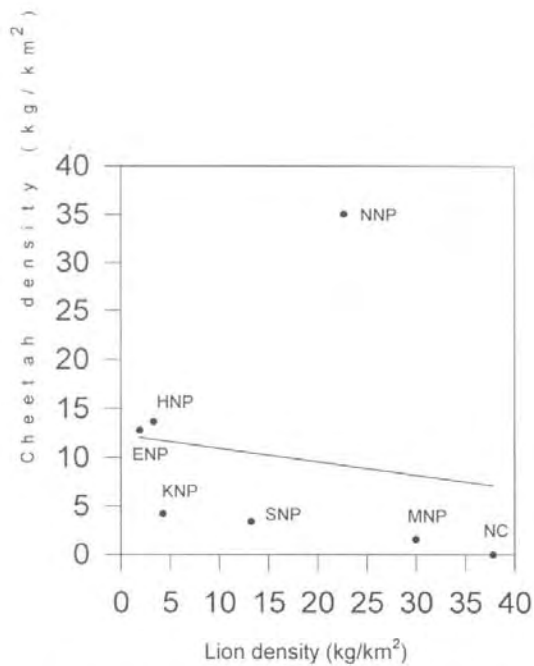
*** This is the area from which the densities of the predators were calculated rather than the total area of KNP

Table 5.5: Ratios of lion and hyena density (animals/km²) in relation to cheetah density (animals/km²) for seven conservation areas of Africa

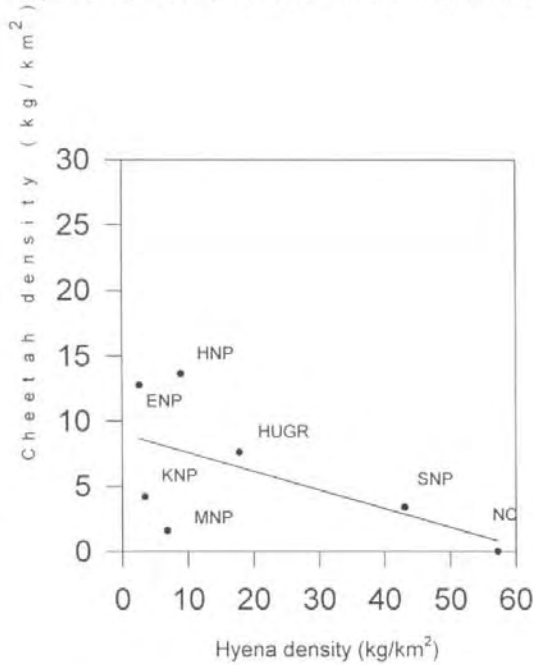
| Conservation area | Prey biomass (15-60 range) kg/km ² | Lion | Hyena | Cheetah |
|--------------------------------------|--|------|-------|---------|
| Hluhluwe-Umfolozi Park | 700 | | 4.36 | 1 |
| Hwange National Park | 30 | 5.83 | 28.33 | 1 |
| Kruger National Park | 246 | 3 | 4.33 | 1 |
| Serengeti ecosystem (1986 - present) | 468 | 6.09 | 35.65 | 1 |
| Etosha National Park | 16 | 6.67 | 16.67 | 1 |
| Nairobi National Park | 461 | 0.71 | | 1 |
| Matusadona National | 1517 | 9.06 | 3.71 | 1 |

Table 5.6: Ratio of lion and hyena biomass (kg/km²) and prey biomass (kg/km²) in the 15-60 kg range, compared to cheetah biomass for eight conservation areas of Africa.

| Conservation area | Ratio lion and hyena/prey densities | Rank | Cheetah biomass | Rank |
|---|--|-------------|------------------------|-------------|
| Hluhluwe-Umfolozi Park | 0.03 | 6 | 7.61 | 4 |
| Hwange National Park | 0.42 | 1 | 13.64 | 2 |
| Kruger National Park | 0.03 | 7 | 4.19 | 5 |
| Serengeti ecosystem (1986 - present) | 0.12 | 4 | 3.38 | 6 |
| Ngorongoro Crater | 0.19 | 3 | 0 | 8 |
| Etosha National Park | 0.29 | 2 | 12.78 | 3 |
| Nairobi National Park | 0.08 | 5 | 35.06 | 1 |
| Matusadona National Park | 0.03 | 8 | 1.58 | 7 |



a) The relationship between lion and cheetah biomass



b) The relationship between hyena and cheetah biomass

Figure 5.4: The effect of a) lion and b) hyena biomass on cheetah biomass in eight conservation areas of Africa where all three species occur

HUGR Hluhluwe-Umfolozi Game Reserve; HNP Hwange National Park; ENP Etosha National Park
 KNP Kruger National Park; SNP Serengeti National Park; NC Ngorongoro Crater; NNP Nairobi
 National Park; MNP Matusadona National Park

