# The impact of lion predation on the large ungulates of the Associated Private Nature Reserves, South Africa.

by

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Submitted in partial fulfilment of the requirements

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in Wildlife Management

Centre for Wildlife Management

Faculty of Natural and Agricultural Sciences

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0002

Supervisor: Prof. Dr. J. du P. Bothma

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***“The wildlife of today is not ours to dispose***

***of as we please. We have it in trust.***

**We must account for it to those**

**who come after.”**

***Motto* of the**

**Timbavati Private Nature Reserve (1977)**

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## ABSTRACT

A predator-prey study was undertaken to determine the impact of lion *Panthera leo* predation on the declining populations of large ungulates in the Associated Private Nature Reserves, an open system with the Kruger National Park.

The determination of prey population trends and their spatial distribution in relation to predator habitats are fundamental to studying predator-prey relationships. A combination of aerial counting and road strip censusing techniques were used to determine the prey population trends in the Associated Private Nature Reserves. The age and sex structure, habitat selection and seasonal abundance of the most abundant lion prey in the study area were compared with that of ungulate populations elsewhere in African savannas.

The population dynamics of the lions in the Associated Private Nature Reserves were investigated by using the call-in counting technique. The total number of lions, mean pride size, lion density, and the age and sex structure of the lions in the study area was compared with that of lions in other African savanna woodland habitats.

The range dynamics and habitat selection of four focal lion groups in the Associated Private Nature Reserves were studied. An adult lioness from each of the C, S and M prides, and an adult male from the N coalition were immobilized and then fitted with radio-collars. The range use and habitat selection of the lions in the present study were compared with that of their preferred prey, and with that of lions in other African savannas.

In African savanna ecosystems, rainfall is regarded as the key component driving the system. Ecological modelling was therefore used to better understand the interrelationship between rainfall, prey population trends and lion predation in the Associated Private Nature Reserves. The overall conclusions of the ecological modelling were then compared with the results of the present study on lion predation in the Associated Private Nature Reserves.

The predation rate and prey selection of the lions in the Associated Private Nature Reserves was determined by using a combination of short-term continual predation observations and historical lion kill data. The prey selection of the lions in the present study was compared with that of historical lion kill data to determine whether the predation pressure shifted from the preferred blue wildebeest and Burchell’s zebra to the more abundant impala, and the larger buffalo and giraffe. The killing and consumption rates of the focal lion groups in the present study were used to determine the impact of lion predation on the large ungulate populations in the Associated Private Nature Reserves. Lion predation data for the present study were compared with that of lions in other African savannas.

The results of the present study were used to test the hypothesis that the apparent decrease in the large ungulate populations in the Associated Private Nature Reserves from 1980 to 2003 was due to a combination of lion predation, climatic fluctuation, the change in habitat over time, the removal of the boundary fences between the Associated Private Nature Reserves and the Kruger National Park, and the change in the aerial counting method from 1992 to 1996.

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# CHAPTER 1

# INTRODUCTION

The relationship between a predator and its prey in nature is a delicate one, especially where man has influenced this dynamic equilibrium. In areas such as the Kruger National Park and the surrounding private nature reserves, these natural wildlife areas have been fenced, necessitating management of intervention (Mills & Shenk 1992). These fences may cut off the natural movement routes of animals and it has then often become necessary to supply artificial sources of water and food. The western boundary fence of the Kruger National Park and many of the internal fences within the surrounding private nature reserves were removed in 1993, to create a more open and larger ecological system. The requirements for the management of such an ecological system were best described by Giles (1969) when he defined wildlife management as: the science and art of changing the characteristics and interactions of habitats, wild animal populations, and humans in order to achieve specific human goals by utilising a wildlife resource. These goals are often for recreative activities such as hunting, wildlife viewing, hiking or for ecological and economic reasons (Hin 2000). The wildlife resource must be utilised in such a way that a balance is maintained between the economic and ecological characteristics of the particular ecosystem.

Predator-prey relationships are highly complex and are dependent upon the dynamics of the particular ecosystem. The data needed to measure the impact of predation on their prey include many parameters that are difficult to measure and include: the number of predators and prey in the area; how the predators select their prey with respect to species, sex, age and physical condition; how often the predators kill; the fecundity and survival rates of the prey; and the contribution of mortality other than predation to the population dynamics of the prey (Mills & Shenk 1992). The African lion *Panthera leo* (Linnaeus 1758) has been identified as the major predator of large herbivores in the

Central District of the Kruger National Park (Mills & Shenk 1992) and in the Klaserie Private Nature Reserve (Kruger 1988), followed by the spotted hyaena *Crocuta crocuta* (Henschel & Skinner 1990). In his study Kruger (1988) determined that lions accounted for 68% of all the prey animals that were killed by the large predators in the Klaserie Private Nature Reserve. The other main large predators that preyed on large herbivores in the Klaserie Private Nature Reserve were the leopard *Panthera pardus*, cheetah *Acinonyx jubatus* and wild dog *Lycaon pictus*. Henschel and Skinner (1990) found that the spotted hyaena killed only half the food that it consumed in the Kruger National Park, scavenging the other half. This was also found to be the case in the Timbavati Private Nature Reserve (Hirst 1969). In his study, Hirst (1969) concluded that lions in the Timbavati Private Nature Reserve were able to adapt their feeding habits to existing conditions, scavenging when carcasses were available. In the Etosha National Park the lions and the spotted hyaenas adapt their feeding habits during the occasional anthrax epidemics among the larger ungulates when both the lions and spotted hyaenas do not have to hunt because of the abundance of carcasses for scavenging. Although the lions will still continue to do some hunting, the spotted hyaenas then scavenge almost exclusively.

In more recent studies (Owen-Smith 1990; Mills, Biggs & Whyte 1995) it was found that environmental factors have a significant effect on predator-prey relationships and, often in combination with predation-regulated large herbivore populations. In African savanna ecosystems rainfall is widely regarded as the key component driving the system (Coe, Cumming & Phillipson 1976; East 1984; Mills & Retief 1984; Owen-Smith 1990).

A number of studies in the Central District of the Kruger National Park (Smuts 1978, Whyte & Joubert 1988, Mills, Biggs & Whyte 1995) have found that lion predation on both the migratory and sedentary blue wildebeest *Connochaetes taurinus* and Burchell's zebra *Equus burchellii* subpopulations was of major importance in the decline of both these herbivores during a period of unusually high rainfall. Tall grass conditions and a tendency for herds to fragment then increased the vulnerability of the blue wildebeest and zebras to predation. Whyte and Joubert (1988) found that in the Kruger National Park the wetter cycles induced prey population declines while drier cycles favoured prey population growth. In their study Whyte and Joubert (1988) concluded that long-term weather cycles have always occurred in the Kruger National Park, and that the blue wildebeest populations will fluctuate in accordance with these cycles.

The continual decline in the large herbivore subpopulations of the Associated Private Nature Reserves since 1983 prompted the need for the present study. The blue wildebeest and Burchell's zebra subpopulations in particular were focused on. Because lion predation accounted for 96% of all the Burchell's zebras, and 99% of all the blue wildebeest that were killed in the Klaserie Private Nature Reserve by large predators (Kruger 1988), the present study focused on lion predation. In doing so, the interrelationship between rainfall, predation by lions and the population trends of large herbivores in the Associated Private Nature Reserves were considered. A number of secondary factors which may influence this interrelationship were also considered. These were: the historical mismanagement of the area, the change in the aerial counting method from 1992 to 1996, the removal of the internal fences within the Associated Private Nature Reserves and the dismantling of the eastern boundary fence with the Kruger National Park.

The present study therefore tested the hypothesis that the continual decline in the large ungulate populations in the Associated Private Nature Reserves was due to a combination of lion predation, fluctuation in rainfall, the removal of the internal boundary fences, the change in the aerial counting method from 1992 to 1996; and habitat changes as a result of historical mismanagement of the area. To test this hypothesis the following key questions were researched:

- Are the environmental conditions and habitat requirements of the prey species in question still being met in the Associated Private Nature Reserves, or has the habitat changed so much over time that it became more suitable for some prey species and less suitable for other prey species.

- What is the density of lions in the Associated Private Nature Reserves?
- What is the kill frequency and prey selection of the lions in the Associated Private Nature Reserves?
- Are there other factors that act in combination with lion predation or alone to regulate the large ungulate populations in the Associated Private Nature Reserves?
- What are the management implications to maintain the dynamic equilibrium between the lions, their prey and the environment in the Associated Private Nature Reserves?

These key questions were investigated in the chapters that follow. Chapter 5 is written as a separate article in itself, to be submitted to a peer-reviewed scientific journal. This chapter therefore complies with the stylistic regulations of the intended publication. The methods for the different aspects of the study are described under Methods in each relevant chapter. A complete list of the references that were cited is given at the end of the thesis.

# CHAPTER 2

# STUDY AREA

## LOCATION AND HISTORY

The Associated Private Nature Reserves are located in the Limpopo province of the Republic of South Africa, between latitudes 24º 34' S and 24º 03' S and longitudes 31º 03' E and 31º 31' E (Figure 2.1). The Associated Private Nature Reserves were amalgamated in June 1993 when the internal fences between the Klaserie Private Nature Reserve, the Timbavati Private Nature Reserve and the Umbabat Private Nature Reserve were removed, and the boundary fence on their east with the Kruger National Park was dismantled (Figures 2.1 and 2.2). This created an open ecological system between the Associated Private Nature Reserves and the Kruger National Park, allowing for local and seasonal movements of animals. A fourth private nature reserve, the Balule Private Nature Reserve, is also one of the Associated Private Nature Reserves, but at the time of this study, its boundary fences with the Klaserie Private Nature Reserve had not yet been dismantled. The Balule Private Nature Reserve is therefore fenced off but it has a low density of large predators at present. It was therefore not included in the present study. The Associated Private Nature Reserves border the Kruger National Park and geographically occur on the same latitude as the Central District of that Park.

The approximate sizes of the three reserves are: the Klaserie Private Nature Reserve: 628 km², the Timbavati Private Nature Reserve: 650 km², and the Umbabat Private Nature Reserve: 250 km². This study was therefore conducted in an area of approximately 1500 km² in the combined Klaserie, Timbavati, and Umbabat Private Nature Reserves.

The Associated Private Nature Reserves have a chequered history of land-use practices and management approaches which has led to habitat change and degradation. Before

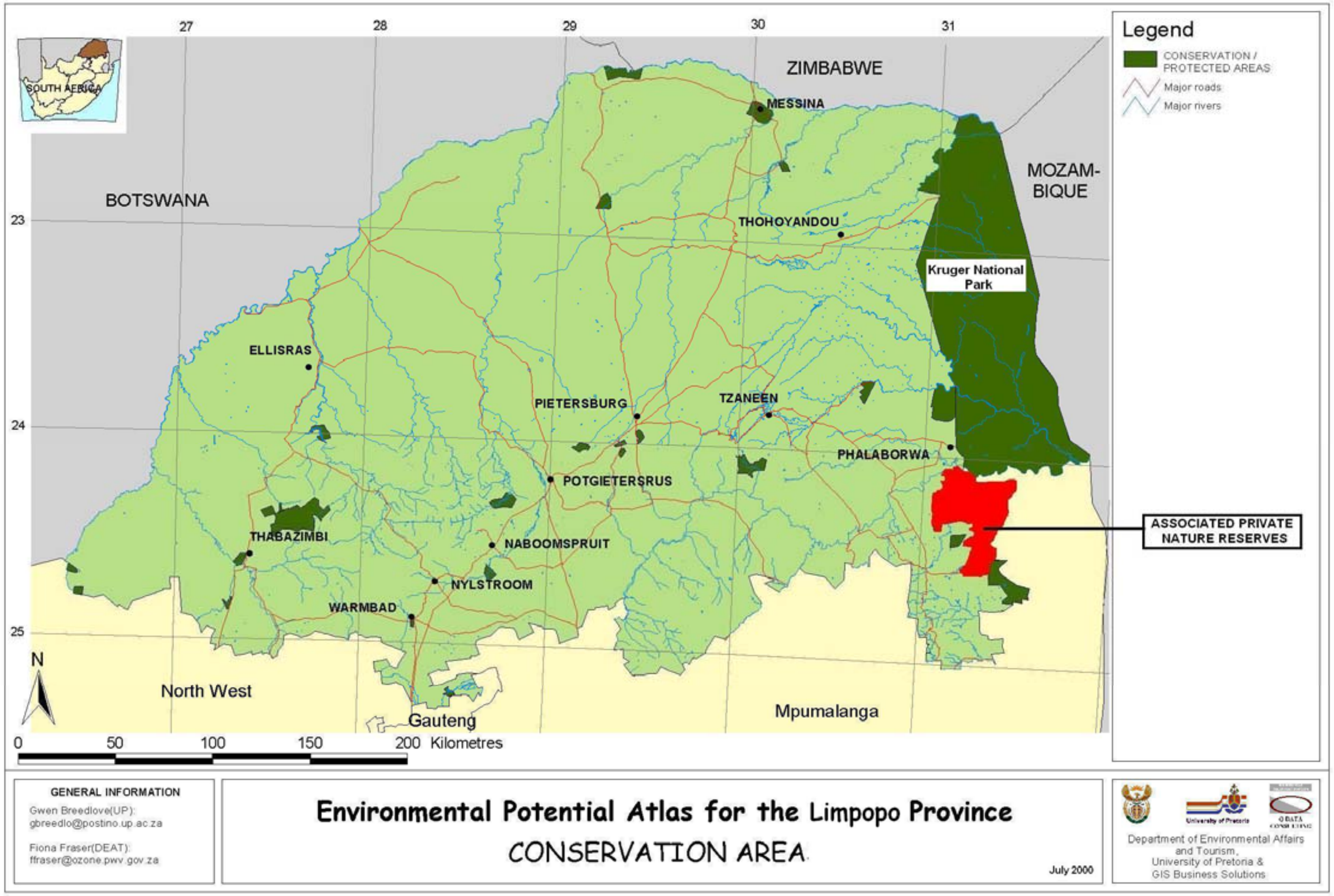


**Figure 2.1**: The Associated Private Nature Reserves within the Limpopo province of South Africa.

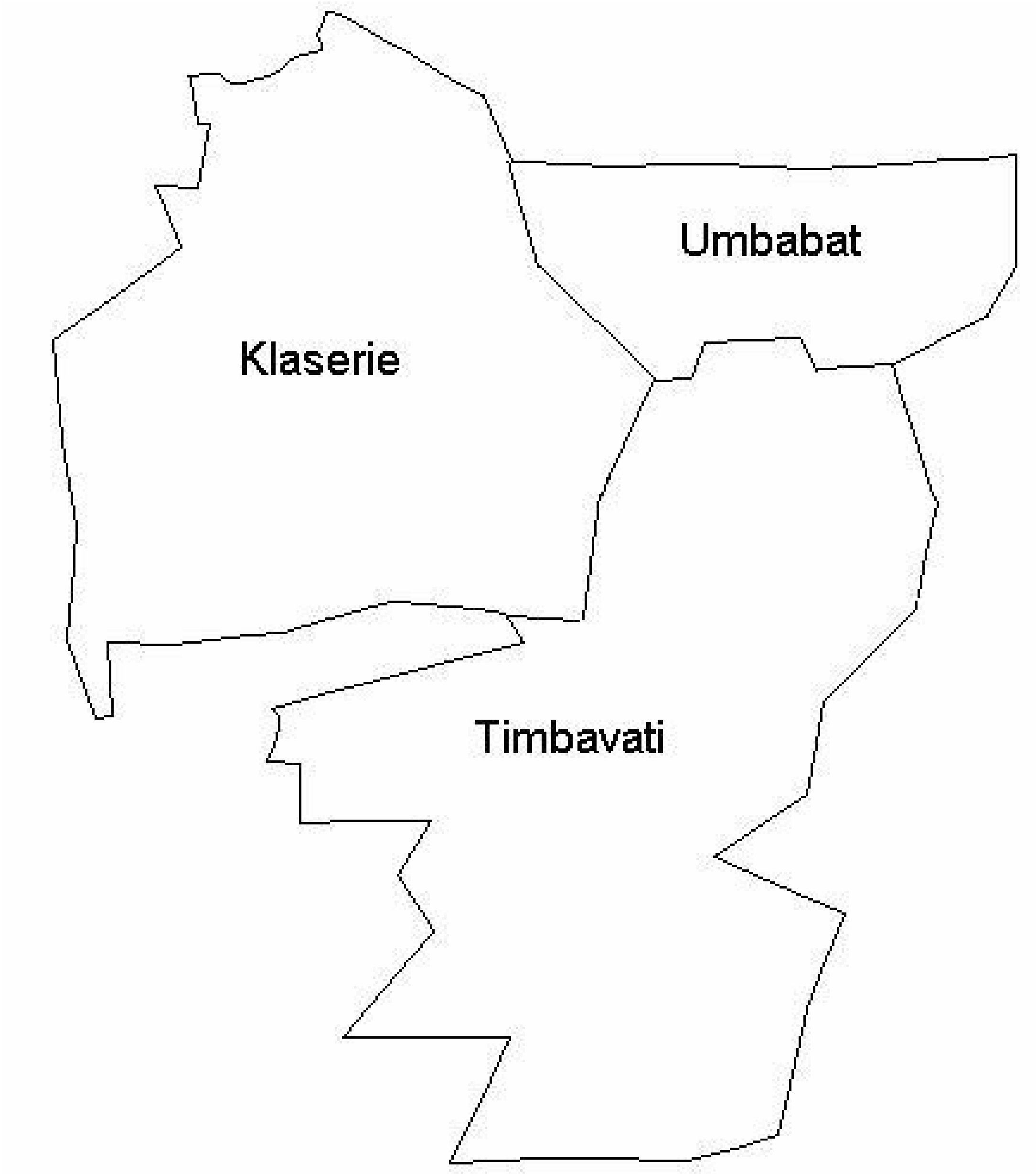


**Figure 2.2**: The three private nature reserves that comprised the Associated Private Nature Reserves until September 2005. The present study was conducted in this area from March 2000 to September 2002.

the formation of the individual private nature reserves in the 1960's and 1970's, the dominant form of land-use was cattle farming. The bushveld vegetation was not suited to farming cattle, and overstocking caused overgrazing and bush encroachment. The construction of dams increased the grazing pressure in certain areas, and along with the exclusion of veld fires further encouraged bush encroachment and caused soil erosion. The structure and composition of the vegetation therefore changed to suit certain animal species and not others. According to Porter (1970) that is why the impala *Aepyceros melampus* became so numerous in later years even though it did not occur in the Timbavati Private Nature Reserve at the turn of the century. The change in vegetation also had detrimental effects on other ungulates such as the roan antelope *Hippotragus equinus*, sable antelope *Hippotragus niger*, tsessebe *Damaliscus lunatus lunatus*, Burchell's zebra *Equus burchellii* and blue wildebeest *Connochaetes taurinus*. Currently, the blue wildebeest and Burchell's zebra populations are declining, and the roan antelope, sable antelope and tsessebe have disappeared from the Associated Private Nature Reserves. The present study investigated the current management strategies and endeavoured to make recommendations to the reserve management.

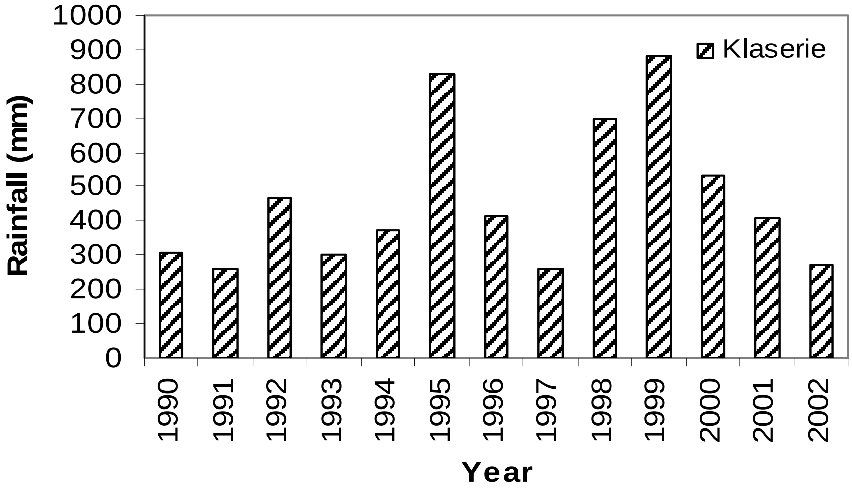
The human element in the Associated Private Nature Reserves is comprised of private landowners, private game lodge staff and reserve management staff. Conservation and eco-tourism are integral components, and management decisions have to meet both economic and ecological objectives. The Associated Private Nature Reserves have a decision-making committee with representatives from each of its member entities. The Associated Private Nature Reserves have formed a partnership with the Kruger National Park and have adopted the management principles as set out in the Kruger National Park Master Plan.

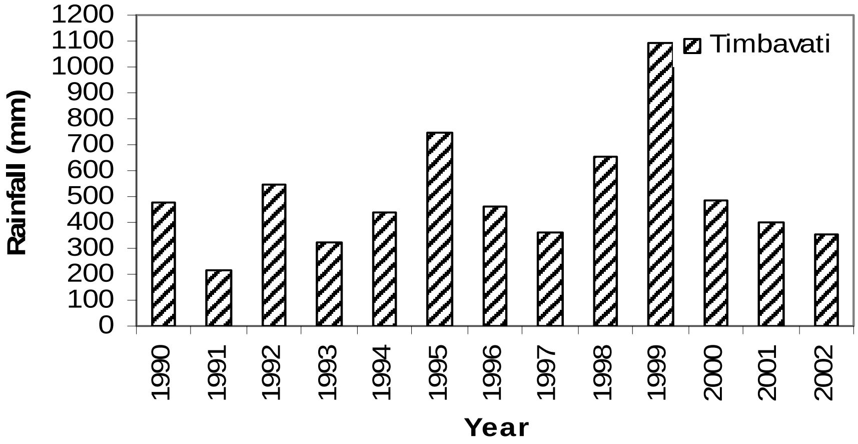
## CLIMATE

The Associated Private Nature Reserves are situated in a summer rainfall area of South Africa. The climate is typified by a summer wet season, which is roughly confined to the period from October to March, with the majority of precipitation occurring from December to February (Weaver 1995). The remainder of the year tends to be dry, with rare occurrences of precipitation.

The mean annual precipitation varies considerably between the reserves because precipitation tends to be highly localised in the Lowveld of South Africa (Figure 2.3). Rainfall patterns in the Lowveld as a whole follow wet and dry cycles, which conform roughly to a 20-year oscillation consisting of 10 years of above, followed by 10 years of below mean annual rainfall (Tyson & Dyer 1975; Gertenbach 1980). Currently the area is in year five of a dry cycle (Peel 2003). Fluctuations in Burchell's zebra and blue wildebeest populations in the Kruger National Park were found to conform to these wet and dry climatic cycles (Gertenbach 1980; Whyte & Joubert 1985; Mills, Biggs & Whyte 1995). Mills *et al.* 1995 conducted a study on the relationship between rainfall, lion predation and population trends in African herbivores. The study was conducted in the central district of the Kruger National Park, an area of comparable vegetation and rainfall, and was therefore used later in this study for comparative purposes. The Computing Centre for Water Research calculates annual rainfall from July to June the following year. In doing so, the long-term mean rainfall for the Klaserie, Timbavati and Umbabat Private Nature Reserves was 464 mm, 585 mm and 452 mm respectively.

Temperatures tend to be high during the day, but they drop at night by 10 to 15ºC. Temperature data that were collected by the Warden of the Klaserie Private Nature Reserve from 1975 to 1991 showed a mean daily maximum temperature for the wet season (October to March) of 32.6 ºC and a mean daily minimum temperature then of 20.5 ºC. The mean daily maximum temperature for the dry season (April to September)





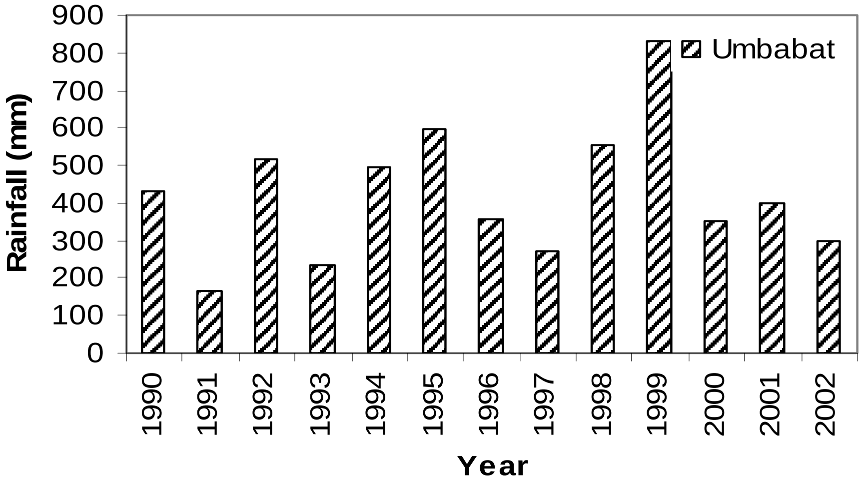


**Figure 2.3**: Recent annual rainfall for the Klaserie, Umbabat and Timbavati Private Nature Reserves from 1990 to 2002. Source: Peel (2003).

was 28.4 ºC and the mean daily minimum temperature is then 10.8 ºC (Kruger 1988).

## VEGETATION, SOILS AND GEOMORPHOLOGY

The study area occurred in the Arid Lowveld of the Savanna Biome, as described by Acocks (1988). The vegetation in the Associated Private Nature Reserves may be classified as Mopane Bushveld in the north, Mixed Lowveld Bushveld in the central and western areas, and Sweet Lowveld Bushveld in the south and east (Low & Rebelo 1996; Van Rooyen & Bredenkamp 1998). *Combretum apiculatum*, *C. zeyheri* and *C. collinum, Sclerocarya birrea* and *Terminalia sericea* form dominant components of the vegetation on granite. *Acacia nigrescens* and *Sclerocarya birrea* are the dominant species on gabbro.

The Associated Private Nature Reserves contain five distinct landscapes, based on the system developed in the Kruger National Park by Gertenbach (1983). The Timbavati and Umbabat Private Nature Reserves are located in the triangle formed by the Olifants River, the Timbavati River and the western boundary of the Kruger National Park and consists of *Combretum - Colophospermum mopane* Woodland which is intersected by Thornveld on Gabbro.

The *Combretum - Colophospermum mopane* Woodland landscape has a substratum of mainly granite and gneiss, which is intersected by numerous intrusions of dolerite. The terrain is undulating and is drained by the tributaries of the Timbavati River. The altitude varies from 300 to 500 m above sea level. Historically the *Combretum - Colophospermum mopane* Woodland landscape provided suitable habitat for the sable antelope, African elephant *Loxodonta africana*, African buffalo *Syncerus caffer*, Greater kudu *Tragelaphus strepsiceros*, impala and Burchell's zebra.

The Thornveld on Gabbro landscape is also referred to as a gabbro intrusion (Gertenbach 1983). It is characterised by a thorn savanna with a dense grass cover. This landscape is a series of islands of gabbro origin, sometimes linked by narrow dykes. The terrain is flat to slightly undulating with prominent koppies and an altitude of between 550 to 600 m above sea level. The most southern distribution of roan antelope in the Lowveld is associated with this landscape type (Gertenbach 1978). This gabbro intrusion into the Timbavati Private Nature Reserve was an area of great importance to the migratory herds of the Kruger National Park until it was fenced off in 1961 (Whyte 1985) (Figure 2.4). The large gabbro areas present in the Orpen/Timbavati area formed a choice blue wildebeest range, to which they would move after the spring rains (Whyte 1985). Burchell's zebra and blue wildebeest favoured the largest parts of this landscape before the erection of fences, especially after fire. Other wild herbivores that occur by preference in this landscape are the greater kudu, impala, giraffe *Giraffa camelopardalis*, waterbuck *Kobus ellipsiprymnus*, warthog *Phacochoerus africanus*, buffalo and elephant.

The dominant landscapes in the Klaserie Private Nature Reserve area were a mixed *Combretum - Terminalia* Woodland in the south, with Olifants River Rugged Veld in the north, and *Combretum - Colophospermum mopane* Woodland in the east. The Klaserie Private Nature Reserve was flat to gently undulating with a general slope from the southwest to the northeast and an altitude of 303 to 535 m above sea level (Weaver 1995). The major drainage is the Klaserie River which flows northeast through the reserve. The southeast section of the Klaserie Private Nature Reserve is drained by the Ntsiri River. Both the Klaserie and Ntsiri Rivers drain into the Olifants River outside the reserve boundary (Kruger 1988). The parent materials on the reserve are predominantly granites and gneisses (Figure 2.4). Historically the Klaserie Private Nature Reserve was used on a seasonal basis by Burchell's zebra and blue wildebeest herds before the erection of the fences. Weaver (1995) found an association between Burchell's zebra and

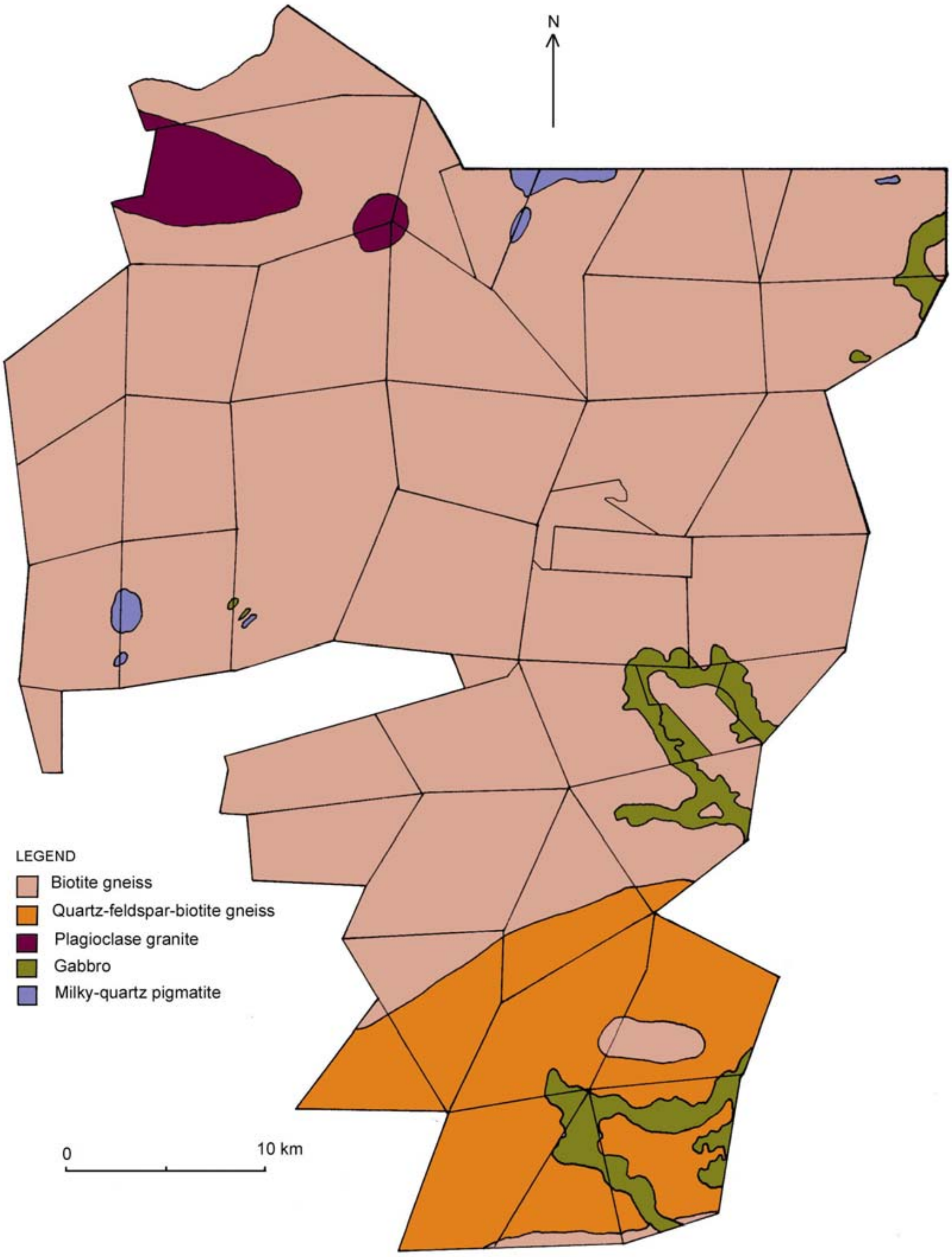


**Figure 2.4**: The geology of the Associated Private Nature Reserves, South Africa. Source: Van Rooyen (2005)

blue wildebeest distribution and the following three habitat types in the south of the Klaserie Private Nature Reserve: *Acacia nigrescens* - *Grewia* spp. Woodlands, Southwestern Mixed Woodlands and, *Combretum apiculatum* - *Sclerocarya birrea*, *Grewia* spp. Short Woodland Southern Extension.

The study by Van Rooyen & Purchase (2005) was the first attempt to map the vegetation of the entire Associated Private Nature Reserves. This study classified the vegetation in the Associated Private Nature Reserves into 24 vegetation types (Appendix A). Van Rooyen (2005) later clumped these 24 vegetation types into 11 management units for management purposes and the objectives of the present study (Figure 2.5). A detailed description of the vegetation, geology, land types and soils in the Associated Private Nature Reserves is given by Van Rooyen (2005).

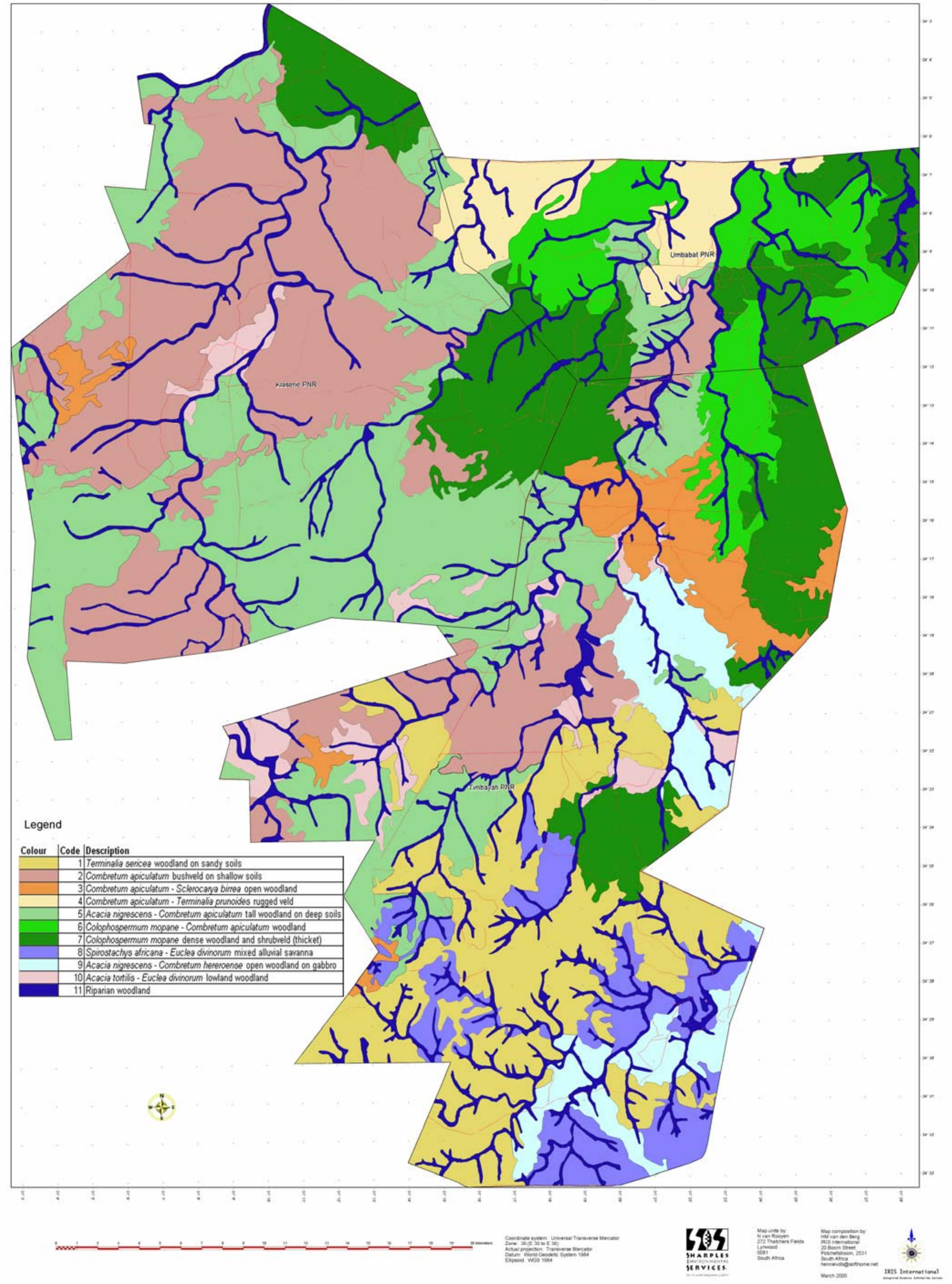


**Figure 2.5**: A simplified vegetation map for the Associated Private Nature Reserves showing the 11 management units that were determined by Van Rooyen (2005).

# CHAPTER 3

# GENERAL METHODS

The specific methods used in determining the different aspects of the present study are described under Methods in each relevant chapter.

# CHAPTER 4

# PREY DYNAMICS

## INTRODUCTION

The determination of prey population trends and their spatial distribution in relation to predator habitats are imperative to the success of any wildlife management programme. This is particularly true for wildlife areas that practise sustainable utilisation. The Associated Private Nature Reserves employ a consumptive approach to their wildlife management strategy by hunting, shooting rations and the sale of live animals (Weaver 1995). It is important for the wildlife managers of these nature reserves to know the size of the animal population from which they are harvesting. However, this figure is a meaningless statistic unless it can be related to population trends (Thomson 1992).

An understanding of prey population dynamics and the relationship between the prey animals and their habitats is basic to the study of predator-prey relationships. The interactions between predators and their prey are bi-directional. Predators affect prey populations and their behaviour, and the ecological factors that affect prey species in turn influence the predators of that prey (Funston 1999).

### Population dynamics

The number of prey in an area, the age and sex structure of that prey population, and the physical condition of the prey are some of the main factors that have to be considered in predation studies (Mills & Shenk 1992). The age and sex structure of the prey population influence the selection of prey by lions. Prey dispersion determines the range size of predators, and prey richness limits the group size of social predators (Macdonald 1983).

The selection of an appropriate counting technique is influenced by the cost, the size of the area, the type of animals to be counted, the type of habitat, the available manpower and the purpose for which the count is required. There is no single comprehensive counting technique that is suitable for all types of animal in all habitat types. The most consistent (precise) methods give a more constant margin of error and are therefore more reliable for effective wildlife management (Bothma 2002).

The use of aerial surveys as a management tool in the monitoring of large ungulates began in 1935 (Cahalane 1938). The use of aircraft, particularly helicopters, has grown consistently since 1950 and at present is being universally applied to count ungulate populations (Reilly 2002). In open bushveld areas aerial counting methods are the most widely used and are suitable techniques for determining prey population trends. However, in dense bushveld or forested areas, such as in the Associated Private Nature Reserves, a combination of aerial counting and road strip censusing methods produces the best results (Weaver 1995; Bothma 2002). This is the combination of counting methods that is being applied in the Associated Private Nature Reserves, and therefore the results upon which the inferences about the prey populations and their habitat selection were made in the present study.

### Ungulate-habitat dynamics

Large herbivores have specific habitat preferences and are therefore unevenly distributed in a specific habitat (Pienaar 1974; Hirst 1975; Vermaak 1996). Habitats are selected by ungulate species according to their specific requirements in terms of food, shelter and breeding needs, and these requirements influence the adaptations of the ungulates to various vegetation types (Thompson 1986).

Ecological separation between African ungulates reduces interspecific competition and prevents competitive exclusion between ungulate species (Weaver 1995). The dynamic equilibrium between ungulates and the habitat in which they occur may be disrupted by various phenomena, such as excessive herbivore impact, habitat degradation and artificial measures such as fencing, water provision, and systematic burning. The consequent change in habitat may either favour certain prey species, negatively affect others, or have no influence at all (Pienaar 1969; Funston 1999).

Vegetation constitutes a major component of the habitat of large herbivores (Bredenkamp 1981). Since physical habitat features such as the vegetation types present affect prey distribution, such habitat features are also indirectly expected to affect predator distribution (Krüger 1996*).* The hunting success of a predator may be affected by the type of habitat and the habitat conditions in which their prey animals occur. Lions prefer using the cover of grass, bushes and shrubs when hunting their prey, and therefore the density of the vegetation in which lion prey are found may affect their hunting success (Funston 1999). Rainfall determines habitat quality and structure through its influence on vegetation, and it can induce changes in habitat suitability that are capable of substantially modifying predator-prey relations (Smuts 1978; Whyte & Joubert 1988; Mills, Biggs & Whyte 1995). Rainfall is therefore the key factor that drives African savanna ecosystems (Coe *et al.* 1976).

The vegetation in the Timbavati and Umbabat Private Nature Reserves was broadly classified into 11 vegetation types by Hirst (1975) and Zambatis (1980). In the Klaserie Private Nature Reserve, 14 types of vegetation were classfied (Zambatis 1985). The vegetation in the Associated Private Nature Reserves was classified into 24 vegetation types and 11 wildlife management units by Van Rooyen *et al.* (2005). The field staff of the Associated Private Nature Reserves monitor visible changes in habitat condition by using annual fixed-point photography of the vegetation. The Range and Forage Institute conducts vegetation condition assessments annually in the Associated Private Nature

Reserves and presents their findings and recommendations in an annual ecological monitoring report to the committee that manages the respective private nature reserves (Peel 2003).

The vegetation in the Associated Private Nature Reserves has changed over time (Porter 1970; Kruger 1988; Weaver 1995). Because ungulates have specific habitat requirements (Thompson 1986), any change in the vegetation types in the Associated Private Nature Reserves will affect the prey communities found there. Therefore the present study tested the following hypotheses:

- That the vegetation in the study area was gradually changing from an open savanna to a dense woodland vegetation
- That the basic habitat preferences of the ungulate species in the study area were still being met
- That the age and sex structure of the ungulate species present were in proportion to that expected for most African savannas
- That the total biomass of all the animals, the prey biomass and the feeding class proportions for the most abundant lion prey reflected the expected values for African savannas (Coe *et al.* 1976; Collinson & Goodman 1982)

## METHODS

### Population dynamics

*Aerial counting method*

The technique of aerial counting of prey was based on the design applied in the Kruger National Park (Joubert 1983; Viljoen & Retief 1993). This technique was modified by the South African National Parks from a total count to a sample count in 1994, and the distance sampling method (Thomas *et al.* 2002) was applied in the Kruger National Park in 1998 (Reilly, Harley, Kruger & Whyte in prep.). The distance sampling method estimated the total population with the aid of a correction factor for undercounting as a result of a deteriorating detection probability further away from the sampling transect – the perpendicular distance of the animal from a sampling line or point (Burnham & Anderson 1984; Buckland, Anderson, Burnham & Laake 1993). The distance sampling technique was cost- and time-effective and gave a better estimate of the actual number of animals in the Kruger National Park (Whyte pers. comm.)[1]. The present study suggested that the distance sampling method was not suitable for the Timbavati, Klaserie or Umbabat Private Nature Reserves or any area smaller than 100 000 ha (Reilly pers.comm.)[2]. The sampling precision of the distance sampling technique was not adequate for detecting changes in the population trends of rare ungulates in these areas. Furthermore, a suitable technique is yet to be developed to determine how historical data (total counts) can be compared with distance sampling data.

The aerial counts were done at the end of the dry season according to the method of Joubert (1983). Parallel strips approximately 800 m apart were flown at a height of 60 m above ground level in a westerly direction at an airspeed of 145 to 160 km/h. The aerial counts were done between 08:00 and 12:30 by using a fixed-wing aircraft or a helicopter that could seat six observers. From 1983 to 1999 the data were recorded directly on to a 1:100 000 map but from 2000 to 2004 they were digitised onto a computer that was connected to a Global Positioning System. The Timbavati and Umbabat Private Nature Reserves used a fixed-wing aircraft survey from 1983 to 2001, and a Bell Jet Ranger helicopter from 2002 to the present. Total counts were done in the Timbavati and Umbabat Private Nature Reserves from 1983 to 1999, but the distance sampling method was applied from 2000 to 2002. The aerial counts for the Klaserie Private Nature Reserve

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were total counts. A Bell Jet Ranger helicopter was used from 1983 to 1991 and from 1997 to the present, and a fixed-wing aircraft from 1992 to 1996. From 1992 to the present a separate helicopter count was done for elephants and buffaloes in the Associated Private Nature Reserves. The influence of the change in the aerial counting methods, from fixed-wing counts to helicopter counts, on the detection and interpretation of prey population dynamics in the study area was reviewed in Chapter 8.

The population trends of the most abundant types of lion prey in the Associated Private Nature Reserves were derived from aerial counts (Joubert 1999) and from the ecological monitoring reports of Peel (2003). The most abundant types of lion prey in the Associated Private Nature Reserves were the impala *Aepyceros melampus*, the blue wildebeest *Connochaetes taurinus*, Burchell's zebra *Equus burchellii*, the greater kudu *Tragelaphus strepsiceros*, the Cape buffalo *Syncerus caffer*, the giraffe *Giraffa camelopardalis*, the warthog *Phacochoerus africanus* and the waterbuck *Kobus ellipsiprymnus*. From the ecological monitoring reports of Peel (2003), the total biomass of animals counted and the total prey biomass were calculated for the Timbavati, Klaserie, Umbabat, and the combined Associated Private Nature Reserves. The total biomass of animals in the study area was then compared with that estimated using Coe, Cumming & Phillipson (1976). Coe *et al.* (1976) examined 12 natural African ecosystems with a mean annual rainfall of < 700 mm to determine the relationship between the total biomass of animals that could be sustained in a given wildlife area and its rainfall.

Large herbivores may be classified according to four feeding classes depending on their feeding preferences. The most abundant large herbivores in the Associated Private Nature Reserves were classified according to these four feeding classes following Collinson & Goodman (1982):

- bulk grazers: buffalo, Burchell's zebra, waterbuck and white rhinoceros

- selective grazers: blue wildebeest and warthog
- mixed feeders: African elephant and impala
- browsers: giraffe and greater kudu

The proportions of bulk grazers, selective feeders, mixed feeders and browsers in the Associated Private Nature Reserves were compared with the recommended proportion of 45:20:20:15 for these feeding classes respectively (Collinson & Goodman 1982; Peel 2003). Although this ratio is outdated, it was used in the present study because the Agricultural Research Council's Range and Forage Institute still uses this ratio when doing the ecological monitoring surveys for the Associated Private Nature Reserves, from which management decisions are made.

*Road strip censusing method*

The methods used by Weaver (1995) to study herbivore vegetation use patterns in the Klaserie Private Nature Reserve were also used for this part of the present study. The herbivore distribution patterns were correlated with their proximity to roads or established bush tracks in the Klaserie Private Nature Reserve. Burchell's zebra were most likely to be found within 40 to 60 m of a road or bush track, and the blue wildebeest within 40 to 225 m of it (Weaver 1995).

Road strip censuses were done within each vegetation type in the Associated Private Nature Reserves. For the Timbavati, Klaserie and Umbabat Private Nature Reserves, two surveys were done in the wet season (October to March) and in the dry season (April to September), respectively. A total of 17 survey routes were used to census the entire study area. Using a vegetation map of the study area (Zambatis 1983), the transect length of each survey route within each vegetation type was chosen to be proportional to the relative surface area of the respective vegetation types. The road transect lengths varied from 15 to 40 km and totalled 425 km. The road transects were done in the early morning and the late afternoon (Hirst 1969; Wentzel 1989; Von Holdt 1999) and were established along existing roads and tracks due to the large area to be surveyed and the length of the required sampling routes. Within the Associated Private Nature Reserves, the roads and tracks traverse all the habitat types present, and it was therefore possible to establish representative transects within each vegetation type, with a minimum of observer bias (Schutte 1986). The speed of travel was adjusted to the individual habitat type and respective season. Observation speeds during the wet season tended to be slower due to the poor condition of the roads. To minimise observer bias and to avoid double counting any individuals on the same day, the route direction was reversed for each alternate survey (Weaver 1995).

Specific herbivore data were recorded for each observation: the species, time, GPS location, odometer reading, habitat type, total number of animals for each species, and the number of animals in each age and sex class. These data were recorded for the impala, blue wildebeest, Burchell's zebra, greater kudu, buffalo, giraffe, waterbuck and warthog only, because these were the most abundant types of lion prey in the Associated Private Nature Reserves and the Kruger National Park (Kruger 1988; Whyte & Joubert 1988; Mills & Shenk 1992; Mills & Biggs 1993).

The age classes that were used in this study only differentiated between adults and juveniles. Age classes were determined for each of the eight most abundant types of lion prey by using the age classification of Bothma *et al*. (1996). The prey observations during road strip censuses were weighted by the number of animals observed in the wet (October to March) and the dry season (April to September) respectively, to compare prey abundance seasonally. Chi-squared analyses were used to test the significance of the differences in the population data between years for the respective private nature reserves. The differences in the population data between the various private nature reserves were also tested for significance.

## Ungulate-habitat dynamics

The data from the ecological monitoring reports for the Associated Private Nature Reserves were used to investigate the habitat dynamics and preferences of the ungulates in the study area from 1991 to 2003 (Peel 2003). The conclusions drawn from these data were then compared with those from previous studies (Hirst 1969, Hirst 1975, Kruger 1988 and Weaver 1995).

### *Vegetation dynamics*

The indices that were used to determine the annual change in the vegetation in the Associated Private Nature Reserves were grass cover and the grass standing crop for the herbaceous layer, while sapling density was used as an index of the change in the woody layer. Previous studies have shown that rainfall determines the primary productivity of vegetation, and hence the regional aggregate and species-specific biomass densities of large herbivores and carnivores in African savannas (Coe *et al.* 1976; East 1984; Van Orsdol *et al.* 1985). The habitat data for the study area were therefore compared with the annual fluctuation in rainfall to determine whether there was any correlation. It was assumed that the previous year's rainfall had a greater affect on a current year's vegetation dynamics than that of the current year (Peel 2003). The grass standing crop and the sapling density in the study area were also compared from 1996 to 2002 as an index of vegetation change.

### *Ungulate-habitat dynamics*

The aerial counting data for the prey populations in the Associated Private Nature Reserves and the Animal Movements Extension Program for Arcview 3.2 were used to estimate the habitat selection of the eight most abundant types of lion prey in the Associated Private Nature Reserves. For analysis, the GPS locations and the herd sizes of the eight types of lion prey were stored as GIS ArcInfo point covers (Mills & Gorman 1997). By superimposing these data onto a digitised vegetation map of the Associated Private Nature Reserves (Van Rooyen *et al.* 2005) the number of animals per vegetation type was calculated for each of the eight most abundant types of lion prey in the Timbavati, Klaserie and Umbabat Private Nature Reserves.

The habitat preferences of the most abundant lion prey were then calculated by comparing patterns of habitat use with habitat availability. For the Associated Private Nature Reserves, the habitat availability was calculated by dividing the surface area covered by vegetation type $x$ by the total surface area of the reserve. A habitat selection index was then calculated for each of the vegetation types in the ranges used by the focal lions by using the following Index of Jacobs (1974):

$S = [U – A] / [(U + A) – 2UA]$

where: $S$ = selection of vegetation type $x$

$U$ = the proportion of use of vegetation type $x$

$A$ = the proportion of vegetation type $x$ available in the range of a lion or pride

A habitat selection value of 0 indicated that a vegetation type was used in the same ratio as its proportional occurrence, a positive value (maximum +1.0) indicated preference of use for a specific vegetation type and a negative value (minimum -1.0) indicated that the vegetation type was not being used.

A preference index in itself, however, is of limited use because it does not involve a statistical test, and only provides a ratio of habitat use to habitat availability (Alldredge & Ratti 1986). The habitat selection data were therefore analysed by using the method described by Neu *et al.* (1974). Chi-squared analyses were used to determine whether there was any significant evidence of selection for a specific vegetation type by the various prey animals. The observed counts of prey in each vegetation type were compared with the expected counts if each vegetation type were used in proportion to its availability. When a significant difference in use versus availability was detected, a Bonferroni Z-statistic was used to determine which vegetation types were used more or less often by the various prey animals than expected by constructing 95% simultaneous confidence intervals around the proportion of the prey animals recorded in each vegetation type (Marcum & Loftsgaarden 1980; Beyers *et al.* 1984; Allredge & Ratti 1992; Pienaar *et al.* 1992). The confidence intervals were calculated by using the following equation of Allredge & Ratti (1992): $U \pm Z_{1-\alpha/2k}\,[U(1-U)/n]^{1/2}$

where: U = the proportion of use by the various prey animals

$Z_{1-\alpha/2k}$ = the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$

k = the number of vegetation types

n = the total number of observations of the eight types of lion prey

Bonferroni confidence intervals were calculated for the habitat selection of the eight most abundant prey animals in the Associated Private Nature Reserves ($\alpha = 0.05$, $k = 12$ and $Z_{1-\alpha/2k} = 2.80$). The results indicated whether each vegetation type was used significantly more or less than expected compared with the percentage availability of the corresponding vegetation type.

## RESULTS

### Prey population dynamics

Figures 4.1, 4.2, 4.3 and 4.4 show the aerial count data for the eight most abundant types of lion prey in the Timbavati, Klaserie, Umbabat and the Associated Private Nature Reserves from 1980 to 2003. The annual count data were significantly different for the period of observation in the Timbavati ($\chi^2$ = 26170.479 df = 98; $P \leq 0.01$), Klaserie ($\chi^2$ = 43078.187; df = 161; $P \leq 0.01$) and Umbabat Private Nature Reserves ($\chi^2$ = 6493.399; df = 70; $P \leq 0.01$). The combined count data for the Associated Private Nature Reserves differed significantly between the years of the respective aerial counts ($\chi^2$ = 16123.947; df = 63; $P \leq 0.01$). The results of the aerial counting from 1991 to 2003 differed significantly between years for the Timbavati, Klaserie and Umbabat Private Nature Reserves (Figs. 4.1 to 4.4). All the prey populations in the Associated Private Nature Reserves, except for the buffalo population, showed a decreasing trend over the total counting period. Only the buffalo population increased from 1991 to 2003.

### *Total animal biomass and prey biomass*

The total biomass of animals and the available prey biomass for lions for the Timbavati, Klaserie, Umbabat and the combined Associated Private Nature Reserves appear in Fig. 4.8 and Tables 4.1 to 4.4. The total biomass of animals in 2001, 2002 and 2003 for the Timbavati, Klaserie and the Associated Private Nature Reserves was greater than the maximum recommended animal biomass in these areas (Table 4.1) (Coe *et al.* 1976; Peel 2003). The total biomass of animals in the Umbabat Private Nature Reserve in 2001 was at the maximum recommended biomass of animals for the sustainable management of that area. In 2002 and 2003 the total biomass of animals in the Umbabat Private Nature Reserve was significantly greater than that expected (Peel 2003).

The available prey biomass for lions in the Timbavati, Klaserie and the Umbabat Private Nature Reserves differed significantly from each other ($\chi^2$ = 1359.316; df = 60; $P \leq 0.01$). The prey biomass in the Timbavati, Klaserie and the Associated Private Nature Reserves from 2001 to 2003 was greater than the minimum recommended biomass of animals for

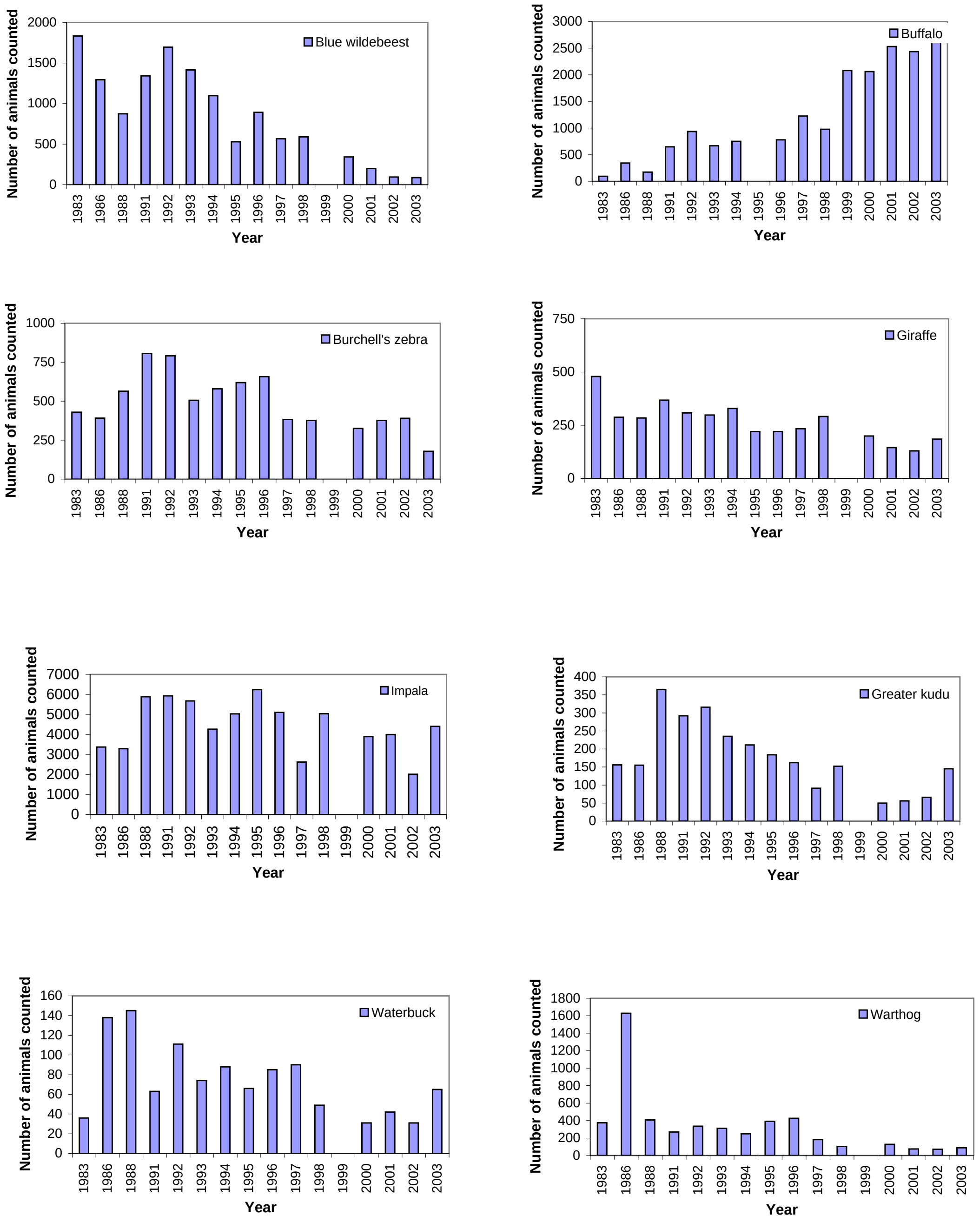

**Figure 4.1:** Trends in the number of prey animals of lions counted during aerial counting for the eight most abundant types of lion prey in the Timbavati Private Nature Reserve from 1983 to 2003. Source of data: Peel (2003).

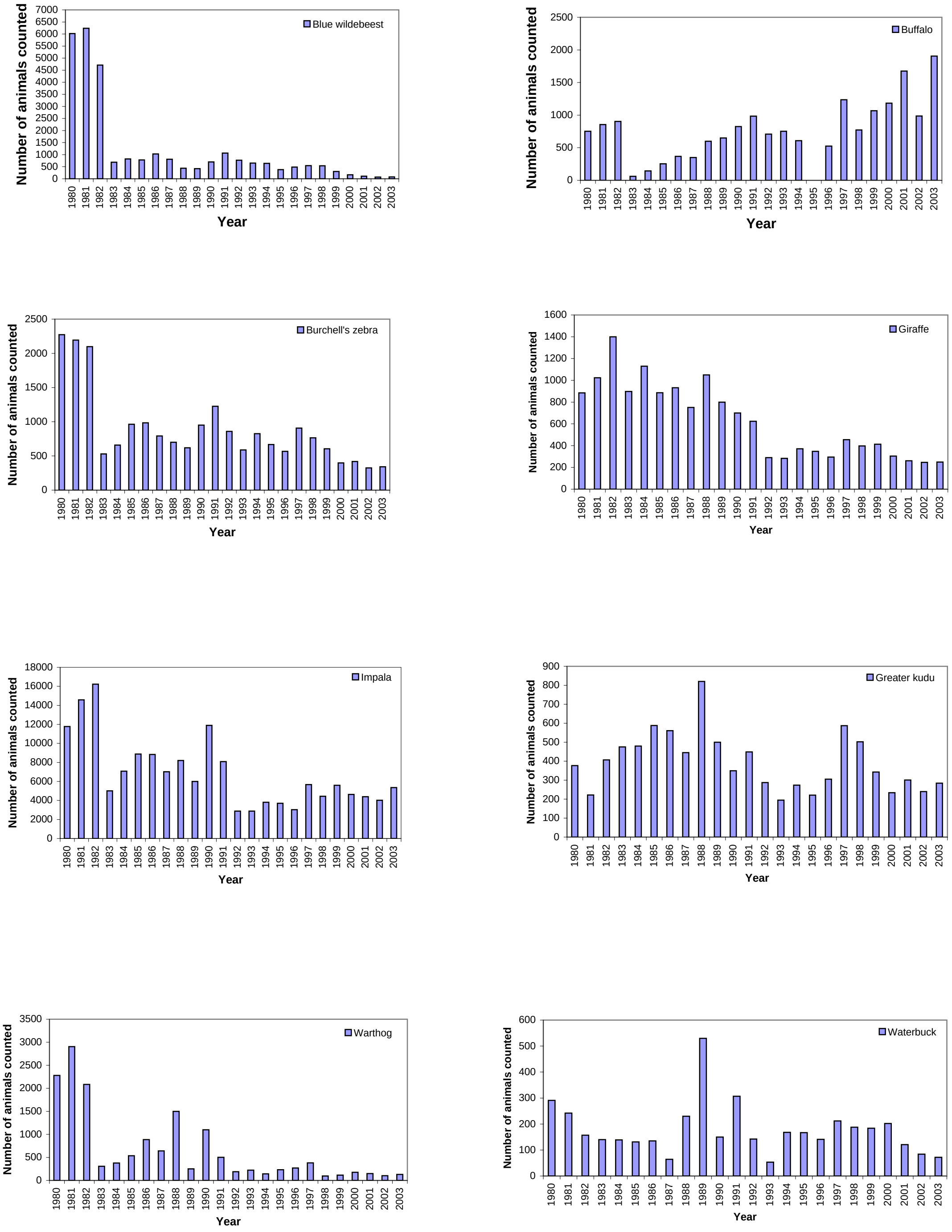

**Figure 4.2:** Trends in the number of prey animals of lions counted during aerial counting for the eight most abundant types of lion prey in the Klaserie Private Nature Reserve from 1980 to 2003. Source of data: Peel (2003).

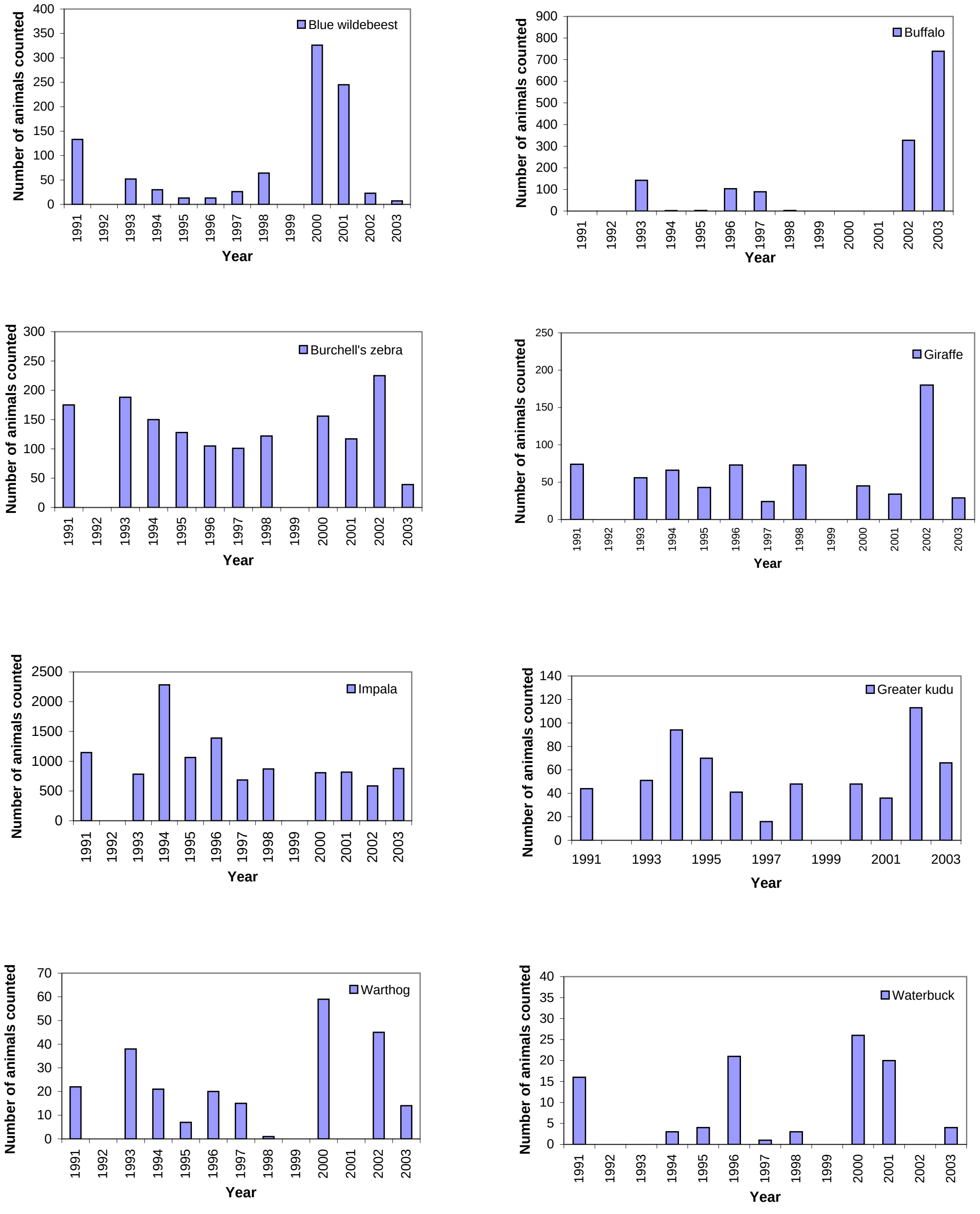

**Figure 4.3:** Trends in the number of prey animals of lions counted during aerial counting for the eight most abundant types of lion prey in the Umbabat Private Nature Reserve from 1991 to 2003. Source of data: Peel (2003).

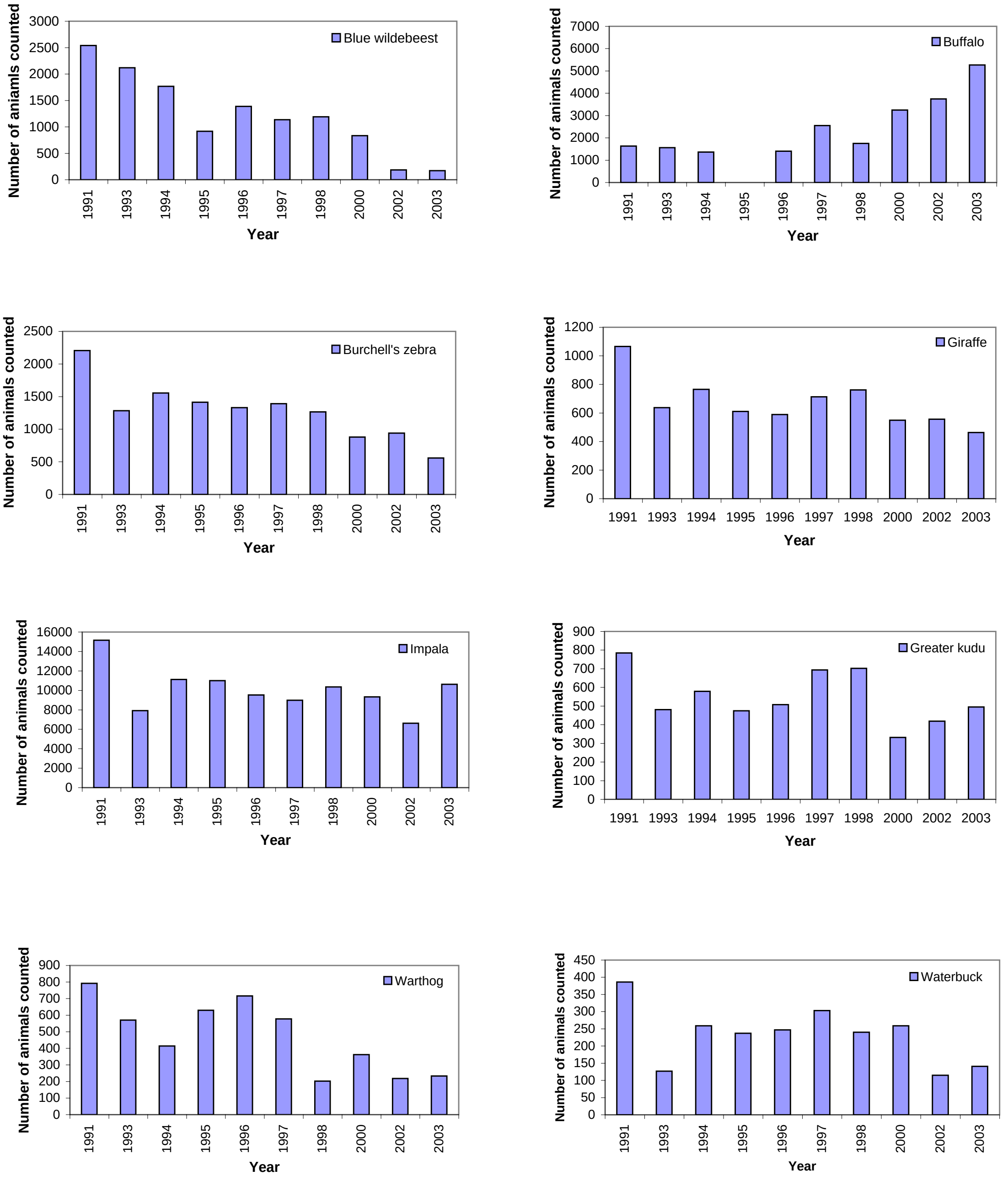

**Figure 4.4:** Trends in the number of prey animals of lions counted during aerial counting for the eight most abundant types of lion prey in the Associated Private Nature Reserve from 1991 to 2003. Source of data: Peel (2003).

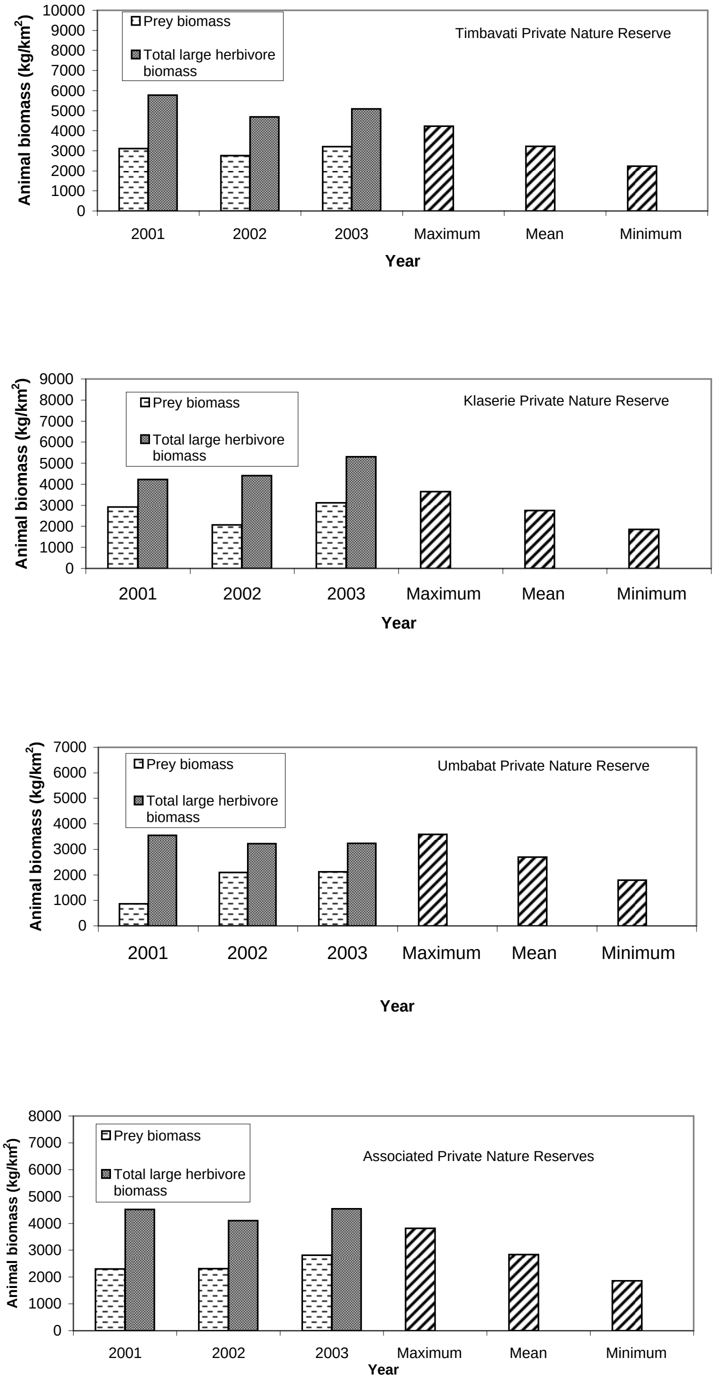

**Figure 4.8:** The prey biomass and total biomass of large herbivores in the Associated Private Nature Reserves and its component private nature reserves from 2001 to 2003. The data were compared to the maximum, mean and minimum recommended large herbivore biomass for those areas (Coe *et al.* 1976) Source of data: Peel (2003).

Table 4.1: *Chi-squared tests comparing the actual biomass (kg/km²) of animals in the Timbavati, Klaserie, Umbabat and the combined Associated Private Nature Reserves with the maximum expected biomass of animals for the respective areas based on Coe et al. (1976) from 2001 to 2003.*

| **AREA** | **YEAR** | **TOTAL ANIMAL BIOMASS** | **MAXIMUM RECOMMENDED ANIMAL BIOMASS** | **CHI-SQUARED TESTS** | | |
|---|---|---|---|---|---|---|
| | | | | $\chi^2$ | **P** | **df** |
| Timbavati Private Nature Reserve | 2001 | 5773 | 4225 | 741.383 | ≤ 0.05 | 9 |
| | 2002 | 4683 | 4225 | 58.122 | ≤ 0.05 | 9 |
| | 2003 | 5090 | 4225 | 270.650 | ≤ 0.05 | 9 |
| Klaserie Private Nature Reserve | 2001 | 4230 | 3650 | 169.198 | ≤ 0.05 | 9 |
| | 2002 | 4410 | 3650 | 211.562 | ≤ 0.05 | 9 |
| | 2003 | 5300 | 3650 | 1171.305 | ≤ 0.05 | 9 |
| Umbabat Private Nature Reserve | 2001 | 3550 | 3590 | 0.126 | > 0.05 | 9 |
| | 2002 | 3222 | 3590 | 34.347 | ≤ 0.05 | 9 |
| | 2003 | 3235 | 3590 | 425.962 | ≤ 0.05 | 9 |
| Associated Private Nature Reserves | 2001 | 4518 | 3820 | 767.215 | ≤ 0.05 | 7 |
| | 2002 | 4105 | 3820 | 738.478 | ≤ 0.05 | 7 |
| | 2003 | 4542 | 3820 | 784.775 | ≤ 0.05 | 7 |

Table 4.2: *Chi-squared tests comparing the prey biomass (kg/km$^2$) of animals in the Timbavati, Klaserie, Umbabat and the combined Associated Private Nature Reserves with the minimum, mean and maximum expected biomass of animals for the respective areas based on Coe et al. (1976) in 2001.*

| **AREA** | **PREY BIOMASS** | **RECOMMENDED ANIMAL BIOMASS** | | | **CHI-SQUARED TEST** | | |
|---|---|---|---|---|---|---|---|
| | | **minimum** | **mean** | **maximum** | **$\chi^2$** | **P** | **df** |
| Timbavati Private Nature Reserve | 3210 | 2225 | ~ | ~ | 436.081 | ≤ 0.05 | 7 |
| | | ~ | 3225 | ~ | 0.070 | > 0.05 | 7 |
| | | | | 4225 | 243.827 | ≤ 0.05 | 7 |
| Klaserie Private Nature Reserve | 2919 | 1850 | ~ | ~ | 617.654 | ≤ 0.05 | 7 |
| | | ~ | 2750 | ~ | 38.005 | ≤ 0.05 | 7 |
| | | | | 3650 | 246.419 | ≤ 0.05 | 7 |
| Umbabat Private Nature Reserve | 865 | 1800 | ~ | ~ | 4859.715 | ≤ 0.05 | 7 |
| | | ~ | 2695 | ~ | 12430.157 | ≤ 0.05 | 7 |
| | | | | 3590 | 20688.445 | ≤ 0.05 | 7 |
| Associated Private Nature Reserves | 2508 | 1860 | ~ | ~ | 225.607 | ≤ 0.05 | 7 |
| | | ~ | 2840 | ~ | 88.861 | ≤ 0.05 | 7 |
| | | | | 3820 | 450.759 | ≤ 0.05 | 7 |

Table 4.3: *Chi-squared tests comparing the prey biomass (kg/km$^2$) of animals in the Timbavati, Klaserie, Umbabat and the combined Associated Private Nature Reserves with the minimum, mean and maximum expected biomass of animals for the respective areas based on Coe et al. (1976) in 2002.*

| **AREA** | **PREY BIOMASS** | **RECOMMENDED ANIMAL BIOMASS** | | | **CHI-SQUARED TEST** | | |
|---|---|---|---|---|---|---|---|
| | | **minimum** | **mean** | **maximum** | $\chi^2$ | **P** | **df** |
| Timbavati Private Nature Reserve | 2837 | 2225 | ~ | ~ | 455.822 | ≤ 0.05 | 7 |
| | | ~ | 3225 | ~ | 146.621 | ≤ 0.05 | 7 |
| | | | | 4225 | 3617.974 | ≤ 0.05 | 7 |
| Klaserie Private Nature Reserve | 2074 | 1850 | ~ | ~ | 166.313 | ≤ 0.05 | 7 |
| | | ~ | 2750 | ~ | 680.732 | ≤ 0.05 | 7 |
| | | | | 3650 | 2324.484 | ≤ 0.05 | 7 |
| Umbabat Private Nature Reserve | 2101 | 1800 | ~ | ~ | 261.705 | ≤ 0.05 | 7 |
| | | ~ | 2695 | ~ | 540.366 | ≤ 0.05 | 7 |
| | | | | 3590 | 2488.801 | ≤ 0.05 | 7 |
| Associated Private Nature Reserves | 2226 | 1860 | ~ | ~ | 232.568 | ≤ 0.05 | 7 |
| | | ~ | 2840 | ~ | 664.797 | ≤ 0.05 | 7 |
| | | | | 3820 | 2665.003 | ≤ 0.05 | 7 |

Table 4.4: *Chi-squared tests comparing the prey biomass (kg/km²) of animals in the Timbavati, Klaserie, Umbabat and the combined Associated Private Nature Reserves with the minimum, mean and maximum expected biomass of animals for the respective areas based on Coe et al. (1976) in 2003.*

| **AREA** | **PREY BIOMASS** | **RECOMMENDED ANIMAL BIOMASS** | | | **CHI-SQUARED TEST** | | |
|---|---|---|---|---|---|---|---|
| | | **minimum** | **mean** | **maximum** | $\chi^2$ | **P** | **df** |
| Timbavati Private Nature Reserve | 3209 | 2225 | ~ | ~ | 524.767 | ≤ 0.05 | 7 |
| | | ~ | 3225 | ~ | 9.805 | > 0.05 | 7 |
| | | | | 4225 | 612.488 | ≤ 0.05 | 7 |
| Klaserie Private Nature Reserve | 3123 | 1850 | ~ | ~ | 875.521 | ≤ 0.05 | 7 |
| | | ~ | 2750 | ~ | 155.543 | ≤ 0.05 | 7 |
| | | | | 3650 | 276.183 | ≤ 0.05 | 7 |
| Umbabat Private Nature Reserve | 2126 | 1800 | ~ | ~ | 177.515 | ≤ 0.05 | 7 |
| | | ~ | 2695 | ~ | 300.670 | ≤ 0.05 | 7 |
| | | | | 3590 | 1384.405 | ≤ 0.05 | 7 |
| Associated Private Nature Reserves | 2819 | 1860 | ~ | ~ | 1061.468 | ≤ 0.05 | 7 |
| | | ~ | 2840 | ~ | 8.492 | > 0.05 | 7 |
| | | | | 3820 | 1682.506 | ≤ 0.05 | 7 |

those areas (Fig. 4.8) (Tables 4.2 to 4.4) (Coe *et al.* 1976; Peel 2003). In the Umbabat Private Nature Reserve the prey biomass of lions in 2002 and 2003 was greater than the minimum recommended biomass for that area, but in 2001 it was less than that recommended for the sustainable management of that area.

*Feeding class proportions*

The proportion of bulk grazers, selective feeders, mixed feeders and browsers present during the present study was significantly different to generally recommended guidelines (Collinson & Goodman 1982; Peel 2003) for the Timbavati ($\chi^2$ = 376.762; df = 18; P ≤ 0.01), Klaserie ($\chi^2$ = 438.941; df = 21; P ≤ 0.01), Umbabat ($\chi^2$ = 207.219; df = 18; P ≤ 0.05) and the combined Associated Private Nature Reserves ($\chi^2$ = 805.639; df = 21; P ≤ 0.05) (Fig. 4.9). When compared to the recommended proportions for the four feeding classes (Collinson & Goodman 1982), the proportion of bulk grazers approached the recommended proportion, the proportion of selective feeders and browsers was lower than the guideline, and the proportion of mixed feeders was greater than the recommended proportion.

*Age structure, sex ratio and seasonal abundance*

Figures 4.5, 4.6 and 4.7 show the age and sex structure, and the seasonal abundance of the eight most abundant types of lion prey in the Associated Private Nature Reserves. The proportion of adults was significantly greater than that of juveniles in all the populations of the eight types of lion prey in the Timbavati ($\chi^2$ = 1021.736; df = 7; P ≤ 0.05), Klaserie ($\chi^2$ = 539.677; df = 7; P ≤ 0.05) Umbabat ($\chi^2$ = 244.292; df = 7; P ≤ 0.05), and the Associated Private Nature Reserves ($\chi^2$ = 809.102; df = 7; P ≤ 0.05) (Fig. 4.5). This observed age structure was consistent with that of most ungulate populations in the African savannas. The proportion of juveniles relative to adults in the populations of the giraffe, Burchell's zebra and the blue wildebeest was, however, lower than the generally recommended 30

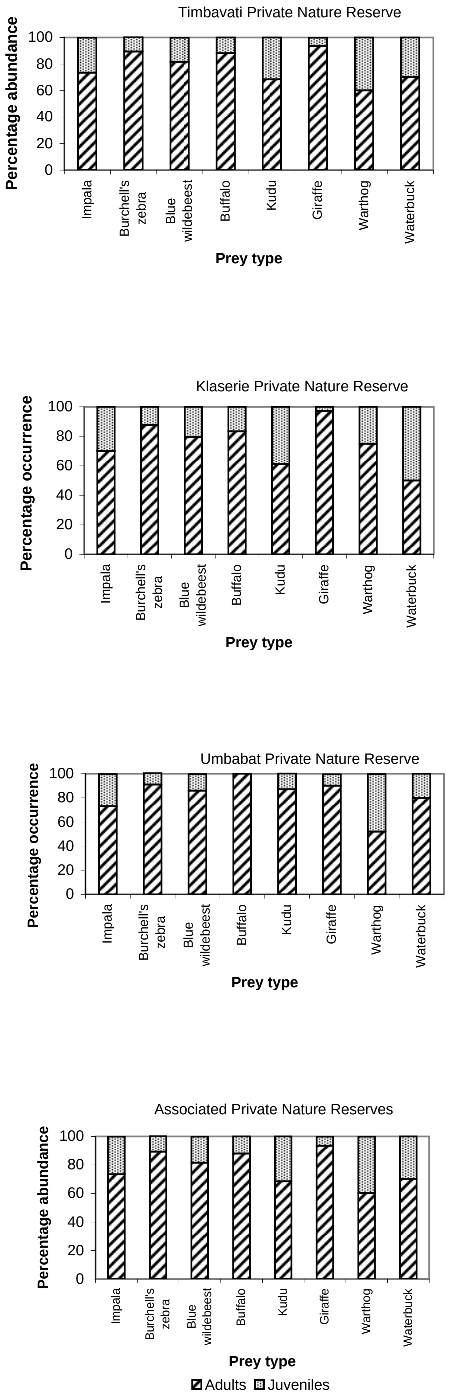

**Figure 4.5:** The age structure of the eight most abundant types of lion prey in the Associated Private Nature Reserves from 1985 to 2002, based on road strip census data.

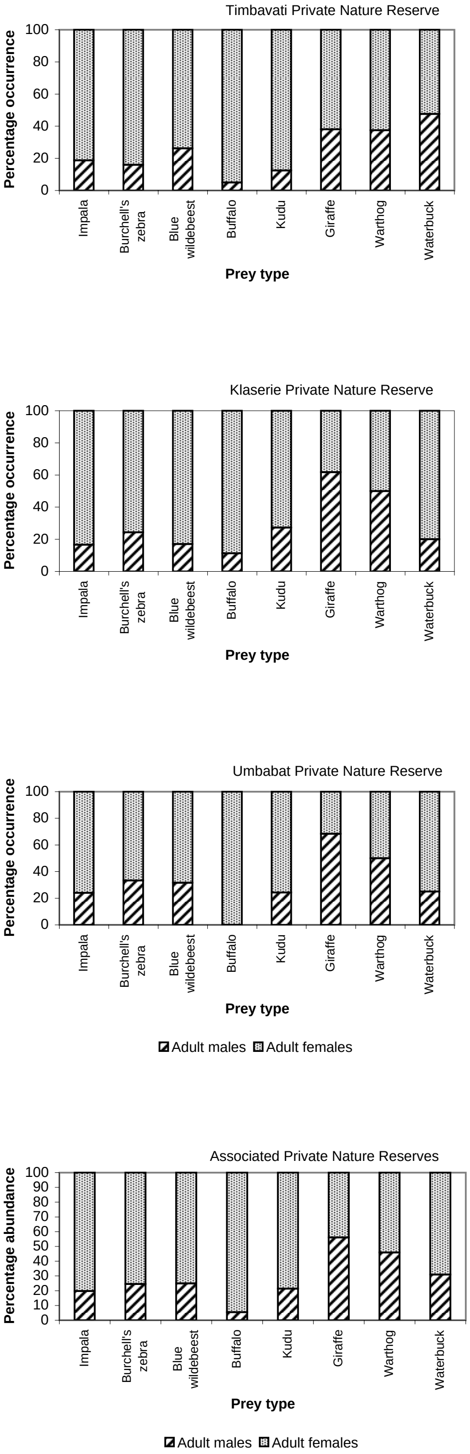

**Figure 4.6:** The sex ratio of the eight most abundant types of lion prey in the Associated Private Nature Reserves from 1985 to 2002, based on road strip census data.

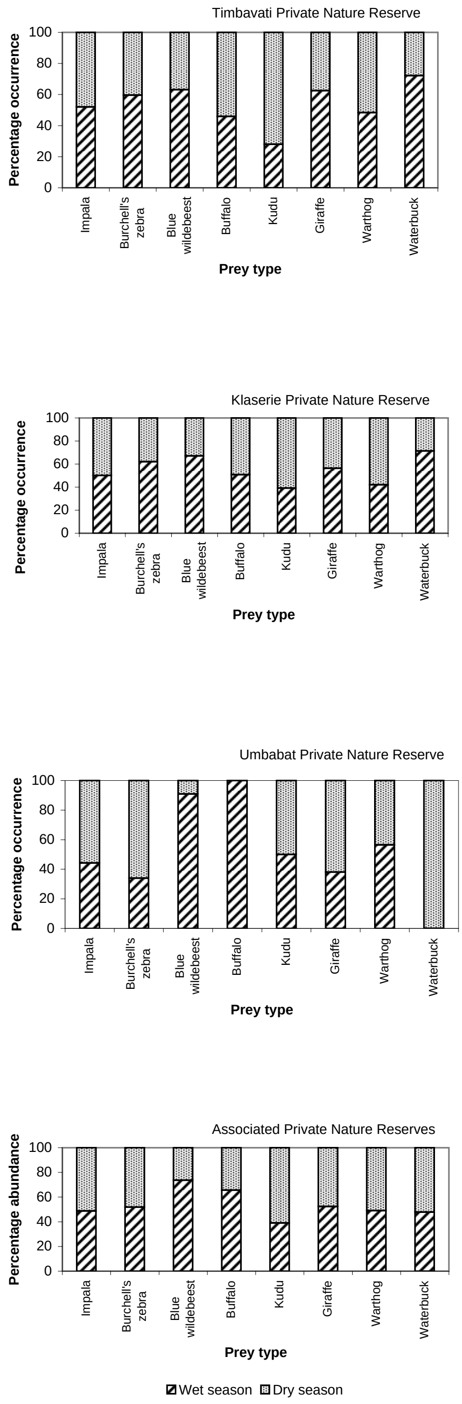

**Figure 4.7:** The seasonal abundance of the eight most abundant types of lion prey in the Associated Private Nature Reserves from 1985 to 2002, based on road strip census data.

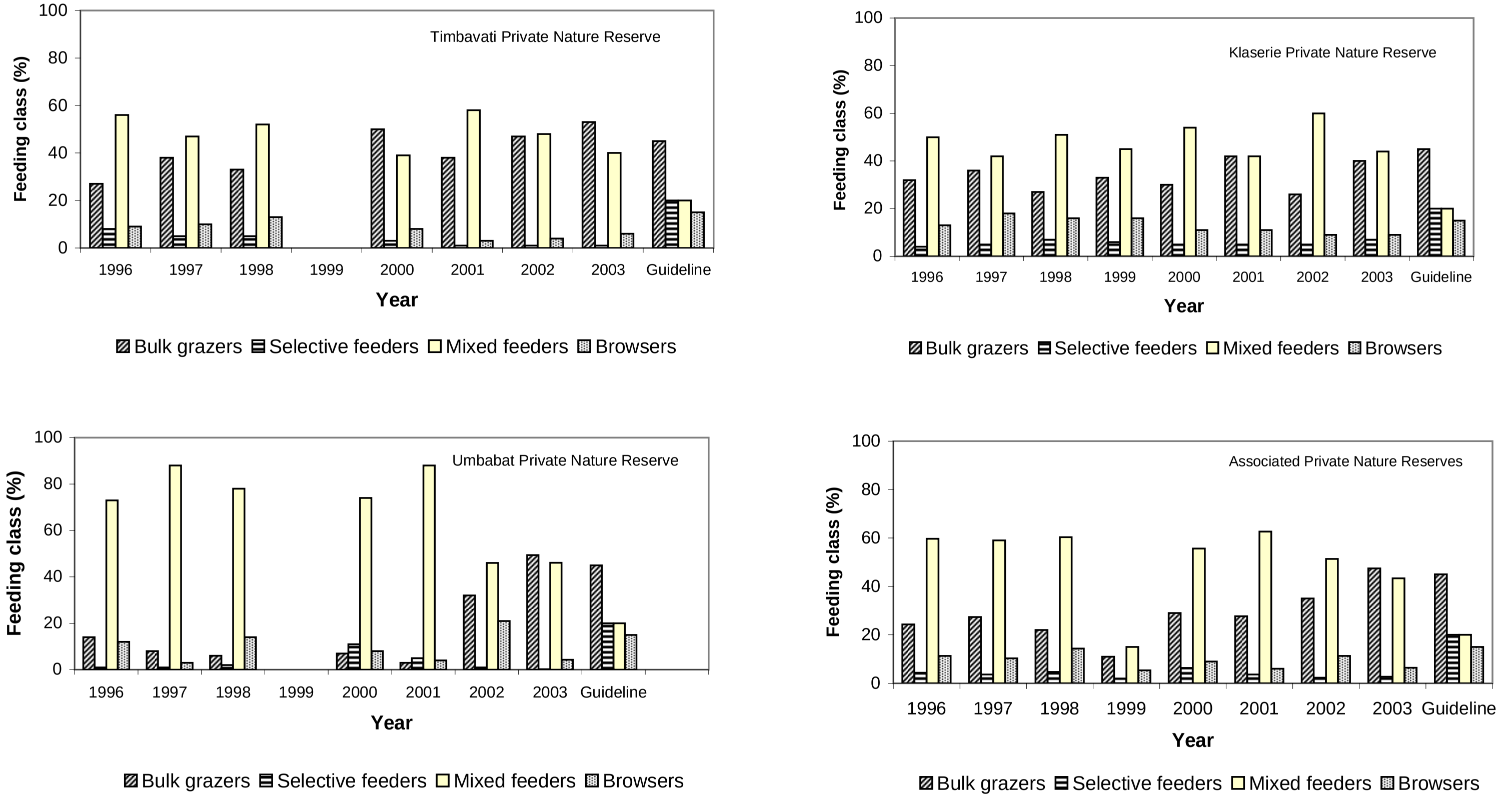

**Figure 4.9:** The feeding class proportions for the prey biomass in the Timbavati, Klaserie and the Umbabat Private Nature Reserves, and combined for the Associated Private Nature Reserves from 1996 to 2003. The calculated proportions were compared with the guideline proportions of Collinson & Goodman (1982). For the Timbavati and the Umbabat Private Nature Reserves no data were available in 1999. Source of data: Peel (2003).

to 40% (Bothma 2002).

The sex ratio of the adult animals was significantly biased towards females in all the prey populations of the Timbavati ($\chi^2$ = 344.811; df = 7; $P \leq 0.05$), Klaserie ($\chi^2$ = 148.458; df = 7; $P \leq 0.05$), Umbabat ($\chi^2$ = 188.249; df = 7; $P \leq 0.05$) and the Associated Private Nature Reserves ($\chi^2$ = 852.078; df = 7; $P \leq 0.05$) (Fig. 4.6). This skewed sex ratio was as was expected, based on that of most ungulate populations in the African savannas (Bothma 2002).

Greater numbers of prey were observed in the wet season than the dry season for all types of lion prey in the Timbavati ($\chi^2$ = 17.016; df = 7; $P \leq 0.05$), Klaserie ($\chi^2$ = 14.085; df = 7; $P \leq 0.05$) and the Associated Private Nature Reserves ($\chi^2$ = 423.432; df = 7; $P \leq 0.05$) (Fig. 4.7). In the Umbabat Private Nature Reserve, however, a greater number of prey animals were observed in the dry season than the wet season for all types of lion prey ($\chi^2$ = 56.454; df = 7; $P \leq 0.05$), which was different from what normally occurs in the African savannas where prey abundance is usually greater in the wet season than the dry season (Peel 2003).

### Vegetation dynamics

The vegetation dynamics from 1996 to 2002 in the Associated Private Nature Reserves appear in Fig. 4.10. The distance between neighbouring perennial grass plants in the study area decreased as annual rainfall increased. The distance between neighbouring perennial grass plants conversely increased from 1999 to 2002, indicating that perennial grass cover decreased for that period.

A significant relationship existed between the grass standing crop and the fluctuation in annual rainfall ($R^2$ = 0.695; $P \leq 0.05$). An increase in the grass standing crop was

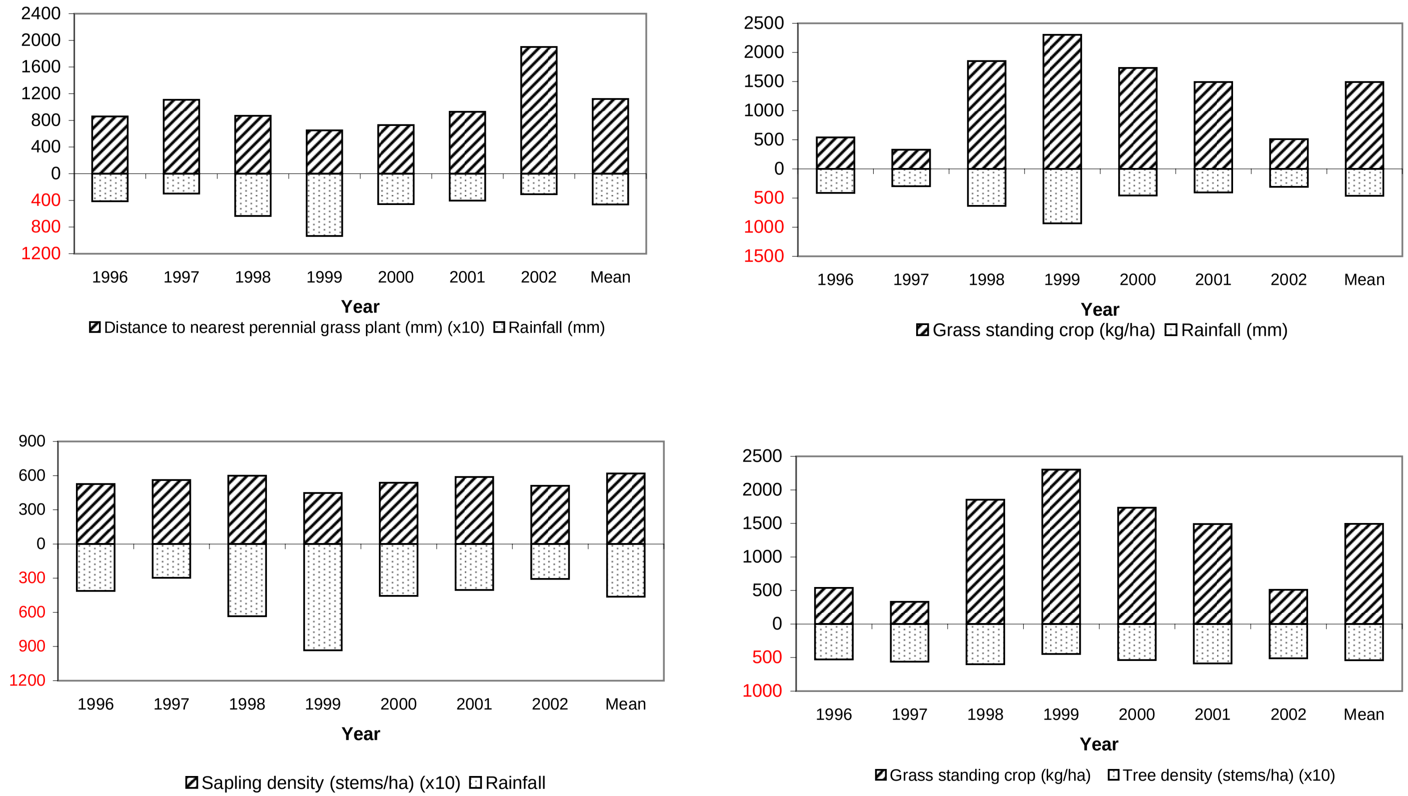

**Figure 4.10:** The vegetation dynamics in the Associated Private Nature Reserves from 1996 to 2002, based on the ecological monitoring reports of Peel (2003). The perennial grass cover, grass standing crop and sapling density were determined annually relative to fluctuations in rainfall. The grass standing crop was also compared to the tree density in the study area between years.

correlated with an increase in annual rainfall. From 2000 to 2002 annual rainfall decreased below the long-term mean and the grass standing crop decreased accordingly to below its long-term mean. The grass standing crop in the study area decreased from 1999 to 2002 (Fig. 4.10).

The sapling density from 1996 to 2002 did not vary significantly from the long-term mean and was therefore considered stable ($\chi^2$ = 8.543; df = 6; $P > 0.05$). The annual rainfall did, however, fluctuate significantly from 1996 to 2002 ($\chi^2$ = 17426.69; df = 6; $P \leq 0.05$) and there was no correlation between sapling density and annual rainfall ($R^2$ = 0.353; $P > 0.05$).

When the annual tree density in the Associated Private Nature Reserves was compared with the annual standing crop of grass in that area, there was no correlation ($R^2$ = 0.276 ; $P > 0.05$). The tree density changed from a maximum of 599 stems/ha in 1998 to a minimum of 447 stems/ha in 1999, whereas the grass standing crop fluctuated from 331 kg/ha in 1997 to 2302 kg/ha in 1999.

**Ungulate-habitat dynamics**

A total of 15 209 observations was used to determine the habitat selection of the eight most abundant types of lion prey in the Associated Private Nature Reserves (Table 4.5). The most frequently utilised vegetation types by all eight types of lion prey were the *Combretum apiculatum* Bushveld on shallow soils (20.2%) and the *Acacia nigrescens* – *Combretum apiculatum* Tall Woodland on deep soils (21.3%). These were open woodland vegetation types that had a grass cover from 42 to 75%, a low percentage of tree canopy cover (2 to 20%), and rock cover that varied from 0 to 40% (Van Rooyen 2005). The chi-square analyses showed a significant difference in habitat use as opposed to its availability for the blue wildebeest ($\chi^2$ = 365.844; df = 11; $P \leq 0.05$), the buffalo ($\chi^2$ =

1785.478; df = 11; $P \leq 0.05$), Burchell's zebra ($\chi^2$ = 164.833; df = 11; $P \leq 0.05$), giraffe ($\chi^2$ = 205.820; df = 11; $P \leq 0.05$), impala ($\chi^2$ = 3871.010; df = 11; $P \leq 0.05$), greater kudu ($\chi^2$ = 90.481; df = 11; $P \leq 0.05$), warthog ($\chi^2$ = 53.641; df = 11; $P \leq 0.05$), and the waterbuck ($\chi^2$ = 336.913; df = 11; $P \leq 0.05$) in the combined Associated Private Nature Reserves.