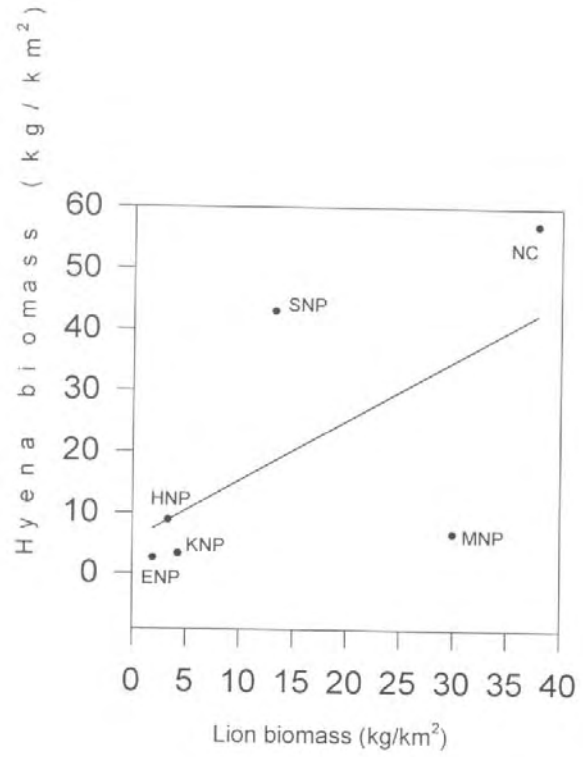


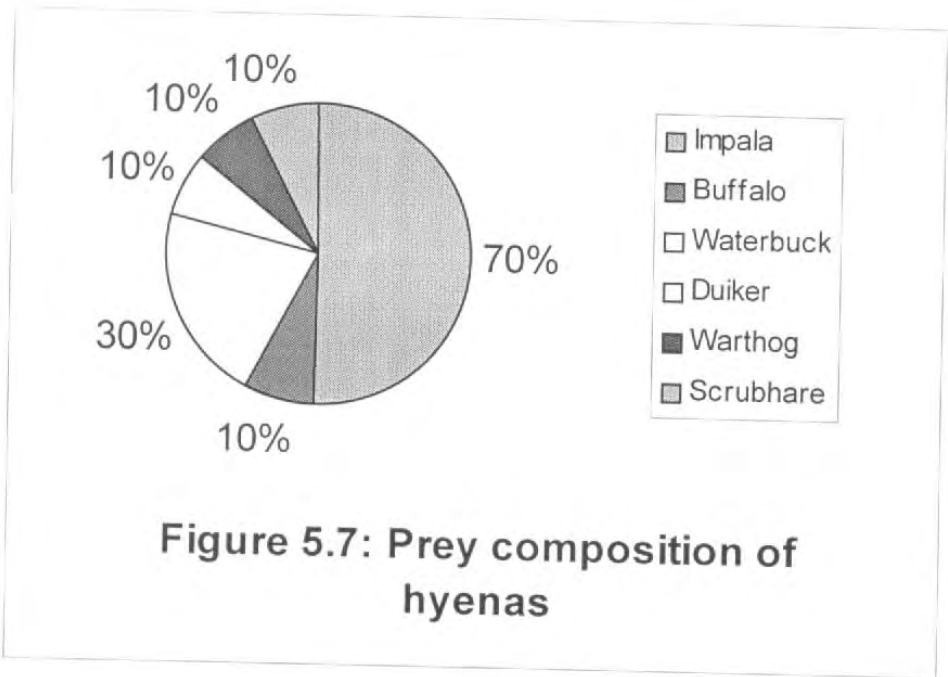
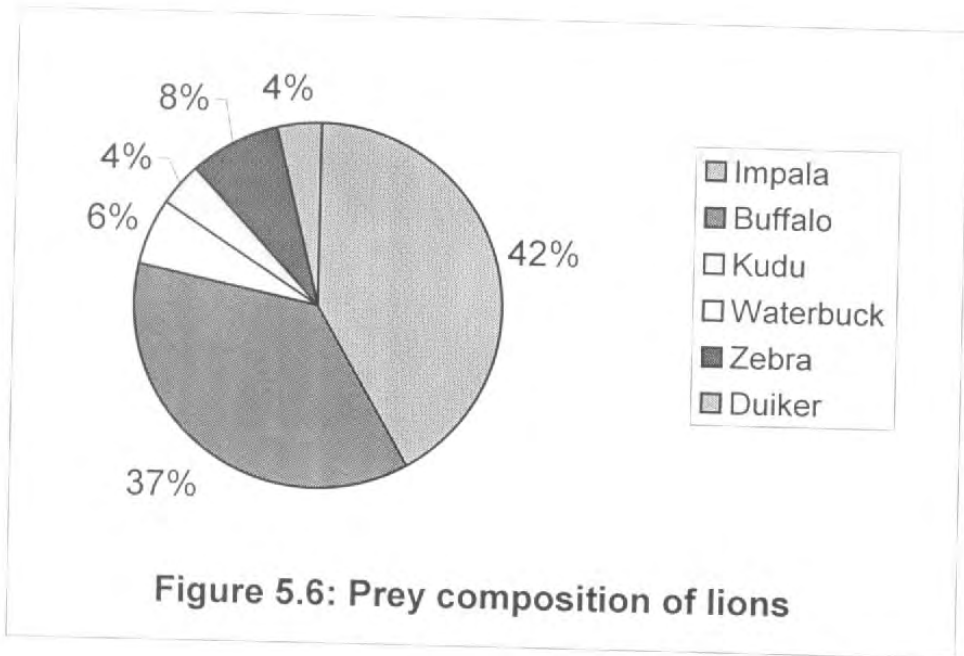
Figure 5.5: The relationship between lion biomass and hyena biomass for six conservation areas of Africa

HUGR Hluhluwe-Umfolozi Game Reserve; HNP Hwange National Park; ENP Etosha National Park
 KNP Kruger National Park; SNP Serengeti National Park; NC Ngorongoro Crater; NNP Nairobi
 National Park; MNP Matusadona National Park

5.3.4 *Hyaena and lion prey composition*

A total of 18 lion scats and 10 hyaena scats were collected altogether. Six prey species were recorded for lions and six for hyaenas (Figures 5.6 and 5.7). A total of 29 lion kills were recorded. The data from analysis of the lion scats was not significantly different from those collected from kills (Chi-square test for heterogeneity) and the two data sets were pooled for analysis. Impala (*Aepyceros melampus*) constituted the majority of lion and hyaena prey composition, 42% and 70% respectively. (Figures 5.6 and 5.7).

However, it is known that smaller prey species are over represented in scat analysis because of the higher skin to flesh ration in smaller prey species (Henschel and Skinner, 1990). Impala and buffalo (*Syncerus caffra*) are probably preyed on in equal proportion by lions in MNP. Other species killed included buffalo, waterbuck (*Kobus ellipsiprymnus*), kudu (*Tragelaphus imberbis*), zebra (*Equus burchelli*), duiker (*Sylvicapra grimmia*), warthog (*Phacochoerus aethiopicus*) and scrubhare (*Lepus saxatilis*). Lions exhibited a very low preference for impala (PSR = 0.46) and a very high preference for buffalo (PSR = 9.25). Hyaenas showed a preference for waterbuck (PSR = 1.00) over impala (PSR = 0.75). The proportion of adult impala and buffalo killed by lions was greater than for juveniles, 67% and 83% respectively (Figure 5.8).



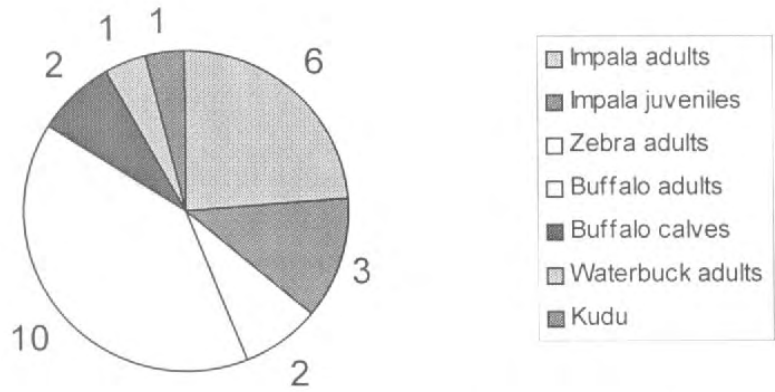


Figure 5.8: Proportion of adults and juveniles of prey species killed by lions

5.3.5 Habitat preferences of lions and cheetahs

There were 39 sightings (June – July) of lions and 56 sightings (February – July) of cheetahs by the two guides. According to this analysis, lions showed a preference for the treeline (PR = 15.8) and the foreshore (PR = 6.73) but did not utilise the woodland as much as would be expected (PR = 0.09). The same pattern was shown by the cheetahs although their preference for the treeline (PR = 16.4) was slightly greater than shown by lions. They also did not use the foreshore as much as the lions (PR = 4.65). There was no evidence that lions were showing any preference for any habitat type in the early morning or late evening (Table 5.7). However, the cheetahs appeared to use the treeline more often in the early evening than the early morning ($n = 29$, $\chi^2 = 6.461$, $df = 2$, $P = 0.04$; Table 5.7).

5.4 Discussion

The number of lions and hyaenas in MNP has increased slightly over the four years since the cheetahs were first released. In spite of the high density of lions, cheetahs are still present. The low density of hyaenas probably means that they have little effect on the number of cheetahs in MNP.

There appears to be little overlap in prey selection between cheetahs (Section 4.3.3) and lions (Figure 5.6) in MNP. Cheetahs take predominantly impala and show a preference

Table 5.7: Number of sightings (observed and expected) of lion and cheetah in MNP in the early morning (05:30-09:00) and early evening (16:00-19:00)

| Species | Time of Day | Habitat type | | | | | | Total |
|----------------|--------------------|--------------|------|----------|------|----------|------|-------|
| | | Foreshore | | Treeline | | Woodland | | |
| | | Obs | Exp | Obs | Exp | Obs | Exp | |
| Lion | 05:30-09:00 | 16 | 17.9 | 5 | 4.31 | 3 | 1.85 | 24 |
| | 16:00-19:00 | 13 | 11.1 | 2 | 2.69 | 0 | 1.15 | 15 |
| | Total | | 29 | | 7 | | 3 | |
| Cheetah | 05:30-09:00 | 9 | 8.28 | 1 | 3.62 | 5 | 3.1 | 15 |
| | 16:00-19:00 | 7 | 7.72 | 6 | 3.38 | 1 | 2.9 | 14 |
| | Total | | 16 | | 7 | | 6 | |

for waterbuck whereas lions, while taking a large number of impala, specialise on buffalo.