The preferred vegetation types of the eight most abundant types of lion prey in the Associated Private Nature Reserves appear in Table 4.5. The other vegetation types were either not used by the ungulates being studied or they were utilised in proportion to their availability.

The blue wildebeest showed a preference of use for the *Combretum apiculatum – Sclerocarya birrea* Open Woodland (15.3% of all observations) and the *Acacia nigrescens – Combretum hereroense* Open Woodland on gabbro (28.8%). The percentage utilization of these two vegetation types by the blue wildebeest was significantly greater than their availability (5.6 and 3.8% respectively). Of the available habitat 44.1% was preferred, 42.6% was not being used and 13.3% was utilised in proportion to its availability by the blue wildebeest.

The buffalo preferred the *Acacia nigrescens – Combretum apiculatum* Tall Woodland on deep soils (31.0% of all observations), the *Terminalia sericea* Woodland on sandy soils (21.0%), *Combretum apiculatum – Sclerocarya birrea* Open Woodland (15.5%), and the *Acacia tortilis – Euclea divinorum* Lowland Woodland (12.3%). The other vegetation types (20.2% of all observations) were utilised significantly less by the buffalo than was expected by their availability.

For the Burchell's zebra the preferred vegetation types were the *Acacia nigrescens – Combretum apiculatum* Tall Woodland on deep soils (26.6% of all observations) and

Riparian Woodland (18.9%). The percentage utilization of Riparian Woodland (18.8% of all observations) by Burchell's zebra was significantly greater than its availability (9.7% of all observations) (Table 4.5).

The giraffe in the Associated Private Nature Reserves utilised only five of the 12 available vegetation types (52.7% of the total surface area). The preferred vegetation types were the *Acacia nigrescens – Combretum apiculatum* Tall Woodland on deep soils (26.6% of all observations) and the *Acacia nigrescens – Combretum hereroense* Open Woodland on gabbro (14.6%). The percentage utilization of the latter (14.6% of all observations) by the giraffe was significantly greater than its availability (3.8% of the total surface area).

This study showed that the impala utilised only four of the 12 available vegetation types (42.5% of the total surface area). A preference of use was shown for the *Combretum apiculatum* Bushveld on shallow soils (25.9% of all observations), *Acacia tortilis – Euclea divinorum* Lowland Woodland (12.0%) and the Riparian Woodland (19.8%).

The greater kudu in the Associated Private Nature Reserves utilised nine of the 12 available vegetation types (88.5% of the total surface area). As was expected by their habitat preferences in other areas of southern Africa (Skinner & Smithers 1990), the Riparian Woodland was preferred, the *Combretum apiculatum – Terminalia prunioides* Rugged Veld was utlilized in proportion to its availability, and the *Acacia nigrescens – Combretum hereroense* Open Woodland on gabbro was not utilised. The kudu preferred the Riparian Woodland (20.6% of all observations) although this vegetation type was only 9.7% of the available habitat.

The warthog utilised eight of the 12 available vegetation types (81.5% of the total surface area). A preference of use was shown by the warthog for Riparian Woodland (18.8% of all observations), although this vegetation type was only 9.7% of the available habitat.

The waterbuck in the Associated Private Nature Reserves utilised four of the 12 available vegetation types (41.2% of the total surface area). The preferred vegetation type of the waterbuck was Riparian Woodland (51.0% of all observations), although this vegetation type was only 9.7% of the available habitat.

## DISCUSSION

The prey dynamics and habitat conditions in the Timbavati and Klaserie Private Nature Reserves have previously been investigated by Hirst (1969), Hirst (1975), Zambatis (1985), Kruger (1988), Weaver (1995) and Peel (2003), but the present study was the first attempt to describe the prey population dynamics of lions for the Associated Private Nature Reserves.

### Prey population dynamics

The enumeration of ungulates by using aerial counting methods is a commonly used tool in the management of wildlife in South Africa (Hensbergen, Berry & Juritz 1996).

The main objective of aerial counting is generally the determination of population trends in ungulates rather than their absolute abundance (Eiselen 1994). Although aerial counts are usually substantial underestimates of the true size of the population (Caughley 1974; Melton 1978; Eltringham 1979; Bothma *et al.* 1990), a reliable estimate may be obtained by maximizing the precision of the annual counts (Reilly 2002).

The most important factor that determines the precision of an aerial count is consistency in the type of aircraft, pilot and observers, flying speed, climatic and environmental conditions (Bothma 2002). The lack of consistency in the type of aircraft used and the infrequency of the aerial surveys in the Associated Private Nature Reserves from 1980 to 2003 has made the interpretation of the results difficult and inconclusive. The aircraft, pilot and observers were not consistent during the counting period, and the distance sampling method (Buckland *et al.* 1993; Thomas *et al.* 2002; Kruger, Reilly & Whyte in prep.) was applied in the survey for 2000, 2001 and 2002. The distance sampling method is not compatible with standard counting methods, and is not suitable for all ungulate species (Reilly 2004). The distribution patterns of blue wildebeest, warthog and waterbuck in the combined Associated Private Nature Reserves are not compatible with the distance sampling method. Blue wildebeest occur in large heterogeneous concentrations that violate the sampling assumption of homogeneity. This leads to over- or underestimation, with commensurate lack of precision (Kruger, Reilly & Whyte in prep.). Because there were only 170 blue wildebeest in the Associated Private Nature Reserves at the time of this study (Peel 2003), reliable and consistent counts are required to monitor annual changes in the population.

The aerial counting method for the Associated Private Nature Reserves was not standardised until 2003. The population trends obtained for the respective private nature reserves were, therefore, not directly comparable. The broad population trends of the ungulates in the Timbavati, Klaserie and the Umbabat Private Nature Reserves were, however, similar (Peel 2003). The populations of all the most abundant types of lion prey, except the buffalo, decreased from 1991 to 2003. These population decreases were a consequence of starvation mortalities during the drought in 1981, 1991 and 1997, and the regulation of the already-low prey populations by lion predation (Kruger 1988; Weaver 1995) (Chapter 8). Secondary factors that had an effect on prey population trends were the removal of the boundary fences between the Associated Private Nature Reserves and the Kruger National Park in 1993, and the change in the aerial counting method from 1992 to 1996. The possible influence of these factors on the ungulate populations in the study area was investigated in Chapter 8.

*Total biomass and prey biomass*

Even in large unfenced areas, such as the Kruger National Park of 20 000 km$^2$, there has to be a balance between the total biomass of animals present and the available habitat. This is particularly true for areas that were previously fenced, such as the Associated Private Nature Reserves (Weaver 1995). The fluctuation in prey biomass between years gives an indication of the impact of predation on a particular prey base.

The total biomass of animals in the Associated Private Nature Reserves from 2001 to 2003 was greater than the maximum recommended biomass that could be sustained in that area (Coe *et al.* 1976; Peel 2003). This was so because of the increase in the number of elephants, buffaloes and white rhinoceroses that moved into the Associated Private Nature Reserves when its boundary fence with the Kruger National Park was removed in 1993. To avoid habitat degradation and the competitive exclusion of other ungulate species, the number of elephants, buffaloes and white rhinoceroses in the Associated Private Nature Reserves should be below the ecological carrying capacity of that area. The inclusion of the Balule and Olifants River Private Nature Reserves, a combined area of 30 000 ha, into the open system of the Associated Private Nature Reserves in 2005, will increase the ecological carrying capacity of the study area and provide more habitat for the existing populations of megaherbivores. Moreover, the rotation of the availability of water in the large number of artificial waterholes in the Associated Private Nature Reserves may cause less movement of elephant and buffalo from the Kruger National Park to these private nature reserves.

Although the prey biomass in the Timbavati, Klaserie and Umbabat Private Nature Reserves was below the minimum expected biomass during the period from 1991 to 2000 (Peel 2003), the prey biomass in the Associated Private Nature Reserves from 2001 to 2003 was greater than the minimum expected guideline. Therefore the prey biomass in the Associated Private Nature Reserves has increased during the period of study. The prey biomass in the Associated Private Nature Reserves is affected by lion predation, climatic changes and habitat factors (Weaver 1995). The relationship between lion predation, rainfall and prey population trends was investigated in Chapter 8.

### *Feeding class proportions*

An imbalance in the proportion of animals in the four feeding classes may cause the competitive exclusion of an animal species by another and eventual habitat degradation (Collinson & Goodman 1982). In the Associated Private Nature Reserves, the proportion of bulk grazers and mixed feeders was greater than the recommended guideline of Collinson & Goodman (1982), and the proportion of selective feeders and browsers was lower than that guideline. The proportion of bulk grazers in the study area has increased steadily since the removal of the boundary fence with the Kruger National Park in 1993. Buffalo did not occur in the study area before the removal of the boundary fence, and a large number of elephants and white rhinoceroses has moved into the area from the Kruger National Park. These animals are water dependent (Skinner & Smithers 1990), and the large number of artificial waterholes in the Associated Private Nature Reserves probably assisted them in moving into this area from the Kruger National Park (Weaver 1995).

The proportion of selective feeders and browsers in the Associated Private Nature Reserves has decreased over time as a consequence of starvation mortalities after a series of droughts in 1981, 1991 and 1997 (Kruger 1988) (Chapter 8). The blue wildebeest and warthog populations, in particular, both decreased by 94% in 1981. The habitat in the Associated Private Nature Reserves changed from a formerly open savanna with dense vegetation along the rivercourses, to a current dense woodland vegetation (Porter 1970; Weaver 1995). This woodland vegetation was more suitable to the habitat preferences of the impala, a mixed feeder, and less suitable for plain's herbivores such as the blue wildebeest and Burchell's zebra (Kruger 1988). The proportion of impala therefore increased and that of blue wildebeest decreased. Various lion studies in African savannas have shown that the blue wildebeest is a preferred prey for lions (Schaller 1972; Smuts 1982; Mills & Shenk 1992; Sunquist & Sunquist 2002). The impact of lion predation on the prey populations in the Associated Private Nature Reserves was studied in Chapter 7.

### *Age structure, sex ratio and seasonal abundance*

A knowledge of the age and sex structure in a prey population is important to understand the reproductive potential of that population, and therefore the potential for population growth (Weaver 1995). In most ungulate populations, the population structure should be biased towards adult females and 30 to 40% of the population should consist of young animals to ensure productivity and therefore population growth (Kruger 1988; Bothma 2002). In natural systems where predators are present, most prey animals could have a mortality rate of nearly 50% in their first year (Bothma 2002). However, animal mortalities as a result of a shortage of food in critical times remain the most important limiting factor for ungulates (Pienaar 1969; Kruuk 1972; Sinclair *et al.* 1985; Kruger 1988).

The age and sex structure of the ungulate populations in the Associated Private Nature Reserves was consistent with that of ungulate populations elsewhere in African savannas. The proportion of juveniles relative to adults in the populations of the giraffe, Burchell's zebra and the blue wildebeest was, however, lower than the recommended 30 to 40%, causing a reduced productivity in these populations and hence creating a decreasing population trend. Either insufficient progeny were being produced or there was a high mortality rate among the young because of poor habitat conditions or shortages of food (Kruger 1988; Bothma 2002). Preliminary results from faecal analyses of the various prey populations in the study area also suggested the possibility of a dietary deficiency in phosphorus and nitrogen that may lead to low reproductive rates (Peel 2003).

Primary plant production is greater in the wet season than the dry season. Therefore the abundance of prey will be greater in the wet season than the dry season (Peel 2003). This is particularly true for ungulates, such as the blue wildebeest, that move seasonally to areas of better grazing in response to the occurrence of rainfall (Mills & Shenk 1992). Many African ungulates give birth to their offspring in the wet season when habitat conditions are more favourable, increasing the abundance of prey animals at that time (Schaller 1972). This was evident for the prey abundance in the Timbavati, Klaserie and the Associated Private Nature Reserves. In the Umbabat Private Nature Reserve, however, the dense mopane (*Colophospermum mopane*) vegetation made the observation of prey animals in the wet season difficult, and prey abundance therefore appeared to be greater than in the dry season.

### Vegetation dynamics

Vegetation composition is rarely constant, and changes in habitat characteristics may have dramatic effects on habitat selection by animals (Schooley 1994). The vegetation composition in the Associated Private Nature Reserves, consequently, has changed from an open savanna to a dense woodland as a result of herbivore impact, artificial water provision and a lack of systematic burning (Porter 1970; Weaver 1995).

The vegetation change in the Associated Private Nature Reserves from 1996 to 2002 was consistent with earlier successive vegetation studies that were done in that area by Hirst (1969), Porter (1970), Kruger (1988), and Weaver (1995). The grass standing crop fluctuated annually in synchrony with changes in rainfall, whereas the tree density remained constant from 1996 to 2002. The observed decrease in the available grazing habitat was of concern because of the continual decrease in the number of selective grazers in the Associated Private Nature Reserves (Hirst 1969; Kruger 1988; Weaver 1995; Peel 2003). The woody layer has a greater resilience to climatic fluctuations than the herbaceous layer and it therefore has a competitive advantage when annual rainfall is below the long-term mean (Weaver 1995; Peel 2003). The expected dry cycle in the area of the Associated Private Nature Reserves (Peel 2003) suggests that there is an imperative for the reserve management to protect the available grazing habitats. This may be achieved by mechanical vegetation removal techniques, systematic burning, and by restricting herbivore access to areas being improved by rotating water availability in artificial waterholes (Weaver 1995).

### Ungulate-habitat dynamics

The habitat preferences of ungulates is influenced by the availability of water and food of necessity, but the physical structure of the habitat is the decisive factor if water and food are available in more than one place (Joubert 1996). The eight types of lion prey that were studied in the Associated Private Nature Reserves also showed particular habitat preferences that were related to their feeding preferences.

Because the blue wildebeest, Burchell’s zebra, buffalo, waterbuck, warthog and impala preferred open woodland habitat types and feed predominately on grass (Bothma, Van Rooyen & Du Toit 1996), it was not surprising that these animals utilised the *Combretum apiculatum* Bushveld on shallow soils and the *Acacia nigrescens – Combretum apiculatum* Tall Woodland on deep soils. The giraffe and greater kudu are browsers and their habitat requirements were met by the above vegetation types. The giraffe preferred open bushveld, and the greater kudu preferred bushveld savanna with broken and rocky terrain (Bothma, Van Rooyen & Du Toit 1996). Specific habitat preferences included the following:

### *Blue wildebeest*

Blue wildebeest are generally classed as selective grazers that prefer grasslands and open bushveld, and are not usually found in dense bushveld (Bothma, Van Rooyen & Du Toit 1996; Van Rooyen, Bredenkamp & Theron 1996). This was confirmed by the present study. The blue wildebeest in the Associated Private Nature Reserves preferred open woodland vegetation. Because 42.6% of the available habitat in the study area was not used by the blue wildebeest, this prey animal appeared to have specific habitat preferences. Moreover, the proportion of preferred habitat that was available (9.4% of the total surface area) was considerably lower than the proportion that was being utilised (44.1% of all observations). It therefore appeared that the habitat requirements of the blue wildebeest in the Associated Private Nature Reserves were not being met. This concurs with earlier studies that were done in the Timbavati and Klaserie Private Nature Reserves by Hirst (1975), Kruger (1988) and Weaver (1995). The change in the vegetation dynamics of the Associated Private Nature Reserves over time is therefore the most likely reason for the continual decrease in the blue wildebeest population in this area. As suggested by Weaver (1995), the proportion of suitable grazing habitat in the Associated Private Nature Reserves may be increased by mechanical vegetation removal techniques, systematic burning, and by restricting herbivore access to those areas being improved by rotating water availability in artificial waterholes.

### *Buffalo*

Buffalo are bulk grazers that prefer open bushveld, do not usually utilize grasslands and may be found in dense bushveld (Van Rooyen, Bredenkamp & Theron 1996). The buffalo in the Associated Private Nature Reserves showed distinct habitat preferences in the present study. Four of the available vegetation types (79.8% of the total surface area) were preferred and the other eight vegetation types (20.2%) were not utilised. The buffalo in the study area did, however, show a broad habitat tolerance by utilizing habitat varying from open bushveld to dense riverine vegetation. However, there was a difference in the habitat preference of the buffalo herds when compared with the bulls, with the herds preferring the open bushveld vegetation types and the bulls the dense woodland vegetation in the riverine areas (Turner pers. obs.).

The buffalo population in the Associated Private Nature Reserves has continued to increase since the removal of the boundary fences between the Associated Private Nature Reserves and the Kruger National Park in 1993. Buffalo are water-dependent (Skinner & Smithers 1990) and large numbers of these animals therefore moved from the Kruger National Park into the Associated Private Nature Reserves, where there is an abundance of artificial waterholes (Weaver 1995).

*Burchell's zebra*

The preferred habitat of the Burchell's zebra is open bushveld, savanna and grassland, although they may be found in dense bushveld (Van Rooyen, Bredenkamp & Theron 1996). In the combined Associated Private Nature Reserves only 9.4% of the available surface area of habitat was open woodland vegetation. The Burchell's zebra there preferred the *Acacia nigrescens – Combretum apiculatum* Tall Woodland on deep soils and Riparian Woodland because these vegetation types covered 29.3% of the available surface area of habitat. The present study agreed with that of Weaver (1995), that the continual decrease in the Burchell's zebra population in this area is most likely because of the change in habitat over time and that the proportion of suitable grazing habitat will have to be increased to provide more habitat for these plains' animals.

*Giraffe*

Giraffe occur in a wide variety of open bushveld and savanna associations, but may be found in dense bushveld (Skinner & Smithers 1990; Van Rooyen, Bredenkamp & Theron 1996). The habitat preferences of the giraffe in the Associated Private Nature Reserves concurred with this concept. The dense woodland and shrubveld vegetation types were not utilised and the open woodland vegetation types were preferred. The proportion of *Acacia nigrescens – Combretum hereroense* Open Woodland available was, however, significantly less than the proportion in which it was utilised by the giraffe. This suggests that the habitat preferences of the giraffe in the Associated Private Nature Reserves are not being met. The giraffe population in this area continued to decrease from 2001 to 2003 because of the change in habitat over time. As with the Burchell's zebra and blue wildebeest in the Associated Private Nature Reserves, the proportion of open woodland vegetation will have to be increased to provide more habitat for the giraffe.

### *Impala*

Impala are mixed feeders that prefer open bushveld vegetation (Van Rooyen, Bredenkamp & Theron 1996). While impala generally do not utilize open grassland they occur on the ecotone between open bushveld and woodland and will graze on open grassland with a flush of green grass (Skinner & Smithers 1990). In the present study, the impala showed distinct habitat preferences by utilizing only four of the 12 available vegetation types and 42.5% of the available surface area of habitat. They preferred the bushveld, lowland woodland and riparian woodland vegetation, but did not utilize the open woodland vegetation types. This was not expected because the impala is a mixed feeder that can feed on both grass and browse. The impala population in the Associated Private Nature Reserves has, however, continued to increase during this study suggesting that its habitat requirements are being met or that the change in habitat over time is favouring them.

### *Greater kudu*

The greater kudu prefers savanna woodland vegetation and does not occur in deserts, forests or in open grasslands. It is partial to areas of broken, rocky terrain with a cover of woodland and a nearby water supply (Skinner & Smither 1990). It was found in the present study that the greater kudu had a broad habitat preference by utilizing nine of the 12 available vegetation types and 88.5% of the available surface area of habitat. The habitat requirements of the greater kudu in the Associate Private Nature Reserves therefore appeared to have been met or the current habitat favours them.

*Warthog*

Warthog occur in open bushveld, grassland, vleis and floodplains with short grass. Although the warthog in the present study were observed in eight of the 12 available vegetation types, their preference was for the Riparian Woodland. Of the available vegetation types, seven were being utilised in proportion to their availability suggesting that sufficient suitable habitat is available to the warthog in the Associated Private Nature Reserves. The continued decrease in the warthog population during this study is therefore not likely to be related to habitat availability. The population decrease was, however, more probably a consequence of starvation mortalities during the droughts in 1981, 1991 and 1997 (Kruger 1988) (Chapter 8). It is therefore possible that the warthog population in the Associated Private Nature Reserves may continue to decrease because another drought cycle is expected (Peel 2003).

*Waterbuck*

The preferred habitat of the waterbuck is open bushveld, vleis and floodplains, and grassland (Van Rooyen, Bredenkamp & Theron 1996). Throughout their range waterbuck are associated with water, being dependent on it (Skinner & Smithers 1990). The waterbuck in the Associated Private Nature Reserves in the present study occurred in only four of the 12 available vegetation types. As was expected, a preference was shown for the Riparian Woodland vegetation in the riverine areas. The proportion of this vegetation type utilised (51% of all observations) by the waterbuck, however, was significantly greater than its availability (9.7% of the available surface area of habitat). This confirmed the preference shown by waterbuck for vegetation associated with water. An unfavourable change in habitat over time in the Associated Private Nature Reserves is most likely contributing to the continual decline in the waterbuck population in this area.

## CONCLUSIONS

An understanding of prey population dynamics and the relationship between the prey animals and their habitat is the foundation for the study of predator-prey relationships. The present study was the first attempt to describe the prey dynamics in the Associated Private Nature Reserves.

The aerial counting methods used in the Timbavati, Klaserie and Umbabat from 1983 to 2003 were not consistent, making the interpretation of prey population trends difficult. The prey populations in the Associated Private Nature Reserves, except for the buffalo population, showed a decreasing trend for the counting period. However, more reliable and consistent counts are required for monitoring population trends in the future and for making responsible management decisions.

The age structure, sex ratio and the seasonal abundance of the prey populations in the Associated Private Nature Reserves was as expected. For all eight types of lion prey the proportion of adult females was greater than adult males. In most ungulate populations, 30 to 40% of the population consisted of young animals and will ensure productivity and population growth (Bothma 2002). However, the proportion of juveniles in the populations of the giraffe, Burchell’s zebra and the blue wildebeest was lower than recommended for ungulate populations by Collinson & Goodman (1986) and Peel (2003). This may reflect the fact that the populations of giraffe, Burchell's zebra and blue wildebeest in the Associated Private Nature Reserves are decreasing. The abundance of prey in the study area was greater in the wet season than the dry season, as was expected.

The prey biomass in the Associated Private Nature Reserves from 2001 to 2003 was lower than the mean recommended guideline for that area, although the total biomass of animals in the Associated Private Nature Reserves from 2001 to 2003 was greater than the maximum expected biomass (ecological carrying capacity) for that area (Coe *et al.* 1976). When compared to the recommended proportions for the four feeding classes (Collinson & Goodman 1982), the proportion of bulk grazers and mixed feeders was greater than expected in natural systems, and the proportion of selective feeders and browsers was lower than it. An imbalance in the proportion of animals in the four feeding classes may cause the competitive exclusion of certain prey species by others and eventually lead to habitat degradation (Collinson & Goodman 1982).

The habitat changes in the Associated Private Nature Reserves from 1996 to 2002 were similar to those observed in earlier vegetation studies that were done in that area (Hirst 1969; Porter 1970; Kruger 1988; Weaver 1995). The expected dry cycle in the area of the Associated Private Nature Reserves (Peel 2003) suggested that the reserve management may in future have to protect the available grazing habitats. This may be achieved by mechanical vegetation removal techniques, systematic burning, and by restricting herbivore access to those areas being improved by rotating water availability in artificial waterholes (Weaver 1995).

The habitat preferences of the eight most abundant types of lion prey were similar to the preferences found for these prey types in other areas of southern Africa. For the blue wildebeest, Burchell's zebra, giraffe and waterbuck in the Associated Private Nature

Reserves, however, a current trend away from their suitable habitat appeared to be contributing to a continual decrease in the size of their populations.

## CHAPTER 5

# Lion population dynamics in the Associated Private Nature Reserves, Limpopo province, South Africa

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## ABSTRACT

The population dynamics of the lions *Panthera leo* in the Associated Private Nature Reserves were investigated by using the call-in counting technique. Two surveys were done by using 64 call-in stations, in November 2000 and November 2001. The lion population in the Associated Private Nature Reserves was found to be stable from November 2000 to November 2001. The total population size in November 2000 and November 2001 was 156 lions and 148 lions, respectively. These population estimates were similar to the one of 172 lions determined in an independent study by Funston (2004). The mean number of lion prides was 13, the mean pride size was 10 lions and the mean lion density was 8.0 lions per 100 km$^2$. When compared with lions in other African savanna woodland habitats, the lions in the Associated Private Nature Reserves were found to be at intermediate densities and pride sizes. The age and sex structure of the adult lions in the study area were consistent with that of other areas in Africa, where adults contribute >50% to the population and the number of adult females outnumber adult males. In contrast, however, a greater proportion of the subadults and cubs in the Associated Private Nature Reserves were males than females. This skewed sex ratio may be due to the male-biased litters that result from trophy hunting of lions in the Associated Private Nature Reserves.

*Key words:* lion, *Panthera leo*, Felidae, population size, density, age structure, sex ratio

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## INTRODUCTION

A reliable estimate of the number of lions *Panthera leo* in an area is fundamental to lion conservation and management. In areas where lions are harvested or hunted, there is a risk of overexploitation. Therefore a prerequisite to managing that risk is an accurate estimate of the size of the lion population in the prescribed area (Loveridge, Lynam & Macdonald 2001). An estimate of the number of lions in an area is also necessary when investigating the impact of lion predation on its prey (Mills & Shenk 1992).

Large carnivores are difficult to count because of their secretive nature, primarily nocturnal habit, and low densities (Gros, Kelly & Caro 1996). Counting techniques that are usually used on large herbivores are not appropriate for large carnivores (Mills 1997). Accordingly, methods have been developed specifically for estimating large carnivore numbers. The criteria that were used to select an appropriate counting technique for the present study were: feasibility, accuracy, expense and the technical requirements for the particular circumstances (Gittleman 1989).

The size of the lion population in the Associated Private Nature Reserves has not been reliably estimated before the present study. While Hirst (1969) did a predator-prey study in the Timbavati Private Nature Reserve he did not estimate the number of lions present. The mass capture technique of Smuts, Whyte & Dearlove (1977) was used to estimate the number of lions in the Klaserie Private Nature Reserve in 1978 and 1980 (P.C. Viljoen unpubl. data). These surveys were unsuccessful with seven lions being marked from the 20 calling stations (35%) in the first study, and 11 lions from the 56 calling stations (20%) in the second study. This success rate was lower than the 61% capture success rate of Smuts *et al.* (1977) for lions in the Kruger National Park. In his report to the management committee of the Klaserie Private Nature Reserve, Viljoen gave no reason for the low success rate of his lion survey. The most probable reason is that the lions became habituated to the tape-recorded sounds that were broadcast during the 10 hour duration of calling at each call-in station and failed to respond.

The current paper is a first attempt at investigating the lion population dynamics in the entire Associated Private Nature Reserves. Lion pride size varies from area to area according to the availability of prey, and it is correlated with the lean-season abundance of prey (Van Orsdol *et al.* 1985). Because lion density varies in accordance with the variation in pride size, lion density is correlated with the availability of prey and will also vary from area to area (Van Orsdol *et al.* 1985). Being an open system with the Kruger National Park, it was expected that the lion population dynamics in the Associated Private Nature Reserves would be similar to that of the lions in the Kruger National Park.

## STUDY AREA

The Associated Private Nature Reserves consists of adjacent and privately-owned reserves in the Limpopo province, South Africa, between latitudes 24° 03' S and 24° 34' S and longitudes 31° 03' E and 31° 31' E. The Associated Private Nature Reserves (1530 km²) were formed in June 1993 when the internal fences between the Klaserie Private Nature Reserve (628 km²), the Timbavati Private Nature Reserve (650 km²), and the Umbabat Private Nature Reserve (250 km²) were removed, as was the boundary fence on their east with the Kruger National Park. This created an open ecological system between the Associated Private Nature Reserves and the Kruger National Park, allowing for local and seasonal movements of animals.

The topography in the Associated Private Nature Reserves consists of undulating open hills, lowlands and mountains with moderate to high relief. The altitude of the area varies from 300 to 543 m above sea level (N. van Rooyen unpubl. report). The Associated Private Nature Reserves are situated in a summer rainfall area of South Africa (Weather Bureau 1998). The long-term mean annual rainfall for the Klaserie, Timbavati and Umbabat Private Nature Reserves is 464mm, 585mm and 452mm respectively (Computing Centre for Water Research). Temperatures tend to be high during the day, but they drop at night by 10 to 15° C. The mean daily minimum temperature for the Associated Private Nature Reserves in January is 20.1° C and for June 8.9° C. The hottest month is January with a mean daily maximum temperature of 31.7° C. The coldest month is June with a mean daily maximum temperature of 24.7° C (Weather Bureau 1998).

The study area was in the Savanna Biome, specifically the Arid Lowveld as described by Acocks (1988). The vegetation in the Associated Private Nature Reserves may be classified as Mopane Bushveld in the north, Mixed Lowveld Bushveld in the central and western areas, and Sweet Lowveld Bushveld in the south and east (Low & Rebelo 1996; Van Rooyen & Bredenkamp 1998). *Combretum apiculatum*, *C. zeyheri* and *C. collinum, Sclerocarya birrea* and *Terminalia sericea* form important components of the vegetation on granite. *Acacia nigrescens* and *Sclerocarya birrea* are the dominant species on gabbro.

## METHODS

The modified mass capture technique (Smuts *et al.* 1977; Mills 1985; Mills & Gorman 1997; Mills, Juritz & Zucchini 2001) was tested in the Klaserie Private Nature Reserve in August 1999 as a precursor to the present study (Rowles 1999). Although geographical closure is a fundamental assumption of population estimation (Otis *et al.* 1978), the modified mass capture technique was used by Ogutu & Dublin (1998) to effectively estimate the lion population dynamics in the open system of the Maasai Mara National

Reserve in south-west Kenya. This method was found to be effective for the Klaserie Private Nature Reserve and the lion population in this 650 km$^2$ reserve was surveyed in 2.5 nights. Based on the successful use of this method in the Klaserie Private Nature Reserve (Rowles 1999), and on the advice of M.G.L. Mills (pers. comm.), this method was used in the present study to survey the lion population in the Associated Private Nature Reserves. However, the extensive size of the study area and constraints on the time and assistance of the reserve management staff necessitated the adaptation of the counting method. The lodge traversing area in the Timbavati Private Nature Reserve (280 km$^2$) was therefore not surveyed by using the call-in counting technique, because the field guides from the seven lodges traversed that area twice daily. These field guides were able to provide the necessary information on the pride composition and structure for the lions in their traversing area. The lion survey was therefore done in the remaining 1250 km$^2$ of land of the Associated Private Nature Reserves in November 2000 and 2001. Double counting of these lions was avoided by using the photographic identikit for the lions in the lodge traversing area that was provided by Tanda Tula Game Lodge. Because the lodge traversing area forms only 18% of the surface area of the Associated Private Nature Reserves, it was not expected that the different methodology that was used for this area would be of major consequence to the total lion count.

A separate lion survey was done for each of the private nature reserves that comprise the Associated Private Nature Reserves. Because the call-in counting technique is labour-intensive and time-consuming, and the aim of the present study was to determine the population dynamics for the total lion population in the entire Associated Private Nature Reserves, a single lion count was done in each of the Associated Private Nature Reserves in 2000 and 2001 respectively. For efficiency and accuracy two field teams were used, each team with its own vehicle and broadcasting equipment. The call-in stations were spaced 6 km apart, each having an animal response radius of 2.5 km (Rowles 1999). The field teams were therefore positioned so that their call-in stations were further apart than the calibrated response distance of 2.5 km (Rowles 1999) to avoid confusing the lions with more than one broadcast simultaneously (Mills 1985; Ogutu & Dublin 1998).

Since lions are predominantly active between sunset and sunrise (Kruger 1988; Mills & Biggs 1993; Funston 1999), broadcasting was started just before sunset. The lions were lured by using an amplifier and horn speaker to broadcast tape-recorded sounds of lions feeding and squabbling at a kill, combined with the sounds of spotted hyaenas *Crocuta crocuta* mobbing lions and the distress calls of a grey duiker *Sylvicapra grimmia*. An impala *Aepyceros melampus* carcass was first dragged behind a vehicle for 500 m along the road in either direction of the bait tree. The scent trail from the dragged carcass provided a further incentive for lions to visit the call site. The carcass was then hoisted into the tree, where it was tied down 2.5 m above the ground. As a safety precaution, the carcass was transported to the bait station site on a trailer and was separated from the observation vehicles during broadcasting. This was done because the lions may be attracted to the blood from the carcass and the observers would then be in danger of being attacked by the lions.

The horn speaker consisted of two speakers facing 180º from each other that were mounted on the roof of the vehicle, about 2 m above the ground. The broadcast was done for 10 minutes, followed by a 5-minute interval of silence whereafter the calls were repeated. After 30 minutes the speaker was rotated through 90º to ensure a total coverage of the entire area. A total of 60 minutes was therefore spent at each call-in station. It was recommended (M.G.L. Mills pers.comm.) that a dominant lion in each of the responding lion prides be temporarily marked with a coloured paint-ball mark fired from a compressed-air gun. Such marking of lions was necessary to prevent recounting the same lions. This approach was used for the survey that was done in November 2000, but it was abandoned in the second survey because the lions could be identified by the researcher and the field staff without marking them.

Pertinent data on the lions that showed up at the call-in stations were documented. These data included: the time, GPS location, number of animals, age and sex structure of the pride, resident or nomadic status (Ogutu & Dublin 2002) and any visible marks or scars that could be used for individual identification (Pennycuick & Rudnai 1970). By photographing both profiles of a lion, the unique cheek- or eye-spot patterns (facial markings where the whiskers emerge) can be used to identify individual lions. This technique was applied in the present study by combining the researcher's own photographic records of the lions in the Associated Private Nature Reserves with the identikit compiled by Tanda Tula Game Lodge and photographs provided by the reserve management staff and landowners. All the data were recorded on field sheets to ensure the consistency and accuracy of the collected data.

Using the lion count data the total number of lions that responded in November 2000 and 2001 was calculated with 95% confidence intervals. The pride composition of the lions in the Timbavati, Klaserie, Umbabat and the entire Associated Private Nature Reserves respectively were calculated separately by using the lion count data. At the time of this study there were, however, no resident lions in the Umbabat Private Nature Reserve. Lion density was estimated by equating the call-in census to one involving randomly located circular sample sites (call sites) with fixed 2.5 km radii (Ogutu & Dublin 1998). The sample lion density estimate was then calculated by dividing the total number of lions responding per survey by the sample area (1250 km$^2$). The standard error for this density estimate was calculated by using Jolly's (1969) method 1 for equal-sized sampling units. Lion density was expressed as the number of lions per 100 km$^2$.

The lions were assigned to age and sex categories that were based on those of Schaller (1972). The age and sex data for the lions in the Timbavati, Klaserie and the entire Associated Private Nature Reserves were compared for 2000 and 2001. These data were first compared within each of the reserves, and then between them. Without replicate lion counts no measure of variance could be calculated and the age and sex data could therefore not be compared statistically in all cases (Prof Groeneveld pers. comm.). The lion density values and pride sizes that were calculated for the lions in the study area could therefore not be compared statistically with those of lions in other African savannas (Prof Groeneveld pers. comm.). Several recent studies have described the failings of statistical hypothesis testing and the arbitrariness of *P*-values (Johnson 1999; Guthery *et al.* 2001; Eberhardt 2003). The distinction is made between statistical significance and biological significance and in doing so, more meaning alternatives are suggested, e.g. estimation and confidence intervals, analysis of variance or covariance, and regression (Anderson *et al*. 2001). In the present study, chi-squared analyses and other statistical tests were used when possible.

By using the repeated measures analysis of variance of the General Linear Modelling Program (SAS 2001), it was tested whether the mean pride size in 2000 differed from that in 2001, independent of the area in which the lions occurred. Repeated measures analyses were then used to compare the mean pride size in 2000 with that in 2001 for the Timbavati, Klaserie and the entire Associated Private Nature Reserves. Finally, the mean pride size in the Timbavati and Klaserie Private Nature Reserves were compared between areas, independent of the year of the counts.

Because lion pride size and lion density vary according to the availability of prey (Van Orsdol *et al.* 1985), the prey abundance in the Associated Private Nature Reserves was determined in the wet (October to March) and the dry season (April to September). The road strip censusing method (Norton-Griffiths 1978) that was used by Weaver (1995) to study herbivore vegetation use patterns in the Klaserie Private Nature Reserve was used for this part of the present study. A total of 17 survey routes were used to census the entire study area. Using a vegetation map of the study area (Zambatis 1983), the transect length of each survey route within each vegetation type was chosen to be proportional to the relative surface area of the respective vegetation types. All prey animals sighted within 100 m on either side of the road transect line were counted and a range finder was used to estimate the distance of animals from the line. The speed of travel was adjusted to the individual habitat type and respective season. Observation speeds during the wet season tended to be slower due to the poor condition of the roads. To minimise observer bias and to avoid double counting any individuals on the same day, the route direction was reversed for each alternate survey (Weaver 1995). Prey abundance was calculated as the number of large ungulates within each road transect. To compare prey abundance seasonally, the prey observations during road strip censuses were weighted by the number of animals observed in the wet (October to March) and the dry season (April to September) respectively. The prey abundance in the Associated Private Nature Reserves was then compared to that in other African savannas.

## RESULTS

A population of 156 lions (range: 137 - 186) was estimated for the Associated Private Nature Reserves in November 2000, including those lions that were found within the traversing area of the Timbavati lodges (Table 1). The total number of lions that responded in the November 2000 count was 126.7 ± 24.51 (95% c.l.) and the number of call-in stations to which lions responded was 35 (n = 64 call-in stations; 55%) (Figure 1). In November 2001 there was an estimated 148 lions (range: 120 – 173) in the study area, including the lions in the traversing area of the Timbavati lodges (Table 1). The total number of lions that responded in the 2001 lion count was 105 ± 25.9 (95% c.l.) and the

**Table 1**: *The actual number of lions counted in the Timbavati, Klaserie and the entire Associated Private Nature Reserves in 2000 and 2001, based on the results of the call-in counting technique (Mills, Juritz & Zucchini 2001) and data from the Timbavati lodges.There were no resident or nomadic lions observed in the Umbabat Private Nature Reserve.*

| **LION CLASS** | **ASSOCIATED PRIVATE NATURE RESERVES** | | | | **TIMBAVATI PRIVATE NATURE RESERVES** | | | | **KLASERIE PRIVATE NATURE RESERVES** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2000 | | 2001 | | 2000 | | 2001 | | 2000 | | 2001 | |
| | Number | % | Number | % | Number | % | Number | % | Number | % | Number | % |
| Territorial males | 25 | 16.0 | 17 | 11.5 | 19 | 19.2 | 14 | 14.9 | 6 | 10.5 | 3 | 5.6 |
| Nomadic males | 15 | 9.6 | 16 | 10.8 | 6 | 6.1 | 6 | 6.4 | 9 | 15.8 | 10 | 18.5 |
| Pride females | 50 | 32.1 | 51 | 34.5 | 36 | 36.4 | 36 | 38.3 | 14 | 24.6 | 15 | 27.8 |
| Subadult males | 22 | 14.1 | 19 | 12.8 | 11 | 11.1 | 8 | 8.5 | 11 | 19.3 | 11 | 20.4 |
| Subadult females | 12 | 7.7 | 16 | 10.8 | 5 | 5.1 | 6 | 6.4 | 7 | 12.3 | 10 | 18.5 |
| Male cubs | 18 | 11.5 | 11 | 7.4 | 14 | 14.1 | 11 | 11.7 | 4 | 7.0 | 0 | 0.0 |
| Female cubs | 11 | 7.1 | 6 | 4.1 | 8 | 8.1 | 6 | 6.4 | 3 | 5.3 | 0 | 0.0 |
| Unknown | 3 | 1.9 | 12 | 8.1 | 0 | 0.0 | 7 | 7.4 | 3 | 5.3 | 5 | 9.3 |
| Total | 156 | 100 | 148 | 100 | 99 | 100 | 94 | 100 | 57 | 100 | 54 | 100 |

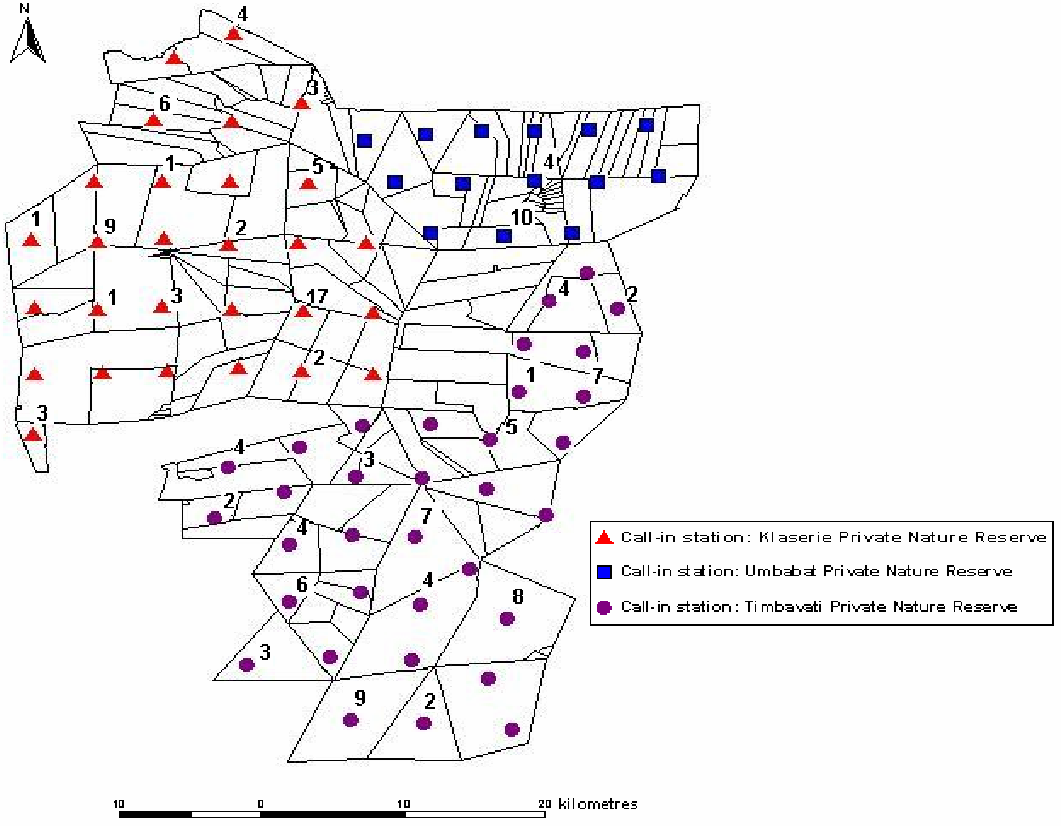

**Figure 1:** The number of lions observed at call-in stations in the Associated Private Nature Reserves in November 2000, based on the call-in counting technique (Mills, Juritz & Zucchini 2001). The Timbavati lodge traversing area was excluded from the count.

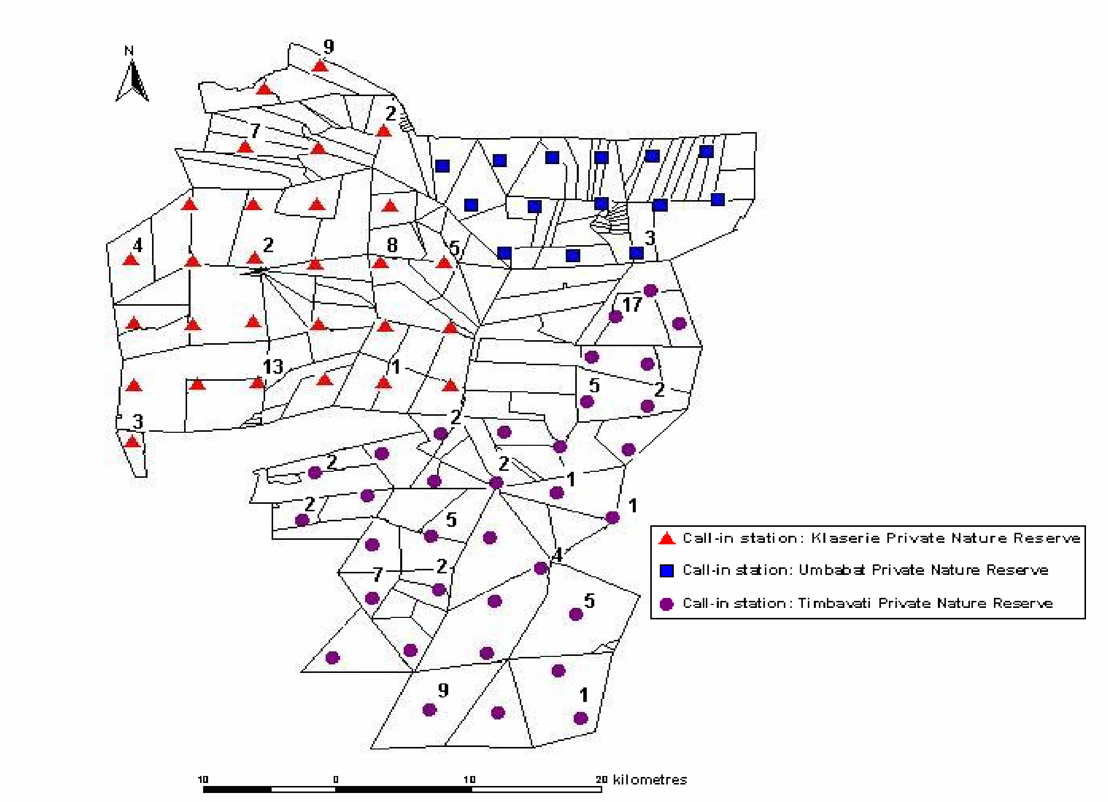

**Figure 2:** The number of lions observed at call-in stations in the Associated Private Nature Reserves in November 2001, based on the call-in counting technique (Mills, Juritz & Zucchini 2001). The Timbavati lodge traversing area was excluded from the count.

number of call-in stations to which lions responded was 25 (n = 64 call-in stations; 39%) (Figure 2). The lion response frequency for the count in 2000 was similar to that in 2001 ($\chi^2$ = 1.67; df = 1; P > 0.05). The number of lions in the Associated Private Nature Reserves in 2000 was not significantly different from that in 2001 (Wilk's Lambda Statistic = 0.832; df = 1; P > 0.05) (Table 1). The total number of lions that were estimated for the Associated Private Nature Reserves was similar to the estimate of 172 lions that was determined in an independent study by Funston (2004).

**Pride size and composition**

The population of 156 lions in the study area in November 2000 consisted of 138 resident and 15 nomadic lions (Table 1). Three of the lions that responded during this count were not nomadic lions or from a resident pride. The resident lions belonged to 13 prides, 10 of which occurred in the Timbavati Private Nature Reserve with the other three prides in the Klaserie Private Nature Reserve. The number of lion prides did not change from November 2000 to November 2001. The total number of lions in the study area in November 2000 was likewise similar to that found in November 2001 (Wilk's Lambda Statistic = 0.832; df = 1; *P* > 0.05). The number of resident lions present did not change significantly from 2000 to 2001 ($\chi^2$ = 4.719; df = 5; *P* > 0.05), and neither did the number of nomadic lions in the study area ($\chi^2$ = 0.106; df = 1; *P* > 0.05) (Table 1). The largest group of nomadic male lions in the study area was a coalition of five adult males.

In the Timbavati and Klaserie Private Nature Reserves the mean pride size in November 2000 was similar to that in November 2001 (Wilk's Lambda Statistic = 0.968; df = 1; P > 0.05) (Table 2). However, the mean pride size in the Associated Private Nature Reserves changed significantly from 2000 to 2001 (Wilk's Lambda Statistic = 0.709; df = 1; P ≤ 0.05) (Table 2). This was unexpected because there was no significant difference between the mean pride sizes in the Timbavati and Klaserie Private Nature Reserves for

**Table 2**: *The mean ± SD of the pride size of the lions in the Klaserie, Timbavati and the entire Associated Private Nature Reserves and its component reserves for 2000 and 2001, based on derived data from the call-in technique (Mills; Juritz & Zucchini 2001). There were no resident lions in the Umbabat Private Nature Reserve at the time of the present study.*

| **AREA** | **YEAR** | **PRIDE SIZE** | | **NUMBER OF PRIDES** |
|---|---|---|---|---|
| | | Mean ± SD | Range | |
| Timbavati Private Nature Reserve: | 2000 | 9.1 ± 3.5 | 2 - 14 | 10 |
| | 2001 | 7.5 ± 5.7 | 2 - 20 | 10 |
| Klaserie Private Nature Reserve: | 2000 | 15.1 ± 5.9 | 8 - 19 | 3 |
| | 2001 | 12.2 ± 1.7 | 10 - 13 | 3 |
| Associated Private Nature Reserves: | 2000 | 10.4 ± 4.6 | 2 - 19 | 13 |
| | 2001 | 8.5 ± 5.4 | 2 - 20 | 13 |

2000 and 2001 (Type III sum of squares = 1.747; df = 1; $P > 0.05$). The true difference ($\sigma$) between the mean pride size in 2000 and 2001 in the Associated Private Nature Reserves, at the 0.95 confidence level, was $1.245 \leq \sigma \leq 1.338$. For the Associated Private Nature Reserves the mean pride size in 2000 differed from the mean pride size in 2001 by a minimum of 1.245 lions and a maximum of 1.338 lions. This is not biologically significant because pride size varies according to prey availability, when there is an emigration of subadult males and during a pride takeover by adult male lions (Van Orsdol *et al.* 1985). The mean pride size in the Associated Private Nature Reserves from November 2000 to November 2001 was therefore considered to be stable.

The mean pride size of 10.0 lions in the Associated Private Nature Reserves was similar to that of 11.8 that was found in the Kruger National Park many years earlier (Smuts 1976), but smaller than the one of 17.0 in the Serengeti National Park (Van Orsdol, Hanby & Bygott 1985), 19.4 for the Ngorongoro Crater (Hanby, Bygott & Packer 1995), and the one of 22.0 for the Maasai Mara National Reserve (Ogutu & Dublin 2002). The mean pride size in the Associated Private Nature Reserves was, however, greater than that of 4.2 lions in the more arid South African portion of the Kgalagadi Transfrontier Park (Mills, Wolf, Le Riche & Meyer 1978).

**Population density**

The mean lion density in the Associated Private Nature Reserves was 7.9 ± 0.8 (95% c.l.) in November 2000, and 6.8 ± 1.3 (95% c.l.) in November 2001. The lion density in the Associated Private Nature Reserves in 2000 and 2001 was similar to that in the Kruger National Park, lower than that in the Serengeti National Park, Ngorongoro Crater and the Maasai Mara National Reserve, and greater than that on the Maasai Steppe and in the Kgalagadi Transfrontier Park (Lamprey 1964; Hofer & East 1995; Hanby, Bygott & Packer 1995; Ogutu & Dublin 1998; Funston *et al.* 2001) (Table 3). The arid Maasai Steppe of

**Table 3**: *Comparison of the mean lion density (lions per 100 km²) and the seasonal change in prey density (kg per km²) in the Associated Private Nature Reserves in November 2000 and 2001, with the lion densities found in other areas of Africa.*

| **AREA** | **LION DENSITY** | | **PREY DENSITY** | | |
|---|---|---|---|---|---|
| | Density | Source | Wet season | Dry season | Source |
| Associated Private Nature Reserves | 8.0 | Present study | 3160 | 2945 | Present study |
| Etosha National Park | 2.8 | Stander (1992) | ~ | ~ | ~ |
| Kgalagadi Transfrontier Park | 0.2 | Funston *et al.* (2001) | ~ | ~ | ~ |
| Kruger National Park | 10.5 | Smuts (1982) | ~ | ~ | ~ |
| Maasai Steppe | 0.3 | Lamprey (1964) | ~ | ~ | ~ |
| Maasai Mara National Reserve | 29.4 | Ogutu & Dublin (1998) | 10 335 | 26 092 | Ogutu & Dublin (2002) |
| Ngorongoro Crater | 40.0 | Schaller (1972) | 11 693 | 12 000 | Hanby *et al.* (1995) |
| Savuti Marsh | 20.0 | Viljoen (1997) | 27 000 | 2000 | Viljoen (1997) |
| Serengeti National Park | 16.0 | Schaller (1972) | 20 000 | 1000 | Schaller (1972) |

~ No data available

Tanzania has the lowest known natural lion density in Africa at 0.3 lions per 100 $km^2$, and the lion density of 40 lions per 100 $km^2$ in the Ngorongoro Crater National Park is one of the highest in African savannas (Lamprey 1964). The lions in the Associated Private Nature Reserves were therefore at an intermediate density.

The prey density in the study area was similar in the wet and the dry season from 2000 to 2002 ($\chi^2$ = 2.101; df = 2; $P > 0.05$). When compared with other areas in Africa, the prey density in the wet season was lower in the Associated Private Nature Reserves than in the Ngorongoro Crater, Serengeti Plains, and the Savuti Marsh (Table 3). For the dry season, however, the prey density in the study area was lower than that in the Ngorongoro Crater and greater than the prey density on the Serengeti Plains and the Savuti Marsh (Table 3).

### Age composition and sex ratio

Adults formed > 50% of all the prides in the Timbavati and Klaserie Private Nature Reserves, and the total lion population in the Associated Private Nature Reserves, (Table 4). This was comparable to the proportion of adults in the lion populations of the Serengeti Plains (57%) (Schaller 1972), the Kruger National Park (53.3%) (Smuts 1976) and the Etosha National Park (51%) (Stander 1990). There was no significant difference between the age composition of the lions in the Timbavati and Klaserie Private Nature Reserves in November 2000 and 2001 respectively ($\chi^2$ = 3.104; df = 2; $P > 0.05$) (Table 4). The proportion of adult lions in the Timbavati Private Nature Reserve was similar to that in the Klaserie Private Nature Reserve in November 2000 and 2001. However, the proportion of subadults in the Klaserie Private Nature Reserve was greater than in the Timbavati Private Nature Reserve in November 2000 and 2001, and the proportion of cubs in the Timbavati Private Nature Reserve was greater than in the Klaserie Private Nature Reserve in November 2000 and 2001.

**Table 4**: *The lion population structure in the Timbavati, Klaserie and the entire Associated Private Nature Reserves in November 2000 and 2001 based on data from the call-in counting technique of Mills, Juritz & Zucchini (2001) and the Timbavati lodge data. These age and sex categories were used: AM = adult male, AF = adult female, SM = subadult male, SF = subadult female, CM = male cubs, and CF = female cubs. There was no resident lion pride in the Umbabat Private Nature Reserve at the time of the present study.*

| **AREA** | | **AGE AND SEX COMPOSITION** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **Adults** | | | **Subadults** | | | **Cubs** | | |
| | | Percentage males | Percentage females | AM : AF | Percentage males | Percentage females | SM : SF | Percentage males | Percentage females | CM : CF |
| Timbavati Private Nature Reserve | 2000 | 25.3 | 36.4 | 1 : 1.4 | 11.1 | 5.1 | 1 : 0.5 | 14.1 | 8.1 | 1 : 0.6 |
| | 2001 | 21.3 | 38.3 | 1 : 1.8 | 8.5 | 6.4 | 1 : 0.8 | 11.7 | 6.4 | 1 : 0.5 |
| Klaserie Private Nature Reserve | 2000 | 26.3 | 24.6 | 1 : 0.9 | 19.3 | 12.3 | 1 : 0.6 | 7.0 | 5.3 | 1 : 0.8 |
| | 2001 | 24.1 | 27.8 | 1 : 1.2 | 20.4 | 18.5 | 1 : 0.9 | 0.0 | 0.0 | ~ |
| Associated Private Nature Reserves | 2000 | 25.6 | 32.1 | 1 : 1.3 | 14.1 | 7.7 | 1 : 0.5 | 11.5 | 7.1 | 1 : 0.6 |
| | 2001 | 22.3 | 34.5 | 1 : 1.5 | 12.8 | 10.8 | 1 : 0.8 | 7.4 | 4.1 | 1 : 0.6 |

~ No data available

The sex ratio of the lions in all age categories did not differ significantly from November 2000 to November 2001 for the Timbavati Private Nature Reserve ($\chi^2 = 9.385$; df = 5; $P > 0.05$), the Klaserie Private Nature Reserve ($\chi^2 = 7.481$; df = 5; $P > 0.05$) or the entire Associated Private Nature Reserves ($\chi^2 = 3.622$; df = 5; $P > 0.05$). In November of 2000 and 2001 the proportion of males to females in the Associated Private Nature Reserves was similar (Table 4).

## DISCUSSION

The call-in counting method is a less intensive, cheaper and more practical form of the mass capture technique for lions (Smuts *et. al.* 1977). Ogutu & Dublin (1998) applied this technique to determine the size of the lion population in the Maasai Mara National Reserve. The high precision and low bias of their estimate showed that the call-in counting method was reliable and could be employed to effectively monitor carnivore populations despite the lack of geographical closure of their study area (Loveridge, Lynam & Macdonald 2001). This counting method also seemed to be effective for estimating the minimum number of lions in the Associated Private Nature Reserves, as shown by the statistically similar results for the survey in 2000 and 2001, and the similarity between the results of the present study with that of the independent study of Funston (2004). As expected, the results of the present study were similar to those for the lions in the adjoining Kruger National Park (Smuts 1976; Funston 1999). The proportion of lions that responded to call-in stations in the Associated Private Nature Reserves was also similar to that found by Ogutu & Dublin (1998) and Funston *et al.* (2001) in two totally different environmental conditions than that of the present study.

### Pride size and composition

Lions live either as resident prides that defend territories, or as nomads that roam over wide areas in search of prey or to establish territories (Schaller 1972). A lion pride is a stable and long-term group of related females and their cubs, and adult males that are dominant in that pride at the time (Packer *et al.* 1988). Pride size is generally stable and is best reflected by the number of adult females because the females are the core members of the pride. The variation in pride size is principally based on whether subadult females remain in their natal pride or move away from that pride (Funston 1999). This may be influenced by the availability of prey and lion population density. However, the most important factor appears to be the emigration of non-receptive subadult females from a pride when a pride is taken over by new adult males (Packer & Pusey 1983; Hanby & Bygott 1987; Pusey & Packer 1987).

Based on the similar mean pride size, total population size and the number of lion prides in 2000 and 2001, the lion population in the Associated Private Nature Reserves was considered to be stable for that period. A greater number of nomadic lions was observed in the study area in 2001 than in 2000. The pride takeover of three prides by intruding males during this study was a possible cause for this. The consequent emigration of the surviving adult male lions and the subadult male and female lions from these prides may, therefore, have increased the number of nomadic lions in the study area in 2001. The largest male coalition in the Associated Private Nature Reserves consisted of a group of five nomadic male lions and was the. This coalition was of the same size as the largest coalition that was observed in the Kruger National Park by Smuts (1976) and Funston (1999). Such a coalition size is large when compared with male coalitions in other African savannas (range: 1 – 7 lions; Hanby *et al.* 1995).

Lion pride size varies from area to area according to the availability of prey, and it is correlated with the lean-season abundance of prey (Van Orsdol *et al.* 1985). The prey availability, and therefore the mean pride size of the lions, in the Associated Private

Nature Reserves was lower than that on the Serengeti Plains, the Ngorongoro Crater and the Maasai Mara National Reserve, but greater than that in the more arid Kgalagadi Transfrontier Park (Schaller 1972; Hofer & East 1995; Hanby *et al.* 1995; Ogutu & Dublin 1998; Funston *et al.* 2001). As expected, the mean pride size in the Associated Private Nature Reserves was similar to that in the adjacent Kruger National Park (Smuts 1976).

In more mesic areas, such as the Ngorongoro Crater, prey availability is similar in the wet and dry seasons (Hanby *et al.* 1995). However, in less mesic areas prey availability may vary seasonally, such as on the Serengeti Plains where more prey animals are available in the wet than the dry season (Schaller 1972; Hanby *et al.* 1995). Although the mean lion pride size in the Associated Private Nature Reserves was not determined seasonally, the prey availability in the wet season was similar to that in the dry season (Table 3), suggesting that the mean pride size in the wet season may well have been similar to that in the dry season.

### Population density

Lion density varies from area to area in accordance with the variation in lion pride size (Van Orsdol *et al.* 1985). In areas where prey is more abundant lion pride size is greater, and consequently lion density is greater. This was also true in the present study. The lion density in the Associated Private Nature Reserves was lower than that on the resource-rich Serengeti Plains and the Ngorongoro Crater, and greater than in the more arid and prey-poor Maasai Steppe and Kgalagadi Transfrontier Park (Lamprey 1964; Schaller 1972; Funston *et al.* 2001). The lions in the Associated Private Nature Reserves occurred at intermediate densities that were comparable to that found in other African savanna woodland habitats.

The lion density in a specific area of its habitat may vary according to local prey availability (Van Orsdol *et al.* 1985; Hanby & Bygott 1987; Pusey & Packer 1987; Packer *et al.* 1988). In unfenced areas where prey migrate, such as the Serengeti Plains, prey availability is greater in the wet season than the dry season, and lion density follows this trend (Schaller 1972). Stander (1997) found a similar situation for lions in the Kaudom Game Reserve in northeastern Namibia. Although the lion density in the Associated Private Nature Reserves was not compared seasonally in the present study, the similar prey availability in the wet and dry season suggested that the lion density in the wet season could also be similar to that in the dry season. The dry climatic cycle that is currently being experienced in the Associated Private Nature Reserves (Peel 2003) suggests that prey availability, and therefore lion density, are likely to decrease in the immediate future.

### Age composition and sex ratio

The population dynamics of lions varies from region to region because of environmental and other variables (Bothma & Walker 1999). When ecological conditions are poor, lion survival rates are lower, particularly for the cubs and subadults whose food intake declines then because potential prey is less abundant (Schaller 1972; Bertram 1973; Betram 1975; Packer *et al.* 1988). The age structure of the adult lions in the Associated Private Nature Reserves was consistent with that of other savanna areas in Africa, with adults contributing >50% to the population (Schaller 1972; Smuts 1976; Stander 1990; Funston & Mills 1997; Bothma & Walker 1999; Ogutu & Dublin 2002). Lion reproductive and cub survival rates are in balance with the abundance of their resources, especially food (Hanby *et al.* 1995). It is therefore of interest that in the present study in the Klaserie Private Nature Reserve no cubs were counted in the lion count that was done in 2001. This lack of cubs was the result of infanticide that occurred in one pride, while the second pride was in an inter-litter phase and the adult females of the third pride had young cubs that still did not move around with the pride at the time of the counts. Moreover, Smuts *et* *al.* (1977) and Funston *et al.* (2001) found that lion cubs are seldom, if ever, brought to call-in stations by their mothers.

The sex ratio of lions also varies from region to region (Bothma & Walker 1999). In the Associated Private Nature Reserves the adult females outnumbered the adult males, as they did in the Etosha National Park (Stander 1990), the Serengeti Plains (Schaller 1972) and the Kruger National Park (Smuts 1976). In contrast, however, a greater proportion of the subadults and cubs in the study area were males than females. Generally, the sex ratio of lion cubs does not differ significantly from parity, and differential mortality does not occur until lions become subadults, when there is a bias towards males (Betram 1973; Smuts 1976; Packer & Pusey 1987; Creel & Creel 1997). However, variations in sex ratio at birth do occur, with increasing male-biased litters occurring in areas where adult males are hunted as trophies (Yamazaki 1996; Creel & Creel 1997; Whitman & Packer 1997; Whitman *et al.* 2004). The male-biased litters in the Associated Private Nature Reserves where trophy hunting of lions occurs, may be the reason for this skewed sex ratio. The sex ratio for the total lion population in the Associated Private Nature Reserves, however, approached parity, as in the Etosha National Park (Stander 1990), Serengeti Plains (Schaller 1972) and the Kruger National Park (Smuts 1976).

## CONCLUSIONS

The call-in counting method provided a minimum estimate of the lion population size and density in the Associated Private Nature Reserves. This population estimate was validated by the results of the independent study by Funston (2004). Lions in the Associated Private Nature Reserves live at intermediate densities and have intermediate pride sizes when compared with those in other areas such as the Serengeti National Park, Kruger National Park, Maasai Mara National Reserve, Etosha National Park and the Kgalagadi Transfrontier National Park. The age and sex structure of the lions in the present study were comparable to that of lions in other savanna areas of Africa.

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# CHAPTER 6

# RANGE SIZE, DISTRIBUTION AND HABITAT SELECTION

## INTRODUCTION

It is important to determine an animal's range size and shape, and patterns of habitat utilisation for most ecological and behavioural studies (Harris *et al.* 1990). The distribution, range size and habitat selection of predators have been variously attributed to the predators' energy requirements (Mace, Harvey & Clutton-Brock 1982), reproductive status (Frame, Malcolm & Lawick 1979), habitat productivity and food availability (Macdonald 1983), differential visibility and mobility within habitats (Creel & Creel 1995), and the presence or not of other predators (Barnett 1994).

The basic pattern of felid social organisation is one in which males occupy larger, exclusive ranges that encompass the ranges of several females (Sunquist & Sunquist 1989). The social structure and territorial behaviour of lions affects their range use and distribution (Kilian 2003). A territory is commonly defined as that area within a range that is actively defended by the occupier against animals of the same species (Lawrence 1998). Lions either live as resident prides that defend territories within a defined range, or as nomads that roam over a wide, undefended area searching for prey or territories (Schaller 1972). A lion pride consists of a group of related females and their cubs, and two to four adult males that are associated with the pride at that time (Schaller 1972). Female lions usually occupy separate adjacent ranges, whilst the range of pride males may overlap with those of several females. In contrast to females, coalitions of males are considered to defend access to a group of pride females rather than a demarcated territory (Bygott *et al.* 1979; Packer *et al.* 1988).

Male lions in the Kruger National Park seem to have three distinct phases of range use (Funston 1999). Dispersing or evicted males experience a non-territorial phase during which they do not have a resource to defend (females or habitat), until they attempt to take over a pride (Bygott *et al.* 1979; Pusey & Packer 1987; Packer *et al*. 1988). When the males are successful in taking over a pride they replace the previous coalition of males and maintain regular contact with the pride females (Packer & Pusey 1983). The resource defended during the take-over phase is thus the pride females. Following the birth of a cohort of cubs the resident males move into the territory maintenance phase, where the males spend more time patrolling the territory and less time in the company of the females and cubs. The most important resources defended during this phase, however, are the cubs and possibly the core area of range in which the pride females raise them (Funston 1999).

Lions may extend their ranges in response to changing prey distributions. Consequently the range of one pride may overlap with that of a neighbouring pride (Schaller 1972; Hanby, Bygott & Packer 1995). Ranges occupied by nomadic lions may be 10 times larger than that of prides (Schaller 1972).

The most important determinants of lion range size and distribution are prey availability and habitat preference (Funston 1999). Range size is inversely correlated with lean season prey availability (Van Orsdol, Bygott & Bygott 1985). The range size of a lion pride is related to the size of the pride and the distribution of its prey, and the size of the lion pride varies according to the availability of prey (Van Orsdol 1985). Prey distribution and availability changes in accordance with habitat type. Therefore lions select certain habitats in preference to others (Macdonald 1983).

Habitat selection is an active process whereby animals in an area use the portions of that area that best satisfy their fundamental requirements of food, reproduction and rest (Brewer 1994). Lions occur in various habitat types in Africa, ranging from arid landscapes in the Etosha National Park and the Kgalagadi Transfrontier Park (Stander 1992; Funston *et al.* 2001), to semi-arid savannas such as the Kruger National Park (Funston 1999), the grasslands of the Maasai steppe (Saba 1979), and the mesic savannas of the Serengeti Ecosystem and the Ngorongoro Crater (Schaller 1972; Hanby *et al.* 1995; Sunquist & Sunquist 2002). Physical habitat features including vegetation type affect prey distribution and consequently also predator distribution. Various types of prey prefer specific habitat types, and are therefore unevenly distributed throughout an area (McNaughton & Georgiades 1986). Consequently, physical vegetation structure is an important factor in lion habitat selection because it affects the visibility and mobility of lions. The amount of cover for hunting also influences lion hunting success (Krüger 1996). Vegetation type was therefore investigated in the present study as an ecological determinant of lion distribution and range size in the Associated Private Nature Reserves. In doing so, the hypothesis that the range use and habitat selection of the lions in the Associated Private Nature Reserves was similar to that of lions in other African savannas was tested. This hypothesis was tested by studying the following four key questions:

- That the range size and use of the lions in the Associated Private Nature Reserves were comparable to that of the lions in other African savannas.
- That the habitat selected by the lions in the study area was proportional to the availability of the respective habitat types within the ranges of those lions.
- That the habitat selected by the lions in the study area was proportional to the availability of the respective habitat types within the Associated Private Nature

Reserves.

- That the habitat selection by the lions in the Associated Private Nature Reserves was similar to that of the lions in other African savannas.

## METHODS

The range dynamics and habitat selection of four focal lion groups in the Associated Private Nature Reserves were studied. The C, S and M prides had the largest pride size, and the N coalition consisted of the largest group of nomadic males in the study area (Chapter 5). The N coalition was the only male coalition that was studied because other male coalitions were either not habituated to being followed by a vehicle, or their ranges extended into the Kruger National Park. The selected lion groups were lured to capture sites and the focal lions were immobilised (Mills 1985; Ogutu & Dublin 2002). An adult lioness from each of the C, S and M prides, and an adult male from the N coalition were fitted with radio-collars. The focal lions are referred to as females C, S, and M and male coalition N.

The radio-collars were made by Rowles[1] by using Telonics™ (Mesa, Arizona, USA) transmitters (148 to 152 MHz), with dental acrylic housings and collars of conveyor belting. The collars were fitted to the lions and were secured by using pop-rivets. An AOR AR8000 digital receiver and a four-element Yagi antenna were used to locate the radio signals from the collars. Signals were received at a distance up to 8 km, depending on the topography and the density of the vegetation in which the collared animal occurred. The radio-collars were replaced on two occasions. One of the collars was replaced due to a faulty battery, and a second collar was replaced due to irreparable damage from being chewed by other lions.

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[1] Mr C. Rowles, Warden, Klaserie Private Nature Reserve, P.O. Box 150, Hoedspruit, South Africa, 1380.

Subsequent to the collar being damaged, thicker conveyor belting from an elephant collar was used and no further problems of this kind were encountered.

### Radio-tracking

The focal lion groups were located by using radio-tracking, opportunistic sightings and reports from the field staff at the lodges. These focal lion groups were radio-located each day from a vehicle for 10 consecutive days during three separate sessions, during the period from 26 May 2001 to 25 August 2002 (Chapter 7). The field staff in the Associated Private Nature Reserves assisted with data collection by radio-locating the focal animals when they were not being tracked by the researcher. A directional antenna was used to detect a radio signal and to determine the direction from which the radio signal was being transmitted. The perceived signal strength increases as the distance between the receiver and the transmitter decreases (Amlaner & Macdonald 1980). The position of the observer was determined by using a global positioning system (GPS), and noted on a map. A compass bearing of the direction of the signal was then taken, and a vector was then drawn from the position of the observer towards the origin of the signal. The observer then travelled towards the signal and repeated this procedure from a second or more points at regular time and distance intervals. The estimated location of the lion is at the point where the drawn vectors intersected and the signal strength was at the greatest. When the signal strength was at its maximum, the signal was non-directional and the animal could be located visually either from the vehicle or on foot.

### Range use analysis

The ranges of the focal lion groups were based on plots of all radio-locations for a single collared animal in each group, during the period of study (Kenward 1987). For each of the collared animals, continual observation data were combined with the radio-locations provided by the field staff of the Associated Private Nature Reserves. For range analysis purposes, the minimum time interval between consecutive radio-locations was one day. This ensured that the locations for each lion group were independent of one another, preventing auto-correlation of the data and a resultant underestimation of range size (Swihart & Slade 1985; Reynolds & Laundre 1990).

Two methods of range analysis were applied to the data, the minimum convex polygon method and the kernel analysis method. These methods allow for both statistical and spatial analysis of range size (Harris *et al.* 1990). The data were subjected to these analyses by using the ArcView Global Information System package (ArcView 3.2). The Spatial Analyst Extension and the Animal Movement Extension for ArcView were used to perform the range analysis (Hooge 1999).

### *The minimum convex polygon method*

The minimum convex polygon method is the simplest and one of the oldest techniques of range size calculation (Mohr 1947). It is still the most widely used method due to its comparability between studies (Harries *et al.* 1990). The peripheral fix points were joined to create a convex polygon area that included all the location points (Worton 1987). The disadvantages of this method are that the range size is highly correlated to the total number of observations, and that it includes areas that are never visited by the focal animal. The outermost location points may in fact be the result of occasional excursions outside the range, and the inclusion of these points could overestimate the actual range size of the animal (Mizutani & Jewell 1998). A limitation of calculating the minimum convex polygon method when using Arcview 3.2 is that this computer programme is only capable of determining the 100% utilisation distribution because no peeling option is available. Yet, the minimum convex polygon method was used here because it is the only range analysis method that is comparable between studies. The other range size estimators use different algorithms for their estimation of range size (Harris *et al.* 1990).

### *The kernel analysis method*

The kernel method of analysis is a probabilistic method of range size and use analysis that attempts to assess an animal's probability of occurrence at each point in space. This method relies on placing a probability density (kernel) on each location point (Worton 1989; Seaman & Powell 1996). The range size and use of an animal is determined in terms of the relative amount of time that the animal spends in different areas of the range (Worton 1989; Seaman & Powell 1996). The kernel method with a 95% isopleth is used to remove the effect of outliers on the calculation of range size. The core areas of use of the range of an animal are defined by using 75% and 50% isopleths (Mizutani & Jewell 1998).

Many authors feel that the kernel method with a 95% isopleth gives a reliable representation of the range of an animal (Jaremovic & Croft 1987; Mizutani & Jewell 1998; Broomhall 2001). In cases where accuracy is critical, such as in arid environments where range size might be used to calculate the size of viable conservation areas, an adaptive kernel method should be used in conjunction with a least-squares cross-validation (Worton 1989; Melville 2005). Hemson *et al.* (2005) determined, however, that least-squares cross-validation failed at large sample sizes and had significant variation at small sample sizes. In the present study, where the sample size was small and accuracy was not critical, a fixed kernel method gave enough information to determine the range dynamics of the lions in the Associated Private Nature Reserves.

## Habitat selection

A measure of habitat selection by the lions in the Associated Private Nature Reserves was obtained by comparing patterns of habitat use with habitat availability (Neu, Byers & Peek 1974). The approach used was based on that of Mills & Gorman (1997) when studying the habitat selection of wild dogs in the southern district of the Kruger National Park. The habitat selection of the focal lion groups (females C, S and M, and male coalition N) was first considered within their respective ranges. The habitat selection of the lions and their most abundant prey was then considered at the landscape level to investigate which habitats were selected for from within the whole study area. For the focal lions the percentage of radio-locations that occurred in the various vegetation types of their respective ranges was then compared with the percentage of radio-located kills within those vegetation types (Table 6.4 to 6.7).

A digitised vegetation map for the Timbavati, Klaserie and Umbabat Private Nature Reserves (Van Rooyen *et al.* 2005) and the ArcView Global Information System package (ArcView 3.2) were used to determine the proportion of each vegetation type in the range of the four lion groups, and in the whole study area. A minimum convex polygon was derived that encompassed every location point, including all excursions, for each of the radio-collared lions. The surface area of each of the various vegetation types in the ranges of the focal lion groups was then determined. This was done to exclude any areas that the lions had not visited (Kilian 2003). The location fixes for each of the collared lions within the different vegetation types was then counted. The habitat selection data for the eight most abundant types of lion prey were determined in Chapter 4.

The habitat preference of the focal lions was calculated by comparing patterns of habitat use with habitat availability, as was done in Chapter 4 for the eight most abundant types of lion prey. Habitat availability was calculated by dividing the surface area covered by vegetation type $x$ by the total area of the Associated Private Nature Reserves. A habitat selection index was then calculated for each of the vegetation types in the ranges of the focal lions (Jacobs 1974). The habitat selection data were analysed by using the method of Neu *et al.* (1974). Chi-square analyses were done to establish whether a specific vegetation type was preferred or was not being used by the relevant focal lion or prey animal. In those cases where the chi-square values were significant, the Bonferroni approach was used to determine which habitat types were preferred or were not being used (Marcum & Loftsgaarden 1980; Pienaar 1992). The habitat preferences of the focal lions and their most abundant prey were then compared in the entire surface area of the Associated Private Nature Reserves.

## RESULTS

### Radio telemetry

For females C, S and M, and male coalition N sufficient locations were obtained to allow meaningful analyses of range size (≥ 25 locations) (Mituzani & Jewell 1998; Broomhall 2001; Melville 2004) and the results appear in Figs. 6.1 to 6.10. In all, 364 radio-locations were recorded during the study period. The number of locations for male coalition N and female M from May 2001 to August 2002 was greater than that for females C and S because a greater number of radio-locations were provided by the field staff of the Klaserie Private Nature Reserve than by the Timbavati Private Nature Reserve (Table 6.1).

### Range use analysis

The range size estimates for the focal lions that were monitored from May 2001 to August 2002 appear in Table 6.1. The mean range size for female lions in the Associated Private

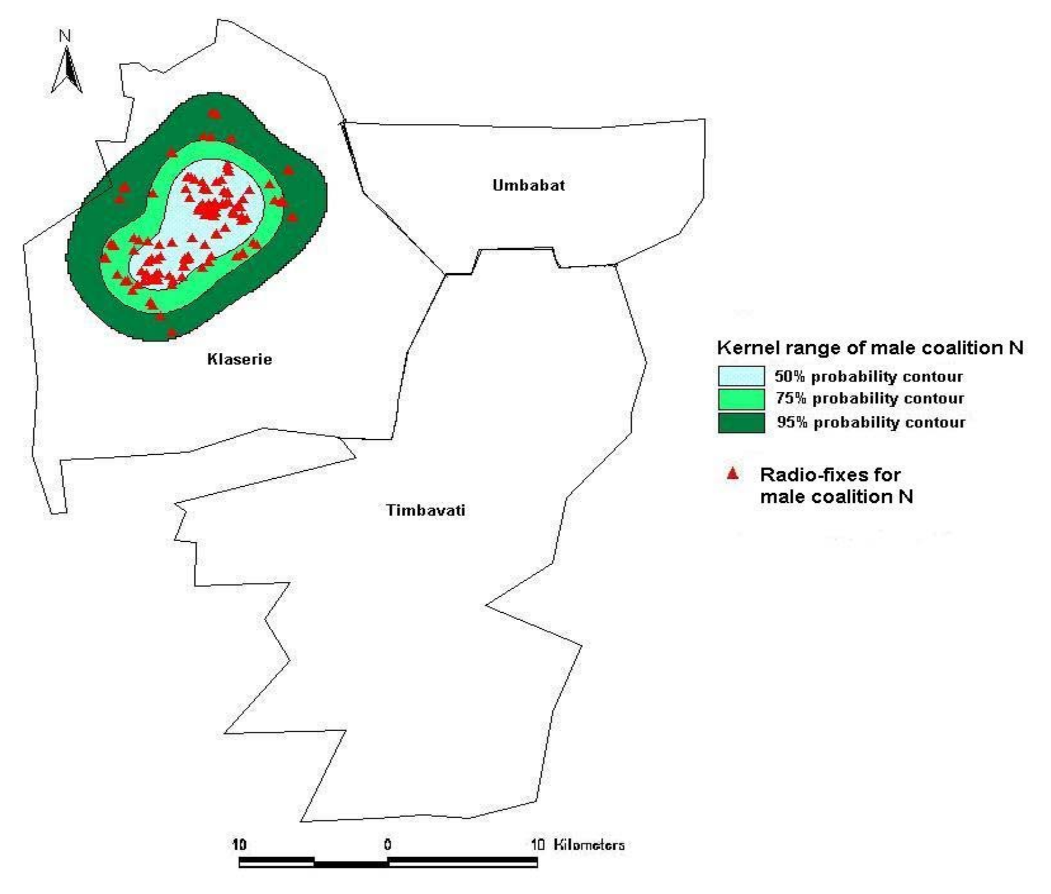

**Figure 6.1**: Range use of male coalition N in the Klaserie Private Nature Reserve from May 2001 to August 2002, based on the kernel range analysis method (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

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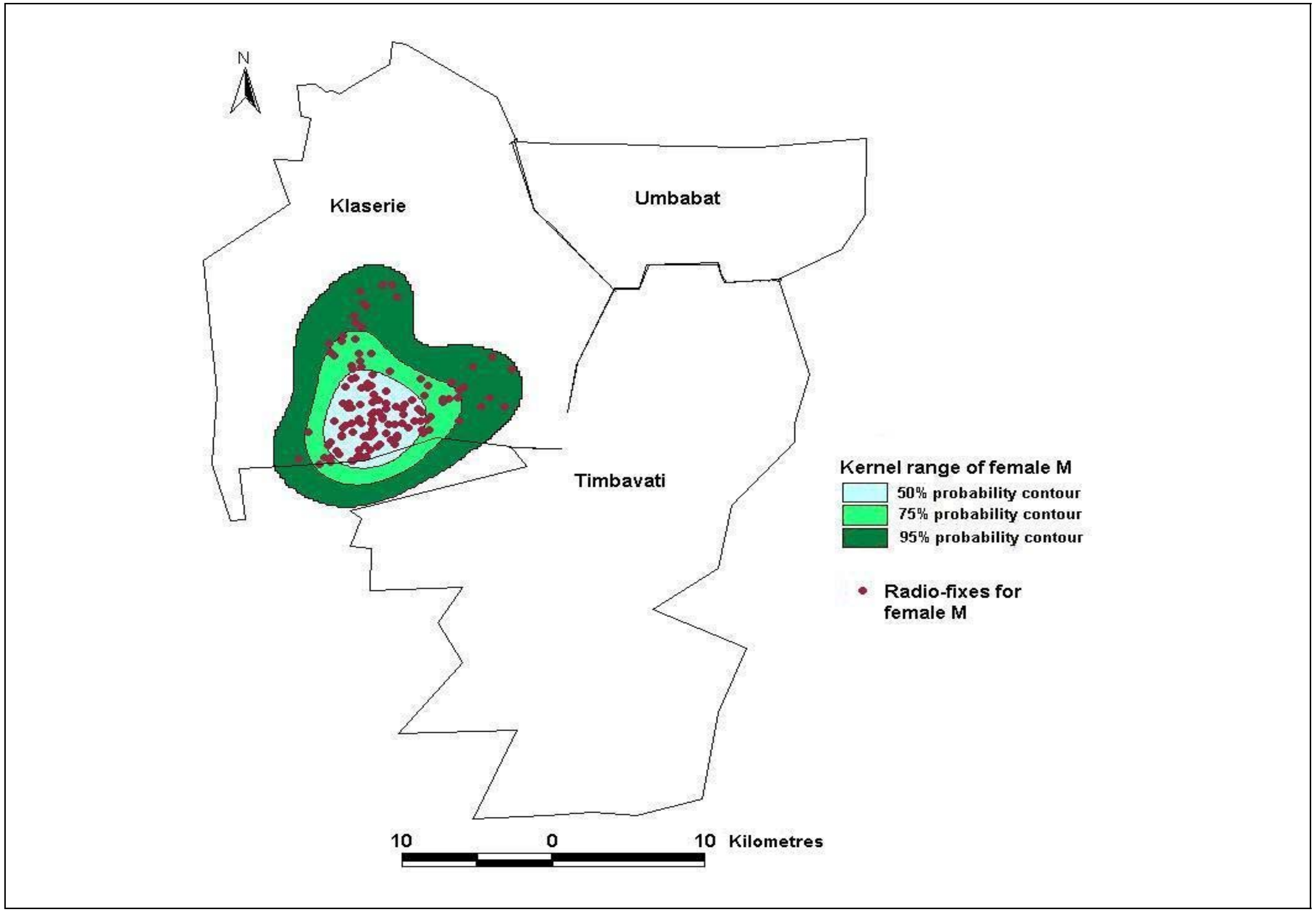

**Figure 6.2**: Range use of female M in the Klaserie Private Nature Reserve from May 2001 to August 2002, based on the kernel range analysis method (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

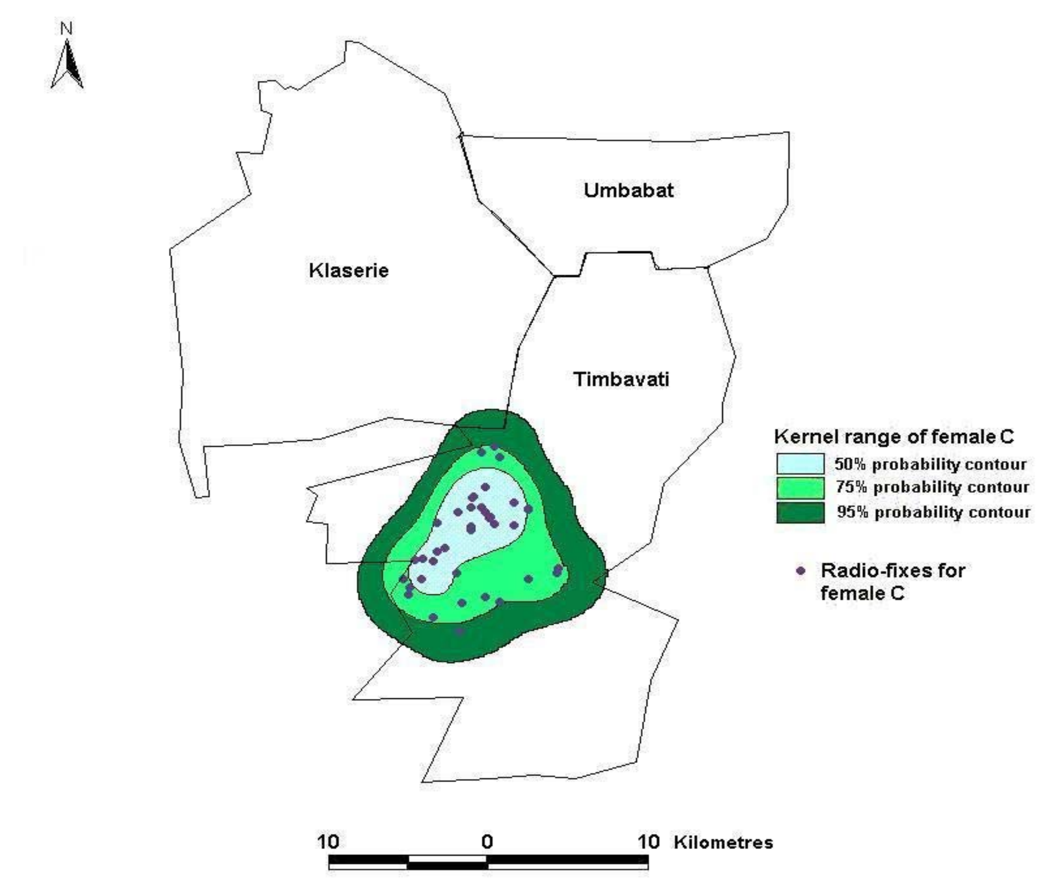

**Figure 6.3**: Range use of female C in the Timbavati Private Nature Reserve from May 2001 to August 2002, based on the kernel range analysis method (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

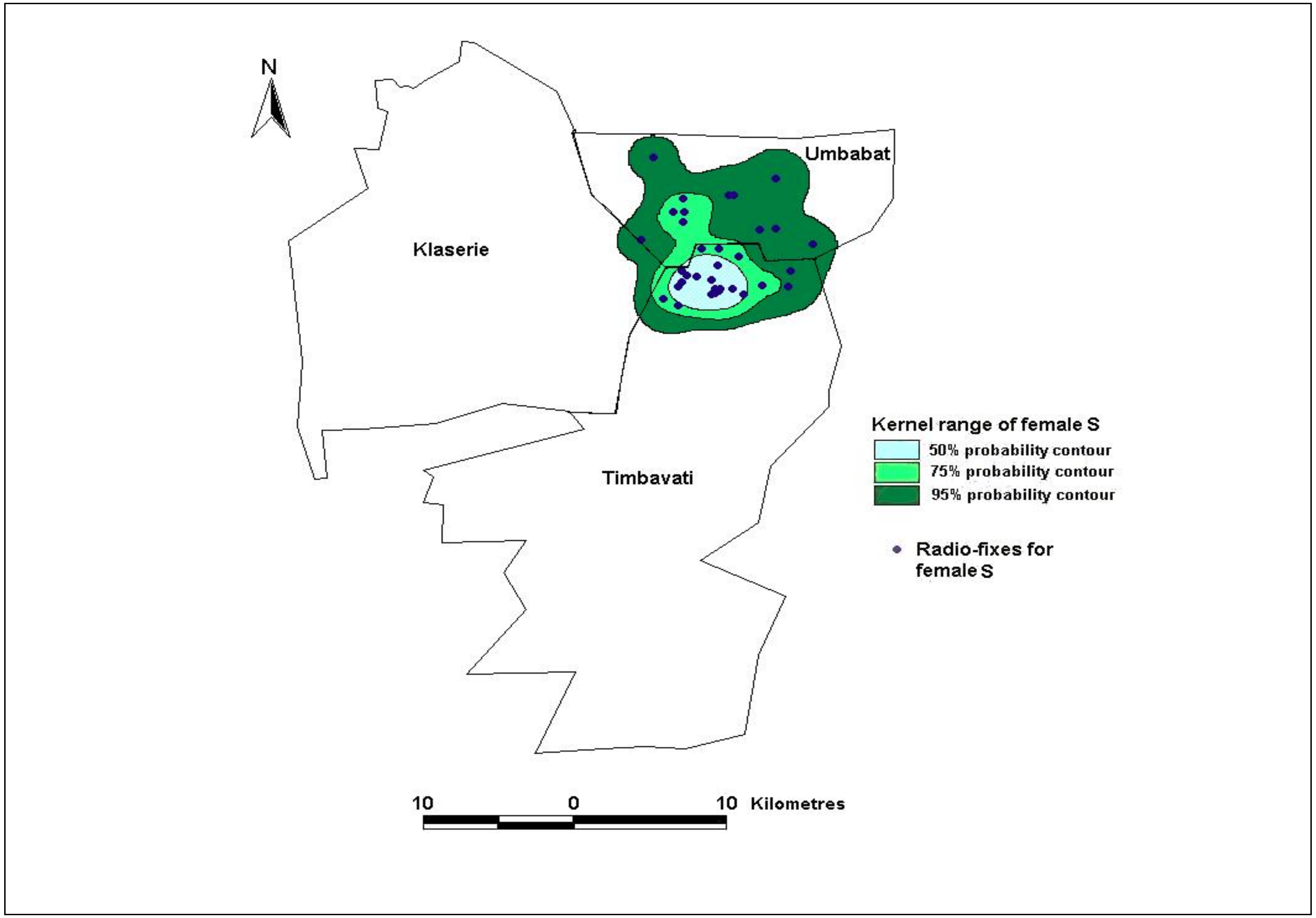

**Figure 6.4**: Range use of female S in the Timbavati Private Nature Reserve from May 2001 to August 2002, based on the kernel range analysis method (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

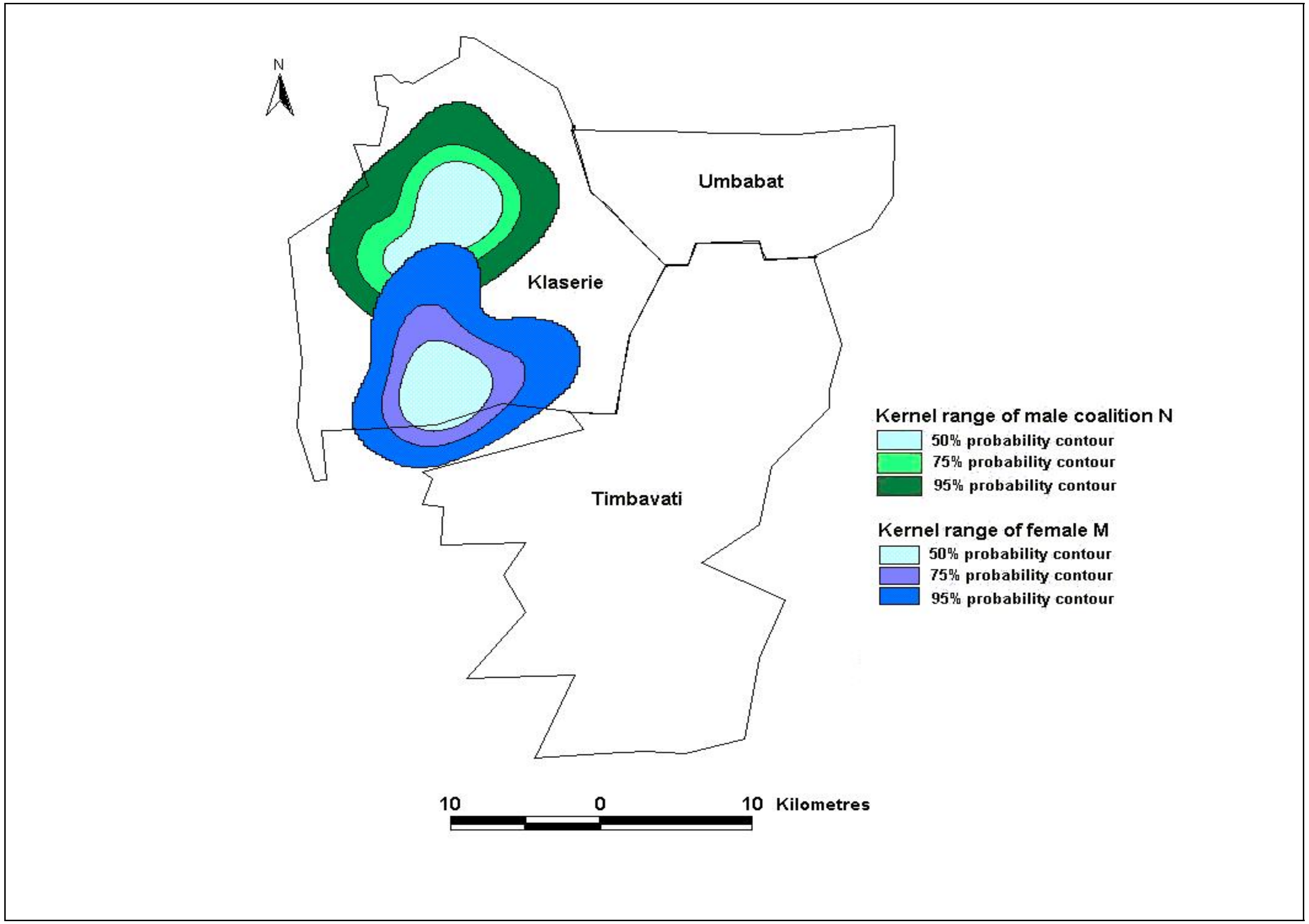

**Figure 6.5**: The overlap in range use of male coalition N and female M in the Klaserie Private Nature Reserve from May 2001 to August 2002, based on the kernel range analysis method (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

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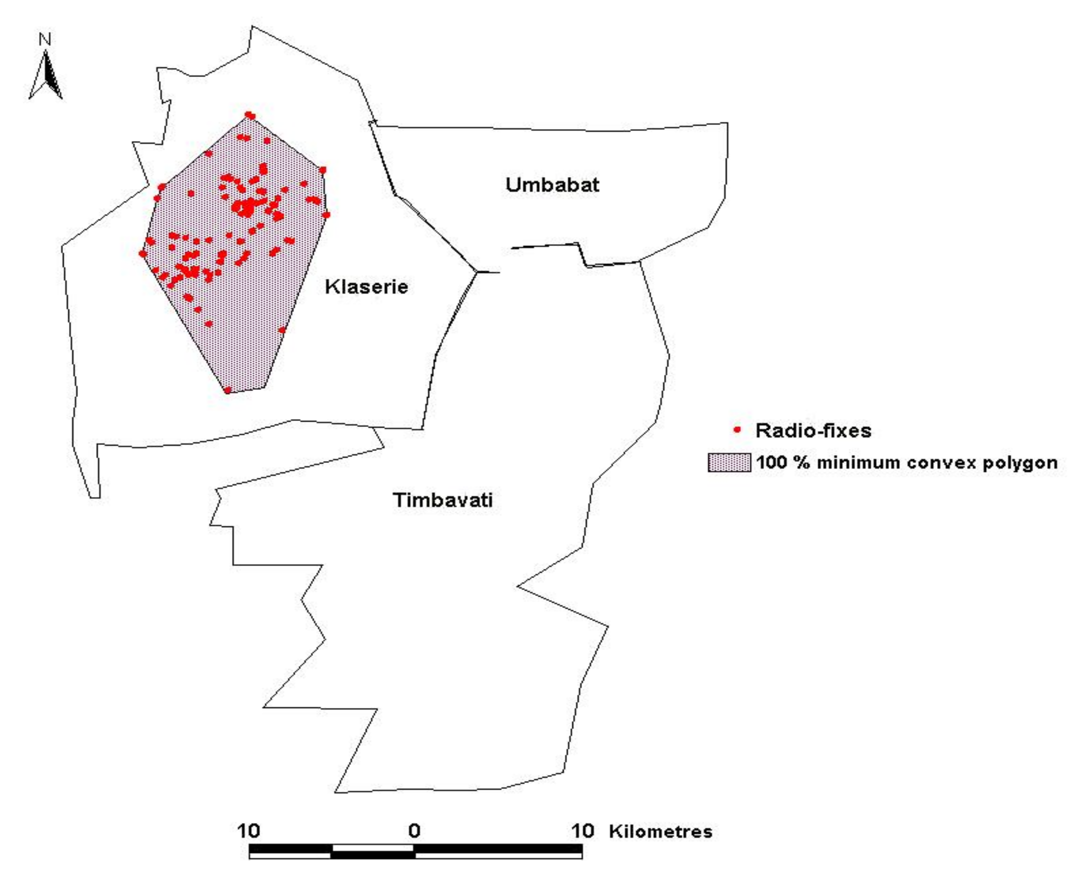

**Figure 6.6**: Range use of male coalition N in the Klaserie Private Nature Reserve from May 2001 to August 2002, based on the 100% minimum convex polygon range analysis method (Worton 1987) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

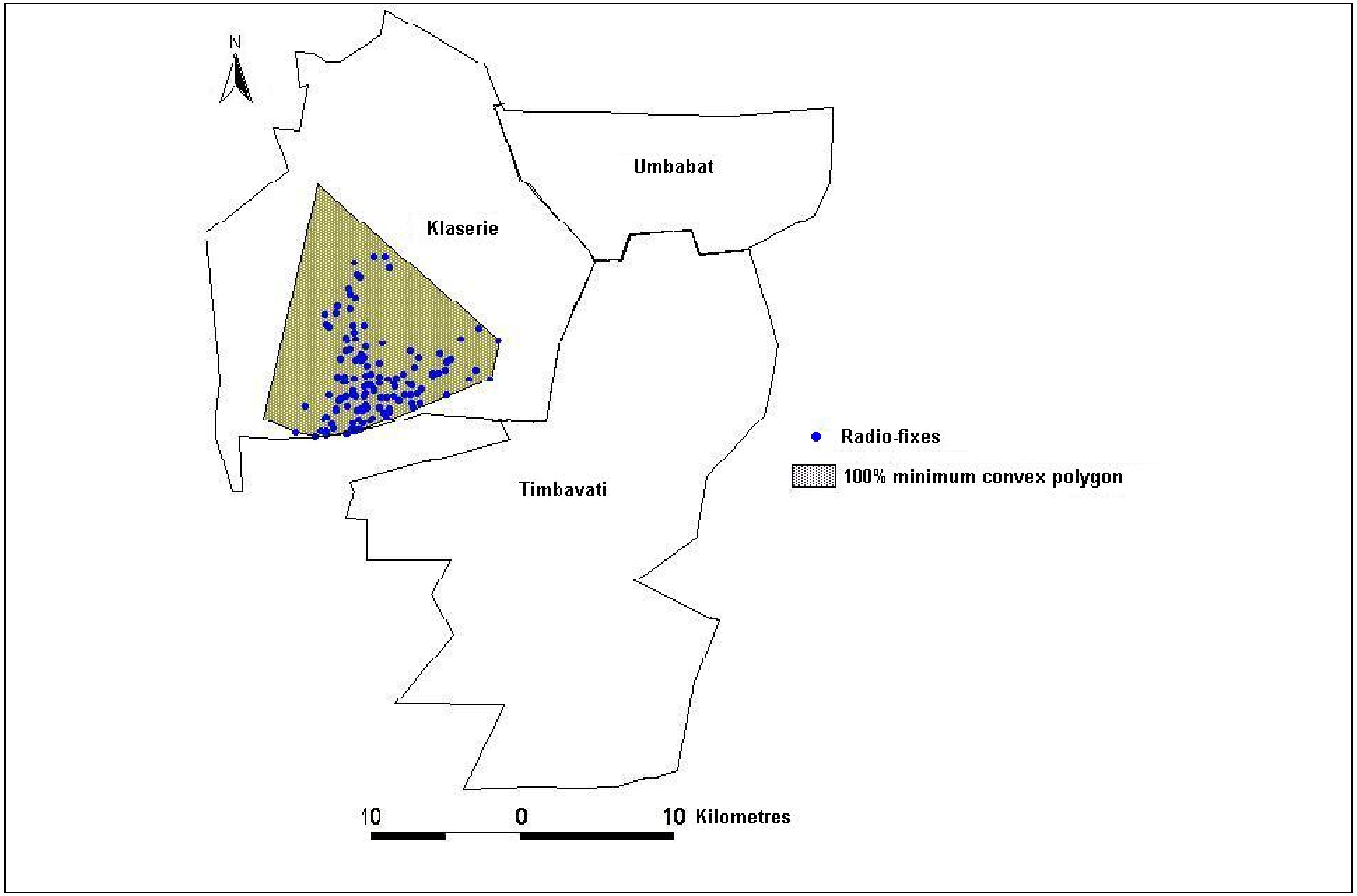

**Figure 6.7**: Range use of female M in the Klaserie Private Nature Reserve from May 2001 to August 2002, based on the 100% minimum convex polygon range analysis method (Worton 1987) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