In Kruger National Park (KNP) lions are the dominant predator (accounting for 54% of total predation) as they can take advantage of the buffalo, especially during drought years (Mills, 1995) and have exclusive access to zebra and wildebeest, *Connochaetus taurinus* (Mills and Biggs, 1993). A similar situation seems to occur in MNP. In Kruger and Kalahari lions and hyaenas kill the same species but select for adults and juveniles respectively (Mills and Biggs, 1993; Mills, 1990). In none of the areas where large predators have been studied has there been any overlap in the preferences for prey of lions and cheetahs (Mills and Biggs, 1993; Mills 1990; Schaller 1972).

Hyaenas overlap considerably with cheetahs in their prey selection in MNP, taking predominantly impala and showing a preference for waterbuck (Figure 5.7). However, due to the low density of hyaenas competition for prey is probably insignificant. In Etosha National Park hyaenas specialised on springbok, *Antidorcas marsupialis* (Gasaway, Mossestad and Stander, 1991). In Chobe hyaenas fed on impala during the dry season but specialised on zebra foals during the wet (Cooper, 1990). In the Kalahari they specialised on juvenile wildebeest and gemsbok, *Oryx gazella*, springbok were not an important part of their diet (Mills, 1990). Scavenging was not an important method of obtaining food in any of the above parks. In KNP where the numbers of hyaenas and lions is approximately equal, they scavenge 50% of their food from lion kills and killed mainly kudu and waterbuck. In MNP there is probably little opportunity to scavenge as

the very high density of lions presents too much of a threat. An adult male hyaena was killed during the study period and lions exhibited very aggressive behaviour to hyaenas during the predator surveys (Section 5.3.1). Although impala are abundant there is little medium size prey available for hyaenas as there is in the other conservation areas of Africa which were compared to MNP (Section 5.3.3). These two factors may contribute to the low density of hyaenas compared to lions in MNP. The productive foreshore habitat appears to be dominated by the lion prides which may further restrict the access of hyaenas to suitable food (Figures 5.2 and 5.3).

Cheetahs and lions had the same habitat preferences, although cheetahs used the treeline more in the early evening than lions did (Table 5.7). This is similar to what was observed in KNP where cheetahs and lions used the plains and the thickets to the same degree (Mills and Biggs, 1993). This could result in severe competition but as each species is selecting for different prey this similar habitat preference is probably not important. During the study period, cheetahs were often observed near lions sometimes with kills (within 500m). Caro (1994) argues that although competition over carcasses is often cited as having an adverse effect on cheetahs in the wild, studies in the Serengeti have shown that hyaenas and lions only take 9% of the flesh that is killed by cheetahs. The Serengeti is characterised by open habitat and in areas of thicker vegetation, such as MNP, kleptoparasitism is unlikely to be a serious threat. Habitat use in MNP by these two large predators is likely to be in response to prey abundance rather than avoidance of other large predators. However, a more thorough investigation is necessary before any strong conclusions as to the extent of any overlap in habitat use can be made.

If there is little evidence for competition between cheetahs, lions and hyaenas over prey or habitats then some other factor must explain the low biomass of cheetahs in MNP despite a very large prey population. For the available prey biomass in MNP, which is extremely high compared to other parks of Africa because of the productive foreshore habitat, the biomass of cheetahs is relatively low (Table 5.4). Only Ngorongoro Crater, which has the highest densities of lions and hyaenas in Africa, has a lower biomass of cheetahs (Table 5.4). In fact for the available biomass in MNP, only lions have a correspondingly high biomass (Table 5.4). MNP is also the only park where there are more lions than hyaenas (Table 5.5, Figure 5.5). Laurenson (1995) argues that the number of lions has the greatest negative influence on the number of cheetahs because they prey on cheetah cubs and the figures for MNP seem to agree with this hypothesis (Figure 5.4). For the number of hyaenas present the biomass of cheetahs is less than would be expected, suggesting another influence (Figure 5.4b). For the number of lions present the cheetah biomass of MNP is as would be expected (Figure 5.4a) especially if NNP is removed from the analysis. NNP is very close to Nairobi and the number of cheetahs in this park may not reflect an entirely natural situation. The effect of large numbers of visitors especially on cheetah has been known to affect the behaviour of cheetahs in the Serengeti, causing them to hunt in the middle of the day (Mills, pers comm) and the situation in NNP may be similar. MNP is also not a “natural situation” as cheetahs have been introduced. However, the lion and hyaena populations have not been directly manipulated, and since the release of cheetahs there has been no further interference by humans. The three predator species can be argued to be interacting as

“naturally” as is possible in any National Park. The dominance of lions in MNP appears to be limiting the other two predator species to numbers well below what could be supported by the available prey. The lack of any significant relationship between the ratio of lion and hyaena biomass to prey biomass, and cheetah biomass (Table 5.6) suggests that in any environment one predator may become dominant and restrict the numbers of the other predators to below that which could be supported by the available prey i.e prey abundance is not the only factor influencing the number of predators. In MNP it is probably only the extremely large impala population and the presence of safe habitat (woodland and treeline) that enables the cheetahs to persist despite the adverse effect of the high density of lions.

CHAPTER SIX: Population Viability analysis of cheetahs in Matusadona National Park

6.1 Introduction

The purpose of the Matusadona cheetah translocation project was to establish a viable breeding population of cheetahs (Anon, 1994). Matusadona National Park (MNP) was chosen as a suitable park to re-introduce cheetahs as it was assumed that cheetahs had occurred there prior to the filling of Lake Kariba although there was no evidence of this. It was also assumed that there was suitable habitat and a plentiful supply of prey (Zank, 1995). As there was no feasibility study carried out before the release of the cheetahs the minimum number required to establish a viable population was not known. A total of 14 adults and three cubs were released (Zank, 1995).

In 1995 a population viability analysis (PVA) was carried out, in retrospect, to determine if the introduced population of cheetahs would persist in MNP (Zank, 1995). PVA involves predicting whether a population of animals will persist in an environment for an arbitrarily chosen time by simulating the dynamics of the population, usually with the help of a computer model (Lacy, 1993). The PVA carried out in 1995 was not able to use parameters of the MNP population itself as these were not available, but used parameters obtained from other studies of cheetahs in Africa. The conclusion of this PVA was that the cheetah population in MNP would not be viable in the long term as the juvenile mortality rate was likely to be very high because of the high density of lions present

(Zank, 1995). Lions are known to prey on cheetah cubs and cause significant levels of mortality (Laurenson, 1995).

Most PVAs to date have focused on the effects of genetic drift and inbreeding on the probability of small populations going extinct (Lacy, 1993). The output of this type of analysis was simply the minimum number of animals that would need to be present to prevent the population from going extinct, what is known as a minimum viable population (Boyce, 1992). However, some authors argue that it is the knowledge of the use of an environment and its resources by a species that is more important in predicting the success of a population rather than genetic theory (Simberloff, 1988; Boyce, 1992). They argue that habitat degradation or reduction are the two greatest threats to most endangered species and the responses to these threats, which will determine the long term survival of a population, depending on the species in question (Simberloff, 1988; Boyce, 1992). Macdonald, Mace and Rushton (1998) compared the output of different PVA software and found that for the same set of data the predictions of persistence varied considerably depending on the model used. They concluded that a PVA should be viewed as a process which highlights areas where the behaviour and use of an environment by the species in question are most likely to influence whether a population of animals belonging to that species will persist into the future. Each PVA would, therefore, be unique to a species in a particular environment (Schaffer, 1990).