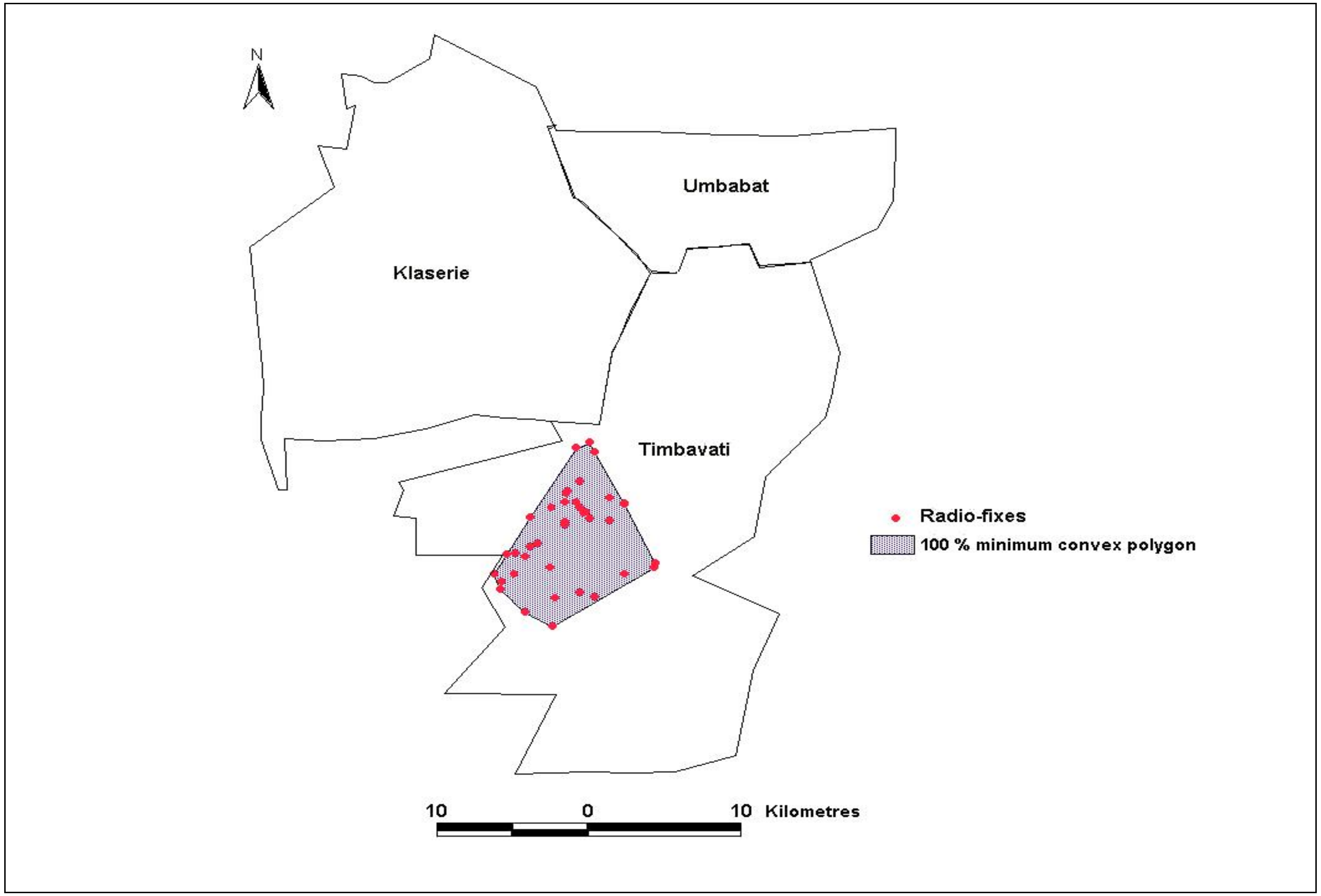

**Figure 6.8:** Range use of female C in the Timbavati Private Nature Reserve from May 2001 to August 2002, based on the 100% minimum convex polygon range analysis method (Worton 1987) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

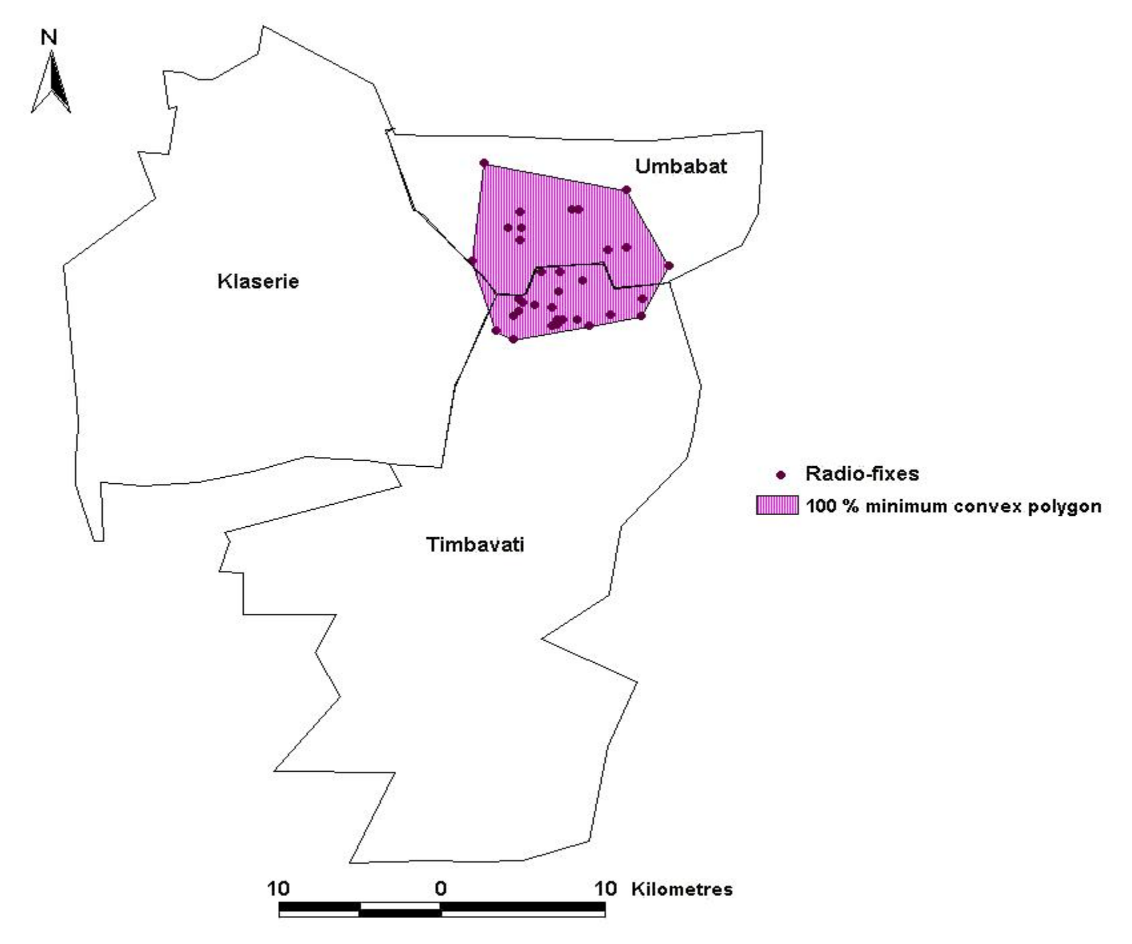

**Figure 6.9**: Range use of female S in the Timbavati Private Nature Reserve from May 2001 to August 2002, based on the 100 % minimum convex polygon range analysis method (Worton 1987) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

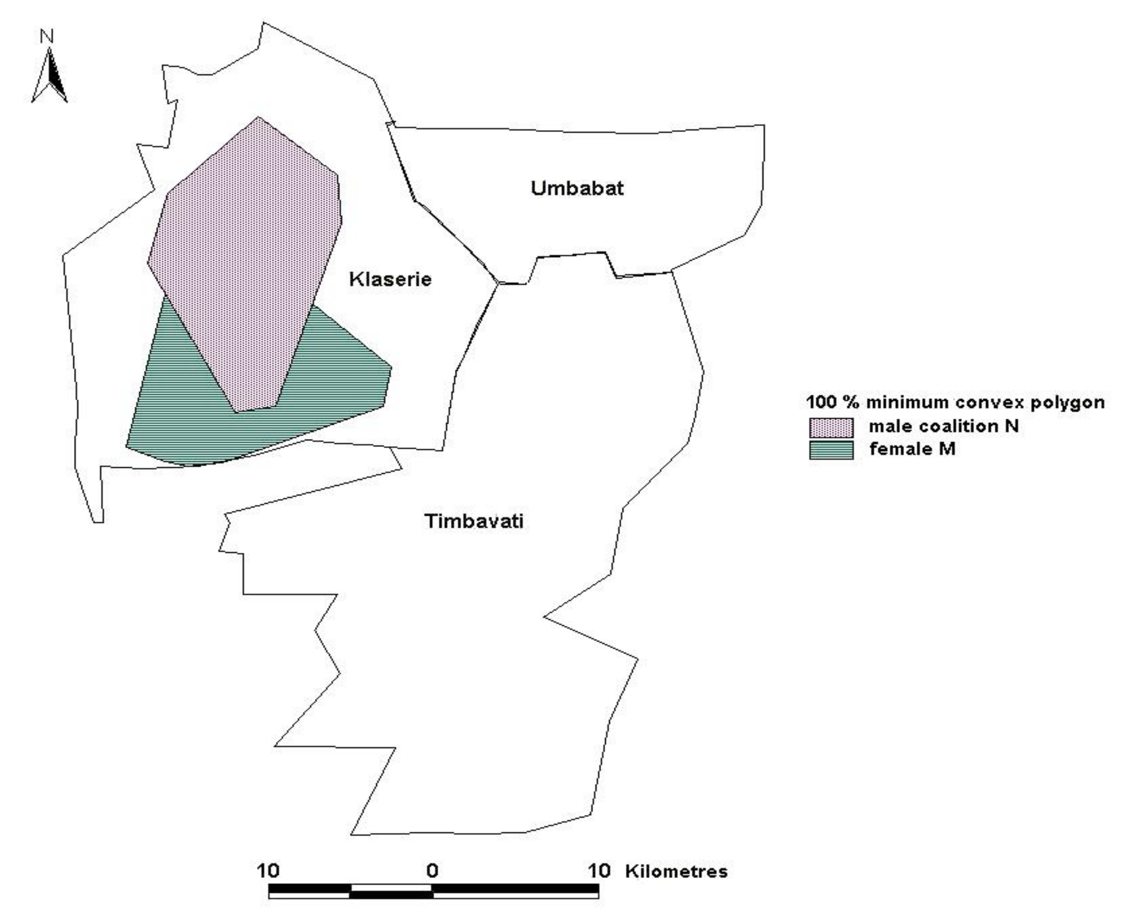

**Figure 6.10:** The overlap in range use of the male coalition N and female M in the Klaserie Private Nature Reserve from May 2001 to August 2002, based on the 100% minimum convex polygon range analysis method (Worton 1987) and the Animal Movement Extension for Arcview 3.2 (Hooge 1999).

**Table 6.1**: *Range sizes (km$^2$) or the focal lion groups studied in the Associated Private Nature Reserves in South Africa from May 2001 to August 2002, based on the kernel analysis and minimum convex polygon (MCP) methods of range analysis.*

| **ITEM** | **RANGE SIZE** | | | |
|---|---|---|---|---|
| | Male N | Female M | Female C | Female S |
| Number of radio locations: | 151 | 137 | 34 | 42 |
| Method used | | | | |
| Kernel: 95% probability contour | 193.9 | 185.5 | 222.2 | 180.1 |
| Kernel: 75% probability contour | 93.4 | 79.4 | 118.7 | 56.7 |
| Kernel: 50% probability contour | 47.4 | 36.7 | 46.2 | 19.8 |
| MCP: 100% contour | 157.6 | 171.5 | 104.7 | 108.5 |

Nature Reserves was 121.3 km$^2$ ± 112.35 (SD) when using the 100% minimum convex polygon method (n = 133 locations), and 195.9 km$^2$ ± 56.91 (SD) based on the 95% probability contour of the kernel analysis method. For females C, S and M the core area of use varied from 19.8 km$^2$ to 46.2 km$^2$ (50% probability contour of the kernel analysis method) (Figures 6.2 to 6.4). The mean size of the core area utilised by female lions in the Associated Private Nature Reserves was 34.2 km$^2$ ± 33.22 (SD). These range sizes of lion prides in the Associated Private Nature Reserves were in accordance with the results of other lions studies in similar habitats (Table 6.2).

Male coalition N was located on 151 occasions and the size of their range was estimated at 157.6 km$^2$ (100% minimum convex polygon method) and 193.9 km$^2$ (95% probability contour of the kernel analysis method) (Figs. 6.1 and 6.6) (Table 6.1). The core area utilised by male coalition N was 47.4 km$^2$ (50% probability contour of the kernel analysis method). The range size of male coalition N was similar to the mean range size for females C, S and M based on the 100% minimum convex polygon method ($t = 0.696$; df = 2; $P > 0.05$) and the 95% probability contour of the kernel analysis method ($t = 0.076$; df = 2; $P > 0.05$). There was no significant difference in the size of the core area utilised by male coalition N and the mean size of the core area utilised by female lions in the study area ($t = 0.853$; df = 2; $P > 0.05$). These results were consistent with range use patterns for lions in the Kruger National Park (Funston 1999).

The ranges of male coalition N and female M overlapped (Figures 6.5 and 6.10). Based on the kernel range analysis method the area of overlap was 74.9 km$^2$, whereas the 100% minimum convex polygon method indicated that the area of overlap was 6.7 km$^2$ (Figure 6.10). There was no apparent overlap between the range of females C, S, and M.

**Table 6.2**: *Comparison of the mean range sizes (km²) and prey density (kg/km²) of lions in the Associated Private Nature Reserves with other studies. Sources of data: Present study, Bothma & Walker (1999), Sunquist & Sunquist (2002). The range sizes of the lions in the present study were based on the 100% minimum convex polygon method.*

| **AREA** | **RANGE SIZES** | | | **PREY DENSITY** | | | |
|---|---|---|---|---|---|---|---|
| | Males | Females | Source | Wet season | | Dry season | Source |
| Associated Private Nature Reserves | 194 | 84 - 172 | Turner (current study) | 3160 | | 2945 | Present study |
| Central Kalahari Game Reserve | ~ | 702 - 3900 | Owens & Owens (1984) | ~ | | ~ | ~ |
| Etosha National Park | ~ | 150 - 2075 | Stander (1992) | ~ | | ~ | ~ |
| Kaudom Game Reserve | ~ | 1055 - 1745 | Stander (1997) | ~ | | ~ | |
| Kruger National Park | 167 | 100 - 150 | Whyte (1985); Funston (1999) * | ~ | | ~ | ~ |
| Ngorongoro Crater | ~ | 45 | Schaller (1972) | 11 693 | | 12 000 | Bothma & Walker (1999) |
| Phinda Resource Reserve | 130 | 53 | Hunter (1998) | ~ | 1996 [a] | ~ | Hunter (1998) |
| Savuti Marsh | ~ | 300 | McBride (1990) | 27 000 | | 2000 | Bothma & Walker (1999) |
| Serengeti National Park | ~ | 200 | Hanby *et al.* (1995) | 20 000 | | 1000 | Bothma & Walker (1999) |
| Welgevonden Private Game Reserve | 251 | 101 - 233 | Kilian (2003) | ~ | 1860 [b] | ~ | Kilian (2003) |

~ No data available

* Data for the range size of female lions in the Kruger National Park were based on Whyte (1985)

[a b] not known whether the values for the prey density in the Phinda Resource Reserve and the Welgevonden Private Game Reserve are for the wet or dry season

### Habitat selection

Table 6.3 shows that the *Combretum apiculatum* Bushveld on shallow soils and the *Acacia nigrescens* – *Combretum apiculatum* Tall Woodlands on deep soils covered most of the Associated Private Nature Reserves. As was expected, the *Combretum apiculatum* Bushveld on shallow soils and the *Acacia nigrescens* – *Combretum apiculatum* Tall Woodlands on deep soils were also the most frequently utilised vegetation types by the focal lions and their most abundant prey, and the focal lions killed most of their prey in these vegetation types (Table 6.3).

Females C, S and M, and male coalition N had no particular habitat preferences within their respective ranges (Table 6.4 to 6.7). Not one of the vegetation types was preferred by the focal lions, and there was no particular vegetation type that all the focal lions did not utilize. Moreover they were all utilised in proportion to their availability.

The preferred vegetation types of the focal lions and the eight most abundant types of their prey in the Associated Private Nature Reserves appear in Tables 6.8 to 6.11. At the landscape level, the focal lions and their most abundant prey showed distinct habitat preferences. There was a partial overlap in the preferred vegetation types of the lions and that of their most frequently killed prey. The lions preferred the *Combretum apiculatum* Bushveld on shallow soils and the *Acacia nigrescens* – *Combretum apiculatum* Tall Woodlands on deep soils. The buffalo and giraffe showed a preference for the *Acacia nigrescens* – *Combretum apiculatum* Tall Woodlands on deep soils, whilst the impala and Burchell's zebra preferred the *Combretum apiculatum* Bushveld on shallow soils. Although the blue wildebeest, greater kudu, warthog and waterbuck in the study area showed no preference of use for the preferred vegetation types of the lions, they utilised these vegetation

**Table 6.3**: *Habitat selection at the landscape level by the lions and their most abundant prey in the Associated Private Nature Reserves, South Africa, based on range analyses for male coalition N and females C, S and M, and the simplified vegetation map of Van Rooyen et al. (2005). The percentage of prey killed by the lions (Chapter 6) in each vegetation type is also shown.*

| **VEGETATION TYPE** | **AREA IN KM$^2$** | **PERCENTAGE OF AVAILABLE HABITAT** | **PERCENTAGE OF HABITAT USED BY FOCAL LIONS** | **PERCENTAGE CONTRIBUTION OF ANIMALS KILLED BY FOCAL LIONS** | **PERCENTAGE OF HABITAT USED BY THE MOST ABUNDANT LION PREY** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Blue wildebeest | Burchell's zebra | Buffalo | Giraffe | Impala | Greater kudu | Warthog | Waterbuck |
| *Terminalia sericea* Woodland on sandy soils | 144.3 | 10.0 | 1.7 | 3.5 | 2.9 | 21.0 | 5.5 | 4.2 | 7.0 | 9.7 | 11.3 | 0.0 |
| *Combretum apiculatum* Bushveld on shallow soils | 311.0 | 21.5 | 33.1 | 22.8 | 25.3 | 10.4 | 27.5 | 19.1 | 23.7 | 17.4 | 17.1 | 18.7 |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 81.7 | 5.6 | 3.1 | 1.8 | 15.3 | 15.5 | 6.2 | 9.3 | 4.3 | 6.9 | 8.8 | 9.0 |
| *Combretum apiculatum - Terminalia prunoides* Rugged Veld | 33.0 | 2.3 | 0.0 | 0.0 | 0.0 | 0.0 | 1.8 | 3.6 | 0.8 | 1.4 | 0.0 | 0.0 |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 282.9 | 19.6 | 34.8 | 36.8 | 19.4 | 31.0 | 26.6 | 26.6 | 16.5 | 18.5 | 18.8 | 11.6 |
| *Colophospermum mopane - Combretum apiculatum* Woodland | 99.2 | 6.9 | 2.4 | 0.0 | 5.3 | 0.8 | 2.6 | 0.6 | 5.7 | 2.5 | 4.6 | 1.3 |
| *Colophospermum mopane* Dense Woodland and Shrubveld *(thicket)* | 171.6 | 11.9 | 2.7 | 7.0 | 0.0 | 5.4 | 2.2 | 2.1 | 3.2 | 11.3 | 4.2 | 1.3 |
| *Spirostachys africana - Euclea divonorum* Mixed Alluvial Savanna | 52.1 | 3.6 | 1.4 | 1.8 | 0.0 | 0.0 | 0.7 | 0.0 | 1.2 | 1.9 | 5.8 | 0.0 |
| *Acacia nigrescens - Combretum hereroense O* pen Woodland on gabbro | 54.5 | 3.8 | 0.3 | 0.0 | 28.8 | 0.0 | 5.5 | 14.6 | 8.9 | 1.9 | 5.0 | 0.0 |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 63.2 | 4.4 | 5.8 | 5.3 | 0.0 | 12.3 | 2.6 | 7.5 | 10.0 | 7.6 | 5.8 | 7.1 |
| Riparian Woodland | 140.8 | 9.7 | 14.7 | 21.1 | 2.9 | 3.6 | 18.7 | 12.5 | 18.5 | 20.8 | 18.8 | 51.0 |
| Dolerite dykes | 12.5 | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Total | 1446.7 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |

**Table 6.4**: *The habitat selection of male coalition N in the Klaserie Private Nature Reserve, South Africa from May 2001 to August 2002, based on the minimum convex polygon method for range analysis, the habitat selection index of Jacobs (1974) and a chi-square analysis value of $\chi^2$ = 26.545; df = 7; P < 0.01. The relevant 95% Bonferroni confidence intervals (α = 0.05; k = 8; Z = 2.70) are also shown. The simplified vegetation map of Van Rooyen et al. (2005) was used.*

| **VEGETATION TYPE** | **RADIO LOCATIONS** | | **PROPORTION OF HABITAT AVAILABLE** | **HABITAT SELECTION INDEX*** | **CHI-SQUARE CONTRIBUTION** | **BONFERRONI CONFIDENCE INTERVAL** | **HABITAT USE** |
|---|---|---|---|---|---|---|---|
| | Number of locations | Proportion of habitat covered | | | | | |
| *Combretum apiculatum* Bushveld on shallow soils | 56 | 0.533 | 0.575 | -0.08 | 3.497 | (0.413; 0.654) | No pattern |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 4 | 0.038 | 0.012 | 0.53 | 3.801 | (-0.008; 0.084) | No pattern |
| *Combretum apiculatum - Terminalia prunoides* Rugged Veld | 0 | 0.000 | 0.004 | -1.00 | 0.468 | (0.000; 0.000) | Not used |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 17 | 0.162 | 0.279 | -0.33 | 9.165 | (0.073; 0.251) | Not used |
| *Colophospermum mopane* Dense Woodland and Shrubveld (thicket) | 0 | 0.000 | 0.001 | -1.00 | 0.024 | (0.000; 0.000) | Not used |
| *Spirostachys africana - Euclea divonorum* Mixed Alluvial Savanna | 0 | 0.000 | 0.001 | -1.00 | 0.151 | (0.000; 0.000) | Not used |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 12 | 0.114 | 0.048 | 0.43 | 5.868 | (0.037; 0.191) | No pattern |
| Riparian Woodland | 16 | 0.153 | 0.080 | 0.35 | 3.571 | (0.066; 0.240) | No pattern |
| Total | 125 | 1.000 | 1.000 | | 26.545 | | |

* Values between -1 and 0 indicate that the vegetation type was not used by the focal lions
Value of 0 indicates that the focal lions used the vegetation type in accordance with its availability
Values between 0 and +1 indicate that the focal lions preferred the vegetation type

**Table 6.5**: *The habitat selection of female M in the Klaserie Private Nature Reserve, South Africa, from May 2001 to August 2002, based on the minimum convex polygon method for range analysis, the habitat selection index of Jacobs (1974) and a chi square analysis value of $\chi^2$ = 14.548; df = 8; P < 0.01. The relevant 95% Bonferroni confidence intervals (α = 0.05; k = 9; Z = 2.75) are also shown. The simplified vegetation map of Van Rooyen et al. (2005) was used.*

| **VEGETATION TYPE** | **RADIO LOCATIONS** | | **PROPORTION OF HABITAT AVAILABLE** | **HABITAT SELECTION INDEX*** | **CHI-SQUARE CONTRIBUTION** | **BONFERRONI CONFIDENCE INTERVAL** | **HABITAT USE** |
|---|---|---|---|---|---|---|---|
| | Number of locations | Proportion of habitat covered | | | | | |
| *Combretum apiculatum* Bushveld on shallow soils | 32 | 0.264 | 0.375 | -0.253 | 6.439 | (0.159; 0.369) | Not used |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 2 | 0.017 | 0.023 | -0.158 | 0.334 | (-0.014; 0.047) | No pattern |
| *Combretum apiculatum - Terminalia prunoides* Rugged Veld | 0 | 0.000 | 0.001 | -1.000 | 0.186 | (0.000; 0.000) | Not used |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 66 | 0.545 | 0.460 | 0.169 | 0.381 | (0.426; 0.664) | No pattern |
| *Colophospermum mopane - Combretum apiculatum* Woodland | 0 | 0.000 | 0.002 | -1.000 | 0.233 | (0.000; 0.000) | Not used |
| *Colophospermum mopane* Dense Woodland and Shrubveld (thicket) | 0 | 0.000 | 0.004 | -1.000 | 0.481 | (0.000; 0.000) | Not used |
| *Spirostachys africana - Euclea divonorum* Mixed Alluvial Savanna | 0 | 0.000 | 0.002 | -1.000 | 0.248 | (0.000; 0.000) | Not used |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 3 | 0.025 | 0.050 | -0.347 | 1.987 | (-0.012; 0.062) | No pattern |
| Riparian Woodland | 18 | 0.150 | 0.084 | 0.318 | 4.260 | (0.065; 0.235) | No pattern |
| Total | 133 | 1.000 | 1.000 | | 14.548 | | |

* Values between -1 and 0 indicate that the vegetation type was not used by the focal lions
Value of 0 indicates that the focal lions used the vegetation type in accordance with its availability
Values between 0 and +1 indicate that the focal lions preferred the vegetation type

**Table 6.6**: *The habitat selection of female C in the Timbavati Private Nature Reserve, South Africa, from May 2001 to August 2002, based on the minimum convex polygon method for range analysis, the habitat selection index of Jacobs (1974) and a chi square analysis value of* $\chi^2 = 26.813$; *df = 9; P<0.01. The relevant 95% Bonferroni confidence intervals (α = 0.05; k = 10; Z = 2.76) are also shown. The simplified vegetation map of Van Rooyen et al. (2005) was used.*

| **VEGETATION TYPE** | **RADIO LOCATIONS** | | **PROPORTION OF HABITAT AVAILABLE** | **HABITAT SELECTION INDEX*** | **CHI-SQUARE CONTRIBUTION** | **BONFERRONI CONFIDENCE INTERVAL** | **HABITAT USE** |
|---|---|---|---|---|---|---|---|
| | Number of locations | Proportion of habitat covered | | | | | |
| *Terminalia sericea* Woodland on sandy soils | 5 | 0.132 | 0.294 | -0.464 | 3.398 | (-0.020; 0.284) | Not used |
| *Combretum apiculatum* Bushveld on shallow soils | 8 | 0.211 | 0.183 | 0.088 | 0.158 | (0.028; 0.394) | No pattern |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 2 | 0.053 | 0.055 | -0.019 | 0.004 | (-0.047; 0.153) | No pattern |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 13 | 0.342 | 0.144 | 0.511 | 10.375 | (0.130; 0.554) | No pattern |
| *Colophospermum mopane - Combretum apiculatum* woodland | 1 | 0.025 | 0.004 | 0.717 | 4.419 | (-0.045; 0.095) | No pattern |
| *Colophospermum mopane* Dense Woodland and Shrubveld (thicket) | 0 | 0.000 | 0.039 | -1.000 | 1.478 | (0.000; 0.000) | Not used |
| *Spirostachys africana - Euclea divonorum* Mixed Alluvial Savanna | 4 | 0.105 | 0.129 | -0.118 | 0.171 | (-0.032; 0.242) | No pattern |
| *Acacia nigrescens - Combretum hereroense* Open Woodland on gabbro | 1 | 0.026 | 0.004 | 0.754 | 5.204 | (-0.045; 0.097) | No pattern |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 2 | 0.053 | 0.035 | 0.219 | 0.358 | (-0.047; 0.153) | No pattern |
| Riparian Woodland | 2 | 0.053 | 0.114 | -0.393 | 1.249 | (-0.047; 0.153) | No pattern |
| Total | 38 | 1.000 | 1.000 | | 26.813 | | |

* Values between -1 and 0 indicate that the vegetation type was not used by the focal lions
Value of 0 indicates that the focal lions used the vegetation type in accordance with its availability
Values between 0 and +1 indicate that the focal lions preferred the vegetation type

**Table 6.7**: *The habitat selection of female S in the Timbavati Private Nature Reserve, South Africa, from May 2001 to August 2002, based on the minimum convex polygon method for range analysis, the habitat selection index of Jacobs (1974) and a chi square analysis value of* $\chi^2 = 7.318$; *df = 7; P < 0.01. The relevant 95% Bonferroni confidence intervals (α = 0.05; k = 8; Z = 2.70) are also shown. The simplified vegetation map of Van Rooyen et al. (2005) was used.*

| **VEGETATION TYPE** | **RADIO LOCATIONS** | | **PROPORTION OF HABITAT AVAILABLE** | **HABITAT SELECTION INDEX*** | **CHI-SQUARE CONTRIBUTION** | **BONFERRONI CONFIDENCE INTERVAL** | **HABITAT USE** |
|---|---|---|---|---|---|---|---|
| | Number of locations | Proportion of habitat covered | | | | | |
| *Combretum apiculatum* Bushveld on shallow soils | 1 | 0.034 | 0.097 | -0.505 | 1.163 | (-0.057; 0.125) | No pattern |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 1 | 0.034 | 0.025 | 0.154 | 0.100 | (-0.057; 0.125) | No pattern |
| *Combretum apiculatum - Terminalia prunoides* Rugged Veld | 0 | 0.000 | 0.027 | -1.000 | 0.783 | (0.000; 0.000) | Not used |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 6 | 0.207 | 0.136 | 0.249 | 1.088 | (0.004; 0.410) | No pattern |
| *Colophospermum mopane - Combretum apiculatum* woodland | 6 | 0.207 | 0.292 | -0.225 | 0.723 | (0.004; 0.410) | No pattern |
| *Colophospermum mopane* Dense Woodland and Shrubveld (thicket) | 8 | 0.276 | 0.283 | -0.017 | 0.005 | (0.052; 0.500) | No pattern |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 0 | 0.000 | 0.014 | -1.000 | 0.406 | (0.000; 0.000) | Not used |
| Riparian Woodland | 7 | 0.242 | 0.126 | 0.377 | 3.050 | (0.027; 0.457) | No pattern |
| Total | 29 | 1.000 | 1.000 | | 7.318 | | |

* Values between -1 and 0 indicate that the vegetation type was not used by the focal lions
Value of 0 indicates that the focal lions used the vegetation type in accordance with its availability
Values between 0 and +1 indicate that the focal lions preferred the vegetation type

**Table 6.8**: *A comparison of the habitat selection of the lions in the Associated Private Nature Reserves of South Africa with that of the blue wildebeest and buffalo from May 2001 to August 2002, based on range analysis data for the focal lions, aerial counting data for the prey animals (Chapter 4), and in conjunction with 95% Bonferroni confidence intervals ($\alpha = 0.05$; $k = 12$; $Z = 2.80$).The vegetation types used were based on the simplified vegetation map of Van Rooyen et.al. (2005).*

| VEGETATION TYPE | HABITAT SELECTION | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Lions** | | | **Blue wildebeest** | | | | **Buffalo** | | | |
| | Proportion of habitat available | Bonferroni confidence interval | Habitat selection * | $\chi^2$ | ***P*** | Bonferroni confidence interval | Habitat selection | $\chi^2$ | ***P*** | Bonferroni confidence interval | Habitat selection |
| *Terminalia sericea* Woodland on sandy soils | 0.100 | (-0.004; 0.038) | Not used | 8.471 | < 0.05 | (-0.007; 0.066) | Not used | 270.811 | < 0.05 | (0.186; 0.234) | Preferred |
| *Combretum apiculatum* Bushveld on shallow soils | 0.215 | (0.254; 0.408) | Preferred | 1.138 | > 0.05 | (0.160; 0.346) | No pattern | 128.074 | < 0.05 | (0.086; 0.122) | Not used |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 0.056 | (0.002; 0.059) | No pattern | 28.528 | < 0.05 | (0.076; 0.230) | Preferred | 397.846 | < 0.05 | (0.134; 0.177) | Preferred |
| *Combretum apiculatum - Terminalia prunoides* Rugged Veld | 0.022 | (0.000; 0.000) | Not used | 3.740 | < 0.05 | (0.000; 0.000) | Not used | 49.522 | < 0.05 | (0.000; 0.000) | Not used |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 0.196 | (0.270; 0.426) | Preferred | 0.003 | > 0.05 | (0.109; 0.279) | No pattern | 149.476 | < 0.05 | (0.283; 0.337) | Preferred |
| *Colophospermum mopane - Combretum apiculatum* Woodland | 0.069 | (-0.001; 0.049) | Not used | 0.635 | > 0.05 | (0.005; 0.101) | No pattern | 123.180 | < 0.05 | (0.002; 0.013) | Not used |
| *Colophospermum mopane* Dense Woodland and Shrubveld (thicket) | 0.119 | (0.001; 0.054) | Not used | 20.230 | < 0.05 | (0.000; 0.000) | Not used | 79.433 | < 0.05 | (0.041; 0.068) | Not used |
| *Spirostachys africana - Euclea divonorum* Mixed Alluvial Savanna | 0.036 | (-0.005; 0.033) | Not used | 6.120 | > 0.05 | (0.000; 0.000) | Not used | 81.036 | < 0.05 | (0.000; 0.000) | Not used |
| *Acacia nigrescens - Combretum hereroense* Open Woodland on gabbro | 0.038 | (-0.006; 0.013) | Not used | 280.132 | < 0.05 | (0.191; 0.386) | Preferred | 85.538 | < 0.05 | (0.000; 0.000) | Not used |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 0.044 | (0.020; 0.096) | No pattern | 7.480 | < 0.05 | (0.000; 0.000) | Not used | 316.157 | < 0.05 | (0.103; 0.142) | Preferred |
| Riparian Woodland | 0.097 | (0.089; 0.205) | No pattern | 8.006 | < 0.05 | (-0.007; 0.066) | Not used | 86.396 | < 0.05 | (0.025; 0.047) | Not used |
| Dolerite dykes | 0.008 | (0.000; 0.000) | Not used | 1.360 | > 0.05 | (0.000; 0.000) | Not used | 18.008 | < 0.05 | (0.000; 0.000) | Not used |

*** Not used: habitat is utilized in a smaller proportion than its availability by the focal lions and their eight most abundant types of prey**
**No pattern: habitat is utilized in the same proportion as its availability by the focal lions and their eight most abundant types of prey**
**Preferred: habitat is utilized in a greater proportion than its availability by the focal lions and their eight most abundant types of prey**

**Table 6.9**: A comparison of the habitat selection of the lions in the Associated Private Nature Reserves of South Africa with that of the Burchell's zebra and giraffe from May 2001 to August 2002, based on range analysis data for the focal lions, aerial counting data for the prey animals (Chapter 4), and in conjunction with 95% Bonferroni confidence intervals (α = 0.05; k = 12; Z = 2.80).The vegetation types used were based on the simplified vegetation map of Van Rooyen et.al. (2005).

| **VEGETATION TYPE** | **HABITAT SELECTION** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Lions** | | | **Burchell's zebra** | | | | **Giraffe** | | | |
| | Proportion of habitat available | Bonferroni confidence interval | Habitat selection * | $\chi^2$ | ***P*** | Bonferroni confidence interval | Habitat selection | $\chi^2$ | ***P*** | Bonferroni confidence interval | Habitat selection |
| *Terminalia sericea* Woodland on sandy soils | 0.100 | (-0.004; 0.038) | Not used | 11.084 | < 0.05 | (0.028; 0.082) | Not used | 11.351 | < 0.05 | (0.011; 0.072) | Not used |
| *Combretum apiculatum* Bushveld on shallow soils | 0.215 | (0.254; 0.408) | Preferred | 9.059 | < 0.05 | (0.221; 0.328) | No pattern | 0.894 | > 0.05 | (0.131; 0.251) | No pattern |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 0.056 | (0.002; 0.059) | No pattern | 0.383 | > 0.05 | (0.033; 0.091) | No pattern | 7.986 | < 0.05 | (0.048; 0.137) | No pattern |
| *Combretum apiculatum - Terminalia prunoides* Rugged Veld | 0.022 | (0.000; 0.000) | Not used | 0.337 | > 0.05 | (0.002; 0.034) | No pattern | 2.909 | > 0.05 | (0.007; 0.064) | No pattern |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 0.196 | (0.270; 0.426) | Preferred | 13.482 | < 0.05 | (0.213; 0.318) | Preferred | 8.297 | < 0.05 | (0.198; 0.333) | Preferred |
| *Colophospermum mopane - Combretum apiculatum* Woodland | 0.069 | (-0.001; 0.049) | Not used | 14.877 | < 0.05 | (0.007; 0.045) | Not used | 19.288 | < 0.05 | (-0.006; 0.018) | Not used |
| *Colophospermum mopane* Dense Woodland and Shrubveld (thicket) | 0.119 | (0.001; 0.054) | Not used | 43.190 | < 0.05 | (0.004; 0.040) | Not used | 27.094 | < 0.05 | (-0.001; 0.043) | Not used |
| *Spirostachys africana - Euclea divonorum* Mixed Alluvial Savanna | 0.036 | (-0.005; 0.033) | Not used | 12.470 | < 0.05 | (-0.003; 0.018) | Not used | 12.060 | < 0.05 | (0.000; 0.000) | Not used |
| *Acacia nigrescens - Combretum hereroense* Open Woodland on gabbro | 0.038 | (-0.006; 0.013) | Not used | 4.126 | < 0.05 | (0.028; 0.082) | No pattern | 103.340 | < 0.05 | (0.092; 0.200) | Preferred |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 0.044 | (0.020; 0.096) | No pattern | 4.183 | < 0.05 | (0.007; 0.045) | No pattern | 7.142 | < 0.05 | (0.034; 0.115) | Not used |
| Riparian Woodland | 0.097 | (0.089; 0.205) | No pattern | 47.275 | < 0.05 | (0.142; 0.236) | Preferred | 2.780 | > 0.05 | (0.075; 0.176) | Not used |
| Dolerite dykes | 0.008 | (0.000; 0.000) | Not used | 4.368 | < 0.05 | (0.000; 0.000) | Not used | 2.680 | > 0.05 | (0.000; 0.000) | Not used |

*** Not used: habitat is utilized in a smaller proportion than its availability by the focal lions and their eight most abundant types of prey**
**No pattern: habitat is utilized in the same proportion as its availability by the focal lions and their eight most abundant types of prey**
**Preferred: habitat is utilized in a greater proportion than its availability by the focal lions and their eight most abundant types of prey**

**Table 6.10**: A comparison of the habitat selection of the lions in the Associated Private Nature Reserves of South Africa with that of the impala and greater kudu from May 2001 to August 2002, based on range analysis data for the focal lions, aerial counting data for the prey animals (Chapter 4), and in conjunction with 95% Bonferroni confidence intervals ($\alpha = 0.05$; $k = 12$; $Z = 2.80$).The vegetation types used were based on the simplified vegetation map of Van Rooyen et.al. (2005).

| **VEGETATION TYPE** | **HABITAT SELECTION** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Lions** | | | **Impala** | | | | **Greater kudu** | | | |
| | Proportion of habitat available | Bonferroni confidence interval | Habitat selection * | $\chi^2$ | ***P*** | Bonferroni confidence interval | Habitat selection | $\chi^2$ | ***P*** | Bonferroni confidence interval | Habitat selection |
| *Terminalia sericea* Woodland on sandy soils | 0.100 | (-0.004; 0.038) | Not used | 55.587 | < 0.05 | (0.069; 0.084) | Not used | 0.066 | > 0.05 | (0.057; 0.136) | No pattern |
| *Combretum apiculatum* Bushveld on shallow soils | 0.215 | (0.254; 0.408) | Preferred | 89.658 | < 0.05 | (0.246; 0.271) | Preferred | 3.824 | < 0.05 | (0.121; 0.222) | No pattern |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 0.056 | (0.002; 0.059) | No pattern | 14.797 | < 0.05 | (0.041; 0.053) | Not used | 1.249 | > 0.05 | (0.035; 0.103) | No pattern |
| *Combretum apiculatum - Terminalia prunoides* Rugged Veld | 0.022 | (0.000; 0.000) | Not used | 77.314 | < 0.05 | (0.006; 0.012) | Not used | 1.359 | > 0.05 | (-0.002; 0.029) | No pattern |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 0.196 | (0.270; 0.426) | Preferred | 12.953 | < 0.05 | (0.170; 0.191) | Not used | 0.517 | > 0.05 | (0.129; 0.232) | No pattern |
| *Colophospermum mopane - Combretum apiculatum* Woodland | 0.069 | (-0.001; 0.049) | Not used | 6.361 | < 0.05 | (0.056; 0.069) | No pattern | 12.166 | < 0.05 | (0.004; 0.046) | Not used |
| *Colophospermum mopane* Dense Woodland and Shrubveld (thicket) | 0.119 | (0.001; 0.054) | Not used | 601.429 | < 0.05 | (0.030; 0.040) | Not used | 0.173 | > 0.05 | (0.070; 0.154) | No pattern |
| *Spirostachys africana - Euclea divonorum* Mixed Alluvial Savanna | 0.036 | (-0.005; 0.033) | Not used | 146.728 | < 0.05 | (0.010; 0.016) | Not used | 0.191 | > 0.05 | (0.008; 0.056) | No pattern |
| *Acacia nigrescens - Combretum hereroense* Open Woodland on gabbro | 0.038 | (-0.006; 0.013) | Not used | 385.928 | < 0.05 | (0.000; 0.000) | Not used | 4.460 | < 0.05 | (0.000; 0.036) | Not used |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 0.044 | (0.020; 0.096) | No pattern | 1330.720 | < 0.05 | (0.111; 0.129) | Preferred | 9.864 | < 0.05 | (0.040; 0.111) | No pattern |
| Riparian Woodland | 0.097 | (0.089; 0.205) | No pattern | 1068.288 | < 0.05 | (0.187; 0.209) | Preferred | 53.476 | < 0.05 | (0.152; 0.260) | Preferred |
| Dolerite dykes | 0.008 | (0.000; 0.000) | Not used | 81.248 | < 0.05 | (0.000; 0.000) | Not used | 3.496 | > 0.05 | (0.000; 0.000) | Not used |

*** Not used: habitat is utilized in a smaller proportion than its availability by the focal lions and their eight most abundant types of prey**
**No pattern: habitat is utilized in the same proportion as its availability by the focal lions and their eight most abundant types of prey**
**Preferred: habitat is utilized in a greater proportion than its availability by the focal lions and their eight most abundant types of prey**

**Table 6.11**: A comparison of the habitat selection of the lions in the Associated Private Nature Reserves of South Africa with that of the warthog and waterbuck from May 2001 to August 2002, based on range analysis data for the focal lions, aerial counting data for the prey animals (Chapter 4), and in conjunction with 95% Bonferroni confidence intervals ($\alpha = 0.05$; $k = 12$; $Z = 2.80$).The vegetation types used were based on the simplified vegetation map of Van Rooyen et.al. (2005).

| **VEGETATION TYPE** | **HABITAT SELECTION** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Lions** | | | **Warthog** | | | | **Waterbuck** | | | |
| | Proportion of habitat available | Bonferroni confidence interval | Habitat selection * | $\chi^2$ | ***P*** | Bonferroni confidence interval | Habitat selection | $\chi^2$ | ***P*** | Bonferroni confidence interval | Habitat selection |
| *Terminalia sericea* Woodland on sandy soils | 0.100 | (-0.004; 0.038) | Not used | 0.375 | > 0.05 | (0.055; 0.170) | No pattern | 15.500 | < 0.05 | (0.000; 0.000) | Not used |
| *Combretum apiculatum* Bushveld on shallow soils | 0.215 | (0.254; 0.408) | Preferred | 2.178 | > 0.05 | (0.103; 0.239) | No pattern | 0.561 | > 0.05 | (0.099; 0.275) | No pattern |
| *Combretum apiculatum - Sclerocarya birrea* Open Woodland | 0.056 | (0.002; 0.059) | No pattern | 4.253 | < 0.05 | (0.036; 0.139) | No pattern | 3.261 | > 0.05 | (0.026; 0.155) | No pattern |
| *Combretum apiculatum - Terminalia prunoides* Rugged Veld | 0.022 | (0.000; 0.000) | Not used | 5.280 | < 0.05 | (0.000; 0.000) | Not used | 3.410 | > 0.05 | (0.000; 0.000) | Not used |
| *Acacia nigrescens - Combretum apiculatum* Tall Woodland on deep soils | 0.196 | (0.270; 0.426) | Preferred | 0.088 | > 0.05 | (0.117; 0.258) | No pattern | 5.045 | < 0.05 | (0.044; 0.188) | Not used |
| *Colophospermum mopane - Combretum apiculatum* Woodland | 0.069 | (-0.001; 0.049) | Not used | 1.867 | > 0.05 | (0.008; 0.084) | No pattern | 7.069 | < 0.05 | (-0.012; 0.038) | Not used |
| *Colophospermum mopane* Dense Woodland and Shrubveld (thicket) | 0.119 | (0.001; 0.054) | Not used | 12.061 | < 0.05 | (0.006; 0.078) | Not used | 14.662 | < 0.05 | (-0.012; 0.038) | Not used |
| *Spirostachys africana - Euclea divonorum* Mixed Alluvial Savanna | 0.036 | (-0.005; 0.033) | Not used | 3.325 | > 0.05 | (0.016; 0.101) | Not used | 5.580 | < 0.05 | (0.000; 0.000) | Not used |
| *Acacia nigrescens - Combretum hereroense* Open Woodland on gabbro | 0.038 | (-0.006; 0.013) | Not used | 0.909 | > 0.05 | (0.011; 0.089) | No pattern | 5.890 | < 0.05 | (0.000; 0.000) | Not used |
| *Acacia tortillis - Euclea divonorum* Lowland Woodland | 0.044 | (0.020; 0.096) | No pattern | 1.121 | > 0.05 | (0.016; 0.101) | No pattern | 2.562 | > 0.05 | (0.013; 0.129) | No pattern |
| Riparian Woodland | 0.097 | (0.089; 0.205) | No pattern | 20.265 | < 0.05 | (0.117; 0.258) | Preferred | 272.133 | < 0.05 | (0.397; 0.622) | Preferred |
| Dolerite dykes | 0.008 | (0.000; 0.000) | Not used | 1.920 | > 0.05 | (0.000; 0.000) | Not used | 1.240 | > 0.05 | (0.000; 0.000) | Not used |

*** Not used: habitat is utilized in a smaller proportion than its availability by the focal lions and their eight most abundant types of prey**
**No pattern: habitat is utilized in the same proportion as its availability by the focal lions and their eight most abundant types of prey**
**Preferred: habitat is utilized in a greater proportion than its availability by the focal lions and their eight most abundant types of prey**

types in proportion to their availability.

## DISCUSSION

The ranging behaviour and habitat use of a predator are integral to a study of predator-prey dynamics. The range use and habitat selection of a predator are correlated with prey availability and the habitat preferences of their preferred prey (Sunquist & Sunquist 2002). The spatial use patterns and habitat selection of the lions in the Associated Private Nature Reserves have not previously been determined. Radio-telemetry appeared to be an effective method for locating lions when gathering data for range use analysis in the Associated Private Nature Reserves.

### Range use

The lions in the Associated Private Nature Reserves followed the general pattern of range use of lions elsewhere in African savannas. The focal prides occupied a defended territory or core area within a defined range, and the male coalition N had an undefended range. The range size of the males and females was in accordance with that of lions in habitats with similar prey abundance. The small sample size for the males in the present study prevented a conclusive comparison between the genders for the lions in the Associated Private Nature Reserves.

The range size of lions across various habitats is inversely correlated with lean season prey availability (Van Orsdol *et al.* 1985). Evidence from earlier lion studies has shown that the range sizes of lions in arid savannas such as the Etosha National Park, Kaudom Game Reserve, Savuti Marsh and the Kgalagadi Transfrontier Park were larger than that in the more mesic savannas of the Serengeti National Park and the Ngorongoro Crater (Schaller 1972;

McBride 1990; Stander 1990; Stander 1997; Hanby *et al.* 1995; Funston 2001; Kilian 2003). The range sizes of the lion prides in the Associated Private Nature Reserves followed the same trend. The mean range size of females C, S and M was larger than that for females in the more mesic and prey-rich Ngorongoro Crater (Hanby *et al.* 1995) and Lake Manyara National Park (Schaller 1972), but smaller than in the more arid and prey-poor Central Kalahari Game Reserve (Owens & Owens 1984) and Kaudom Game Reserve (Stander 1997) (Table 6.2).

The range size of male coalition N was also as expected when compared to the range sizes of male lions in other African savannas. The range size of male coalition N (158 km$^2$) was smaller than the range sizes of male lions in the arid Kalahari Gemsbok National Park (2000 km$^2$) (Eloff 2002) and the less mesic Welgevonden Private Game Reserve (251 km$^2$) (Kilian 2003). Based on the kernel analysis method the range size of male coalition N was similar to that of non-territorial male lions in the semi-arid savanna of the Kruger National Park (167 km$^2$) (Funston 1999). This observation was expected given that the prey availability in the Associated Private Nature Reserves (115 prey animals/lion) (Chapter 7) was comparable to that in the Kruger National Park (110 prey animals/lion) (Bothma & Walker 1999).

The Phinda Resource Reserve was the only other area for which data were available for the range size of male lions (Hunter 1998). The range size of male coalition N was larger than the range sizes of males in the Phinda Resource Reserve, even though the prey density in the Phinda Resource Reserve (1996 kg/km$^2$) was lower than that in the Associated Private Nature Reserves (3160 kg/km$^2$) (Table 6.2). This is most likely so because the ranges of the reintroduced lions in the Phinda Resource Reserve were limited by the presence of fences (Kilian 2003). In contrast to the Phinda Resource Reserve, the Associated Private Nature

Reserves are an open system with the Kruger National Park. It was therefore not surprising that the range use patterns of the lions in the study area were similar to that of the lions in the Kruger National Park.

The range use of lions in the Associated Private Nature Reserves therefore appeared to follow similar patterns to that of lions in other African savannas, being smaller than those of lions in arid, prey-poor, savannas and greater than in more mesic, prey-rich savannas.

## Habitat selection

The lions show a wide habitat tolerance, and the only type of vegetation in which they are not generally found is dense forest. Visibility is the common factor throughout the various habitat types that lions use. When compared with tigers, jaguars and leopards, lions prefer more open areas. Being a stalk-and-ambush predator, the lions must, however, have some form of cover to enable it to approach its prey to within striking distance (Schaller 1972).

The habitat requirements of lions are sufficient suitable prey, denning sites and drinking water (Hanby *et al.* 1995). The structure of the vegetation influences prey availability and hunting success (Funston 1999). The habitat selection of lions is therefore related to the habitat preferences of their prey as well as the type or structure of the vegetation. Lions usually find their prey by searching slowly through suitable habitats (Schaller 1972). They are, however, opportunistic feeders that use whatever prey is easiest to find and in certain areas they readily scavenge (Bothma & Walker 1999).

The habitat utilization of the lions in the Associated Private Nature Reserves followed the above expected patterns. The vegetation types that covered the largest surface area and were utilised the most by the preferred lion prey were also utilised most frequently by the focal lions. Not surprisingly, the number of prey animals killed by the focal lions was greatest in these vegetation types that were most frequently used by the lions. However, the vegetation type in which a prey animal was killed was not necessarily an indication of the vegetation type in which the lions began the hunt. It was therefore not an infallible index of the habitat selection by the focal lions, although it did validate the occurrence of the preferred habitat types for these lions.