This chapter describes the output of a PVA carried out using population parameters for the cheetah population obtained during the current study, and compares the results to

those of the 1995 PVA. It also addresses the question of which factors of the MNP cheetahs' ecology will have the greatest effect on the future viability of the population.

6.2 Methods

I performed a PVA was carried out using the computer simulation program VORTEX (version 8.01, Lacy, Hughes and Miller, 1998). This simulation model is a Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events on wildlife populations (Lacy, 1993). It models population dynamics as discrete, sequential events that occur according to probabilities that are random variables (Lacy, 1993).

The simulation process was begun by answering a series of questions about the population parameters and life history attributes of the population either from a knowledge of the population itself or from the literature. Although each question asked could not be included in this section the main questions and answers are described below:

- The population was assumed to be isolated and so migration was not included in the simulation. MNP has two large rivers, a lake and a mountain range as its borders, all of which may be barriers to movement of cheetahs. It is also unlikely that there is a large enough cheetah population outside the park to provide individuals to migrate into the park.

- Inbreeding depression was not incorporated into the simulation. Cheetahs are known to be highly inbred probably for a very long time (O'Brien, Wildt and Bush , 1986). Lacy (1992) argues that if a species has been inbred for a long period of time then they will have lost a large proportion of deleterious alleles and be resistant to further inbreeding.
- Environmental variation in survival was correlated with environmental variation in reproduction as cheetah mothers are known to abandon cubs if they cannot obtain enough food (Laurenson, 1995).
- All males were assumed to be in the breeding pool. Male cheetahs appear to adopt two strategies to find mates, either holding a territory or roaming over a large area looking for mates (Caro and Collins, 1987). It can be assumed that most males will find and mate with at least one female.
- Reproduction was assumed to be density independent as there is no evidence from previous studies of cheetahs that the number of females which breed and produce cubs decreases with increasing population size.
- Average age at the time of death was taken to be eight years. Two of the original adult cheetahs released in 1993 were still alive in 1998, which makes them at least eight years old.

- Studies of cheetahs show that the sex ratio of cubs is close to unity (Pettifer, 1981, Laurenson, Caro and Borner, 1992).
- The average litter size in MNP is three cubs (See section 3.3.1). For the simulation, all females were assumed to breed, 3% producing one cub, 9% producing two cubs and 88% producing three cubs.
- Juvenile mortality was entered as 60% altogether. Cheetahs do not reach maturity until the age of two and it was not known if most of the mortality occurred before or after the age of one. To test for the significance of this division in mortality, two simulations were run keeping all the other parameters the same. The first simulation used a value of 20% mortality for before the age of one and 40% mortality for cubs before the age of two, and the second simulation entered the values in reverse.
- Adult mortality was entered as 20.5% for each sex. Males between the ages of three and four were entered as having a mortality rate of 10%, and each age group after as 5%. Young adult males are known to suffer the greatest mortality because of being forced into suboptimal habitat by already established adult males (Mills and Hess, 1997; Laurenson *et al*, 1992).
- The age structure of the population was entered as follows, based on knowledge of the cheetahs in MNP; there were three females and one male below the age of two

(juveniles); five females and three males between the ages of three and five and two females and three males between the ages of six and eight.

- Three simulations were run with different calculated carrying capacities keeping all other parameters the same. The first simulation used a carrying capacity of 65 animals, calculated from the average equilibrium density of 0.17 cheetahs/km² in areas under 500 km² determined by East (1981). The second simulation was run using a carrying capacity of 40 animals estimated from the sustained yield of edible biomass, calculated in section 4.3.4. The third simulation was run using a carrying capacity of 24 calculated using the equation below

$$P = F \{ 1 + S_r + [F_c/F \times C_b] + [S_{ad}/F \times S_s] \} \quad (\text{Gros, Kelly and Caro, 1997})$$

Where P = population size, F = number of adult females, S_r = adult sex ratio = number of females/number of males, F_c = number of adult females accompanied by cubs, C_b = average number of cubs accompanying their mother, regardless of cub age, S_{ad} = number of subadult groups, including singletons and S_s = average size of subadult groups. For the MNP cheetah population this gives total population of

$$P = 7 \{ 1 + 1.17 + [0.29 \times 3] + [0.14 \times 3] \}$$

$$P = 7 \{3.46\}$$

$$P = 24.22 \sim 24$$

This equation assumes that F is the maximum number that MNP can support because of the ranging behaviour of the individual females (Gros, Kelly and Caro, 1997). It is likely to be an underestimate.

- To keep the simulation simple it was assumed that there would be no catastrophies.
- MNP does not allow any animals to be hunted and so the simulation was run without the effect of harvesting on the population.

Each simulation was run a 100 times for 100 years. A population with a 95% chance of surviving for 100 years was assumed to be viable.

6.3 Results

The viability of the cheetah population of MNP as predicted by VORTEX, appears to be influenced most strongly by the value entered for the carrying capacity of the environment (Table 6.1). Assuming that the mortality values calculated in this study are accurate, if the carrying capacity is greater than 25 animals the probability that the population will persist is 100%, with none of the simulations going extinct. Whether juvenile mortality is greater in the first or second year does not affect the probability that the population will persist for a 100 years for any value of carrying capacity above 25 animals (Table 6.1).

At a carrying capacity of 25 or less the probability that the cheetah population will go extinct increases to 20% if juvenile mortality is greater in year two of a cheetah's life, or to 14% if the juvenile mortality is greater in year one of a cheetah's life (Table 6.1).

(For examples of output data from VORTEX see Appendix V)

Table 6.1: Results of VORTEX simulations of the persistence of the cheetah population in MNP using different values for juvenile mortality carrying capacity.

| Simulation | Juvenile mortality (Yr 1) % | Juvenile mortality (Yr 2) % | Carrying capacity (No. of animals) | Probability of success % | No. of extinctions | Mean final Population size |
|-------------------|------------------------------------|------------------------------------|---|---------------------------------|---------------------------|-----------------------------------|
| 1 | 20 | 40 | 65 | 100 | 0 | 64.46 |
| 2 | 40 | 20 | 65 | 100 | 0 | 64.05 |
| 3 | 20 | 40 | 40 | 100 | 0 | 37.8 |
| 4 | 40 | 20 | 40 | 100 | 0 | 38.85 |
| 5 | 20 | 40 | 24 | 80 | 20 | 21.2 |
| 6 | 40 | 20 | 24 | 86 | 14 | 20.57 |

6.4 Discussion

The above simulations show that the current level of juvenile mortality (60%) in the cheetah population of MNP is low enough to enable the population to persist for a 100 years, if the carrying capacity of MNP is determined by available area or prey (Table 6.1). This is consistent with the findings of the previous PVA carried out in 1995 (Zank, 1995). This previous PVA had used higher levels of juvenile mortality (72-73%) because of the high density of lions in MNP. Lions are known to prey on cheetah cubs killing as many as 73.6% of cubs from birth to independence in the Serengeti (Laurenson, 1995). Hyenas also prey on cheetah cubs but as the density of hyenas in MNP was very low this predation effect on cub survival was assumed to be negligible (Zank, 1995). The 1995 PVA recommended that with such a high juvenile mortality the MNP population be supplemented with 3 adult cheetahs every five years to maintain the population. However, the same PVA showed that the population would be viable if juvenile mortality was below 65%. Evidence from this study suggests that juvenile mortality is less than what was predicted in 1995, despite a higher density of lions (0.317 animals/km² compared to 0.2 animals/km²) and hyenas (0.13 animals/km² compared to 0.08 animals/km²) present in 1998. If this level of juvenile mortality is accurate and remains the same the population has a 100% chance of persisting for 100 years. The current population of 17 animals appears to be a large enough founder population to ensure the successful establishment of cheetahs in MNP.

Simberloff (1988) argues that a PVA must be based on a thorough understanding of the basic ecology of the species in question. Thomas (1990) goes on to argue that there is a need for a better understanding of the environment in which the population is living if a PVA is to be conclusive. The basic ecology of the cheetahs in MNP is better understood than in 1995 when the first PVA was carried out but there are still significant gaps in the understanding of the dynamics of the population and the way they are utilising the environment. The simulations of VORTEX done in this chapter emphasise the need for a better understanding of how many cheetahs the environment of MNP can support. Carrying capacities calculated using available area and prey predicted a 100% chance of the population persisting (Table 6.1). A carrying capacity calculated from the observed use of the environment by the cheetahs predicted that the population would not be viable (Table 6.1).

A retrospective PVA carried out on a population of Lord Howe Island Woodhen, *Tricholimnas sylvestris*, illustrated that predictions of population size and persistence were unrealistically high if carrying capacity was determined using the available area (Brook, Lim, Harden and Frankham, 1997). Predictions of final population size and persistence were more realistic if a lower carrying capacity, based on observed maximum population sizes known from historical data, was used (Brook *et al*, 1997). It appeared that the distribution of the woodhen was connected to the occurrence of Kentan palm, *Howea fosteriana* vegetation associations found on igneous soils. This meant that that some areas of the island were unsuitable and remained unoccupied (Brook *et al*, 1997). The study concluded that assessments of population viability must correctly estimate the

potential carrying capacity of the habitat. At the present moment the carrying capacity of MNP for cheetahs is not known and has only been estimated from the size of the park. Studies of cheetahs in the Serengeti have illustrated that the total available area is not always fully utilised by the animals present (Caro and Collins, 1987; Caro, 1994). Areas of the Serengeti that are devoid of cover but have high densities of prey were avoided by the cheetahs, and areas with persistent low densities of prey were also not utilised. Although cheetahs are not strongly territorial they do appear to avoid areas where other cheetahs are already present (Eaton, 1974; Pettifer 1981). The home ranges of the cheetahs in MNP appear to be restricted by the need to include a certain amount of productive habitat (foreshore) and cover (woodland and treeline) (Chapter 4). If this is really the situation, and it seems likely, then the number of cheetahs that can be supported by MNP is lower than predictions based on area (East, 1981) or available prey (Chapter 4). The carrying capacity of MNP is certainly less than 40 animals but it is not clear whether it is less than the critical 25 animals. There is an urgent need to determine the average home range size and location of more cheetahs in MNP, especially females, to ascertain if it is this behaviour which will limit the cheetah population size to below 25 animals. As environmental changes in food availability occur in MNP it is also necessary to measure juvenile and adult mortality of cheetahs over a longer period of time to determine if they ever reach critical levels for population viability.

CHAPTER SEVEN: Overall conclusions and management recommendations

7.1 Overall conclusions:

7.1.1 Population Viability Analysis (PVA)

From evidence to date it appears that a viable cheetah population has indeed been established in Matusadona National Park (MNP). The juvenile mortality rate of the cheetahs is lower than was previously predicted (Chapter three) despite the high density of lions (Chapter five). The reasons why juvenile mortality in MNP is lower than expected are not clear. Studies in the Serengeti have shown that, although lions are responsible for most mortality of cubs before three months, hyaenas kill more cheetah cubs after they have begun to move with their mother (Laurenson, 1995). The density of hyaenas in MNP is very low in comparison to other areas of Africa (Chapter Five) and they are unlikely to be able to kill a significant number of cheetah cubs resulting in a lower juvenile mortality rate for cheetah cubs than was reported in the Serengeti. However, even with no predation by hyaenas the juvenile mortality rate of cubs in MNP is less than that caused by lions in the Serengeti (Caro and Laurenson, 1994). The Serengeti area is characterised by areas with little available cover and lions often find cheetah dens, killing all the cubs inside (Laurenson, 1995). MNP has large areas of relatively thick woodland vegetation, which may enable female cheetahs to hide their cubs more successfully reducing the amount of predation by lions. The cheetahs in MNP use the woodland at all times when they are not hunting which may explain how they are able to avoid adverse interactions with lions (Chapter Four).

Subadult and adult mortality of cheetahs in MNP is also very low (Chapter three). However, the population was only recently introduced into MNP and may not have reached a level where intraspecific competition for resources results in high adult mortality. Mills and Hess (1997) report that in the Kruger National Park (KNP) subadult mortality is the highest because these individuals are forced into sub-optimal habitats by the older more established cheetahs. The locations of the home ranges of the cheetahs in MNP suggest that cheetahs need to include areas of foreshore, presumably because it has the density of prey, as well as an area of woodland probably to avoid contact with the other large predators of MNP (Chapter Four). If this is actually the case then the number of available areas is limited and intraspecific competition could become intense resulting in higher levels of subadult, and possible adult, mortality. Population viability analysis shows that the population of cheetahs is viable assuming that present mortality rates stay the same and habitat or the availability of prey determines the carrying capacity of MNP (Chapter Six). However, if the number of cheetahs that can actually use the available prey and habitats is restricted by behavioural patterns and other large predator species and is less than 25 animals, the population may no longer be viable (Chapter Six). Territorial behaviour can limit the number of animals that can utilise an area (Caughley and Sinclair, 1994). Whether this is what is happening in MNP is not clear and needs to be investigated further.

7.1.2 Translocation techniques and strategies

The success of the re-introduction project up until the present enables more information to be added to the list of what factors increase the success of translocation projects. The animals used in this project were wild caught and adapted quickly to the new environment (Zank, 1995). The prey selection and habitat preferences of the cheetahs have not altered since they were first released (Chapter Four), an observation that supports the argument that wild caught animals adapt quicker to new environments than captive bred animals (Griffiths, Scott, Carpenter and Reed, 1989). Linnell, Aanes, Swenson, Odden and Smith (1997) argued that translocations that employed “soft-release” techniques, where animals were kept in enclosures in the new area for a period of time before release, were the most successful. The behaviour of the cheetahs in MNP provides further evidence that such techniques are successful but without comparisons with areas where “hard release” of cheetahs have occurred it is not possible to say if which method is more or less useful for the release of cheetahs. Although the cheetahs initially moved very large distances on being released, data from this study show that they have settled down and their movements cover an area less than half that covered when they were first released (Chapter Four). However, the MNP project emphasises the dangers of the large post release movements that many translocated animals exhibit (Linnell *et al* , 1997). Five out of the 14 adults released into MNP moved out of the boundaries of the park shortly after release and one adult male was subsequently snared.

The most interesting result of the translocation of cheetahs into MNP is that, despite the presence of a large number of competitors, the cheetahs have, so far, successfully established themselves in MNP. The very large prey population, concentrated in a small area, is probably one reason why the cheetahs have been able to find an “empty niche” in the new environment (Griffiths *et al*, 1989). In addition the presence of a sharp boundary (the treeline) between an area of productive food and an area of cover has enabled the cheetahs to hunt successfully as well as avoid adverse interactions with the other large predators of MNP.