The habitat selection of the focal lions within their respective ranges was not as conclusive as was expected. Not one of the focal lions showed a preference for any particular vegetation type. Moreover they utilised all the vegetation types in proportion to their availability. For females C and S this result was most likely influenced by the low number of radio-fixes that were recorded for them. Because the focal lions utilised most of the available vegetation types in their ranges in proportion to their availability, the present study suggested that the habitat requirements of the focal lions were being met.

The results also agreed with the contention of Van Orsdol *et al.* (1985) that the habitat selection of lions is not dependent on the type of vegetation but rather on the habitat preferences of their prey.

## CONCLUSIONS

The range use and habitat selection of lions in the Associated Private Nature Reserves have not previously been studied. The range use of the lions in the present study appeared to follow similar patterns to that of lions in other African savannas. As was expected, the range sizes were smaller than the range sizes of lions in arid, probably prey-poor, savannas and greater than in more mesic, prey-rich savannas. The range use pattern of male lions was not determined conclusively in this study because of the small sample size. It was only possible to study the range use of one male lion coalition due to logistical and time constraints. At the time of the present study, the study of Funston (1999) was the only detailed study that had been done with an emphasis on male lions. The range size of male coalition N in the Klaserie Private Nature Reserve was similar to that of male lions in the Kruger National Park (Funston 1999).

The habitat selection of the lions in the Associated Private Nature Reserves concurred with that of lions generally in the African savannas. The habitat preferences of the focal lions were in accordance with that of their preferred prey. As was observed for the lions in the Kruger National Park (Mills & Gorman 1997), prey distribution appeared to be the main determinant of habitat selection by the lions in the Associated Private Nature Reserves.

# CHAPTER 7

# FEEDING ECOLOGY

## INTRODUCTION

Predation by large carnivores plays an integral role in the dynamic equilibrium of ungulate populations. Predator-prey relationships are complex and the impact of predation is controversial, especially in managed habitats. Although lions were formerly widespread in Africa south of the Sahara Desert the majority of lions now occur in areas that are enclosed with fences and are managed actively. Even the Kruger National Park, in spite of its large size, is not a self-sustaining system. Predation by lions may play a significant role during a period of man-induced instability of the ecosystem (Kruuk 1986). As the largest of Africa's cats, the influence of the lion on its prey must therefore be considered when managing any area in which it occurs.

Many studies have been done to date on lion predation and its influence on prey populations (e.g: Hirst 1969; Pienaar 1969; Schaller 1972; Smuts 1982; Van Orsdol 1985; Mills & Shenk 1992; Hanby *et al.* 1995; Viljoen 1997; Druce *et al.* 2004). These studies all focussed on pride females as the killing lions, because in those ecosystems the females did most of the hunting (Scheel & Packer 1991). However, in the savanna woodlands of the Kruger National Park, Funston (1999) showed that male lions hunted and killed a major portion of their prey. The prey selection, kill frequency and food consumption rate of male lions was also different from that of female lions. Predation by male lions had a significant impact on the buffalo population in particular. Male lions were found to be efficient predators in the savanna woodland areas that have large buffalo and impala populations. It is likely that this is the case in similar woodland savannas where lions occur.

Several studies have suggested that predators regulate low density, resident prey populations (Whyte & Joubert 1988; Mills & Shenk 1992; Mills *et al.* 1995). Fryxell, Greever and Sinclair (1988) also concluded that predators can limit resident herbivores that occur at low population densities. This is unlikely to occur where resident prey populations are present at high densities, or where large migratory prey populations occur. In the Kruger National Park, lion predation has been identified as a significant regulating factor of the blue wildebeest and Burchell's zebra populations under certain ecological conditions (Smuts 1978; Mills & Shenk 1992; Mills *et al.* 1995; Funston 1999). Smuts (1978) showed that lion predation caused a decline in the blue wildebeest and Burchell's zebra populations in the central district of the Kruger National Park during years of high rainfall. Mills and Shenk (1992) found that lion predation affected blue wildebeest populations more severely than those of Burchell's zebra. Lions in the Kruger National Park selected adult blue wildebeest but juvenile Burchell's zebras as prey. The sedentary behaviour of the blue wildebeest seemed to increase their vulnerability to lion predation. A recent study in the Kruger National Park confirmed this trend. Funston (1999) found that lion predation was proportionally heavy on the resident buffalo and blue wildebeest populations, but less so on the semi-migratory Burchell's zebra population.

A similar pattern of lion predation was found in the Timbavati and the Klaserie Private Nature Reserves (Hirst 1969; Kruger 1988). The removal of the internal fences of the Associated Private Nature Reserves and the boundary fence, on the east, with the Kruger National Park has restored the former movement routes of the blue wildebeest and Burchell's zebra subpopulations. They now again move seasonally within the Associated Private Nature Reserves and between the Associated Private Nature Reserves and the Kruger National Park (Weaver 1995). However, the continued decline in the populations of blue wildebeest and Burchell's zebra in the Associated Private Nature Reserves is of concern to the reserve management, the lodges and landowners. This study investigates the impact of lion predation on the eight most abundant prey types of the lions in the Associated Private Nature Reserves.

The following hypotheses were tested:

- Prey selection by the lions in the Associated Private Nature Reserves has switched from medium-sized prey to larger prey.
- Male lions in the Associated Private Nature Reserves select larger prey and have a higher kill rate than adult female lions.
- Lions in different areas of the Associated Private Nature Reserves show particular preferences for prey.
- There is a relationship between seasonal rainfall and lion predation patterns in the Associated Private Nature Reserves.
- The impact of the current level of lion predation on the prey populations in the Associated Private Nature Reserves is sustainable.

The present study is the first predator-prey study that has been undertaken in the area that is now the Associated Private Nature Reserves, since the removal of the fences with the Kruger National Park and the dismantling of the internal fences in 1993. The presence of fences effects the movement of semi-migratory ungulates including the blue wildebeest and Burchell's zebra, and had an impact on predator-prey dynamics at a given time in the past.

## METHODS

The least biased method of studying the feeding ecology of large carnivores is by direct observation through following radio-collared animals in a vehicle for extended periods (Mills 1992). This method was successfully employed by Viljoen (1997), Funston (1999) and Kilian (2003) for their respective study areas in Chobe National Park, Kruger National Park and the Welgevonden Private Game Reserve.

The data that are required to assess the impact of predators on their prey include many parameters, some of which are difficult to measure. However, the type of prey selected by the predator (prey selection), the number of prey animals killed (kill rate) and the estimated amount of meat consumed (consumption rate) have been identified as some of the important factors in predator-prey studies (Mills & Shenk 1992; Mills *et al.* 1995; Funston 1999; Kilian 2003). These aspects will be addressed here.

A parameter such as the kill rate is influenced by the population dynamics of the prey, but it is notoriously difficult to measure in areas where it is impossible to follow tracks for extended periods, except in snow (Mech 1970) or sand (Mills 1990). To overcome this problem, Mills and Shenk (1992) located and then followed radio-collared lions continuously for periods of up to 336 hours (14 days) to record data on activity, prey encounters and group composition. Funston (1999) observed lions only at night for a minimum of three consecutive nights per session, as it was found that 88% of lion kills in the Kruger National Park are made at night (Mills & Biggs 1993). A similar study was done by Kilian (2003) on the Welgevonden Private Game Reserve, in the Limpopo province of South Africa. The dense vegetation of the Associated Private Nature Reserves made the following of lions for continuous periods and the direct observation of kills difficult. Therefore, for the purposes of the present study, the methods of Mills and Shenk (1992) and Funston (1999) were adapted to include data from predator survey forms and historical kill records to investigate the feeding ecology of the lions in the Associated Private Nature Reserves.

### Rainfall

The rainfall data for the Associated Private Nature Reserves were described in detail in

Chapters 2 and 4. Annual rainfall was calculated from July to June, and a wet season (October to March) and a dry season (April to September) were differentiated. The reserve management and various lodges record annual rainfall for the Associated Private Nature Reserves. The Computing Centre for Water Research has based the long-term mean rainfall for each of the components of the Associated Private Nature Reserves on these data. The rainfall data from 1982 to 2003 were used to determine the seasonality of predation by the lions in the Associated Private Nature Reserves.

### Prey population trends

Population estimates for the larger ungulates were made by using aerial counts that were conducted annually, at the end of the dry season, from 1980 to 2003 (Chapter 4). The aerial counts were obtained for the following periods from the reserve management of the Associated Private Nature Reserves and the Agricultural Research Council's Range and Forage Institute (Peel 2003): for the Timbavati Private Nature Reserve from 1983 to 2003, the Umbabat Private Nature Reserve from 1991 to 2003, and the Klaserie Private Nature Reserve from 1980 to 2003. The aerial counts that were done in the Umbabat and Timbavati Private Nature Reserves during the study period (2000 to 2003) were inconsistent and unreliable (Chapter 4). Therefore, the aerial counts for 2003, which are consistent in terms of methodology for all three of the Associated Private Nature Reserves, were used for the Timbavati and Umbabat Private Nature Reserves. The prey biomass that was obtained from these aerial counts was lower than that obtained from the aerial counts from 2000 to 2002 (Chapter 4). Therefore predation rates that were calculated by using these counts were overestimates rather than underestimates. The subsequent estimate of the impact of lion predation on their prey consequently is a worst case scenario.

Sex and age structures for the most abundant types of lion prey were calculated from road strip censuses. The censuses were done seasonally for each of the Associated Private

Nature Reserves from March 2000 to September 2002 (Chapter 4). The road strip censuses were also used to determine the seasonal abundance of prey.

### Predator survey forms and historical records

Predator survey forms were distributed to the reserve management, landowners and the staff of the lodges within the Associated Private Nature Reserves to record all lion sightings. Additional information on lion activity, prey encounters, pride composition and kill information during the study period were also obtained. The management of the Klaserie Private Nature Reserve and the Timbavati lodges provided historical lion kill data for the period from 1983 to 2003.

### Lion observations

Long-term continual observations (Mills & Shenk 1992; Funston 1999; Kilian 2003) where lions were followed in a vehicle for periods of 10 to 20 hours per day (mean =15 ± 5.6 ; n =120 days) and data on activity, prey encounters, lion group composition and kill information (species, sex, and estimated age of the prey) were recorded whenever possible. The use of short-term continual observation data is biased towards larger kills unless the lions are tracked on a step by step basis (Mills & Shenk 1992). A compromise between short-term (2 to 15 hours) and long-term (up to 336 hours) continual observations was used in the present study, due to logistical and habitat constraints. The focus of the present study was on the impact of lion predation on large herbivores. Hence the modified method was considered to be adequate.

Predation observations were conducted on the dominant lion prides in the Klaserie and the Timbavati Private Nature Reserves. At the time of this study there was no resident lion pride in the Umbabat Private Nature Reserve. Adult female lions do most of the killing of blue wildebeest and Burchell's zebra (Van Orsdol 1986; Mills & Shenk 1992; Funston

1999). Therefore, an adult female lion in each of the three focal prides was radio-collared. Because the focus of this study was the impact of lion predation on their prey, the three largest lion prides were selected for observation. They were identified as prides C, S and M. Funston (1999) showed that coalitions of male lions in the Kruger National Park specialise in hunting buffalo on whose numbers they have a significant impact. Within the Associated Private Nature Reserves male lions formed coalitions of two to five individuals during the present study that focused on the N coalition, the largest of the coalitions. The N coalition consisted of five non-territorial males, all older than four years. They had no regular contact with females and did not defend a territory that contained a group of females. A radio-collar was fitted to one member of the coalition to allow radio-tracking of the group.

The focal animal within each pride was the dominant, radio-collared individual (Mills & Shenk 1992; Funston 1999; Kilian 2003). Each lion pride was followed for three sessions of 10 days (mean duration = 15 ± 5.6 hours per day, n = 120 days) from 26 May 2001 to 25 August 2002. Long-term continual observations were done mainly at night because lions are known to hunt predominantly at night, when they make 88% of their kills (Kruger 1988; Mills & Biggs 1993; Funston 1999). A correction factor was applied for the 12% of kills that were made during the day that may have been missed (Funston 1999). During each observation session of 10 days it was unlikely that any of the larger kills that were made on the first nine nights would be missed, although those made on the tenth night could have been missed. However, kills of smaller prey such as impala, blue wildebeest calves and Burchell's zebra foals would most likely be missed on all nights. The kill rate was therefore adjusted by a factor of 1.12 per night for small prey, and by 1.12 for every tenth night for larger prey, to compensate for missed kills (Funston 1999). Observations were made during both seasons to obtain comparative data.

The lions were observed at night by using the methods of Mills & Shenk (1992) and Funston (1999). In both these studies, the focal animals were observed from a vehicle at a distance of 20 to 30 m by using a spotlight that was fitted with a red filter to avoid any possible influence on the predator-prey interactions. When the lions hunted, the spotlight and vehicle engine were switched off so as not to create a distraction.

Following Mills and Shenk (1992), Krüger (1996), Viljoen (1997), Funston (1999) and Kilian (2003), the following specific methods were used:

### Kill rates

The kill rate was calculated from the data that were obtained during the long-term observations (Mills & Shenk 1992; Funston 1999). The kill rate calculations that were used for the C, S and M prides were based on adult females or female equivalents (Van Orsdol 1986). However, for the all-male N coalition adult male lions were used as the unit of a killing lion (Funston 1999). The number of kills that was made was assumed to be related to the pride composition (Van Orsdol 1984; Mills & Shenk 1992; Funston 1999). The annual kill rate per prey type was calculated for a hypothetical year, based on the cumulative kill rate per session for that prey over the observation period and the type of lion group involved (lion prides and non-territorial males). The annual kill rate per lion was then calculated as follows: kill rate per lion per year = (number of prey killed x number of observation hours in a year) ÷ (total number of long-term continual lion observation hours)

The kill rate estimates were multiplied by the number of killing lions of each type of lion group to calculate the estimated proportion of prey that was killed by lions per year from the standing crop of each major type of prey. The kill rate data were then used to calculate the annual kill rate per lion group and the total number of prey animals that were killed annually by each lion group. These data were then used to extrapolate the total number of prey animals that were killed per year by the entire lion population (Chapter 5) in the Associated Private Nature Reserves. This lion harvest was calculated as a percentage of the total standing crop of prey animals available during the chosen observation period (Chapter 4). The impact of lion predation on their prey was measured by using the total kill proportion as an index, and it was compared with the mean recruitment rate for the prey biomass (Peel 2003). The mean recruitment rate of the prey was defined as the annual increment that was added to the prey biomass by births less any management removals (culling, ration shooting and hunting quotas) for all prey types. It includes an estimated natural mortality rate of 3% in the absence of predators (Bothma 1996).

The killing rates for pride females and non-territorial males were tested for significance of difference by comparing them with chi-squared tests obtained by other authors for Botswana (Viljoen 1997) and the Kruger National Park (Pienaar 1969; Mills & Shenk 1992; Funston 1999).

### Food consumption rates

The amount of food consumed was determined from the kill data based on the long-term continual observations from May 2001 to August 2002. The body mass of each prey animal that was killed was determined by using its estimated age and sex and the known live mass for different age classes (Smithers 1990; Bothma 1996). The amount of edible meat for each kill was estimated from published data on dressed carcass mass (Bothma 1996) and it was divided into live prey body mass classes (<25 kg prey: 100% edible, 25 – 100 kg: 90%, 101 – 300 kg: 67%, and > 300 kg: 60%) (Mills 1992; Mills & Biggs 1993). There is no difference between the dressing percentage for male and female ungulate carcasses except for females in a late stage of pregnancy (Ledger 1968). No such females were included in the present study.

The mean daily consumption rate of food per female equivalent (kg per FE per day) was calculated for each lion pride from all the kills that were recorded for that pride during an effective 30 nights of observation (Van Orsdol 1982). The meat consumption rate per adult killing male lion was calculated similarly for the N coalition. A mean consumption rate was calculated for the three focal lion prides and it was then compared with the consumption rate of the N coalition. The following assumptions of Viljoen (1997) and Funston (1999) were made for these calculations:

- Lions of the same sex and size would have similar consumption rates at specific carcasses. This assumption is supported by the fact that there is no social dominance among lions of the same sex and age (Schaller 1972; Packer & Pusey 1985).
- The amount of food consumed by an individual lion is directly proportional to its body mass. Therefore a consumption weighting factor was applied depending on the sex and age of the individuals involved. The consumption of food by an adult male is 1.5 times that of an adult female (Schaller 1972; Van Orsdol 1986).
- All the available meat is utilized by the lions from a given kill.
- Meat loss to other carnivores as the result of interspecific competition is negligible.

The mean food consumption rate and the mean number of killing lions per lion group (Table 7.1) were used to calculate the food consumption in kg per year for the focal lion prides and of the N coalition. The total consumption in kg per year for the entire lion population of the Associated Private Nature Reserves during the observation period was then calculated from these values and the estimated number of lions present in the Associated Private Nature Reserves (Chapter 5). This consumption value was expressed as a percentage of the total prey biomass (kg) present in the Associated Private Nature Reserves during the observation period, and it was in turn compared with the mean recruitment rate of the prey biomass that was obtained from Peel (2003) and calculated as biomass (kg).

**Prey selection**

Prey preference by lions can refer to the type, age and sex class of the prey. It was determined from the long-term observation data, predation field sheets and kill records from individual Timbavati lodges and data for the Klaserie Private Nature Reserve. Only 47 kills were recorded for the focal lion groups during the observation period. These data were therefore combined with the data for the Timbavati lodges and the Klaserie Private Nature Reserve for the same lion groups over the same time period. The kill data for the Klaserie Private Nature Reserve were calculated over four time periods:

1. The period from 1982 to 1992 before the boundary fence with the Kruger National Park was removed.
2. The period from 1993 to 2003 after the above fence had been removed
3. The period from 1979 to 1981 with the greatest blue wildebeest predation pressure
4. The study period from 2000 to 2003.

For the Timbavati Private Nature Reserve, historical lion kill records were obtained from the individual lodges for 1994 to 1999 and from Hirst (1969). The prey selection by the lions in the Ngala Lodge traversing area was compared with that of the other Timbavati lodges. The historical predation trends in the Timbavati and Klaserie Private Nature Reserves were then compared with those that were found in the present study. Kill data recorded from 1994 to 1999 by the Timbavati lodges were compared with those recorded during the present study.

The kill data for the lion population in the entire Associated Private Nature Reserves could not be combined because the long-term field observation data for the focal lion groups were significantly different with the kill records for the lions in the traversing area of the

Timbavati lodges ($\chi^2 = 649.661$; df = 7; $P \leq 0.05$), the Ngala Lodge area ($\chi^2 = 1313.004$; df = 7; $P \leq 0.05$) and the Klaserie Private Nature Reserve ($\chi^2 = 400.437$; df = 7; $P \leq 0.05$).

A predation rating scale was developed for the different types of prey by using the following equation of Pienaar (1969), Mills & Biggs (1993) and Kilian (2003): predation rating = (number of prey killed) ÷ (relative abundance of that prey)

Population estimates of the most abundant types of lion prey were based on aerial counts, while age and sex structures were based on road strip censuses that were done for the Associated Private Nature Reserves (Chapter 4) (Weaver 1995). The frequency, age structure and sex ratio of prey killed were tested for evidence of prey selection. The two age-classes that were used were juveniles (≤ 1 year old) and adults (> 1 year old) and a chi-squared test was used to test the data for significance of difference.

### Seasonality of predation

The seasonality of lion predation in the Associated Private Nature Reserves was analysed by using the kill data that were based on continual observations, or were recorded from predator field sheets, and on the kill records of the Timbavati lodges and the Klaserie Private Nature Reserve (kill rates, age and sex selection). The kill data were weighted by the number of kills that was made in each season. For the focal lion groups the long-term observation data were combined with the data from the Timbavati lodges and the Klaserie Private Nature Reserve to compensate for the low number of kills that were recorded for certain types of prey. The data were tested for significance of difference by using a chi-squared test.

## RESULTS

### Rainfall

The Associated Private Nature Reserves experience wet and dry cycles that conform to a 20-year oscillation consisting of 10 years of above mean rainfall, followed by 10 years below it (Tyson & Dyer 1975; Gertenbach 1980). The long-term mean rainfall for the Klaserie and Timbavati Private Nature Reserves was 464 mm and 585 mm respectively. A dry cycle occurred from 1982 to 1992, and a wet cycle from 1993 to 2002. The study therefore occurred at the end of a wet cycle, during which the Associated Private Nature Reserves received from 7.5% below the long-term mean annual rainfall to 7.5% above it (Peel 2003).

### Lion population

The composition of the four lion groups studied varied from 21 to 43 killing lions (mean = 28 ± 12.3 lions) during the observation period, and comprised 14 to 19% of the total lion population in the Associated Private Nature Reserves. The total range that was occupied by the four lion groups was 1020 km$^2$. This is equal to 68% of the study area (Chapter 6). The mean number of adult females occupying the range of the C and S prides, including the intermittent presence of nomadic lions, was 6.7 and 3.0 respectively (Funston 1999). Similarly, the M pride was comprised of a mean of 6.2 adult female killing lions. The N coalition consisted of five non-territorial adult male lions and this coalition remained constant throughout the study.

### Kill rate

The total number of hours that the C, S and M prides were observed during an effective observation session of 30 nights, per pride, was 438 hours, 419 hours and 462 hours respectively. The N coalition was observed for 481 hours during a total observation session of 30 nights. When Van Orsdol's (1982) weighting factor was applied, this equated to 5840 lion-hours for the C pride, 4380 lion-hours for the S pride, 7300 lion-hours for the M pride, and 3369 lion-hours for the N coalition. The effective number of lion-hours was high due to the large size of the lion prides, with a large number of dependent subadults. For the N coalition the large number of adult killing males resulted in a high number of effective lion-hours. Table 7.1 shows the kill rate estimates and the estimated proportion of prey that was killed per year from the standing crop of each major prey type.

The focal lion prides made 35 kills during 90 nights of observation at a mean kill rate of 1 kill every 2.6 nights. The N coalition, at a mean kill rate of 1 kill every 2.5 nights, made 12 kills during 30 nights of observation. The pride females killed a mean of 17.4 prey animals per lion per year, and the focal lion prides killed a combined total of 277.0 prey animals per year. The N coalition made 31.0 kills per male lion per year and the five non-territorial male lions together killed 156 prey animals per year. The estimated lion population of 148 lions (101 female equivalents and 16 non-territorial males) (Chapter 5) therefore removed a total of 2255 prey animals per year at a rate of 15.2 prey animals per lion per year. The total standing crop of prey was 17 958 animals (Chapter 4). The lion population therefore removed 12.6% of the standing crop of prey animals in the Associated Private Nature Reserves during the study. When compared with the mean recruitment rate of 15.4% for the prey biomass (Peel 2003), the kill rate of the lion population in the Associated Private Nature Reserves from May 2001 to August 2002 therefore seems to be sustainable.

Table 7.2 shows the frequency in which the 10 most abundant types of prey were killed by the focal lion groups and the proportion of a standing crop of each type of prey that was removed by the lions per year. The focal lion prides killed the following prey most often: impala (26%), giraffe (20%), buffalo (17%), greater kudu (14%) and waterbuck (11%). Combined, these five types of prey form 88% of all the prey animals that were killed. The proportion of giraffe (35%) ($\chi^2$ = 372.93, df = 1, $P$ < 0.01) and greater kudu (27%) ($\chi^2$ =

**Table 7.1**: *The kill rate per killing lion per year, the number of the 10 most abundant prey types killed by lions and the population of each prey animal killed from a standing crop in the Associated Private Nature Reserves from 26 May 2001 to 25 August 2002. Kill rates were calculated for pride females (FE) in the C, S and M prides, and for adult males in the N coalition.*

| Prey | Area | Lion group | Number of prey killed | Kill rate per lion per year | Number of killing lions | Mean standing crop* | Number of prey killed per year | Percentage of prey killed per year |
|---|---|---|---|---|---|---|---|---|
| Blue wildebeest | Timbavati | C pride | 0 | 1.5 | 0.0 | 39 | 0 | 0.0 |
| | Timbavati | S pride | 0 | 2.0 | 0.0 | 6 | 0 | 0.0 |
| | Klaserie | M pride | 1 | 1.2 | 6.2 | 51 | 7 | 13.7 |
| | Klaserie | N coalition | 0 | 2.6 | 0.0 | 35 | 0 | 0.0 |
| Buffalo | Timbavati | C pride | 5 | 7.5 | 6.7 | 835 | 50 | 6.0 |
| | Timbavati | S pride | 0 | 2.0 | 0.0 | 300 | 0 | 0.0 |
| | Klaserie | M pride | 1 | 1.2 | 6.2 | 765 | 7 | 0.9 |
| | Klaserie | N coalition | 4 | 10.4 | 5.0 | 540 | 52 | 10.0 |
| Burchell's zebra | Timbavati | C pride | 0 | 1.5 | 0.0 | 78 | 0 | 0.0 |
| | Timbavati | S pride | 0 | 2.0 | 0.0 | 6 | 0 | 0.0 |
| | Klaserie | M pride | 2 | 2.4 | 6.2 | 259 | 15 | 5.8 |
| | Klaserie | N coalition | 1 | 2.6 | 5.0 | 222 | 13 | 5.9 |
| Giraffe | Timbavati | C pride | 5 | 7.5 | 6.7 | 90 | 50 | 55.6 |
| | Timbavati | S pride | 1 | 2.0 | 3.0 | 14 | 6 | 42.9 |
| | Klaserie | M pride | 1 | 1.2 | 6.2 | 76 | 7 | 9.2 |
| | Klaserie | N coalition | 1 | 2.6 | 5.0 | 128 | 13 | 10.2 |
| Greater kudu | Timbavati | C pride | 0 | 1.5 | 0.0 | 38 | 0 | 0.0 |
| | Timbavati | S pride | 2 | 4.0 | 3.0 | 23 | 12 | 52.1 |
| | Klaserie | M pride | 3 | 3.6 | 6.2 | 65 | 22 | 33.8 |
| | Klaserie | N coalition | 1 | 2.6 | 5.0 | 140 | 13 | 9.3 |
| Impala | Timbavati | C pride | 1 | 1.5 | 6.7 | 576 | 10 | 1.7 |
| | Timbavati | S pride | 5 | 10.0 | 3.0 | 362 | 30 | 8.3 |
| | Klaserie | M pride | 3 | 3.6 | 6.2 | 1164 | 22 | 1.9 |
| | Klaserie | N coalition | 1 | 2.6 | 5.0 | 2051 | 13 | 0.6 |
| Nyala | Timbavati | C pride | 0 | 1.5 | 0.0 | ~ | 0 | ~ |
| | Timbavati | S pride | 0 | 2.0 | 0.0 | ~ | 0 | ~ |
| | Klaserie | M pride | 0 | 1.2 | 0.0 | ~ | 0 | ~ |
| | Klaserie | N coalition | 2 | 5.2 | 5.0 | ~ | 26 | ~ |
| Steenbok | Timbavati | C pride | 0 | 1.5 | 6.7 | ~ | 0 | ~ |
| | Timbavati | S pride | 0 | 2.0 | 3.0 | ~ | 0 | ~ |
| | Klaserie | M pride | 0 | 1.2 | 6.2 | ~ | 0 | ~ |
| | Klaserie | N coalition | 1 | 2.6 | 5.0 | ~ | 13 | ~ |
| Warthog | Timbavati | C pride | 1 | 1.5 | 6.7 | 68 | 10 | 14.7 |
| | Timbavati | S pride | 0 | 2.0 | 0.0 | 6 | 0 | 0.0 |
| | Klaserie | M pride | 0 | 1.2 | 0.0 | 118 | 0 | 0.0 |
| | Klaserie | N coalition | 0 | 2.6 | 0.0 | 35 | 0 | 0.0 |
| Waterbuck | Timbavati | C pride | 1 | 1.5 | 6.7 | 45 | 10 | 22.2 |
| | Timbavati | S pride | 2 | 4.0 | 3.0 | 40 | 12 | 30.0 |
| | Klaserie | M pride | 1 | 1.2 | 6.2 | 73 | 7 | 9.6 |
| | Klaserie | N coalition | 1 | 2.6 | 5.0 | 55 | 13 | 23.6 |

*** The mean standing crop for each prey type of the focal lion groups as calculated from the 2003 aerial counts for the Timbavati and Umbabat Private Nature Reserves and the 2001 aerial count for the Klaserie Private Nature Reserve**

**~ Unknown, no aerial count data or road strip census data were available for the nyala or steenbok**

**Table 7.2:** *The percentage of each of the 10 most abundant types of lion prey that was killed and the proportion of each prey killed per year from the standing crop of that prey type, by the focal lion groups in the Associated Private Nature Reserves, Limpopo Province. These data were based on long-term observation data from May 2001 to August 2002. For each prey type the percentage occurrence in the population is shown.*

| **PREY** | **PRIDES** | | **NON-TERRITORIAL MALES** | | **ALL LION GROUPS** | | **OCCURRENCE IN THE PREY POPULATION (%)*** |
|---|---|---|---|---|---|---|---|
| | Kill ratio (%) | Proportion of standing crop per year (%) | Kill ratio (%) | Proportion of standing crop per year (%) | Kill ratio (%) | Proportion of standing crop per year (%) | |
| Blue wildebeest | 3.0 | 17.0 | 0.0 | 0.0 | 2.0 | 12.0 | 1.2 |
| Buffalo | 17.0 | 3.0 | 33.0 | 10.0 | 21.0 | 5.0 | 29.7 |
| Burchell's zebra | 6.0 | 9.0 | 8.0 | 9.0 | 6.0 | 9.0 | 3.8 |
| Giraffe | 20.0 | 51.0 | 9.0 | 16.0 | 17.0 | 39.0 | 2.8 |
| Greater kudu | 14.0 | 30.0 | 9.0 | 14.0 | 13.0 | 25.0 | 3.0 |
| Impala | 26.0 | 3.0 | 8.0 | 1.0 | 21.0 | 3.0 | 57.0 |
| Nyala | 0.0 | 0.0 | 17.0 | ~ | 4.0 | ~ | ~ |
| Steenbok | 0.0 | 0.0 | 8.0 | ~ | 3.0 | ~ | ~ |
| Warthog | 3.0 | 10.0 | 0.0 | 0.0 | 2.0 | 8.0 | 1.5 |
| Waterbuck | 11.0 | 45.0 | 8.0 | 36.0 | 11.0 | 43.0 | 1.1 |
| Total | 100.0 | ~ | 100.0 | ~ | 100.0 | ~ | 100.0 |

*** Based on aerial counts for the Associated Private Nature Reserves from 2000 to 2002.**
**~ No data**

194.53, df = 1, $P < 0.01$) that was removed from their standing crop each year was greater than expected based on their occurrence in the population. The lion prides killed fewer impala and buffalo than expected by their availability, harvesting 3% of the standing crop per year in each case ($\chi^2 = 163.89$, df = 1, $P < 0.01$). The most frequently killed prey of the N coalition was the buffalo (33%), and 10% of the standing crop of buffalo was harvested per year by them. The actual number of other prey animals that was killed by the N coalition was insufficient to make meaningful deductions about the kill frequency of these prey. When the kill data obtained from long-term observations were combined with data from the Timbavati lodges and the Klaserie Private Nature Reserve for the same lion groups over the same period, no differences were found ($\chi^2 = 2.89$; df = 7; $P > 0.05$). Consequently the prey frequency and selection were based on these combined data when prey selection is discussed later.

### Food consumption rate

The kill data for each pride during an effective 30 nights of long-term continual observations indicated a mean consumption rate of 11.5 kg of food per female equivalent per day for pride C, 6.6 kg for pride S, and 4.3 kg for pride M. The food consumption rate of pride C was greater than that of prides S ($\chi^2 = 1737.253$; df = 7; $P \leq 0.05$) and M ($\chi^2 = 2268.965$; df = 7; $P \leq 0.05$). This is probably due to the proportions of buffalo (45%) and giraffe (27%) that were killed by pride C when the non-territorial male lions were with the pride (Table 7.1). The mean combined food consumption rate for the three lion prides was 7.62 kg per female equivalent per day, and for coalition N it was 13.8 kg per male per day. The food consumption rate for the non-territorial male lions was greater than the minimum daily requirement of 8.1 kg per day ($\chi^2 = 4.01$; df = 1; $P \leq 0.05$) that was proposed by Funston (1999) for adult males with a mean body mass of 188kg (Smuts, Robinson & Whyte 1980). The total food consumption per year for the focal lion prides was 63 692 kg per year, and for the N coalition it was 25 185 kg per year. The total food consumption for the estimated 148 lions in the Associated Private Nature Reserves from May 2001 to August 2002 was 361 350 kg per year, and the total prey biomass at that time was 3 943 440 kg. Based on their food consumption rate, the lion population therefore harvested 9.2% of the standing prey biomass of the Associated Private Nature Reserves during the study period. This is less than the calculated mean recruitment rate of 18.6% (733 950 kg) for the prey biomass in the present study. The level of lion predation in the Associated Private Nature Reserves from May 2001 to August 2002 was therefore sustainable.

### Prey selection

The prey selection of the lions in the Associated Private Nature Reserves was calculated for the 10 most abundant types of lion prey during the study period (Table 7.1 to 7.3) and eight types of prey that were known to have been taken historically by lions in the study area (Table 7.5 to 7.7, 7.10 and 7.12). The two most often killed types of prey were the giraffe and buffalo. In the Timbavati Private Nature Reserve the impala had a high relative abundance, and was one of the most often killed prey animals. It therefore serves as a buffer species in lion predation. For the Ngala Lodge traversing area and the Klaserie Private Nature Reserve, the blue wildebeest and Burchell's zebra were major prey in terms of numbers and biomass, and they were killed at a greater frequency than was expected from their relative abundance (Tables 7.8 and 7.10). Therefore they are preferred prey. Over recent years, the relative abundance of the blue wildebeest has declined in the Klaserie Private Nature Reserve and the Ngala Lodge area and the number of buffalo has increased substantially (Hirst 1969; Kruger 1988). The prey selection by the lions in these areas appears therefore to have changed from blue wildebeest to buffalo.

#### Associated Private Nature Reserves

The combined kill data for the focal lion groups in the Associated Private Nature Reserves

**Table 7.3:** *The number of lion kills, the frequency of predation and the percentage of the biomass killed by all the focal lion groups in the Associated Private Nature Reserves, from May 2001 to August 2002. The data were based on long-term observations and kill data from the Timbavati lodges and the Klaserie Private Nature Reserve.*

| **PREY** | **PRIDES** | | | **NON-TERRITORIAL MALES** | | | **ALL LIONS** | | | **PERCENTAGE OF PREY ABUNDANCE *** |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Kills** | | **Percentage of biomass killed** | **Kills** | | **Percentage of biomass killed** | **Kills** | | **Percentage of biomass killed** | |
| | Number | Percentage of prey killed | | Number | Percentage of prey killed | | Number | Percentage of prey killed | | |
| Blue wildebeest | 7 | 7.0 | 3.5 | 0 | 0.0 | 0.0 | 7 | 5.0 | 2.4 | 1.0 |
| Buffalo | 12 | 11.0 | 21.2 | 19 | 59.0 | 73.0 | 31 | 22.0 | 37.0 | 33.0 |
| Burchell's zebra | 7 | 7.0 | 4.6 | 2 | 7.0 | 3.0 | 9 | 7.0 | 4.1 | 3.0 |
| Giraffe | 26 | 25.0 | 53.1 | 4 | 13.0 | 18.0 | 30 | 22.0 | 41.0 | 3.0 |
| Greater kudu | 17 | 16.0 | 7.9 | 2 | 6.0 | 2.0 | 19 | 14.0 | 6.1 | 3.0 |
| Impala | 20 | 19.0 | 3.0 | 1 | 3.0 | 1.0 | 21 | 15.0 | 2.2 | 54.0 |
| Nyala | 0 | 0.0 | 0.0 | 2 | 6.0 | 1.0 | 2 | 1.0 | 1.0 | 0.0 |
| Steenbok | 0 | 0.0 | 0.0 | 1 | 3.0 | 1.0 | 1 | 1.0 | 1.0 | 0.0 |
| Warthog | 7 | 6.0 | 1.1 | 0 | 0.0 | 0.0 | 7 | 5.0 | 0.8 | 2.0 |
| Waterbuck | 10 | 9.0 | 5.7 | 1 | 3.0 | 1.0 | 11 | 8.0 | 4.3 | 1.0 |
| Total | 106 | 100.0 | 100.0 | 32 | 100.0 | 100.0 | 138 | 100.0 | 99.8 | 100.0 |

*** Based on aerial counts for the Associated Private Nature Reserves from 2000 to 2002**

**Table 7.5:** *The percentage kill frequency, proportion of each age and sex class killed, percentage of prey biomass killed, and the percentage mortality due to starvation for the eight most abundant prey types of the lions in the Timbavati Private Nature Reserve from 1964 to 1967. Source: Hirst (1969).*

| **PREY** | **LION KILLS** | | | | | | | | | | **PERCENTAGE OF PREY BIOMASS** | **PRECENTAGE OCCURRENCE IN PREY POPULATION** | **PERCENTAGE MORTALITY FROM STARVATION** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Number** | **Percentage of prey killed** | **Adults** | | **Juveniles** | | **Males** | | **Females** | | | | |
| | | | Percentage killed | Percentage occurrence in the prey population | Percentage killed | Percentage occurrence in the prey population | Percentage killed | Percentage occurrence in the prey population | Percentage killed | Percentage occurrence in the prey population | | | |
| Blue wildebeest | 291 | 53 | 73 | 75 | 27 | 25 | 53 | 20 | 47 | 80 | 41 | 21 | 1 |
| Buffalo | ~ | ~ | ~ | ~ | ~ | ~ | ~ | ~ | ~ | ~ | ~ | ~ | ~ |
| Burchell's zebra | 44 | 8 | 67 | 80 | 33 | 20 | 45 | 25 | 55 | 75 | 6 | 7 | 0 |
| Giraffe | 103 | 19 | 60 | 80 | 40 | 20 | 65 | 44 | 35 | 56 | 42 | 10 | 57 |
| Greater kudu | 40 | 7 | 73 | 80 | 27 | 20 | 50 | 30 | 50 | 70 | 5 | 4 | 34 |
| Impala | 32 | 6 | 65 | 80 | 35 | 20 | 45 | 30 | 55 | 70 | 1 | 56 | 38 |
| Warthog | 6 | 1 | 66 | - | 34 | - | 40 | - | 60 | - | 0 | 1 | 60 |
| Waterbuck | 31 | 6 | 100 | - | 55 | - | 45 | 65 | 55 | 35 | 5 | 1 | 18 |
| Total | 547 | 100 | - | - | - | - | - | - | - | - | 100 | 100 | - |

**~ The relative abundance of buffalo in the Timbavati Private Nature Reserve from 1964 to 1967 was low and the buffalo was not a major prey of lions during that peri**

**- No data available**

**Table 7.6:** *The percentage kill frequency and biomass for the most abundant prey types of the lions in the area of the Timbavati lodges, based on the Timbavati lodges data from 1994 to 1999 and 2000 to 2003. Chi-square analyses were used to test the observed kill frequency with the percentage occurrence of those prey types in the population.*

| **PREY** | **TIMBAVATI LODGES** | | | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1994 to 1999** | | | **2000 to 2003** | | | **1994 to 1999** | **2000 to 2003** | **1994 to 1999** | | | **2000 to 2003** | | |
| | Number of kills | Percentage of biomass killed | Percentage of kills | Number of kills | Percentage of biomass killed | Percentage of kills | | | $\chi^2$ | **P** | **df** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 16 | 2.8 | 6.0 | 7 | 4.1 | 7.0 | 7.0 | 2.6 | 0.299 | > 0.05 | 1 | 6.825 | < 0.05 | 1 |
| Buffalo | 48 | 30.0 | 18.0 | 22 | 35.2 | 21.0 | 23.0 | 35.1 | 2.494 | > 0.05 | 1 | 5.763 | < 0.05 | 1 |
| Burchell's zebra | 24 | 5.5 | 9.0 | 9 | 5.2 | 9.0 | 6.0 | 4.6 | 4.361 | < 0.05 | 1 | 3.715 | > 0.05 | 1 |
| Giraffe | 69 | 50.0 | 26.0 | 23 | 40.6 | 22.0 | 3.0 | 2.4 | 475.586 | < 0.05 | 1 | 168.435 | < 0.05 | 1 |
| Greater kudu | 24 | 3.3 | 9.0 | 13 | 6.2 | 12.0 | 2.0 | 1.2 | 67.163 | < 0.05 | 1 | 100.352 | < 0.05 | 1 |
| Impala | 35 | 1.9 | 13.0 | 12 | 1.6 | 12.0 | 57.0 | 52.1 | 87.543 | < 0.05 | 1 | 32.841 | < 0.05 | 1 |
| Warthog | 19 | 1.1 | 7.0 | 6 | 0.9 | 6.0 | 2.0 | 1.3 | 15.789 | < 0.05 | 1 | 15.979 | > 0.05 | 1 |
| Waterbuck | 27 | 5.4 | 10.0 | 12 | 6.1 | 11.0 | 1.0 | 0.6 | 226.864 | > 0.05 | 1 | 207.393 | < 0.05 | 1 |
| Total | 262 | 100.0 | 100.0 | 104 | 100.0 | 100.0 | 100.0 | 100.0 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the traversing area of the Timbavati lodges from 2000 to 2002.**

**Table 7.7:** *Predation rating for the eight most abundant types of lion prey in the Associated Private Nature Reserves, Limpopo province of South Africa. The data are based on kill records for the lions in the traversing area of the Timbavati lodges from 2001 to 2003.*

| **PREY** | **LION KILLS** | | **PERCENTAGE OF PREY ABUNDANCE*** | **PREDATION RATING **** |
|---|---|---|---|---|
| | Number | Percentage of all prey killed | | |
| Blue wildebeest | 7 | 7.0 | 2.6 | 2.7 |
| Buffalo | 22 | 21.0 | 35.1 | 0.6 |
| Burchell's zebra | 9 | 9.0 | 4.6 | 1.9 |
| Giraffe | 23 | 22.0 | 2.4 | 9.2 |
| Greater kudu | 13 | 12.0 | 1.2 | 10.4 |
| Impala | 12 | 12.0 | 52.1 | 0.2 |
| Warthog | 6 | 6.0 | 1.3 | 4.6 |
| Waterbuck | 12 | 11.0 | 0.6 | 17.9 |
| Total | 104 | 100.0 | 100.0 | ~ |

*** Based on aerial counts in the Associated Private Nature Reserves from 2000 to 2003.**

**** A predation rating < 1.0 indicates a lion killing frequency less than the relative abundance of the prey animal, a predation rating = 1.0 indicates a lion killing frequency equal to the relative abundance of the prey animal, and a predation rating > 1.0 indicates a lion killing frequency greater than the relative abundance of the prey animal.**

**Table 7.8:** *The percentage kill frequency and biomass for the most abundant prey types of the lions in the Ngala Lodge area, based on Ngala Lodge kill data from 1994 to 1999, and 2000 to 2003. Chi-square analyses were used to test the observed kill frequency with the percentage occurrence of those prey types in the population.*

| **PREY** | **NGALA LODGE** | | | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1994 to 1999** | | | **2000 to 2003** | | | **1994 to 1999** | **2000 to 2003** | **1994 to 1999** | | | **2000 to 2003** | | |
| | Number of kills | Percentage of biomass killed | Percentage of kills | Number of kills | Percentage of biomass killed | Percentage of kills | | | $\chi^2$ | **P** | **df** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 71 | 17.0 | 30.0 | 33 | 19.6 | 29.0 | 7.0 | 2.6 | 174.860 | < 0.05 | 1 | 301.204 | < 0.05 | 1 |
| Buffalo | 42 | 36.0 | 18.0 | 28 | 45.9 | 24.0 | 23.0 | 35.1 | 3.155 | > 0.05 | 1 | 3.788 | > 0.05 | 1 |
| Burchell's zebra | 21 | 6.7 | 9.0 | 7 | 4.2 | 6.0 | 6.0 | 4.6 | 3.025 | > 0.05 | 1 | 0.553 | < 0.05 | 1 |
| Giraffe | 34 | 33.6 | 14.0 | 15 | 25.8 | 13.0 | 3.0 | 2.4 | 99.756 | < 0.05 | 1 | 54.282 | < 0.05 | 1 |
| Greater kudu | 5 | 1.1 | 2.0 | 0 | 0.0 | 0.0 | 2.0 | 1.2 | 0.008 | > 0.05 | 1 | 1.495 | > 0.05 | 1 |
| Impala | 45 | 3.3 | 19.0 | 27 | 3.8 | 23.0 | 57.0 | 52.1 | 61.603 | < 0.05 | 1 | 18.082 | < 0.05 | 1 |
| Warthog | 19 | 1.5 | 8.0 | 5 | 0.8 | 5.0 | 3.0 | 1.3 | 19.339 | < 0.05 | 1 | 8.217 | < 0.05 | 1 |
| Waterbuck | 3 | 0.8 | 1.0 | 0 | 0.0 | 0.0 | 1.0 | 0.6 | 0.150 | > 0.05 | 1 | 0.690 | > 0.05 | 1 |
| Total | 240 | 100.0 | 100.0 | 115 | 100.0 | 100.0 | 100.0 | 100.0 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the Ngala Lodge area from 2000 to 2002.**

**Table 7.10:** *The percentage kill frequency and biomass for the most abundant prey types of the lions in the Klaserie Private Nature Reserve, based on lion kill data from the Klaserie Private Nature Reserve from 1982 to 2003. Chi-square analyses were used to test the observed kill frequency with the percentage occurrence of those prey types in the population.*

| **PREY** | **KLASERIE PRIVATE NATURE RESERVE** | | | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1982 to 1992** | | | **1993 to 2003** | | | **1982 to 1992** | **1993 to 2003** | **1982 to 1992** | | | **1993 to 2003** | | |
| | Number of kills | Percentage of biomass killed | Percentage of kills | Number of kills | Percentage of biomass killed | Percentage of kills | | | $\chi^2$ | **P** | **df** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 111 | 10.8 | 19.3 | 108 | 9.5 | 18.4 | 8.5 | 5.0 | 78.614 | < 0.05 | 1 | 210.135 | < 0.05 | 1 |
| Buffalo | 83 | 22.2 | 14.4 | 102 | 21.0 | 17.3 | 4.1 | 14.1 | 149.325 | < 0.05 | 1 | 4.396 | < 0.05 | 1 |
| Burchell's zebra | 102 | 9.9 | 17.7 | 99 | 11.0 | 16.8 | 7.2 | 8.0 | 88.340 | < 0.05 | 1 | 57.395 | < 0.05 | 1 |
| Giraffe | 184 | 51.6 | 31.9 | 140 | 47.6 | 23.8 | 6.6 | 4.5 | 560.588 | < 0.05 | 1 | 487.201 | < 0.05 | 1 |
| Greater kudu | 36 | 2.9 | 6.3 | 49 | 5.3 | 8.3 | 3.7 | 4.4 | 10.123 | < 0.05 | 1 | 20.675 | < 0.05 | 1 |
| Impala | 40 | 0.9 | 6.9 | 24 | 0.7 | 4.1 | 62.6 | 59.5 | 285.013 | < 0.05 | 1 | 303.506 | < 0.05 | 1 |
| Warthog | 5 | 0.1 | 0.9 | 14 | 0.0 | 2.4 | 5.8 | 2.5 | 24.156 | < 0.05 | 1 | 0.033 | > 0.05 | 1 |
| Waterbuck | 15 | 1.6 | 2.6 | 52 | 4.8 | 8.8 | 1.5 | 2.0 | 4.682 | < 0.05 | 1 | 137.692 | < 0.05 | 1 |
| Total | 576 | 100.0 | 100.0 | 588 | 100.0 | 100.0 | 100.0 | 100.0 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the Klaserie Private Nature Reserve from 2000 to 2002.**

**Table 7.12:** *The percentage kill frequency and biomass for the most abundant prey types of the lions in the Klaserie Private Nature Reserve, based on lion kill data from the Klaserie Private Nature Reserve, from 1979 to 1981* and from 2001 to 2003**. Chi-square analyses were used to test the observed kill frequency with the percentage occurrence of those prey types in the population.*

| **PREY** | **KLASERIE PRIVATE NATURE RESERVE** | | | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1979 to 1981*** | | | **2001 to 2003**** | | | **1979 to 1981** | **2001 to 2003** | **1979 to 1981** | | | **2001 to 2003** | | |
| | Number of kills | Percentage of biomass killed | Percentage of kills | Number of kills | Percentage biomass killed | Percentage of kills | | | $\chi^2$ | **P** | **df** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 131 | 50.1 | 44.3 | 17 | 6.2 | 12.0 | 19.5 | 1.4 | 93.040 | < 0.05 | 1 | 112.358 | < 0.05 | 1 |
| Buffalo | 6 | 2.1 | 2.0 | 42 | 42.2 | 30.0 | 2.8 | 19.7 | 0.632 | > 0.05 | 1 | 6.789 | < 0.05 | 1 |
| Burchell's zebra | 43 | 16.4 | 14.5 | 18 | 6.7 | 13.0 | 7.2 | 5.1 | 22.071 | < 0.05 | 1 | 15.719 | < 0.05 | 1 |
| Giraffe | 75 | 27.7 | 25.3 | 36 | 38.0 | 25.0 | 3.4 | 3.6 | 418.990 | < 0.05 | 1 | 184.897 | < 0.05 | 1 |
| Greater kudu | 8 | 0.9 | 2.7 | 10 | 2.6 | 7.0 | 1.1 | 3.6 | 6.912 | < 0.05 | 1 | 4.573 | < 0.05 | 1 |
| Impala | 19 | 1.7 | 6.4 | 7 | 0.6 | 5.0 | 54.1 | 63.0 | 124.390 | < 0.05 | 1 | 76.634 | < 0.05 | 1 |
| Warthog | 7 | 0.2 | 2.4 | 2 | 0.2 | 1.0 | 10.8 | 1.9 | 19.501 | < 0.05 | 1 | 0.189 | > 0.05 | 1 |
| Waterbuck | 7 | 0.9 | 2.4 | 11 | 3.5 | 7.0 | 1.2 | 1.6 | 3.347 | > 0.05 | 1 | 33.173 | < 0.05 | 1 |
| Total | 296 | 100.0 | 100.0 | 143 | 100.0 | 100.0 | 100.0 | 100.0 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Source: Kruger (1988)**
**** Based on road strip counts for the Klaserie Private Nature Reserve from 2000 to 2002.**
**~ Not applicable**

was similar for the long-term field observations and the kill records provided by the Timbavati lodges and the Klaserie Private Nature Reserve from May 2001 to August 2002 ($\chi^2$ = 2.89; df = 7; $P > 0.05$).

Table 7.3 lists the number of kills, the frequency of predation and the percentage of the prey biomass that was killed for the 10 major prey types of the focal lion groups studied. The most frequent prey animals that were killed by the prides were giraffe, impala, greater kudu and buffalo. In terms of biomass killed, the giraffe topped the list, followed by the greater kudu and waterbuck. Although the impala was killed in the second highest frequency, it was only sixth in terms of biomass killed. The giraffe, impala, greater kudu and buffalo, as the four most frequent prey, formed 71% of the total number of prey animals killed and 85% of the total prey biomass killed.

For the N coalition, the buffalo and giraffe were killed most often, both in terms of numbers (72%) and biomass (91%). The four most frequently killed prey animals, in terms of numbers, by the focal lion prides and the N coalition were giraffe, buffalo, impala and greater kudu, and in terms of biomass the buffalo and giraffe.