The results of the latest PVA (Chapter six) suggest that the population will require little long term management (IUCN Re-introduction Specialist Group, 1998). However, the population should continue to be monitored to gain a better understanding of how the introduced cheetahs are using MNP and avoiding adverse interactions with the other large predators.

7.1.3 Large predator guild relationships in MNP

The available prey biomass of smaller prey in MNP is relatively high (1517 kg/km²) compared with other conservation areas of Africa. The number of cheetahs currently present in MNP is much less than could be supported by the available prey, 17 animals compared to 40 animals (Chapter Four). This suggests that there is another factor, or other factors, influencing cheetah numbers. One possibility is that the concentration of prey in a very small area, effectively about 50 km², means that cheetah numbers are restricted by how many can utilise this small area. Another possibility is that the very

high density of lions is restricting the number of cheetahs that can utilise the area.

(Chapter Five)

The results of this study, although not conclusive, indicate that the structure of the large predator guild in MNP is different from other areas of Africa that have been studied (Chapter Five). MNP has a very high density of lions and a very low density of hyaenas and cheetahs despite the availability of prey. The lions appear to be the dominant predator of this park, perhaps because they have exclusive use of the buffalo population. The distribution of lions in MNP suggests that they dominate the foreshore habitat where most of the prey animals are concentrated during the dry season (Figure 5.3). This is a similar situation to the one reported in Kruger National Park (KNP). Lions are the dominant predator there because they have exclusive access to the buffalo and zebra populations (Mills and Biggs, 1993). During dry periods, buffalo become increasingly vulnerable to lion predation as they lose condition (Mills, Biggs and Whyte, 1995). There has been an increase in the number of lions in KNP as a result of the very dry years in the early 1990's (Mills, 1995). The buffalo population in MNP increased in the early 1980's in response to increased growth in the *Panicum repens* grassland (Taylor, 1985). There was a corresponding increase in the lion population but not in the hyaena population. MNP is different from KNP in that it has very small populations of the medium sized prey species, waterbuck, kudu and zebra. Hyaenas are not able to exploit the buffalo population directly but can only use it by scavenging from lion kills. In KNP they scavenge about 50% of their food but also hunt waterbuck and kudu to obtain the other 50% (Mills and Biggs, 1993). As a result hyaena numbers and lion numbers in KNP

are approximately equal (Mills and Biggs, 1993). In MNP the hyaena population cannot support itself on the medium sized prey and were not able to respond to the increase in the buffalo population to the same extent as the lions were. This may be the reason for the current imbalance in numbers of lions and hyaenas in MNP.

Whatever the reason for the large difference in numbers between the lions and hyaenas, MNP is an anomaly in the relationship between lion and hyaena biomass (Chapter Five). Whether the establishment of a viable population of cheetahs would have been possible in an areas with numbers of lions and hyaenas similar to other areas of Africa is not clear. Ngorongoro Crater (NC) has many more hyaenas than lions and there are virtually no cheetahs in this park. For the number of lions present, the number of cheetahs in Serengeti National Park (SNP) is also surprisingly low (Chapter Five). SNP also has a large number of hyaenas compared to lions. Kruger, Etosha and Hwange National Parks where the number of lions and hyaenas is more equal, the biomass of cheetahs is also greater than in either SNP or NC. It could be that hyaenas have a greater negative effect on cheetahs than lions. In areas where hyaenas are dominant they may steal carcasses and harass cheetahs more than in areas where they are not the dominant predator.

At the present moment all this is theoretical, but there is some evidence that the relationships between the three large predator species depend on the environment in question. The abundance and availability of different prey species may play an important role in determining the structure of the large predator guild.

7.1.4 *Translocation as a viable cheetah conservation tool in Zimbabwe*

Although the translocation of cheetahs into MNP has been successful so far, it is unlikely that the translocation of cheetahs is ever to be an effective tool for the overall conservation of cheetahs in Zimbabwe for a number of reasons. The new draft plan for the management for cheetahs in Zimbabwe states as its objective that there should be a “secure free ranging population of 5000” cheetahs in Zimbabwe (Heath and Muchena, 1998). The number of cheetahs likely to exist in protected areas will always be small because of the restricting effects of the other large predators present in such areas. MNP is a case in point. Although the population appears to be viable it will never be very large. The project has not yet ascertained what the effects of the movement of cheetahs out of MNP are on the local population. As all translocations of cheetahs into new areas are likely to result in similar movements it is necessary to determine if there have been any adverse consequences, both ecologically and socially of the translocation before any further translocations of cheetahs are carried out (IUCN Re-introduction Specialist Group, 1998).

Translocation is a very expensive process and requires specialised equipment, trained personnel and time. The cost of translocating each individual cheetah to MNP was approximately US \$ 1730 in 1994. Linnell *et al* (1997) argue that where carnivores are abundant and populations rather than individuals are the management unit, translocation of animals is unlikely to be justified. This is the case in Zimbabwe where cheetahs are abundant on private land. There has been no follow up in the source area of the cheetahs

that were moved to MNP to determine if the reduction in the number of cheetahs has helped in reducing the conflict between the farmers and the cheetahs. However, the project only moved 21 adult cheetahs and this very small number is unlikely to have had a significant effect. As pointed out by Zank (1995) conservation of cheetahs in Zimbabwe should focus on areas outside the National Parks estate, as this is where the largest population can be maintained.

What the MNP cheetah project has demonstrated is that re-introduction of cheetahs into new areas using wild animals is viable and effective even if other large carnivores are present. As a stop gap option cheetahs in Zimbabwe could be moved from areas where they are causing problems to areas that have been identified as suitable, but it must be remembered that this is a short term solution, the long term solution is reducing the conflict between farmers and cheetahs.

7.2 Management recommendations

1. The population of cheetahs in MNP needs to be monitored to determine more accurately the juvenile, subadult and adult mortality rates as these may change over time. It is also necessary to obtain a better understanding of how the cheetahs are using the available area by determining the average home range size of a representative sample, using cheetahs from all areas of the park.

2. The total number of cheetahs in MNP needs to be monitored for up to 10 years after release to analyse whether the predictions of the PVA have been upheld. The results of this analysis suggest that the number of cheetahs will be at the maximum the area can support 10 years after the release of the cheetahs into MNP.
3. It is also necessary to monitor the movement of the cheetahs in and out of MNP. It is known that some individual cheetahs are already moving in and out of MNP and the number of individuals doing so is likely to increase with increasing population size. MNP is surrounded by communal lands and there is a possibility that cheetahs moving out of the park will begin to feed on domestic livestock.
4. In line with recommendation Number 3 is a suggestion that a survey be done in the surrounding communal lands to determine if cheetahs are being seen more than before the translocation and whether they are perceived to be taking domestic stock.
5. If the structure of the large predator guild in MNP is determined by the distribution and abundance of prey then changes in prey population sizes and distribution, as well as changes in the populations of lions and hyaenas, need to be closely monitored to record the effects. It is not known what the effects of changing lion and hyaena numbers will be on the introduced population of cheetahs and management will have to be adaptive, and to a certain extent retroactive rather than proactive.
6. There is need for a follow up study to be carried out in the area that acted as a source of the cheetahs used in the translocation project. These cheetahs were

supposedly “problem” animals and it is necessary to determine if their removal has reduced the stock losses in the source area.