The predation ratings in Table 7.4 indicate the vulnerability of various prey animals to lion predation (Sunquist & Sunquist 1989). The lions killed Burchell’s zebra, blue wildebeest, greater kudu, giraffe, warthog and waterbuck in greater frequencies than expected from their relative abundance ($\chi^2$ = 16.85; df = 5; $P < 0.01$).

Timbavati Private Nature Reserve

The historical prey selection of lions in the Timbavati Private Nature Reserve differed significantly from that in the Ngala Lodge area and in the area of the Timbavati lodges (Tables 7.5, 7.6 and 7.8). Table 7.5 shows the killing frequency of the lions in the

**Table 7.4***:* *Predation rating for all the focal lion groups in the Associated Private Nature Reserves, Limpopo province of South Africa. The data are based on long-term field observations and kill data for the lions in the traversing area of the Timbavati lodges and the Klaserie Private Nature Reserve from May 2001 to August 2002.*

| **PREY** | **LION KILLS** | | **PERCENTAGE OF PREY ABUNDANCE *** | **PREDATION RATING **** |
|---|---|---|---|---|
| | Number | Percentage of all prey killed | | |
| Blue wildebeest | 7 | 5 | 1 | 5.0 |
| Burchell's zebra | 9 | 7 | 3 | 2.3 |
| Buffalo | 31 | 23 | 33 | 0.7 |
| Giraffe | 30 | 22 | 3 | 7.3 |
| Greater kudu | 19 | 14 | 3 | 4.7 |
| Impala | 21 | 16 | 54 | 0.3 |
| Warthog | 7 | 5 | 2 | 2.5 |
| Waterbuck | 11 | 8 | 1 | 8.0 |
| Total | 135 | 100 | 100 | ~ |

*** Based on aerial counts for the ranges of the focal lion groups in the Associated Private Nature Reserves from 2000 to 2002**

**** A predation rating < 1.0 indicates a lion killing frequency less than the relative abundance of the prey animal, a predation rating = 1.0 indicates a lion killing frequency equal to the relative abundance of the prey animal, and a predation rating > 1.0 indicates a lion killing frequency greater than the relative abundance of the prey animal.**

Timbavati Private Nature Reserve from 1964 to 1967. The major prey in terms of numbers and biomass were the blue wildebeest (53%) and giraffe (19%). Although these prey were the second and third most abundant prey types, they were killed at a greater frequency than was expected from their relative abundance ($\chi^2$ = 280.88; df = 1; P < 0.01). Hirst (1969) noted that starvation mortalities killed more impala (38%), greater kudu (34%), giraffe (57%) and warthog (60%) in the Timbavati Private Nature Reserve from 1964 to 1967 than the lions.

*Timbavati lodges*

Table 7.6 indicates the predation pattern for lions in the Timbavati Private Nature Reserve from 1994 to 1999 and from 2000 to 2003, based on data from the Timbavati lodges. These data were statistically similar to the combined long-term data of the present study ($\chi^2$ = 4.87; P > 0.05, df = 7), but was significantly different from the data for the period 1964 to 1967 (Hirst 1969) ($\chi^2$ = 417.289; P ≤ 0.05, df = 7). The predation frequencies in the traversing area of the Timbavati lodges were therefore similar to those for the Associated Private Nature Reserves (2001 to 2002), but different from the historical data (1964 to 1967). The relative occurrence and killing frequency by lions for the blue wildebeest decreased from 1967 to 2003 ($\chi^2$ = 41.22; df = 1; P ≤ 0.05), and the buffalo became the second most abundant prey type with a relative abundance of 35% in 2003. The giraffe was killed in the second highest frequency of all prey that were available in 1967, and most often in 2003 ($\chi^2$ = 0.49; df = 1; P ≤ 0.05), although the relative abundance of the giraffe decreased from 10% in 1967 to 2% in 2003 ($\chi^2$ = 973.11; df = 1; P < 0.01).

For the lions in the traversing area of the Timbavati lodges the most abundant prey in terms of numbers from 1994 to 1999 and from 2000 to 2003, was the giraffe, buffalo, impala and waterbuck. In terms of biomass, the giraffe and buffalo formed 80% and 76% of the total biomass killed respectively (Table 7.6). The impala was the most abundant and the third most frequently killed prey in terms of numbers, although it was the prey with one of the lowest biomass percentages. The highest predation ratings were for the greater kudu, giraffe, waterbuck, warthog, blue wildebeest and Burchell's zebra, being killed in greater frequencies than expected from their relative abundance on the Timbavati Reserve ($\chi^2$ = 526.32; df = 5; P < 0.01) (Table 7.7).

### *Ngala Lodge area*

Based on the lion kill data from the Ngala Lodge, the blue wildebeest was the most frequently killed prey, followed by the impala, buffalo and giraffe (Table 7.8). Buffalo, giraffe and blue wildebeest were the prey animals that were killed in the highest biomass, the kills forming 87% of the total available prey biomass from 1994 to 1999, and 92% from 2000 to 2003. Impala clearly was a buffer prey, being the most abundant prey at almost the lowest biomass, but ranking as the third most frequently killed prey (Table 7.9). Four prey types were killed in greater frequencies than expected from their relative abundance on the Timbavati Private Nature Reserve ($\chi^2$ = 822.75; df = 3; P ≤ 0.05). They are Burchell's zebra, blue wildebeest, giraffe and warthog (Tables 7.6 and 7.8). The frequency with which lions killed the giraffe and blue wildebeest in the Ngala Lodge area was greater than their relative abundance in the population (Tables 7.8 and 7.9). The buffalo was the most frequently killed prey animal of the lions in the Ngala Lodge area in terms of biomass for both time periods (Table 7.8). Although the buffalo was killed with an increased frequency from 2000 to 2003 than from 1994 to 1999, its relative abundance in the area also increased significantly from 1999 to 2003 (Table 7.8).

### Klaserie Private Nature Reserve

The kill data for the lions in the Klaserie Private Nature Reserve was calculated from reserve kill records over four time periods: 1979 to 1982, 1982 to 1992, 1993 to 2003 and 2000 to 2003. The four most frequently killed prey animals during all four time periods

**Table 7.9:** *Predation rating for the eight most abundant prey types in the Associated Private Nature Reserves, Limpopo province of South Africa. The data are based on kill records for the lions in the Ngala Lodge area from 2000 to 2003.*

| **PREY** | **LION KILLS** | | **PERCENTAGE OF PREY ABUNDANCE*** | **PREDATION RATING **** |
|---|---|---|---|---|
| | Number | Percentage of all prey killed | | |
| Blue wildebeest | 33 | 29.0 | 2.6 | 11.1 |
| Buffalo | 28 | 24.0 | 35.1 | 0.7 |
| Burchell's zebra | 7 | 6.0 | 4.6 | 1.3 |
| Giraffe | 15 | 13.0 | 2.4 | 5.4 |
| Greater kudu | 0 | 0.0 | 1.2 | 0.0 |
| Impala | 27 | 23.0 | 52.1 | 0.4 |
| Warthog | 5 | 5.0 | 1.3 | 3.8 |
| Waterbuck | 0 | 0.0 | 0.6 | 0.0 |
| Total | 115 | 100.0 | 100.0 | ~ |

*** Based on aerial counts in the Timbavati Private Nature Reserve from 2000 to 2003. No aerial counts were done by the Timbavati Private Nature Reserve or the Kruger National Park for the Ngala Lodge traversing area from 2000 to 2003**

**** A predation rating < 1.0 indicates a lion killing frequency less than the relative abundance of the prey animal, a predation rating = 1.0 indicates a lion killing frequency equal to the relative abundance of the prey animal, and a predation rating > 1.0 indicates a lion killing frequency greater than the relative abundance of the prey animal.**

were Burchell's zebra, blue wildebeest, buffalo and giraffe, both in terms of numbers and biomass (Tables 7.10 and 7.12). Combined, these prey formed 76% to 86% of the total number and 89% to 96% of the total biomass of prey animals that were killed. The relative abundance of buffalo in the Klaserie Private Nature Reserve increased from 3% in the period from 1979 to 1981, to 20% from 2001 to 2003. The killing frequency of buffalo by lions increased from 2% in the period from 1979 to 1981, to 30% in the period from 2001 to 2003. In contrast to the buffalo, the relative occurrence of blue wildebeest in the total prey population decreased from 19% in 1979 to 1981, to 1% in the period from 2001 to 2003. The killing frequency of blue wildebeest by lions consequently decreased from 44% in 1979 to 1981, to 12% from 2001 to 2003 (Table 7.12).

Tables 7.10 and 7.12 show the kill frequency of the main prey types, their respective biomass proportion and their relative occurrence in the population from 1982 to 2003. Both the relative abundance and the killing frequency of the Burchell's zebra and the blue wildebeest decreased from 1982 to 2003. The giraffe was present in the highest biomass of all prey in the period from 1982 to 2003. However, the killing frequency of the giraffe was greater than was expected by their relative abundance both before and after the boundary fence was removed in 1993 (Table 7.10).

The predation ratings were calculated for the most abundant prey types of the lions in the Klaserie Private Nature Reserve from 2000 to 2003 (Table 7.11). The four most often killed prey, Burchell's zebra, blue wildebeest, buffalo and giraffe, were all killed in greater frequencies than expected from their relative abundance on the Klaserie Private Nature Reserve (Table 7.12). Although the impala was the most abundant prey of the lions in the Klaserie Private Nature Reserve from 1982 to 2003, it was present in the lowest biomass and the killing frequency by lions was lower than was expected from its relative abundance (Tables 7.9 and 7.12).

**Table 7.11:** *Predation rating for the eight most abundant prey types in the Associated Private Nature Reserves, Limpopo province of South Africa. The data are based on kill records for the lions in the Klaserie Private Nature Reserve from 2000 to 2003.*

| **PREY** | **LION KILLS** | | **PERCENTAGE OF PREY ABUNDANCE*** | **PREDATION RATING ** ** |
|---|---|---|---|---|
| | Number | Percentage of all prey killed | | |
| Blue wildebeest | 17 | 12.0 | 1.4 | 8.3 |
| Buffalo | 42 | 30.0 | 19.7 | 1.5 |
| Burchell's zebra | 18 | 13.0 | 5.1 | 2.6 |
| Giraffe | 36 | 25.0 | 3.6 | 6.9 |
| Greater kudu | 10 | 7.0 | 3.6 | 1.9 |
| Impala | 7 | 5.0 | 63.0 | 0.1 |
| Warthog | 2 | 1.0 | 1.9 | 0.5 |
| Waterbuck | 11 | 7.0 | 1.6 | 4.3 |
| Total | 143 | 100.0 | 100.0 | ~ |

*** Based on aerial counts in the Associated Private Nature Reserves from 2000 to 2003.**

**** A predation rating < 1.0 indicates a lion killing frequency less than the relative abundance of the prey animal, a predation rating = 1.0 indicates a lion killing frequency equal to the relative abundance of the prey animal, and a predation rating > 1.0 indicates a lion killing frequency greater than the relative abundance of the prey animal.**

## Age and sex selection of prey

The proportion of prey that was killed in the different age and sex classes for the eight most abundant prey types was calculated from all the lion kill records (Tables 7.13 to 7.20). The observed age and sex selection was compared with the population age and sex structure as calculated from road strip census from June 2000 to August 2002. The lions in the Associated Private Nature Reserves selected the adult males of the major ungulate prey in the same proportion that they occurred in the population, except for the blue wildebeest. Female and juvenile giraffe were selected by the lions at a greater frequency than expected from their relative occurrence in the population.

### Associated Private Nature Reserves

The focal lion prides and the N coalition preyed on the different age classes of all prey except the giraffe in the same frequency in which they occurred in the population. Giraffe juveniles were, however, selected in a greater proportion than their occurrence in the population (Table 7.13). Impala, blue wildebeest, buffalo and kudu males were selected at a greater frequency than expected (Table 7.14). A greater frequency of female giraffe was also selected than expected.

### Timbavati Private Nature Reserve

The historical pattern of prey selection by lions in the Timbavati Private Nature Reserve showed a selection for the adults of all the major prey types, at a lower frequency ($\chi^2$ = 176.32; df = 6; $P < 0.01$) than was expected by their relative occurrence in the population. A greater than expected frequency of occurrence ($\chi^2$ = 261.75; df = 6; $P \leq 0.05$) of males was selected for all major prey animals in the period from 1963 to 1967 (Table 7.5).

**Table 7.13:** *Prey age selection by the focal lion groups for the eight most abundant types of lion prey in the Associated Private Nature Reserves based on long-term field observations and data from the Timbavati lodges and the Klaserie Private Nature Reserve from January 2001 to January 2003. For each prey type the observed age selection by the lions was compared with its percentage occurrence in the population.*

| **PREY** | **LION KILLS** | | | | **PRECENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Adults** | | **Juveniles** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Adults** | **Juveniles** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 6 | 86.0 | 1 | 14.0 | 84.0 | 16.0 | 0.015 | > 0.05 | 1 |
| Buffalo | 24 | 77.0 | 7 | 23.0 | 67.0 | 15.0 | 1.690 | > 0.05 | 1 |
| Burchell's zebra | 8 | 89.0 | 1 | 11.0 | 90.0 | 10.0 | 0.012 | > 0.05 | 1 |
| Giraffe | 22 | 73.0 | 8 | 27.0 | 91.0 | 9.0 | 11.433 | < 0.05 | 1 |
| Greater kudu | 18 | 95.0 | 1 | 5.0 | 80.0 | 20.0 | 2.579 | > 0.05 | 1 |
| Impala | 21 | 84.0 | 4 | 16.0 | 74.0 | 26.0 | 1.299 | > 0.05 | 1 |
| Warthog | 5 | 71.0 | 2 | 29.0 | 57.0 | 43.0 | 0.595 | > 0.05 | 1 |
| Waterbuck | 9 | 82.0 | 2 | 18.0 | 75.0 | 25.0 | 0.273 | > 0.05 | 1 |
| Total | 113 | 81.0 | 26 | 19.0 | 80.0 | 20.0 | ~ | ~ | ~ |

*** Based on road strip counts for the Timbavati Private Nature Reserve from 2000 to 2002.**
**~ No data**

**Table 7.14:** *Prey sex selection by the focal lion groups for the eight most abundant types of lion prey in the Associated Private Nature Reserves based on long-term observations and data from the Timbavati lodges and the Klaserie Private Nature Reserve from January 2001 to 2003. For each prey type the observed sex selection by the lions was compared with its percentage occurrence in the population.*

| **PREY** | **LION KILLS** | | | | **PRECENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Males** | | **Females** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Males** | **Females** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 4 | 67.0 | 2 | 33.0 | 22.6 | 77.4 | 6.651 | < 0.05 | 1 |
| Buffalo | 18 | 75.0 | 6 | 25.0 | 14.9 | 85.1 | 68.213 | < 0.05 | 1 |
| Burchell's zebra | 1 | 12.0 | 7 | 88.0 | 22.2 | 77.8 | 0.438 | > 0.05 | 1 |
| Giraffe | 3 | 14.0 | 19 | 86.0 | 42.9 | 57.1 | 7.670 | < 0.05 | 1 |
| Greater kudu | 10 | 56.0 | 8 | 44.0 | 25.0 | 75.0 | 8.963 | < 0.05 | 1 |
| Impala | 12 | 57.0 | 9 | 43.0 | 24.3 | 75.7 | 12.287 | < 0.05 | 1 |
| Warthog | 2 | 67.0 | 3 | 33.0 | 45.6 | 54.4 | 0.064 | > 0.05 | 1 |
| Waterbuck | 6 | 67.0 | 3 | 33.0 | 37.3 | 62.7 | 3.310 | > 0.05 | 1 |
| Total | 56 | 50.0 | 57 | 50.0 | 22.0 | 78.0 | ~ | ~ | ~ |

*** Based on road strip counts for the Timbavati Reserve from 2000 to 2002.**
**~ No data**

**Table 7.15:** *Prey age selection by lions for the eight most abundant types of lion prey in the Associated Private Nature Reserves based on data from the Timbavati lodges from January 2000 to January 2003. For each prey type the observed age selection by the lions was compared with its percentage occurrence in the prey population.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Adults** | | **Juveniles** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Adults** | **Juveniles** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 5 | 71.4 | 2 | 28.6 | 79.2 | 20.8 | 0.258 | > 0.05 | 1 |
| Buffalo | 18 | 81.8 | 4 | 18.2 | 80.7 | 19.3 | 0.019 | > 0.05 | 1 |
| Burchell's zebra | 7 | 77.8 | 2 | 22.2 | 89.5 | 10.5 | 1.324 | > 0.05 | 1 |
| Giraffe | 23 | 88.5 | 3 | 11.5 | 93.3 | 6.7 | 0.992 | > 0.05 | 1 |
| Greater kudu | 10 | 76.9 | 3 | 23.1 | 57.1 | 42.9 | 2.077 | > 0.05 | 1 |
| Impala | 10 | 83.3 | 2 | 16.7 | 77.3 | 22.7 | 0.245 | > 0.05 | 1 |
| Warthog | 5 | 83.3 | 1 | 16.7 | 53.3 | 46.7 | 2.170 | > 0.05 | 1 |
| Waterbuck | 10 | 83.3 | 2 | 16.7 | 80.8 | 19.2 | 0.051 | > 0.05 | 1 |
| Total | 88 | ~ | 19 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the traversing area of the Timbavati lodges from 2000 to 2002.**

**~ No data**

**Table 7.16:** *Prey sex selection by lions from the eight most abundant types of lion prey in the Associated Private Nature Reserves based on data from the Timbavati lodges from January 2000 to January 2003. For each prey type the observed sex selection by the lions was compared with its percentage occurrence in the population.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Males** | | **Females** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Males** | **Females** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 5 | 71.4 | 2 | 28.6 | 26.2 | 73.8 | 7.391 | < 0.05 | 1 |
| Buffalo | 18 | 81.8 | 4 | 18.2 | 5.0 | 95.0 | 275.765 | < 0.05 | 1 |
| Burchell's zebra | 9 | 75.0 | 3 | 25.0 | 16.0 | 84.0 | 31.192 | < 0.05 | 1 |
| Giraffe | 6 | 23.1 | 20 | 76.9 | 38.1 | 61.9 | 2.487 | > 0.05 | 1 |
| Greater kudu | 5 | 38.5 | 8 | 61.5 | 12.5 | 87.5 | 8.011 | < 0.05 | 1 |
| Impala | 8 | 66.7 | 4 | 33.3 | 18.7 | 81.3 | 18.176 | < 0.05 | 1 |
| Warthog | 2 | 33.3 | 4 | 66.7 | 37.5 | 62.5 | 0.044 | > 0.05 | 1 |
| Waterbuck | 8 | 66.7 | 4 | 33.3 | 47.6 | 52.4 | 1.745 | > 0.05 | 1 |
| Total | 61 | ~ | 49 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the traversing area of the Timbavati lodges from 2000 to 2002.**
**~ No data**

**Table 7.17:** *Prey age selection by lions from the eight most abundant types of lion prey in the Associated Private Nature Reserves based on Ngala Lodge data from January 2000 to January 2003. For each prey type the observed age selection by the lions was compared with its percentage occurrence in the population.*

| PREY | LION KILLS | | | | PERCENTAGE OCCURRENCE IN THE PREY POPULATION | | CHI-SQUARED TEST* | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adults | | Juveniles | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | Adults | Juveniles | $\chi^2$ | P | df |
| Blue wildebeest | 24 | 72.7 | 9 | 27.3 | 79.2 | 20.8 | 0.845 | > 0.05 | 1 |
| Buffalo | 20 | 71.4 | 8 | 28.6 | 80.7 | 19.3 | 1.532 | > 0.05 | 1 |
| Burchell's zebra | 5 | 71.4 | 2 | 28.6 | 89.5 | 10.5 | 2.444 | > 0.05 | 1 |
| Giraffe | 8 | 53.3 | 7 | 46.7 | 93.3 | 6.7 | 38.571 | < 0.05 | 1 |
| Greater kudu | 0 | 0.0 | 0 | 0.0 | 57.1 | 42.9 | ~ | ~ | 1 |
| Impala | 19 | 70.4 | 8 | 29.6 | 77.3 | 22.7 | 0.750 | > 0.05 | 1 |
| Warthog | 3 | 60.0 | 2 | 40.0 | 53.3 | 46.7 | 0.089 | > 0.05 | 1 |
| Waterbuck | 0 | 0.0 | 0 | 0.0 | 80.8 | 19.2 | ~ | ~ | 1 |
| Total | 79 | ~ | 36 | ~ | ~ | ~ | ~ | ~ | |

*** Based on road strip counts for the Ngala Lodge area from 2000 to 2003.**
**~ No data available**

**Table 7.18:** *Prey sex selection by lions from the eight most abundant types of lion prey in the Associated Private Nature Reserves based on Ngala Lodge data from January 2000 to January 2003. For each prey type the observed sex selection by the lions was compared with its percentage occurrence in the population.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Males** | | **Females** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Males** | **Females** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 23 | 69.7 | 10 | 30.3 | 26.2 | 73.8 | 32.223 | < 0.05 | 1 |
| Buffalo | 18 | 64.3 | 10 | 35.7 | 5.0 | 95.0 | 209.115 | < 0.05 | 1 |
| Burchell's zebra | 2 | 28.6 | 5 | 71.4 | 16.0 | 84.0 | 0.831 | > 0.05 | 1 |
| Giraffe | 9 | 60.0 | 6 | 40.0 | 38.1 | 61.9 | 3.052 | > 0.05 | 1 |
| Greater kudu | 0 | 0.0 | 0 | 0.0 | 12.5 | 87.5 | ~ | ~ | 1 |
| Impala | 10 | 37.0 | 17 | 63.0 | 18.7 | 81.3 | 5.981 | < 0.05 | 1 |
| Warthog | 1 | 20.0 | 4 | 80.0 | 37.5 | 62.5 | 0.653 | > 0.05 | 1 |
| Waterbuck | 0 | 0.0 | 0 | 0.0 | 47.6 | 52.4 | ~ | ~ | 1 |
| Total | 63 | ~ | 52 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the Ngala Lodge area for 2000 to 2003.**
**~ No data available**

**Table 7.19:** *Prey age selection by lions from the eight most abundant types of lion prey in the Associated Private Nature Reserves based on data from the Klaserie Private Nature Reserve from January 2001 to January 2003. For each prey type the observed age selection by the lions was compared with its percentage occurrence in the population.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Adult** | | **Juveniles** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Adults** | **Juveniles** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 14 | 82.4 | 3 | 17.6 | 79.7 | 20.3 | 0.076 | > 0.05 | 1 |
| Buffalo | 31 | 73.8 | 11 | 26.2 | 83.3 | 16.7 | 2.743 | > 0.05 | 1 |
| Burchell's zebra | 15 | 83.3 | 3 | 16.7 | 87.5 | 12.5 | 0.286 | > 0.05 | 1 |
| Giraffe | 12 | 33.3 | 24 | 66.7 | 97.1 | 2.9 | 528.118 | < 0.05 | 1 |
| Greater kudu | 7 | 70.0 | 3 | 30.0 | 61.1 | 38.9 | 0.332 | > 0.05 | 1 |
| Impala | 7 | 100.0 | 0 | 0.0 | 70.0 | 30.0 | 3.000 | > 0.05 | 1 |
| Warthog | 2 | 100.0 | 0 | 0.0 | 75.0 | 25.0 | 0.667 | > 0.05 | 1 |
| Waterbuck | 9 | 81.8 | 2 | 18.2 | 50.0 | 50.0 | 4.455 | < 0.05 | 1 |
| Total | 97 | ~ | 46 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the Klaserie Private Nature Reserve from 2001 to 2003.**

**~ Not applicable**

**Table 7.20:** *Prey sex selection by lions from the eight most abundant types of lion prey in the Associated Private Nature Reserves based on data from the Klaserie Private Nature Reserve from January 2001 to January 2003. For each prey type the observed age selection by the lions was compared with its percentage occurrence in the population.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Males** | | **Females** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Males** | **Females** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 11 | 64.7 | 6 | 35.3 | 17.0 | 83.0 | 27.368 | < 0.05 | 1 |
| Buffalo | 24 | 57.1 | 18 | 42.9 | 11.3 | 88.8 | 88.597 | < 0.05 | 1 |
| Burchell's zebra | 3 | 16.7 | 15 | 83.3 | 24.3 | 75.7 | 0.568 | > 0.05 | 1 |
| Giraffe | 14 | 38.9 | 22 | 61.1 | 61.8 | 38.2 | 7.977 | < 0.05 | 1 |
| Greater kudu | 6 | 60.0 | 4 | 40.0 | 27.3 | 72.7 | 5.400 | < 0.05 | 1 |
| Impala | 3 | 42.9 | 4 | 57.1 | 16.7 | 83.3 | 3.457 | > 0.05 | 1 |
| Warthog | 0 | 0.0 | 2 | 100.0 | 50.0 | 50.0 | 2.000 | > 0.05 | 1 |
| Waterbuck | 7 | 63.6 | 4 | 36.4 | 20.0 | 80.0 | 13.091 | < 0.05 | 1 |
| Total | 68 | ~ | 75 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the Klaserie Private Nature Reserve from 2001 to 2003.**
**~ Not applicable**

### *Timbavati lodges*

Table 7.15 shows that lions in the Timbavati lodge traversing area selected the adults of the major prey at a greater frequency than was expected from their availability. Impala, Burchell's zebra, blue wildebeest and buffalo males were also selected at a greater than expected frequency of occurrence (Table 7.16).

### *Ngala Lodge area*

In the Ngala Lodge area the frequency at which juvenile giraffe were killed was greater than expected (Table 7.17). The frequency of impala, blue wildebeest and buffalo males that was selected by lions was also greater than their availability in the population (Table 7.18).

### Klaserie Private Nature Reserve

The age and sex selection of prey by lions was calculated from Klaserie Private Nature Reserve data from 2000 to 2003 (Tables 7.19 and 7.20) but the kill records from 1979 to 1981, and 1982 to 2003 could not be used since no data were available for the age and sex structure of the population for that time. The lions in the Klaserie Private Nature Reserve killed a greater proportion of adults than juveniles for all prey types except the giraffe (Table 7.19). For the giraffe, the frequency in which juveniles were killed was greater than expected. Waterbuck adults were also killed at a greater frequency than expected, as was the males of the blue wildebeest, buffalo, greater kudu and waterbuck (Table 7.20). Giraffe females were selected at a greater than expected frequency of occurrence.

## **Seasonality of predation**

For the long-term observation data, and the data from the Timbavati lodges and the Klaserie Private Nature Reserve, the blue wildebeest was selected for by lions in the wet season, and the giraffe and buffalo in the dry season. The frequency in which the blue wildebeest, giraffe and buffalo were killed by lions was as expected by their relative availability in the wet and dry seasons (Tables 7.21 to 7.24)

### Associated Private Nature Reserves

Table 7.21 shows that except for the buffalo, there was no difference between the observed seasonal selection by lions and prey occurrence in the population. A greater proportion of buffalo was killed in the dry season than the wet season, based on their relative availability in the wet and dry seasons. The lions showed a preference for blue wildebeest and Burchell's zebra in the wet season, and giraffe in the dry season.

### Timbavati Private Nature Reserve

#### *Timbavati lodges*

The lions in the traversing area of the Timbavati lodges selected impala and waterbuck at a greater than their expected frequency of occurrence in the wet season (Table 7.22). For all the other prey animals the seasonal selection by lions was not significantly different from their availability (Table 7.22). The blue wildebeest was selected by lions in the wet season in the same proportion as their expected frequency of occurrence.

#### *Ngala Lodge area*

Table 7.23 shows that lions killed the blue wildebeest at a greater frequency in the dry season than was expected. The seasonal selection by lions for all other prey was in proportion to their availability. Insufficient kills were recorded for Burchell's zebra, warthog, greater kudu and waterbuck to determine their possible seasonal selection by lions.

### Klaserie Private Nature Reserve

Table 7.24 shows that lions selected the giraffe and the waterbuck at a greater frequency

**Table 7.21:** *Seasonal prey selection by the C, S and M prides and the N coalition for the eight most abundant types of lion prey in the Associated Private Nature Reserves based on long-term field observations and data from the Timbavati lodges and the Klaserie Private Nature Reserve from May 2001 to August 2002. For each prey type the observed seasonal the lions was compared with its percentage occurrence in the wet and dry seasons.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Wet season** | | **Dry season** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Wet season** | **Dry season** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 5 | 71.0 | 2 | 29.0 | 87.0 | 13.0 | 1.5007 | > 0.05 | 1 |
| Buffalo | 8 | 26.0 | 23 | 74.0 | 46.8 | 53.2 | 5.4918 | < 0.05 | 1 |
| Burchell's zebra | 6 | 67.0 | 3 | 33.0 | 69.0 | 31.0 | 0.0237 | > 0.05 | 1 |
| Giraffe | 13 | 41.0 | 19 | 59.0 | 47.3 | 52.7 | 0.5777 | > 0.05 | 1 |
| Greater kudu | 6 | 32.0 | 13 | 68.0 | 25.0 | 75.0 | 0.4386 | > 0.05 | 1 |
| Impala | 9 | 43.0 | 12 | 57.0 | 51.9 | 48.1 | 0.6950 | > 0.05 | 1 |
| Warthog | 3 | 43.0 | 4 | 57.0 | 31.6 | 68.4 | 0.4121 | > 0.05 | 1 |
| Waterbuck | 4 | 36.0 | 7 | 64.0 | 48.6 | 51.4 | 0.6563 | > 0.05 | 1 |
| Total | 54 | 39.0 | 83 | 61.0 | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the ranges of the lion groups in the Associated Private Nature Reserves from May 2001 to August 2002.**

**~ Not applicable**

**Table 7.22:** *Seasonal selection of prey by lions from the eight most abundant types of lion prey in the Associated Private Nature Reserves based on data from the Timbavati lodges from January 2000 to January 2003. For each prey type the observed seasonal selection by the lions was compared with its percentage occurrence in the wet and dry seasons.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Wet season** | | **Dry season** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Wet season** | **Dry season** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 5 | 71.4 | 2 | 28.6 | 63.1 | 36.9 | 0.208 | > 0.05 | 1 |
| Buffalo | 11 | 50.0 | 11 | 50.0 | 45.9 | 54.1 | 0.146 | > 0.05 | 1 |
| Burchell's zebra | 3 | 33.3 | 6 | 66.7 | 59.7 | 40.3 | 2.592 | > 0.05 | 1 |
| Giraffe | 14 | 60.9 | 9 | 39.1 | 62.5 | 37.5 | 0.026 | > 0.05 | 1 |
| Greater kudu | 4 | 30.8 | 9 | 69.2 | 28.0 | 72.0 | 0.049 | > 0.05 | 1 |
| Impala | 2 | 16.7 | 10 | 83.3 | 52.0 | 48.0 | 5.993 | < 0.05 | 1 |
| Warthog | 1 | 16.7 | 5 | 83.3 | 48.4 | 51.6 | 2.417 | > 0.05 | 1 |
| Waterbuck | 5 | 41.7 | 7 | 58.3 | 72.2 | 27.8 | 5.585 | < 0.05 | 1 |
| Total | 45 | ~ | 59 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the traversing area of the Timbavati lodges from 2000 to 2002.**

**~ Not applicable**

**Table 7.23:** *Seasonal prey selection by from the eight most abundant types of lion prey in the Associated Private Nature Reserves based on data from the Ngala Lodge from January 2000 to January 2003. For each prey type the observed seasonal selection by the lions was compared with its percentage occurrence in the wet and dry seasons.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Wet season** | | **Dry season** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Wet season** | **Dry season** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 23 | 69.7 | 10 | 30.3 | 87.0 | 13.0 | 8.736 | $< 0.05$ | 1 |
| Buffalo | 13 | 46.4 | 15 | 53.6 | 46.8 | 53.2 | 0.002 | $> 0.05$ | 1 |
| Burchell's zebra | 3 | 42.9 | 4 | 57.1 | 69.0 | 31.0 | 2.245 | $> 0.05$ | 1 |
| Giraffe | 6 | 40.0 | 9 | 60.0 | 47.3 | 52.7 | 0.324 | $> 0.05$ | 1 |
| Greater kudu | 0 | 0.0 | 0 | 0.0 | 25.0 | 75.0 | ~ | ~ | 1 |
| Impala | 12 | 44.4 | 15 | 55.6 | 51.9 | 48.1 | 0.609 | $> 0.05$ | 1 |
| Warthog | 3 | 60.0 | 2 | 40.0 | 31.6 | 68.4 | 1.869 | $> 0.05$ | 1 |
| Waterbuck | 0 | 0.0 | 0 | 0.0 | 48.6 | 51.4 | ~ | ~ | 1 |
| Total | 60 | ~ | 55 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the Ngala Lodge area from 2000 to 2002.**

**~ Not applicable**

**Table 7.24:** *Seasonal selection by lions from the eight most abundant types of lion prey in the Associated Private Nature Reserves based on data from the Klaserie Private Nature Reserve from January 2001 to January 2003. For each prey type the observed seasonal selection by the lions was compared with its percentage occurrence in the wet and dry seasons.*

| **PREY** | **LION KILLS** | | | | **PERCENTAGE OCCURRENCE IN THE PREY POPULATION** | | **CHI-SQUARED TEST*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Wet season** | | **Dry season** | | | | | | |
| | Number of kills | Percentage killed | Number of kills | Percentage killed | **Wet season** | **Dry season** | $\chi^2$ | **P** | **df** |
| Blue wildebeest | 10 | 58.8 | 7 | 41.2 | 67.0 | 33.0 | 0.520 | > 0.05 | 1 |
| Buffalo | 21 | 50.0 | 21 | 50.0 | 50.8 | 49.2 | 0.011 | > 0.05 | 1 |
| Burchell's zebra | 10 | 55.6 | 8 | 44.4 | 62.0 | 38.0 | 0.319 | > 0.05 | 1 |
| Giraffe | 13 | 36.1 | 23 | 63.9 | 56.5 | 43.5 | 6.059 | < 0.05 | 1 |
| Greater kudu | 3 | 30.0 | 7 | 70.0 | 39.1 | 60.9 | 0.350 | > 0.05 | 1 |
| Impala | 3 | 42.9 | 4 | 57.1 | 50.1 | 49.9 | 0.148 | > 0.05 | 1 |
| Warthog | 1 | 50.0 | 1 | 50.0 | 42.1 | 57.9 | 0.051 | > 0.05 | 1 |
| Waterbuck | 4 | 36.4 | 7 | 63.6 | 71.4 | 28.6 | 6.627 | < 0.05 | 1 |
| Total | 65 | ~ | 78 | ~ | ~ | ~ | ~ | ~ | ~ |

*** Based on road strip counts for the Klaserie Private Nature Reserve from 2000 to 2002.**
**~ Not applicable**

in the dry season than expected by their availability. The blue wildebeest and Burchell's zebra were selected by lions in the wet season and the impala was selected in the dry season, at their expected frequency of occurrence. There was no seasonal selection for buffalo by the lions in the Klaserie Private Nature Reserve.

## DISCUSSION

The feeding ecology of the lions in the combined area of the Associated Private Nature Reserves had not previously been studied. The findings from the present study were in accordance with the general pattern of lion predation that has been observed for lions in African savannas.

### Killing rate

Previous studies have shown that the least biased method of studying the feeding ecology of large carnivores is by direct observation when following the lions continually in a vehicle for extended periods (Mills 1992; Mills & Shenk 1992; Funston 1999; Kilian 2003). This approach was followed in the present study too and it yielded significant results. The specific role of male lion predation in savanna woodlands with a high density of buffalo and impala was shown by Funston (1999). The present study supported his conclusions. Predation by the focal lion groups was considered to be representative of lion predation for the Associated Private Nature Reserves because, although the mean number of killing lions in the study comprised 19% of the total lion population, their combined ranges covered 68% of the total study area (Chapter 5).

Lion prides in the Associated Private Nature Reserves have a broader selection for medium-sized prey (101 to 300 kg in mass) (Mills 1992; Mills & Biggs 1993) and kill a greater proportion of this prey category than the non-territorial males that predominantly kill buffalo. Funston (1999) found a similar trend for lions in the Kruger National Park. In the present study, adult male and female lions killed prey at a similar rate. However, in the Kruger National Park, the non-territorial male lions kill a greater proportion of large prey, such as buffalo, than the pride females. The male lions in that area therefore kill prey less often the pride females. Lions in a study in the Savuti region of Chobe National Park show a similar prey selection to those in the Associated Private Nature Reserves, but kill prey more frequently (Viljoen 1997). The lower intake of meat by the lions in Savuti is possibly the reason why those lions have a higher killing frequency than the lions in the Associated Private Nature Reserves.

The impact of predation by male lions in the Associated Private Nature Reserves is reflected by the mean number of prey that are killed per male lion per year. The frequency of 31.0 kills per non-territorial male lion per year was significantly greater than the 17.4 kills per adult pride female per year. A similar trend was found for lions in the Kruger National Park (Funston 1999). However, the killing rate of the non-territorial male lions in the Kruger National Park was lower than that of the N coalition in the Associated Private Nature Reserves. The N coalition was the largest group of five non-territorial male lions in the Associated Private Nature Reserves at the time of the present study. The kill and consumption rates that were calculated for these male lions were therefore a maximum for a non-territorial group of males in the study area.

The present study showed that the biomass of prey in the Associated Private Nature Reserves can sustain the total lion population. However, certain prey populations declined during the period of study and it is likely that there is a variable predator-prey balance over time. The giraffe, in particular, was currently especially vulnerable to predation by the lion prides in the Associated Private Nature Reserves, with 35% of the standing crop per year being harvested by these lions. The lions, however, only shifted their prey selection to target giraffe when the availability of their preferred prey, the blue wildebeest and the Burchell's zebra, declined.

The killing rate of the lion population was, however, an overestimate rather than an underestimate because of the following:

1. The estimate for the total biomass of animals in the Associated Private Nature Reserves was conservative because it is based on the aerial count figures for 2003. These counts were lower than the aerial counts for 2001, for which the distance sampling method (Thomas *et al.* 2002) was used (Peel 2003). This method is not compatible with the aerial counting method (Joubert 1983; Viljoen & Retief 1993) that was used in 2001, and furthermore the distance sampling method is not suitable for any area smaller than 100 000 ha (Reilly pers. comm.)[2]. The reliability of the various counts is discussed in depth in Chapter 4.
2. The mean annual recruitment rate of the prey biomass was also an underestimate because it included the removal of 136 buffalo and 406 impala by the reserve management (Peel 2003).

### Food consumption rates

The estimated amount of food consumed by lions is a more reliable index of the impact of lion predation than the killing frequency of lions for various prey (Viljoen 1997). The consumption rate of lions may be used for comparing the impact of lion predation between different areas. The annual food consumption rate per lion in the Associated Private Nature Reserves was greater than that of the lions in both the Kruger National Park (Funston 1999) and the Chobe National Park (Viljoen 1997). In contrast to the lions in the above two areas, the lions in the Associated Private Nature Reserves selected larger prey

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and killed more frequently. The regular presence of non-territorial male lions with the lion prides in the study area is a possible reason for this difference in prey selection. Similar to the lions of the Kruger National Park, the non-territorial males in the study area had a high killing frequency of prey but they predominantly killed buffalo to sustain their high food consumption rate (Funston 1999). The mean food consumption rate of the focal lion prides and the N coalition were, respectively, greater than the minimum daily meat requirement of 5.9 kg of meat for adult female lions and 9.4 to 13.2 kg of meat for adult male lions as calculated by Funston (1999). Despite the high annual consumption rate of the lion population in the Associated Private Nature Reserves, the present study found that the available prey biomass can sustain the current lion population because the annual increase in prey biomass exceeded the annual food consumption rate of the lion population.

### Prey species selection

The predation by lions in the Associated Private Nature Reserves followed the broad trend of lion predation in African savanna ecosystems (Pienaar 1969; Schaller 1972; Mills & Shenk 1992; Mills *et al.* 1995; Funston 1999). Although lions are opportunistic feeders that select at least 38 types of prey (Bothma & Walker 1999), fewer than five of the larger prey types formed the majority of the diet (Schaller 1972; Smuts 1979; Stander 1991b; Mills & Shenk 1992; Hunter 1998; Funston 1999; Kilian 2003). The selection of prey by lions is influenced by prey size, availability and abundance, and by the climatic and habitat conditions at that time (Mills & Shenk 1992; Mills *et al.* 1995; Viljoen 1997; Bothma & Walker 1999; Funston 1999). The impact of lion predation on their prey may shift when there is an increase in the abundance of certain prey animals and a decline in the number of others (Pienaar 1969).

In the Associated Private Nature Reserves the prey selection by the lions shifted from targeting the declining populations of the blue wildebeest and the Burchell's zebra to taking the more of the abundant impala and buffalo populations (Weaver 1995). The fluctuation in the abundance of prey and the consequent shift in predation pressure may be related to management practices. In the Kruger National Park, predation by lions caused a decline in the blue wildebeest population after man had interfered by putting up boundary fences and had changed the grass burning regime (Smuts 1978). The new western boundary fence that was erected in 1960 (Porter 1970) prevented the seasonal movement of the blue wildebeest to areas of better grazing and beyond the range of the lions. The grass component of savanna ecosystems is encouraged by regular burning (Gertenbach 1983), and the lack of controlled burning in the Kruger National Park encouraged the vegetation to become more dense and less suitable for grazing animals such as the blue wildebeest. Although the fencing off of the Associated Private Nature Reserves has been identified as a cause for the decline in the blue wildebeest population in that area (Chapter 4) (Hirst 1969; Kruger 1988; Weaver 1995), the major decline in the blue wildebeest population occurred 10 years before the subsequent removal of these fences.

The population of blue wildebeest in the Klaserie Private Nature Reserve declined from 6564 animals in 1981 to 426 animals in 1983 through starvation during the severe drought of 1981 (Kruger 1988). The blue wildebeest population continued to decline after 1981 due to a lack of suitable habitat and a vulnerability to lion predation during the wet season (Weaver 1995). The lions then shifted their prey selection from their normally preferred prey, the blue wildebeest and the Burchell's zebra, to the more abundant impala. They also increasingly targeted larger prey such as the buffalo and giraffe (Weaver 1995). Although the giraffe was one of the least abundant prey animals in the study area from 1979 to 2003, it was one of the most frequently killed prey animals of the lions. It is possible that the lions selected the giraffe because they are large, and can therefore provide a high energy return for the energy that is expended per hunt.

The prey selection by the lions in the different areas of the Associated Private Nature Reserves was generally consistent from 1979 to 2003, with the lions in these areas selecting medium to large ungulates. However, there were certain trends that were specific to the individual areas. These will be discussed below. The prey selection of the C, S and M prides will be discussed separately to that of the N coalition, for the entire Associated Private Nature Reserves. For the Klaserie Private Nature Reserve, the Ngala Lodge area and the traversing area of the Timbavati lodges, the prey selection by lion prides and adult male lions combined, will be discussed for the individual areas.

### Associated Private Nature Reserves

The prey selection by the focal lion groups in the Associated Private Nature Reserves was similar to that of the lions in the Kruger National Park (Mills & Shenk 1992; Funston 1999). The pride females killed medium-sized ungulates most frequently, whilst the non-territorial males preferred the larger buffalo and giraffe. In contrast to lion predation in the Kruger National Park, the impala was not the most frequently killed prey type of the pride females in the present study. Although the impala was the most abundant prey animal in the present study, larger prey was selected in preference to the impala. The blue wildebeest, Burchell’s zebra, giraffe, warthog and waterbuck were selected at a killing frequency greater than their relative occurrence in the prey population. The giraffe was the most vulnerable prey animal to predation by the lion prides. The killing frequency of the giraffe was 7.3 times greater than their relative availability in the prey population and 39% of the standing crop of the giraffe was harvested by the lions. The decline of the blue wildebeest, the preferred prey of the lions historically, has led to the increased predation pressure on the giraffe by the lion prides of the Associated Private Nature Reserves.

Timbavati Private Nature Reserve

The prey selection by the lions in the Timbavati Private Nature Reserve was similar to that of the focal lion groups in the Associated Private Nature Reserves and the Kruger National Park (Mills & Shenk 1992; Funston 1999). The lions in these areas showed a preference for medium to large ungulates. Historically, the lions killed a greater number of blue wildebeest in the Timbavati Private Nature Reserve than at present, because there was a greater abundance of blue wildebeest then. When the relative abundance of the blue wildebeest decreased the lions started to select a smaller proportion of these prey animals (Hirst 1975; Kruger 1988; Weaver 1995). However, the blue wildebeest is still a preferred prey of the lions in the Timbavati Private Nature Reserve where the lion kill frequency exceeds their relative abundance. This is particularly true for the lions in the Ngala Lodge area. The frequency with which these lions killed these blue wildebeest remained constant from 1975 to 2000, although the relative abundance of the blue wildebeest declined from 40% to 2% in that time (Hirst 1975; Peel 2003). The gabbro plains of the Ngala Lodge area are a preferred habitat for the blue wildebeest and historically they congregated in large populations on these plains (Hirst 1975; Weaver 1995). However, the overall habitat in the Associated Private Nature Reserves has changed over time with an increase in woody plants. Consequently, the number of grazing animals such as the blue wildebeest decreased and the number of browsing animals and mixed feeders increased (Chapter 4) (Kruger 1988; Weaver 1995).

The lions in the traversing area of the Timbavati lodges preferred different prey to those in the Ngala Lodge area. The giraffe, rather than the blue wildebeest, was the most frequently killed prey animal in the area of the Timbavati lodges. There are two possible reasons:

1. The relative abundance of the blue wildebeest in the Ngala Lodge area was greater than that in the area of the Timbavati lodges.

2. The lion pride sizes around the Timbavati lodges were larger and therefore selected larger prey than in the Ngala Lodge area.

Although aerial count data were not available for the prey in the Ngala Lodge area during the study period, historical evidence and the ecological monitoring reports indicate that the relative abundance of the blue wildebeest was greater in this area than in the area of the Timbavati lodges (Hirst 1969; Hirst 1975; Peel 2003). The lions in the area of the Timbavati lodges shifted their prey selection from the declining blue wildebeest population to the giraffe population (Pienaar 1969), whilst in the Ngala Lodge area the lions continued to select the more abundant blue wildebeest. According to the predator counts for the lions in the study area, the lion pride sizes in the area of the Timbavati lodges were larger than for the prides in the Ngala Lodge area (Chapter 5). Larger prides such as the C, S and M prides have a high food consumption rate and may therefore select larger prey, such as the giraffe, to maximise the energy gained from each hunt (Kruuk & Turner 1967; Caraco & Wolf 1975).

Klaserie Private Nature Reserve

The predation trend of the lions in the Klaserie Private Nature Reserve was similar to that of the lions in the Ngala Lodge area. Historically, the most frequently killed prey in the Klaserie Private Nature Reserve was the blue wildebeest. Earlier it was also the second most abundant potential prey. The lion killing frequency of the blue wildebeest decreased from 44% in 1979 to 12% in 2003, in line with a decrease in the relative abundance of this prey animal from 19% in 1979 to 1% in 2003. The lions in the Klaserie Private Nature Reserve changed their prey selection from the blue wildebeest to the buffalo, when the relative abundance of the buffalo increased from 3% in 1981 to 20% in 2003.

The major prey animals in the Klaserie Private Nature Reserve, except the impala and the warthog, were killed at a greater frequency than their relative abundance. Blue wildebeest, Burchell's zebra, greater kudu, waterbuck and buffalo were therefore vulnerable to lion predation. Although the predation rating for the buffalo in the Klaserie Private Nature Reserve suggests that this animal is vulnerable to predation, this not a true reflection of the impact by lion predation. Buffalo occur in large herds that move across the range of the lion prides, and the aerial count does not allow for this. The high frequency of predation by lions on the preferred blue wildebeest and Burchell's zebra was not alleviated by predation on the numerically more abundant impala. In the Kruger National Park, the impala is a buffer prey to predation by lions on less abundant prey (Hirst 1969; Mills *et al.* 1995; Funston 1999). The lions in the Associated Private Nature Reserves seem to select fewer impala than blue wildebeest or Burchell's zebra, because they have a lower individual animal biomass and therefore a lower energy return than the blue wildebeest and Burchell's zebra. The dismantling of the boundary fences between the Kruger National Park and the Associated Private Nature Reserves in 1993 appears not to have had a major effect on the prey selection by lions in the Klaserie Private Nature Reserve. However, the prey selection of the lions changed in 1983 before the removal of the fences (Kruger 1988; Weaver 1995). These dynamics are discussed in more detail in the proposed predator-prey model in Chapter 8.

### Age and sex selection of prey

Lions may select a specific age and sex class of prey depending on the availability of the prey in those particular categories and the ease with which a particular age or sex class can be killed. When hunting prey that are difficult to capture and kill, such as the giraffe, the lions will kill a greater proportion of young, old or sick individuals (Temple 1987). The lions in the Associated Private Nature Reserves selected juvenile and female giraffe because these categories are more easy to kill and are therefore more vulnerable to lion predation. Also, the males of the larger ungulates are selected by the lions in preference to the females, particularly during the mating season when the physical condition of the adult male ungulates is poor and they are easy to hunt (Schaller 1972).

Historically, the age and sex selection of prey by the lions in the Associated Private Nature Reserves was similar to that found in the present study (Hirst 1969; Kruger 1988). However, the buffalo was not a major prey animal of the lions at that time because of its low relative abundance. In the present study, adult male buffalo were selected by the non-territorial male lions that have the physical strength and the benefit of large group sizes to overpower and kill large prey. A similar trend was found for the male lions in the Kruger National Park (Funston 1999).

### Seasonality of lion predation

Climatic factors may dictate the time that is available for foraging and affect the susceptibility of prey, and/or the efficiency of the predator (Sunquist & Sunquist 1989). In African savanna ecosystems rainfall is widely regarded as the key component that drives the system (Coe, Cumming & Phillipson 1976; Sinclair 1979; East 1984; Mills & Retief 1984; Walker, Emslie, Owen-Smith and Scholes 1987; Owen-Smith 1990). Lion predation has been identified as a significant regulating factor of the blue wildebeest and Burchell's zebra populations in the Kruger National Park under certain ecological conditions (Smuts 1978; Mills & Shenk 1992; Mills *et al.* 1995; Funston 1999). Several studies have shown that lions prey on the Burchell's zebra and the blue wildebeest at a higher rate in periods that receive close to the mean rainfall, while the buffalo and giraffe are preferred in periods of rainfall that are below the mean (Hirst 1969; Mills & Shenk 1992; Mills *et al.* 1995; Funston 1999).

In several lion predation studies the killing frequency of the smaller prey, such as impala, have been shown to be under-represented (Hirst 1969; Kruger 1988; Mills *et al.* 1995;

Funston 1999). Because lions are capable of killing and consuming an impala without leaving any evidence of it, particularly in the wet season when the vegetation is dense, location of impala carcasses is more successful in the dry than the wet season. This creates a disproportionate record of impala kills in the wet season. However, with the impala being the most abundant prey animal in the Associated Private Nature Reserves, with a population that was still increasing at the time of this study, this discrepancy played no significant role.

### Associated Private Nature Reserves

The general prey selection of the lions in the Associated Private Nature Reserves was consistent with that of the lions in the Kruger National Park (Mills & Shenk 1992; Mills *et al.* 1995; Funston 1999). Blue wildebeest and Burchell's zebra were selected by the lions in the wet season, and buffalo and giraffe in the dry season. The buffalo was the only prey that was not selected in the same proportion as its availability in either the wet or dry season. A greater frequency of the buffalo was killed in the dry season than expected by their availability in that season. The decline in the giraffe population at the time of the present study may have caused the lions to select a greater number of the buffalo during the dry season. A similar trend was found for the lions in the Kruger National Park, where the prey selection shifted from a declining waterbuck population to the more abundant blue wildebeest and Burchell's zebra populations in a dry cycle (Pienaar 1969).