7. The investigation into the possibilities of encouraging farmers to maintain cheetahs on their land needs to continue with the knowledge that translocations are expensive and are unlikely to be useful in the long term conservation of cheetahs in Zimbabwe.

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APPENDICES

APPENDIX I

Calculation of the area of foreshore exposed in 1998

In 1954 an aerial survey of the Zambezi valley that was to be flooded by the building of the Kariba dam wall was conducted. These photographs were then used to compile a series of contour maps that were published in 1955. The treeline of Matusadona National Park (MNP) corresponds to the highest water level of the lake. Ordinance survey maps dated 1976 show the shoreline of lake Kariba as this treeline. This shoreline was superimposed onto the contour maps of 1955. The lowest and highest level of Lake Kariba for 1998 were obtained from the Lake Captain and were 1576 feet (480.52m) and 1587 (483.84m) above sea level. The average level of the lake was calculated and this contour line drawn onto the 1955 contour maps. The area between the treeline and this line (1998 lake level) was taken to be equal to the area of the foreshore.

APPENDIX II

Some of the Mammals present in Matusadona National Park

| Common Name | Scientific Name |
|----------------------|---------------------------------|
| African Civet | <i>Civetticivis civetta</i> |
| African wild Cat | <i>Felis lybica</i> |
| Black rhino | <i>Diceros bicornis</i> |
| Buffalo | <i>Syncerus caffra</i> |
| Bushbuck | <i>Tragelaphus scriptus</i> |
| Cheetah | <i>Acinonyx jubatus</i> |
| Common duiker | <i>Sylvicapra grimmia</i> |
| Grysbok | <i>Raphicerus sharpei</i> |
| Impala | <i>Aepyceros melampus</i> |
| Kudu | <i>Tragelaphus strepsiceros</i> |
| Large spotted genet | <i>Genetta tigrina</i> |
| Leopard | <i>Panthera pardus</i> |
| Lion | <i>Panthera leo</i> |
| Porcupine | <i>Hystrix africaeaustralis</i> |
| Sable antelope | <i>Hippotragus niger</i> |
| Scrubhare | <i>Lepus saxatilis</i> |
| Side striped jackal | <i>Canis adustus</i> |
| Spotted hyaena | <i>Crocuta crocuta</i> |
| Warthog | <i>Phacochoerus aethiopicus</i> |
| Waterbuck | <i>Kobus ellipsiprymnus</i> |
| Whitetailed mongoose | <i>Ichneumia albicauda</i> |
| Slender mongoose | <i>Herpestes sanguineus</i> |
| Dwarf mongoose | <i>Helogale parvula</i> |
| Wild dog | <i>Lycaon pictus</i> |
| Zebra | <i>Equus burchelli</i> |

APPENDIX III

Calculation of foreshore block areas to determine density of prey.

At the beginning of the study period the level of Lake Kariba was very low and the foreshore area extensive. The vegetation on the foreshore was also very lush reaching a height of 1m in many places. Therefore, it was not possible to accurately count the number of animals near the shoreline from the road that runs along the foreshore. It was decided to demarcate six prey “blocks” along the foreshore where the view of the shoreline was not obstructed by vegetation or small hills and where the shoreline was close enough to be able to accurately count the number of animals in the block. Conspicuous land features such as termite mounds, road junctions or rocky mounds marked the edges of a block. The shoreline provided one boundary, the foreshore road the other boundary and the distances from the road to the shoreline the other two boundaries forming an irregular four-sided block (Figure 1)

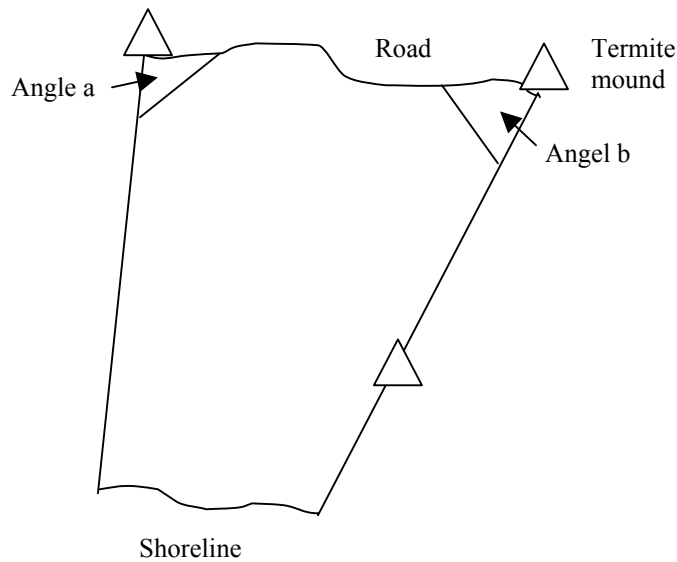


Figure 1: Diagram of a foreshore block

Angles a and b were used to determine the length of the shoreline. It was assumed that the road and the shoreline were straight lines as the area encompassed by the real lines was negligible. The area of the block was determined using a grid containing squares of known area. During the study period the lake level rose significantly reducing the size of the blocks. Two measurements were taken of the block boundaries, one in April (wet season) and one in July (dry season) to enable wet and dry density estimates to be compared accurately.

APPENDIX IV

Example of output data from VORTEX

VORTEX -- simulation of genetic and demographic stochasticity

1 population(s) simulated for 100 years, 100 iterations

Extinction is defined as no animals of one or both sexes.

No inbreeding depression

First age of reproduction for females: 2 for males: 4

Age of senescence (death): 8

Sex ratio at birth (proportion males): 0.50000

Population 1:

Polygynous mating;

100.00 percent of adult males in the breeding pool.

95.00 percent of adult females produce litters.

EV in % adult females breeding = 5.00 SD

Of those females producing litters, ...

3.00 percent of females produce litters of size 1

9.00 percent of females produce litters of size 2

88.00 percent of females produce litters of size 3

20.00 percent mortality of females between ages 0 and 1

EV in % mortality = 3.000000 SD

40.00 percent mortality of females between ages 1 and 2

EV in % mortality = 3.000000 SD

20.00 percent mortality of adult females (2<=age<=3)

EV in % mortality = 3.000000 SD

20.00 percent mortality of males between ages 0 and 1

EV in % mortality = 3.000000 SD

40.00 percent mortality of males between ages 1 and 2

EV in % mortality = 3.000000 SD

10.00 percent mortality of males between ages 2 and 3

EV in % mortality = 3.000000 SD

5.00 percent mortality of males between ages 3 and 4

EV in % mortality = 3.000000 SD

5.00 percent mortality of adult males (4<=age<=5)

EV in % mortality = 3.000000 SD

EVs may be adjusted to closest values possible for binomial distribution.

EV in mortality will be concordant among age-sex classes

but independent from EV in reproduction.

Initial size of Population 1: 17
Age 1 2 3 4 5 6 7 8 Total

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---------|
| 1 | 0 | 1 | 2 | 2 | 1 | 1 | 1 | 9 | Males |
| 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 8 | Females |

Carrying capacity = 30
 EV in Carrying capacity = 5.00 SD

Deterministic population growth rate (based on females, with assumptions of no limitation of mates, no density dependence, and no inbreeding depression):

$r = 0.252$ $\lambda = 1.287$ $R_0 = 2.568$
 Generation time for: females = 3.74 males = 5.65

| Stable age distribution: | Age class | females | males |
|--------------------------|-----------|---------|-------|
| | 0 | 0.203 | 0.203 |
| | 1 | 0.126 | 0.126 |
| | 2 | 0.059 | 0.059 |
| | 3 | 0.037 | 0.041 |
| | 4 | 0.023 | 0.030 |
| | 5 | 0.014 | 0.022 |
| | 6 | 0.009 | 0.017 |
| | 7 | 0.005 | 0.012 |
| | 8 | 0.003 | 0.009 |

Ratio of adult (≥ 4) males to adult (≥ 2) females: 0.604

Population 1

Year 5

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 100, P[S] = 1.000
 Population size = 27.88 (0.57 SE, 5.66 SD)
 Expected heterozygosity = 0.916 (0.002 SE, 0.020 SD)
 Observed heterozygosity = 0.984 (0.003 SE, 0.027 SD)
 Number of extant alleles = 18.03 (0.28 SE, 2.78 SD)

Year 10

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 100, P[S] = 1.000
 Population size = 28.28 (0.53 SE, 5.34 SD)
 Expected heterozygosity = 0.870 (0.003 SE, 0.031 SD)
 Observed heterozygosity = 0.936 (0.005 SE, 0.052 SD)
 Number of extant alleles = 12.30 (0.19 SE, 1.93 SD)

Year 15

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 100, P[S] = 1.000
 Population size = 27.97 (0.55 SE, 5.45 SD)
 Expected heterozygosity = 0.829 (0.004 SE, 0.043 SD)
 Observed heterozygosity = 0.884 (0.008 SE, 0.077 SD)
 Number of extant alleles = 9.57 (0.16 SE, 1.65 SD)

Year 20

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 100, P[S] = 1.000
 Population size = 27.68 (0.54 SE, 5.38 SD)
 Expected heterozygosity = 0.783 (0.006 SE, 0.063 SD)

Observed heterozygosity = 0.841 (0.009 SE, 0.093 SD)
Number of extant alleles = 7.63 (0.15 SE, 1.50 SD)

Year 25

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 28.24 (0.67 SE, 6.65 SD)
Expected heterozygosity = 0.750 (0.008 SE, 0.076 SD)
Observed heterozygosity = 0.798 (0.010 SE, 0.098 SD)
Number of extant alleles = 6.57 (0.12 SE, 1.18 SD)

Year 30

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 28.42 (0.56 SE, 5.60 SD)
Expected heterozygosity = 0.715 (0.009 SE, 0.087 SD)
Observed heterozygosity = 0.774 (0.011 SE, 0.108 SD)
Number of extant alleles = 5.77 (0.12 SE, 1.24 SD)

Year 35

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 28.57 (0.54 SE, 5.37 SD)
Expected heterozygosity = 0.675 (0.011 SE, 0.114 SD)
Observed heterozygosity = 0.730 (0.015 SE, 0.151 SD)
Number of extant alleles = 5.11 (0.12 SE, 1.20 SD)

Year 40

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 28.76 (0.52 SE, 5.21 SD)
Expected heterozygosity = 0.642 (0.012 SE, 0.116 SD)
Observed heterozygosity = 0.694 (0.015 SE, 0.150 SD)
Number of extant alleles = 4.53 (0.12 SE, 1.18 SD)

Year 45

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 27.26 (0.60 SE, 5.96 SD)
Expected heterozygosity = 0.607 (0.013 SE, 0.134 SD)
Observed heterozygosity = 0.649 (0.017 SE, 0.167 SD)
Number of extant alleles = 4.06 (0.11 SE, 1.14 SD)

Year 50

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 26.86 (0.60 SE, 6.02 SD)
Expected heterozygosity = 0.592 (0.013 SE, 0.135 SD)
Observed heterozygosity = 0.625 (0.016 SE, 0.162 SD)
Number of extant alleles = 3.71 (0.10 SE, 1.03 SD)

Year 55

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 28.99 (0.51 SE, 5.10 SD)
Expected heterozygosity = 0.574 (0.015 SE, 0.148 SD)

Observed heterozygosity = 0.607 (0.018 SE, 0.178 SD)
Number of extant alleles = 3.48 (0.10 SE, 0.98 SD)

Year 60

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 28.72 (0.61 SE, 6.08 SD)
Expected heterozygosity = 0.546 (0.015 SE, 0.151 SD)
Observed heterozygosity = 0.592 (0.018 SE, 0.180 SD)
Number of extant alleles = 3.36 (0.10 SE, 0.96 SD)

Year 65

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 27.86 (0.56 SE, 5.61 SD)
Expected heterozygosity = 0.524 (0.014 SE, 0.143 SD)
Observed heterozygosity = 0.562 (0.018 SE, 0.180 SD)
Number of extant alleles = 3.15 (0.09 SE, 0.89 SD)

Year 70

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 27.97 (0.56 SE, 5.62 SD)
Expected heterozygosity = 0.505 (0.016 SE, 0.157 SD)
Observed heterozygosity = 0.544 (0.019 SE, 0.188 SD)
Number of extant alleles = 2.99 (0.09 SE, 0.88 SD)

Year 75

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 28.05 (0.58 SE, 5.75 SD)
Expected heterozygosity = 0.497 (0.017 SE, 0.168 SD)
Observed heterozygosity = 0.541 (0.020 SE, 0.200 SD)
Number of extant alleles = 2.83 (0.09 SE, 0.87 SD)

Year 80

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 27.50 (0.57 SE, 5.73 SD)
Expected heterozygosity = 0.455 (0.018 SE, 0.176 SD)
Observed heterozygosity = 0.484 (0.019 SE, 0.194 SD)
Number of extant alleles = 2.70 (0.08 SE, 0.81 SD)

Year 85

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 27.71 (0.61 SE, 6.06 SD)
Expected heterozygosity = 0.428 (0.018 SE, 0.183 SD)
Observed heterozygosity = 0.459 (0.020 SE, 0.204 SD)
Number of extant alleles = 2.57 (0.08 SE, 0.77 SD)

Year 90

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 27.89 (0.56 SE, 5.60 SD)
Expected heterozygosity = 0.406 (0.019 SE, 0.189 SD)

Observed heterozygosity = 0.433 (0.021 SE, 0.209 SD)
Number of extant alleles = 2.47 (0.08 SE, 0.77 SD)

Year 95

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 28.02 (0.58 SE, 5.78 SD)
Expected heterozygosity = 0.379 (0.020 SE, 0.204 SD)
Observed heterozygosity = 0.402 (0.023 SE, 0.228 SD)
Number of extant alleles = 2.35 (0.08 SE, 0.81 SD)

Year 100

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 27.46 (0.58 SE, 5.77 SD)
Expected heterozygosity = 0.354 (0.021 SE, 0.212 SD)
Observed heterozygosity = 0.377 (0.023 SE, 0.235 SD)
Number of extant alleles = 2.22 (0.08 SE, 0.76 SD)

In 100 simulations of Population 1 for 100 years:
0 went extinct and 100 survived.

This gives a probability of extinction of 0.0000 (0.0000 SE),
or a probability of success of 1.0000 (0.0000 SE).

Mean final population for successful cases was 27.46 (0.58 SE, 5.77 SD)

| Age | 1 | 2 | 3 | Adults | Total |
|-----|------|------|------|--------|-------------|
| | 5.57 | 2.53 | 2.03 | 4.86 | 14.99 Males |
| | 5.70 | | 6.77 | 12.47 | Females |

Across all years, prior to carrying capacity truncation,
mean growth rate (r) was 0.2267 (0.0018 SE, 0.1793 SD)

Final expected heterozygosity was 0.3536 (0.0212 SE, 0.2124 SD)
Final observed heterozygosity was 0.3768 (0.0235 SE, 0.2350 SD)
Final number of alleles was 2.22 (0.08 SE, 0.76 SD)