### Timbavati Private Nature Reserve

In the traversing area of the Timbavati lodges, the impala and the waterbuck were the only two types of prey that were selected seasonally by lions at a greater frequency than was expected by their availability. However, the proportion of waterbuck and impala that was killed by lions in the dry season was higher than expected in the kill data. Impala may be consumed by lions without leaving any evidence while the dense riverine habitat of the waterbuck makes the location of carcasses during the wet season difficult (Mills *et al.* 1995).

In savanna ecosystems lions are more successful at killing blue wildebeest during a period of above mean rainfall when there is adequate vegetation cover (Whyte & Joubert 1988; Mills & Shenk 1992; Mills *et al.* 1995). However, in the Ngala Lodge area the lions killed a greater number of the blue wildebeest in the dry season than was expected by their relative abundance. The blue wildebeest is the preferred prey of the lions in the Ngala Lodge area (Hirst 1975) and may therefore be selected at a greater frequency than their relative abundance independently of changing climatic conditions.

### Klaserie Private Nature Reserve

The giraffe is more vulnerable to lion predation in the dry than the wet season in savanna ecosystems (Hirst 1969; Pienaar 1969; Kruger 1988; Mills *et al.* 1995). The lions in the Klaserie Private Nature Reserve killed a greater proportion of giraffe in the dry season than was expected by their availability. The reason is likely to be a decline in the availability of blue wildebeest and Burchell's zebra, the preferred prey of the lions in the study area. The rainfall during 2002 was less than the long-term mean, resulting in an extended dry season with its habitat conditions, during which the lions selected the giraffe in preference to the blue wildebeest or the Burchell's zebra. This confirms the conclusions of Mills *et al.* (1995) for the lions in the Kruger National Park.

The waterbuck was also killed at a greater than expected frequency in the dry season by the lions in the Klaserie Private Nature Reserve. However, the proportion of waterbuck represented in the kill data was higher than expected for the dry season due to the greater success in locating waterbuck carcasses in the dry season than the wet season.

## CONCLUSIONS

The current impact of lion predation on the total prey population of the Associated Private Nature Reserves was sustainable, although the number of certain prey animals continued to decline during this study. The major prey animals of the lions at the time of the study were the impala, Burchell's zebra, blue wildebeest, buffalo and the giraffe. The non-territorial male lions selected larger prey and killed prey more frequently than the pride females. Predation by male lions was high on the buffalo and the giraffe populations in the study area. The killing and consumption rates of the lion groups in the present study were similar to the predation rates of lions in the Kruger National Park (Funston 1999). Historically, the large herbivore population in the Associated Private Nature Reserves experienced high levels of lion predation. A major decline in some of these prey populations, however, occurred due to starvation during the severe drought in 1981 (Kruger 1988). Several studies have shown that resident prey at high densities are regulated by food availability and not by lion predation (Pienaar 1969; Kruuk 1972; Sinclair, Dublin & Borner 1985). The lions in the study area shifted their prey selection from a declining blue wildebeest and Burchell's zebra population, to the more abundant impala, and the larger buffalo and giraffe. The populations of these preferred blue wildebeest and Burchell's zebra continued to decline during the study because the lion predation pressure on them was greater than their relative abundance. The dense vegetation and wet season conditions were more suitable for lions to hunt the habitat blue wildebeest and the Burchell's zebra in the Associated Private Nature Reserves (Kruger 1988; Weaver 1995). The habitat in these nature reserves changed from an open savanna to a dense woodland vegetation that was less suitable for grazing animals such as the blue wildebeest and Burchell's zebra (Kruger 1988; Weaver 1995). Grazing animals disperse into smaller groups in dense vegetation and are more vulnerable then to lion predation, particularly in the wet season (Smuts 1978). The change in habitat was caused by earlier management actions and climatic fluctuations (Kruger 1988). The management actions that had a detrimental affect on the habitat were overstocking with ungulates, a lack of controlled burning and the erection of numerous artificial waterholes. In the Kruger National Park, management actions were also responsible for the decline in the blue wildebeest population (Smuts 1982). Predation by the lions in the Kruger National Park caused a continuation of the decline in the blue wildebeest populations, after man had interfered by putting in fences and by changing the grass-burning regime.

In large natural areas large predators should be allowed to establish themselves and fulfil their natural role (Bothma 1996). A relatively constant population density of large predators is maintained in an area through social behaviour and changing environmental conditions, provided that there is sufficient food available (Packer & Pusey 1985). In the central Kruger National Park, the removal of a large number of lions and spotted hyaenas in the past, had little effect on the decreasing populations of blue wildebeest and Burchell's zebra (Bothma 1996). The present study has shown that the prey biomass in the open system of the Associated Private Nature Reserves sustained the lion population. Provided that the vegetation in the Associated Private Nature Reserves is managed in such a manner as to promote suitable habitat for the declining prey types, the blue wildebeest should recover by emigration from the Kruger National Park in a typical source to sink effect (Pulliam 1988).

# CHAPTER 8

# MODELLING THE RELATIONSHIP BETWEEN RAINFALL, LION PREDATION AND PREY POPULATIONS

## INTRODUCTION

In Africa, large mammal predator-prey systems are complex due to the variety of species of predator and prey. Predation in large, self-contained ecosystems has little effect on prey populations that are migratory or nomadic (Sinclair, Dublin & Borner 1985; Mills 1990). However, resident prey populations in areas such as the Serengeti and the Kruger National Park may be more heavily influenced by predation (Sinclair 1995; Fryxell, Greever & Sinclair 1988; Whyte & Joubert 1988; Mills & Shenk 1992; Funston 1999). A prey population that has decreased due to some other limiting factor, such as a drought or disease, may then become regulated by lion predation. When the blue wildebeest population in the Kruger National Park was caused to decrease by drought, lion predation retarded the recovery of this population (Pienaar 1969).

Climatic factors may limit the time available for foraging by predators, or affect the effectiveness of predators, and may even affect the susceptibility of the prey to predation (Sunquist & Sunquist 1989). In African savanna ecosystems, rainfall is the key component driving the system (Coe, Cumming & Phillipson 1976; Sinclair 1979; East 1984; Walker *et al.* 1987; Owen-Smith 1990; Mills, Biggs & Whyte 1995). Studies in the Kruger National Park have found that lion predation caused the decrease in the migratory blue wildebeest and the sedentary Burchell’s zebra subpopulations during a period of high rainfall (Smuts 1978a; Whyte & Joubert 1988; Mills & Shenk 1992; Mills, Biggs & Whyte 1995). In the Serengeti National Park, the seasonal fluctuation in rainfall affects prey availability and therefore has an influence on the selection of prey by the lions in that region (Sunquist & Sunquist 2002). When blue wildebeest are abundant on the Serengeti plains in the wet season they are the most frequent lion prey, whereas in the dry season lions kill the more common Thomson's gazelle (*Gazella thomsonii*) and warthog (*Phacochoerus aethiopicus*). A linear relationship has also been found between the population dynamics of ungulates and rainfall. The survival of the calf, juvenile and senescent growth stages of ungulates was greater during a period of above mean rainfall than during a period of mean rainfall or less (Fairall 1985; Owen-Smith 1990).

Early predator-prey studies measured the effect of large mammalian predators on their prey experimentally, by comparing the number of prey in an area where predators were culled, with that in an area where no predators were culled (Smuts 1978b; Whyte 1985). This method of study has a limited conservation value for the predators involved, many of which are endangered species (Mills & Shenk 1992). An alternative method of studying predator-prey relationships is the implementation of a simulation model based on intensive predator-prey observations. Several studies have used such computer modelling to predict the impact of lion predation on their prey populations (eg. Mills & Shenk 1992; Mills, Biggs & Whyte 1995; Funston 1999; Peel & Montagu 1999; Kilian 2003). Simulation models allow the manipulation of several variables relative to each other, and can be used to predict the affect of different ecological conditions on those variables. By modelling prey population dynamics, the possible impact of various management actions can also be simulated.

The modelling of predator-prey relationships requires a knowledge of the predator kill proportion, the preferred prey, the prey population dynamics and the current and predictive environmental conditions. In the present study, these data were available for the Klaserie

Private Nature Reserve from 1985 to 2003. These were the most consistent lion predation data for the Associated Private Nature Reserves, and were taken here as being representative of the entire study area. Previous studies In the Klaserie Private Nature Reserve have indicated that there was a relationship between rainfall, lion predation and prey population trends (Kruger 1988; Weaver 1995). A simulation model was developed to investigate the perceived continued decrease of the ungulate populations in the Associated Private Nature Reserves in more depth. By using a predator-prey model the following hypotheses were therefore tested in the present study for lions and their large ungulate prey:

- The population trends of the larger ungulates in the Klaserie Private Nature Reserve are correlated with fluctuations in annual rainfall.
- The kill proportion of certain types of lion prey is correlated with fluctuations in annual rainfall.
- The size of the prey population determines their kill proportion by lions.
- The removal of the eastern boundary fence of the Klaserie Private Nature Reserve with the Timbavati and Umbabat Private Nature Reserves, and the removal of the western boundary fence of the Kruger National Park with the Timbavati and Umbabat Private Nature Reserves, has influenced prey population trends.
- There is a correlation between the ungulate population trends in the Klaserie Private Nature Reserve and changes in the aerial counting method.

## METHODS

Predator-prey relationships in the African savannas are complex and the environmental conditions are constantly changing. A computer model was therefore developed to aid in the prediction of the dynamics of the relationship between lions and their prey in the Klaserie

Private Nature Reserve. The larger the data-base upon which the computer model is based, the better the predictive ability of the model and its application as a management tool. The model of Mills, Biggs and Whyte (1995) was adopted for use in this part of the present study to investigate the relationships between rainfall, lion predation and the prey population trends in the Klaserie Private Nature Reserve.

**Rainfall**

The rainfall patterns for the Associated Private Nature Reserves were described in detail in Chapters 2 and 4. Annual rainfall was calculated from July in one year to June the following year to reflect a full season of rainfall. The summer rainfall (wet) season starts in October and ends in March, and the winter rainfall (dry) season starts in April and ends in September. The Associated Private Nature Reserves are situated in the Lowveld of South Africa and experience wet and dry cycles that generally conform to a 20-year oscillation consisting of 10 years of above mean rainfall, followed by 10 years below it (Tyson & Dyer 1975; Gertenbach 1980). Most recently, a dry cycle occurred from June 1985 to July 1994 (9 years), and a wet cycle from June 1995 to July 2002 (7 years) in the study area. The long-term mean for rainfall in the Klaserie Private Nature Reserve from 1983 to 2003 is 461 mm (Peel 2003). Rainfall was defined according to four categories (Funston 1999):

- Above mean rainfall: > 7.5% above the long-term mean
- Mean rainfall: 7.5% above the long-term mean to 7.5% below it
- Moderate rainfall: > 7.5% below the long-term mean to 25% below it
- Drought: > 25% below the long-term mean

The reserve management and lodges recorded the annual rainfall for the Associated Private Nature Reserves, and the Computing Centre for Water Research based the mean rainfall for each of the component parts of the Associated Private Nature Reserves on these data. To smooth these data, a recent rainfall mean was calculated from the rainfall of the current and two preceding years.

### Population trends of prey

Population estimates of the larger ungulates were based on aerial counts that were conducted annually at the end of the dry season from 1985 to 2002 (Chapter 4). A fixed-wing aircraft was used from 1992 to 1996, and a four-seater helicopter from 1982 to 1991 and again from 1997 to 2003. Due to the different flying characteristics of a helicopter when it is used to count animals, such population counts were higher than when counts were done with a fixed-wing aircraft (Joubert 1983; Peel *et al.* 1990; Peel & Bothma 1995). The aerial counts for the Klaserie Private Nature Reserve were obtained from the Agricultural Research Council's Range and Forage Institute (Peel 2003). The counts were total counts and no correction factor was therefore applied. The data were smoothed by using a 3- year moving mean.

### Predation

Lions were the major predators of the larger ungulates in the Klaserie Private Nature Reserve, harvesting 68% of the total number of prey killed (Kruger 1988). In the Kruger National Park, lions were also found to be the main predators, removing 54% of the prey biomass (Mills & Biggs 1993). Kill data for the seven most abundant prey types were obtained from the Warden of the Klaserie Private Nature Reserve for the period from 1985 to 2002. These data are biased towards larger prey and underrepresent the smaller prey types (Mills 1992; Mills & Biggs 1993). However, they were considered acceptable for use in the models because the focus of the present study was on the impact of lion predation on the large ungulates.

A predation rating was calculated for the seven most abundant prey types from the kill data and the aerial herbivore counts from 1985 to 2002 (Pienaar 1969) (Chapter 7). The following equation of Mills, Biggs & Whyte (1995) was used to calculate the kill proportion (K) for each prey type: $K = n \div N$

where:

$K$ = the annual kill proportion for each prey type

$n$ = the number of kills per prey type in a given year

$N$ = the total number of kills for all prey types in the same year

### Statistical analyses and model construction

Simple and multiple linear regression, stepwise-regression, and general linear modelling (GLM), were used as model-building tools for the kill data. The statistical programme SAS (2001) and the expertise of Van der Linde (pers. comm.)[1.] and Groeneveld (pers. comm.)[2.] were combined to generate the models. The regressions that were generated were used in spreadsheet models to calibrate the contribution of the relevant parameters in the dynamics of the seven most abundant prey types: the blue wildebeest, Burchell's zebra, buffalo, giraffe, impala, greater kudu and waterbuck. The actual population count for these prey in a particular year were used in the regression equations to estimate each subsequent year's population

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size according to the method of Mills *et al.* (1995). The relevant equation was: $P_T = A + BP_L + CR + D K_L$

where:
$P_T$ = the population count for a particular prey type for a given year
A = a constant
B, C and D = the regression coefficients for the relevant parameters
$P_L$ = the population count for a particular prey type for the previous year
R = the rainfall index in mm
$K_L$ = the lion kill proportion (%) for a particular prey type for the previous year

A regression equation was then developed with a given year's kill proportion ($K_T$) as the dependent variable by using the following equation of Mills *et al.* (1995): $K_T = A + BK_L + CR + DP_L$

where:
$K_T$ = the lion kill proportion for a particular prey type for a given year
$K_L$ = the lion kill proportion for a particular prey type for the previous year
R = the rainfall index in mm
$P_L$ = the population count for a particular prey type for the previous year

The following class categories were introduced to the regression equations as predictors:

*Fence categories*: The presence or absence of the eastern boundary fence between the Klaserie Private Nature Reserve and the Timbavati and Umbabat Private Nature Reserves (removed in 1993), and the western boundary fence between the Kruger National Park and the Timbavati Private Nature Reserve (removed in 1993).

- Fence category 1 = before the removal of the eastern boundary fence of the Klaserie Private Nature Reserve and the Timbavati and Umbabat Private Nature Reserves, and before the removal of the western boundary fence of the Kruger National Park with the Timbavati Private Nature Reserve (1985 to 1992)
- Fence category 0 = after the removal of the eastern boundary fence between the Klaserie Private Nature Reserve and the Timbavati and Umbabat Private Nature Reserves, and after the removal of the western boundary fence between the Kruger National Park and the Timbavati Private Nature Reserve (1993 to 2002)

*Rainfall categories*: the four categories were described earlier in the Methods

*Aerial counting method*:

- H = helicopter counts: 1982 to 1992 and 1997 to 2003
- F = fixed-wing counts: 1992 to 1996

The log values of the independent variables were determined and applied to the regression equations in an attempt to normalise the population counts. This had no effect on the outcome of the models and the crude values were therefore used. A quadratic regression model was used to test whether the data fitted a quadratic curve rather than a linear one. No difference was detected between the relationships from the quadratic regression models and the step-wise linear regression models. Therefore, step-wise linear regression models were used and all correlations were linear. A probability value (*P*) was calculated for each variable in the step-wise regressions, and all variables that were significant at the 75% confidence level were left in the model by the statistical programme SAS (2001). The low confidence level used by SAS (2001) in the step-wise regression analysis was considered acceptable in the present study, because general linear modelling was subsequently applied to the data at the 95% confidence level (Groeneveld pers. comm.). The regression equations and significant variables were used in general linear modeling, and a final set of regression equations was generated. For each of the class categories, general linear modelling provided the least squares means. These means and their probability values were used to test for significance of differences between the means of the various categories. The decision to use a regression as an operative model was dictated by the overall strength of that regression (Mills, Biggs & Whyte 1995). The regression models with the most significant coefficient of determination ($R^2$) and probability value (P) were selected. The greater the coefficient of determination and the lower the probability value, the more closely the data approximated the model (Groeneveld pers. comm.).

The final regression models predicted the relative contribution of rainfall and lion kill proportion in the population trends of the seven prey animals. These models were derived from the significant parameters ($P \leq 0.05$) of the regression equations that were used in general linear modelling. The models were based on two or more parameters depending on the correlation between the relevant parameters. A model consisting of three parameters was used when lion kill proportion and rainfall were uncorrelated ($P > 0.05$). The lower the probability value (P) became below $P = 0.05$, and the greater the coefficient of determination ($R^2$) was above 0, the greater the statistical significance of the model. From the final models that were statistically significant, the predicted dependent variables for each combination of selected independent variables were then calculated, with 95% confidence intervals. These predicted values were compared with the observed values to test the goodness of fit of the predicted models, and to determine whether the results could be extrapolated to make future predictions (Mills, Biggs & Whyte 1995).

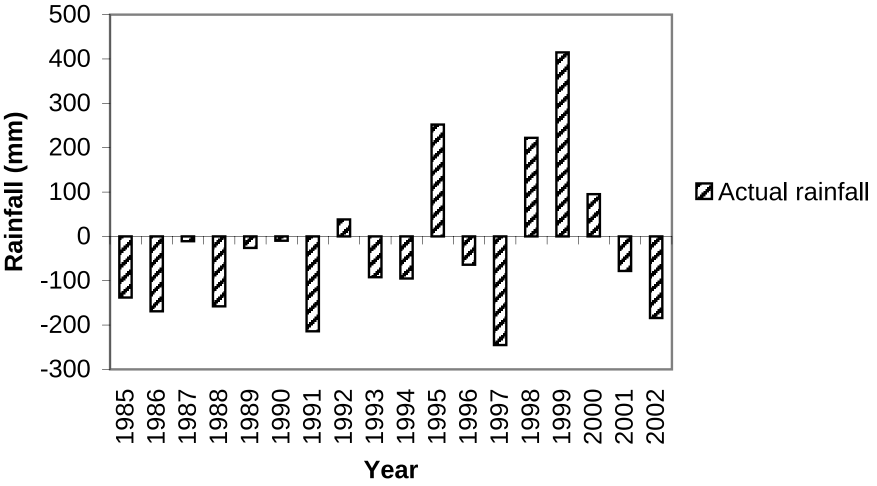
## RESULTS

### Rainfall patterns, population trends and kill proportions

Figure 8.1 shows the actual rainfall and smoothed annual rainfall for the Klaserie Private Nature Reserve from 1985 to 2002. The fluctuation in wet and dry cycles is shown clearly by the smoothed rainfall data. Figure 8.2 shows the population trends for the seven most abundant prey animals of the lions and the lion kill proportion for each prey type in the study area from 1985 to 2002.

The population sizes for each of the seven types of prey fluctuated widely during the period of study (Figure 8.2). Nevertheless, the buffalo was the only prey whose population did not show a long-term decrease from 1985 to 2002. The impala, Burchell's zebra, blue wildebeest and giraffe populations all decreased from 1986 to 1989 (dry years), whilst the buffalo, waterbuck and greater kudu populations increased in that period. From 1989 to 1992 (dry years), the Burchell's zebra, blue wildebeest and buffalo populations increased, and the impala, giraffe, greater kudu and waterbuck populations decreased. A decrease in the numbers of all seven prey types occurred from 1992 to 1996. The magnitude of this population decrease was exaggerated, however, by the change in the aerial counting method during this period (Whyte & Joubert 1988). The buffalo population increased from 1997 to 2002, but all other prey types showed a decrease for the same period.

The kill proportions for the seven types of lion prey fluctuated between years, with the greatest variation occurring in the giraffe and the buffalo (Figure 8.2). The prey types that were killed in the greatest frequency, based on the mean kill proportion from 1985 to 2002, were the giraffe (30%), blue wildebeest (19%), Burchell's zebra (17%) and the buffalo (14%)



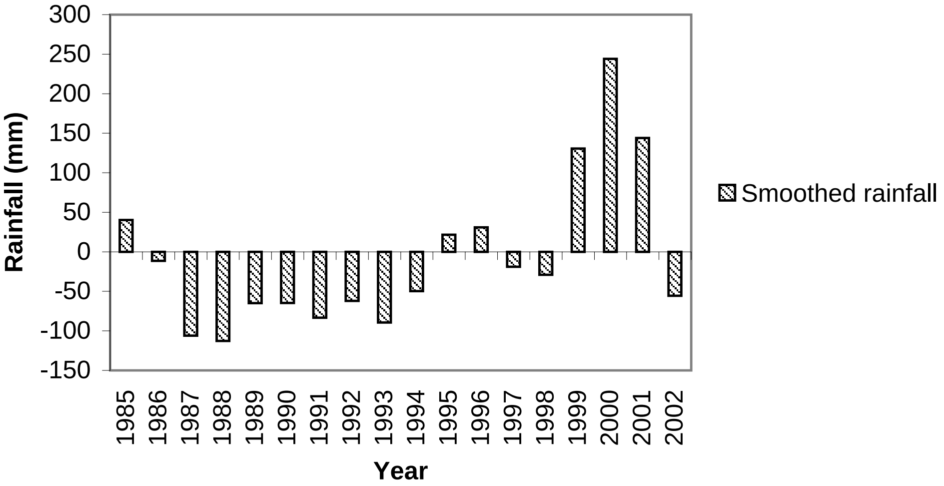


**Figure 8.1**: Actual and 3-year smoothed rainfall for the Klaserie Private Nature Reserve from 1985 to 2002, showing the years for which the rainfall was above the long-term mean of 461 mm (at base line 0) and those below it. Source: Peel (2003)

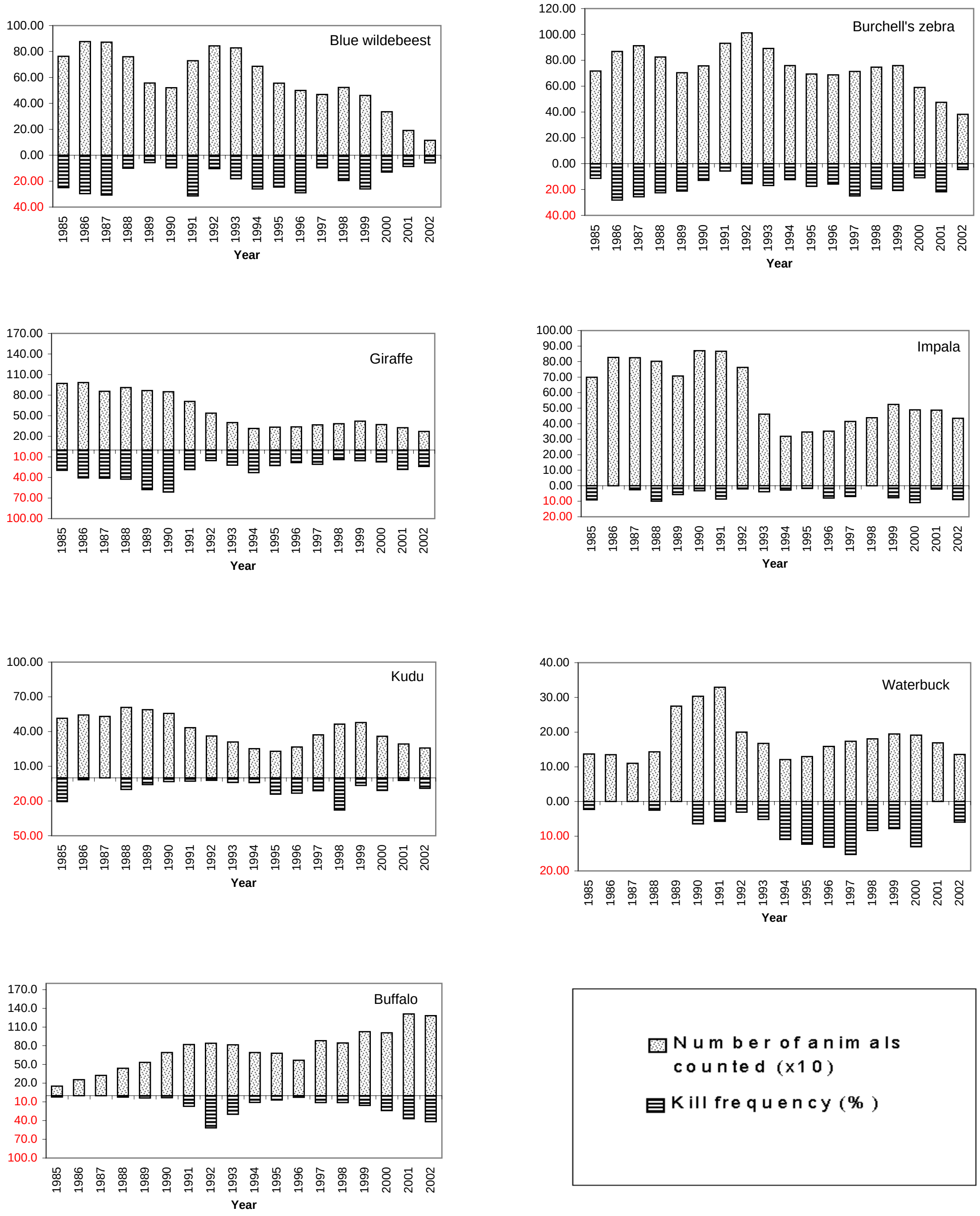


**Figure 8.2:** The number of animals counted during aerial counting and the kill proportion by lions for the seven most abundant types of lion prey in the Klaserie Private Nature Reserve from 1985 to 2002. Sources of data: Peel (2003) and present study.

(Table 8.1). The predation rating (Figure 8.3) for the Burchell's zebra, blue wildebeest and the giraffe shows that these prey animals were killed at a greater than expected frequency based on their abundance from 1985 to 2002. The killing frequency for the impala was less than their relative abundance from 1985 to 2002, as indicated by their predation rating for that period. The predation rating for the buffalo fluctuated during this period, but increased from 1996 to 2002. This period was after the removal of the boundary fence between the Klaserie Private Nature Reserve and the Timbavati and Umbabat Private Nature Reserves in 1993, and during the time when the aerial counting method was changed. The killing frequency for the buffalo from 1998 to 2002 (wet years) was greater than its relative abundance as prey.

### *Mean rainfall and the size of the prey population*

There was no significant relationship between smoothed annual mean rainfall and population size for the seven types of lion prey (Table 8.2).

### *Mean rainfall and lion kill proportion*

The relationship between smoothed annual mean rainfall and kill proportion was not significant for all types of lion prey (Table 8.3).

### *Lion kill proportion and the size of the prey population*

The giraffe was the only prey that showed a significant correlation between its lion kill proportion and population size (Table 8.4). A decrease in the kill proportion of the giraffe was correlated with a decrease in the size of the giraffe population. The kill proportion of the giraffe was positively correlated with the population size of the impala ($R^2 = 0.6433$; $P \leq 0.01$), Burchell's zebra ($R^2 = 0.6088$; $P \leq 0.05$) and blue wildebeest ($R^2 = 0.6478$; $P \leq 0.01$). The lions in the Klaserie Private Nature Reserve changed their prey selection from mainly giraffe

**Table 8.1**: *The mean annual kill frequency of the seven most abundant prey types of the lions in the Klaserie Private Nature Reserve from 1985 to 2002.The prey animals are listed in descending order of the greatest range (minimum and maxiumum) of values for its kill proportion.*

| PREY | MEAN ANNUAL KILL FREQUENCY (%) | STANDARD DEVIATION | RANGE |
|---|---|---|---|
| Buffalo | 14.2 | 0.155 | 0.073 to 0.229 |
| Giraffe | 30.1 | 0.139 | 0.231 to 0.371 |
| Blue wildebeest | 18.9 | 0.092 | 0.143 to 0.235 |
| Burchell's zebra | 16.6 | 0.067 | 0.133 to 0.199 |
| Greater kudu | 8.1 | 0.071 | 0.053 to 0.117 |
| Waterbuck | 6.3 | 0.050 | 0.038 to 0.088 |
| Impala | 5.6 | 0.037 | 0.038 to 0.074 |
| Total | 100.0 | ~ | ~ |

**~ Not applicable**

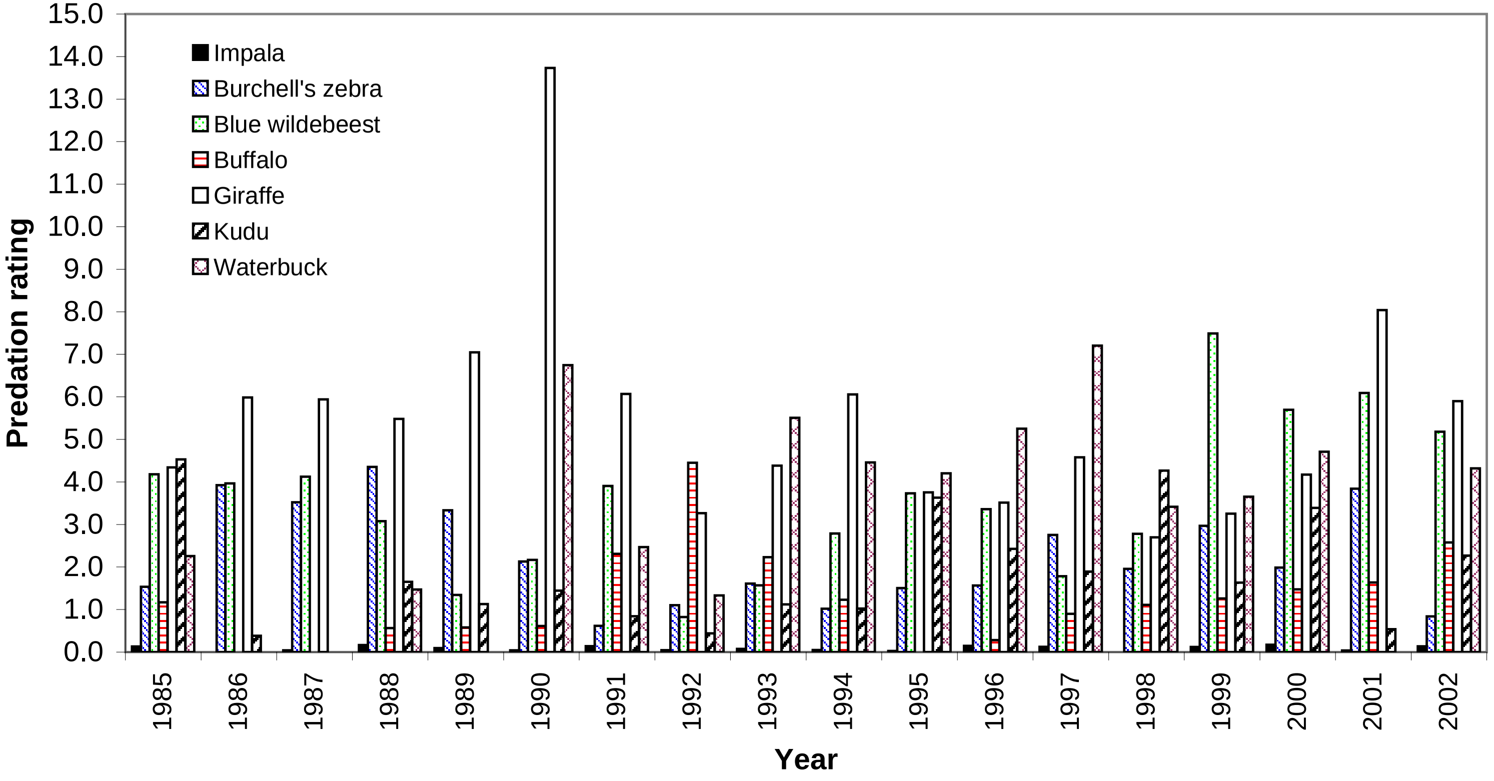


**Figure 8.3**: The predation rating for the seven most abundant prey types of lions in the Klaserie Private Nature Reserve from 1985 to 2002. A predation rating < 1.0 indicates a killing frequency by lions that was less than the relative abundance of the prey animal, a predation rating = 1.0 indicates a killing frequency by lions that was equal to the relative abundance of the prey, and a predation rating > 1.0 indicates a killing frequency by lions that was greater than the relative abundance of the prey animal. Source of data: Rowles (2003) and present study.

**Table 8.2**: *The coefficient of determination and probability values calculated by general linear modelling for the relationship between mean annual rainfall and population size for the most abundant prey types of lions in the Klaserie Private Nature Reserve from 1985 to 2002.The prey animals are listed in descending order of the greatest coefficient of determination.*

| **PREY** | **COEFFICIENT OF DETERMINATION** | ***P-value*** |
|---|---|---|
| Blue wildebeest | 0.3735 | > 0.05 |
| Giraffe | 0.3066 | > 0.05 |
| Impala | 0.2411 | > 0.05 |
| Buffalo | 0.1963 | > 0.05 |
| Burchell's zebra | 0.1922 | > 0.05 |
| Greater kudu | 0.1325 | > 0.05 |
| Waterbuck | 0.0541 | > 0.05 |

**Table 8.3**: *The coefficient of determination and probability values calculated by general linear modelling for the relationship between mean annual rainfall and the kill proportion for the most abundant prey types of the lions in the Klaserie Private Nature Reserve from 1985 to 2002.The prey animals are listed in descending order of the greatest coefficient of determination.*

| **PREY** | **COEFFICIENT OF DETERMINATION** | ***P-value*** |
|---|---|---|
| Waterbuck | 0.4058 | > 0.05 |
| Impala | 0.3911 | > 0.05 |
| Burchell's zebra | 0.2587 | > 0.05 |
| Giraffe | 0.2584 | > 0.05 |
| Greater kudu | 0.1003 | > 0.05 |
| Buffalo | 0.0325 | > 0.05 |
| Blue wildebeest | 0.0212 | > 0.05 |

**Table 8.4**: *The coefficient of determination and probability values for the relationship between the previous year's kill proportion and the population size of the most abundant types of lion prey in the Klaserie Private Nature Reserve from 1985 to 2002. The estimated regression coefficient shows whether the tested relationship was positive or negative. The prey animals are listed in decreasing order of the greatest coefficient of determination.*

| PREY | COEFFICIENT OF DETERMINATION | *P-value* | ESTIMATED REGRESSION COEFFICIENT* |
|---|---|---|---|
| Giraffe | 0.3188 | ≤ 0.05 | -119.80 |
| Burchell's zebra | 0.0909 | > 0.05 | -110.78 |
| Buffalo | 0.0876 | > 0.05 | -78.74 |
| Impala | 0.0392 | > 0.05 | -1278.23 |
| Blue wildebeest | 0.0088 | > 0.05 | -30.73 |
| Greater kudu | 0.0041 | > 0.05 | -14.76 |
| Waterbuck | 0.0004 | > 0.05 | -4.07 |

*** The decrease in the population size of a prey type when the previous year's kill proportion decreases by 10%**

in the dry season (1985 to 1994) to the impala, Burchell's zebra and blue wildebeest in the wet season (1995 to 2002) (Figure 8.2) (Chapter 7).

The population size of the giraffe and buffalo were positively correlated with lion kill proportion (Table 8.5). These prey types were therefore killed more frequently by lions when their population numbers were high. For the other types of prey there was no relationship between population size and lion kill proportion.

### *The effect of the removal of the boundary fence on the size of the prey population*

The population size of the buffalo showed a positive correlation with the removal of the eastern boundary fence of the Klaserie Private Nature Reserve with the Timbavati and Umbabat Private Nature Reserves, and a negative correlation with the other prey animals, except the waterbuck (Table 8.6 and Figure 8.2). The size of the waterbuck population was not correlated with the removal of the eastern boundary fence.

### *The effect of the change in the aerial counting method on the size of the prey population*

A negative linear correlation was found between the change in the aerial counting method from 1992 to 1996 and the population size of the giraffe, impala and greater kudu (Table 8.7). The population sizes of the other prey were not significantly correlated with the change in the aerial counting method, although the populations of all prey types decreased from 1992 to 1996 (Figure 8.2).

**Table 8.5**: *The coefficient of determination and probability values calculated by general linear modelling for the relationship between prey population size and the lion kill proportion for the most abundant types of lion prey in the Klaserie Private Nature Reserve from 1985 to 2002.The prey animals are listed in descending order of the greatest coefficient of determination.*

| PREY | COEFFICIENT OF DETERMINATION | *P-value* | ESTIMATED REGRESSION COEFFICIENT* |
|---|---|---|---|
| Buffalo | 0.5815 | ≤ 0.01 | 0.0290 |
| Giraffe | 0.4453 | ≤ 0.01 | 0.0316 |
| Blue wildebeest | 0.2019 | > 0.05 | 0.0159 |
| Burchell's zebra | 0.0856 | > 0.05 | 0.0093 |
| Waterbuck | 0.0046 | > 0.05 | 0.0003 |
| Greater kudu | 0.0016 | > 0.05 | 0.0017 |
| Impala | 0.0003 | > 0.05 | 0.0002 |

*** The change to the kill proportion of a prey animal for an increase in the size of the prey population by 100 animals.**

**Table 8.6**: *The coefficient of determination and probability values calculated by general linear modelling for the relationship between the removal of the eastern boundary fence of the Klaserie Private Nature Reserve in 1993 and the population size for the most abundant types of lion prey in the Klaserie Private Nature Reserve from 1985 to 2002. The removal of the western boundary fence of the Kruger National Park with the Timbavati Private Nature Reserve in 1993 was a secondary factor for which no data were not available. The prey animals are listed in descending order of the* greatest coefficient of determination.

| | | | **BOUNDARY FENCE** | |
|---|---|---|---|---|
| **PREY** | **COEFFICIENT OF DETERMINATION** | ***P*- value** | Fence category * | Least squares means |
| Giraffe | 0.6469 | ≤ 0.01 | 0 | 337.20 |
| | | | 1 | 795.89 |
| Impala | 0.5013 | ≤ 0.01 | 0 | 572.06 |
| | | | 1 | 7654.11 |
| Blue wildebeest | 0.4433 | ≤ 0.01 | 0 | 387.70 |
| | | | 1 | 759.11 |
| Buffalo | 0.3393 | ≤ 0.05 | 0 | 978.44 |
| | | | 1 | 542.56 |
| Burchell's zebra | 0.3297 | ≤ 0.05 | 0 | 607.10 |
| | | | 1 | 861.33 |
| Greater kudu | 0.3086 | ≤ 0.05 | 0 | 320.20 |
| | | | 1 | 497.78 |
| Waterbuck | 0.0822 | > 0.05 | 0 | 144.73 |
| | | | 1 | 203.11 |

*** Fence category 0 : after the removal of the eastern boundary fence of the Klaserie Private Nature Reserve with the Timbavati and Umbabat Private Nature Reserves (1993 to 2002)**
**Fence category 1 : before the removal of the eastern boundary fence of the Klaserie Private Nature Reserve with the Timbavati and Umbabat Private Nature Reserves (1985 to 1992)**

**Table 8.7**: *The coefficient of determination and probability values calculated by general linear modelling for the relationship between the change in the aerial counting method and the population size for the most abundant types of lion prey in the Klaserie Private Nature Reserve from 1985 to 2002. The prey animals are listed in descending order of the greatest coefficient of determination.*

| **PREY** | **COEFFICIENT OF DETERMINATION** | ***P*- value** | **AERIAL COUNT METHOD** | |
|---|---|---|---|---|
| | | | Category* | Least squares means |
| Impala | 0.4067 | ≤ 0.01 | H | 6769.21 |
| | | | F | 3259.80 |
| Greater kudu | 0.3068 | ≤ 0.05 | H | 457.14 |
| | | | F | 256.40 |
| Giraffe | 0.2479 | ≤ 0.05 | H | 639.21 |
| | | | F | 317.20 |
| Waterbuck | 0.0439 | > 0.05 | H | 183.27 |
| | | | F | 134.20 |
| Buffalo | 0.0255 | > 0.05 | H | 792.43 |
| | | | F | 648.75 |
| Burchell's zebra | 0.0048 | > 0.05 | H | 736.64 |
| | | | F | 702.00 |
| Blue wildebeest | 0.0018 | > 0.05 | H | 556.57 |
| | | | F | 583.40 |

*** H = helicopter count (1982 to 1991 and 1997 to 2003)**
**F = fixed-wing count (1992 to 1996)**

### *The relative contribution of mean rainfall and lion kill proportion to the prey population trends*

Table 8.8 shows the final linear regression models that indicate the relative contribution of smoothed annual mean rainfall and lion kill proportion to the population trends of the seven types of lion prey. For the Burchell's zebra, impala, greater kudu and waterbuck, the two-parameter and three-parameter linear regression models tested were not significant explanatory models for the population size trend of these prey animals (P > 0.05).

*Giraffe*

There was a linear correlation between the size of the giraffe population for a given year and the combined effect of lion kill proportion, mean rainfall and the previous year's population size (Table 8.8). The previous year's population size and rainfall were positively correlated with the size of the giraffe population for a given year, and kill proportion was negatively correlated with the giraffe population size (Table 8.8 and Figure 8.2). The size of the giraffe population during a period of mean rainfall was not significantly different from that during moderate rainfall, above mean rainfall, and drought (Table 8.9). However, the size of the giraffe population increased during periods of mean rainfall and moderate rainfall, and decreased during periods of above mean rainfall and drought (Table 8.9). Rainfall, kill proportion and population size were therefore predictors of the size of the giraffe population for a given year, when considered in combination and separately (Tables 8.2, 8.4, 8.8 and 8.9). The population size of the giraffe decreased after the removal of the boundary fences in 1993 and the change in the aerial counting method from 1992 to 1996 (Tables 8.6 and 8.7).

**Table 8.8**: *The final linear regressions that were calculated using general linear modeling and used to test the relative importance of mean annual rainfall and lion kill proportion in the population trends of the giraffe, buffalo and the blue wildebeest in the Klaserie Private Nature Reserve from 1985 to 2002. The goodness of fit of the final regressions was tested using the coefficient of determination and the probability values calculated during general linear modelling (Mills, Biggs & Whyte 1995). The prey animals are listed in descending order of the most significant regression relationship.The final regression models for the Burchell's zebra, impala, kudu and the waterbuck were not significant* (P>0.05) *and are therefore not included in this table.*

| **PREY** | **THREE-PARAMETER LINEAR REGRESSION EQUATION *** | **GOODNESS OF FIT TEST FOR THE LINEAR REGRESSION EQUATIONS (Samuels 1991)** | | **INDEPENDENT VARIABLES IN THE LINEAR REGRESSION EQUATIONS** | | |
|---|---|---|---|---|---|---|
| | | Coefficient of determination | P-value | Independent variables * | Standard error | *P* -value |
| Giraffe | $P_T$ = -46.221 + 1.206$P_L$+ 322.177R - 837.572$K_L$ | 0.8716 | ≤ 0.01 | A | 116.0987 | > 0.05 |
| | | | | $P_L$ | 0.1773 | ≤ 0.01 |
| | | | | R | 356.4021 | ≤ 0.05 |
| | | | | $K_L$ | 90.9856 | ≤ 0.05 |
| Buffalo | $P_T$ = 121.703 + 0.709$P_L$+ 438.108R -604.170$K_L$ | 0.6464 | ≤ 0.05 | A | 180.9744 | > 0.05 |
| | | | | $P_L$ | 0.2153 | ≤ 0.01 |
| | | | | R | 615.9885 | > 0.05 |
| | | | | $K_L$ | 191.2180 | > 0.05 |
| Blue wildebeest | $P_T$ = 213.413 + 0.887$P_L$ - 44.452R -873.539$K_L$ | 0.6468 | ≤ 0.05 | A | 189.4936 | > 0.05 |
| | | | | $P_L$ | 0.3155 | ≤ 0.05 |
| | | | | R | 841.9265 | > 0.05 |
| | | | | $K_L$ | 162.0945 | > 0.05 |

* Linear regression equation (Mills, Biggs & Whyte 1995): $P_T = A + BP_L + CR + DK_L$

where:

$P_T$ = the population count for a particular prey type for a given year
A = a constant
B, C and D = the regression coefficients for the relevant parameters
$P_L$ = the population count for a particular prey type for the previous year
R = the rainfall index in mm
$K_L$: the lion kill proportion (%) for a particular prey type for the previous year

**Table 8.9**: *The least squares means and probability values for the rainfall categories based on general linear modelling and used here to test the relationship between mean annual rainfall and the population size of the giraffe in the Klaserie Private Nature Reserve from 1985 to 2002. For the blue wildebeest and the buffalo there was no relationship between mean annual rainfall and their population sizes ($P \leq 0.05$) (Table 8.8).*

| | **THE RELATIONSHIP BETWEEN THE LEAST SQUARES MEANS FOR THE RELEVANT RAINFALL CATEGORIES USING FISHER'S TEST (Samuels 1991)** | | | | |
|---|---|---|---|---|---|
| **RAINFALL * CATEGORY** | Least squares means | *P*-value | | | |
| | | 1 | 2 | 3 | 4 |
| 1 | 444.5002 | ~ | ≤ 0.01 | ≤ 0.05 | > 0.05 |
| 2 | 729.6955 | ≤ 0.01 | ~ | > 0.05 | ≤ 0.01 |
| 3 | 656.6075 | ≤ 0.05 | > 0.05 | ~ | ≤ 0.05 |
| 4 | 407.5183 | > 0.05 | ≤ 0.01 | ≤ 0.05 | ~ |

*** Rainfall category 1 - above mean (> 7.5% above the long-term mean)**
**Rainfall category 2 - mean (7.5% above the long-term mean to 7.5% below it)**
**Rainfall category 3 - moderate (> 7.5% below the long-term mean to 25% below it)**
**Rainfall category 4 - drought (> 25% below the long-term mean)**
**~ Not applicable**

### *Buffalo*

The buffalo model indicates that the population size for a given year was significantly correlated with the previous year's population size, but shows no correlation with kill proportion or rainfall (Table 8.8). This supports the results of the preliminary buffalo models that showed no relationship between smoothed annual mean rainfall and either buffalo population size (Table 8.2) or kill proportion (Table 8.3). The buffalo population increased from 1985 to 2002 (Figure 8.2), and this population increase was significantly correlated with the removal of the eastern boundary fence in 1993 (Table 8.6) and the change in the aerial counting method from 1992 to 1996 (Table 8.7). After the removal of the boundary fences the buffalo population increased, and for the period when the aerial counting method changed, the buffalo population decreased (Figure 8.2).

### *Blue wildebeest*

The three-parameter model for the blue wildebeest shows that the previous year's population size was the only significant predictor of the population size of the blue wildebeest for a given year (Table 8.8). Rainfall was not correlated with the population size of the blue wildebeest when tested in combination with the effect of the previous year's population size or when tested separately (Table 8.2). There was no relationship between kill proportion and the size of the blue wildebeest population, when considered in isolation (Table 8.6) or in combination with mean rainfall and the size of the population in the previous year (Table 8.8).

## Observed and predicted prey population trends

Figures 4, 5 and 6 show the observed and the predicted population trends for the giraffe, blue wildebeest and the buffalo. Although the population models for these prey were significant (Table 8.8), the observed and predicted population trends were significantly different for the

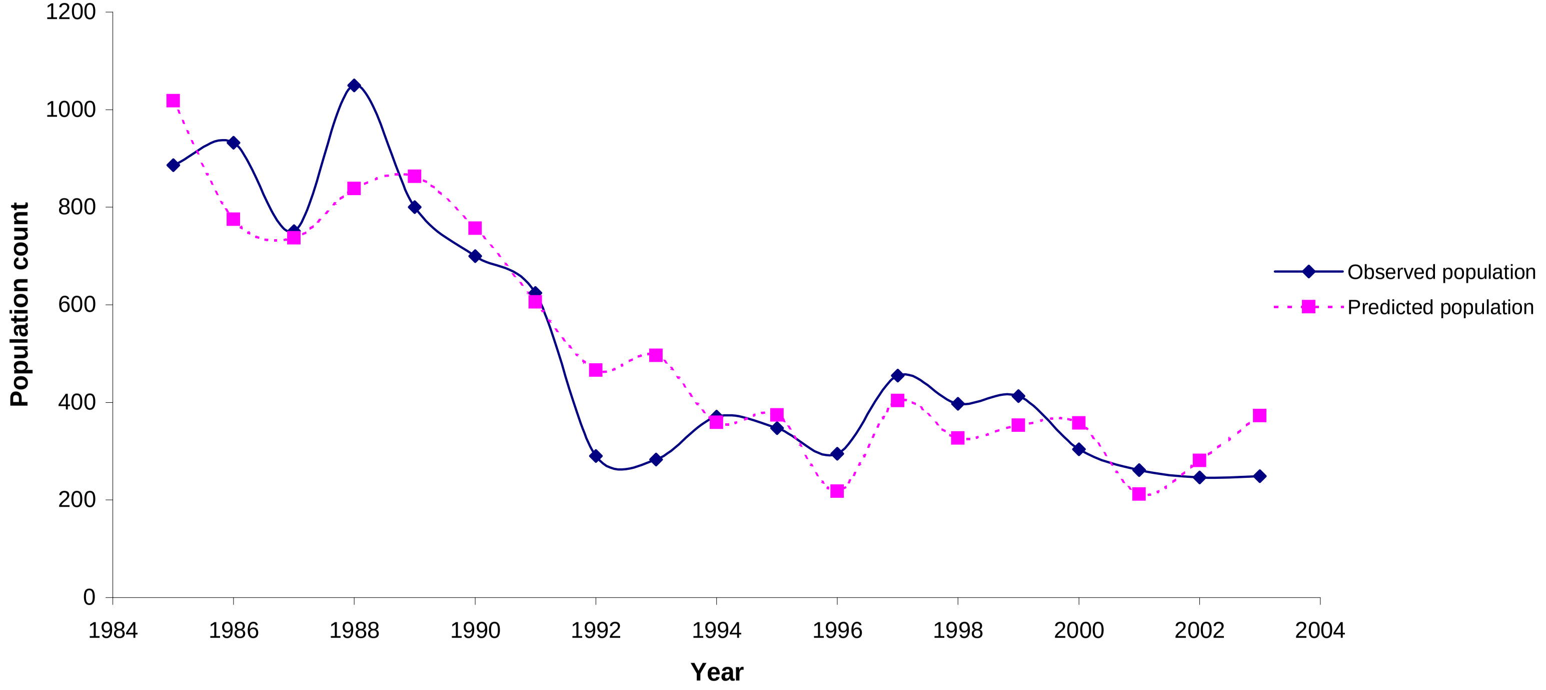


**Figure 8.4**: Observed and predicted population trends for the giraffe in the Klaserie Private Nature Reserve from 1985 to 2003 when using a three-parameter model generated from general linear modelling for the relationship between the size of the giraffe population, lion kill proportion and rainfall, shown in Table 8.8 (Mills, Biggs & Whyte 1995)

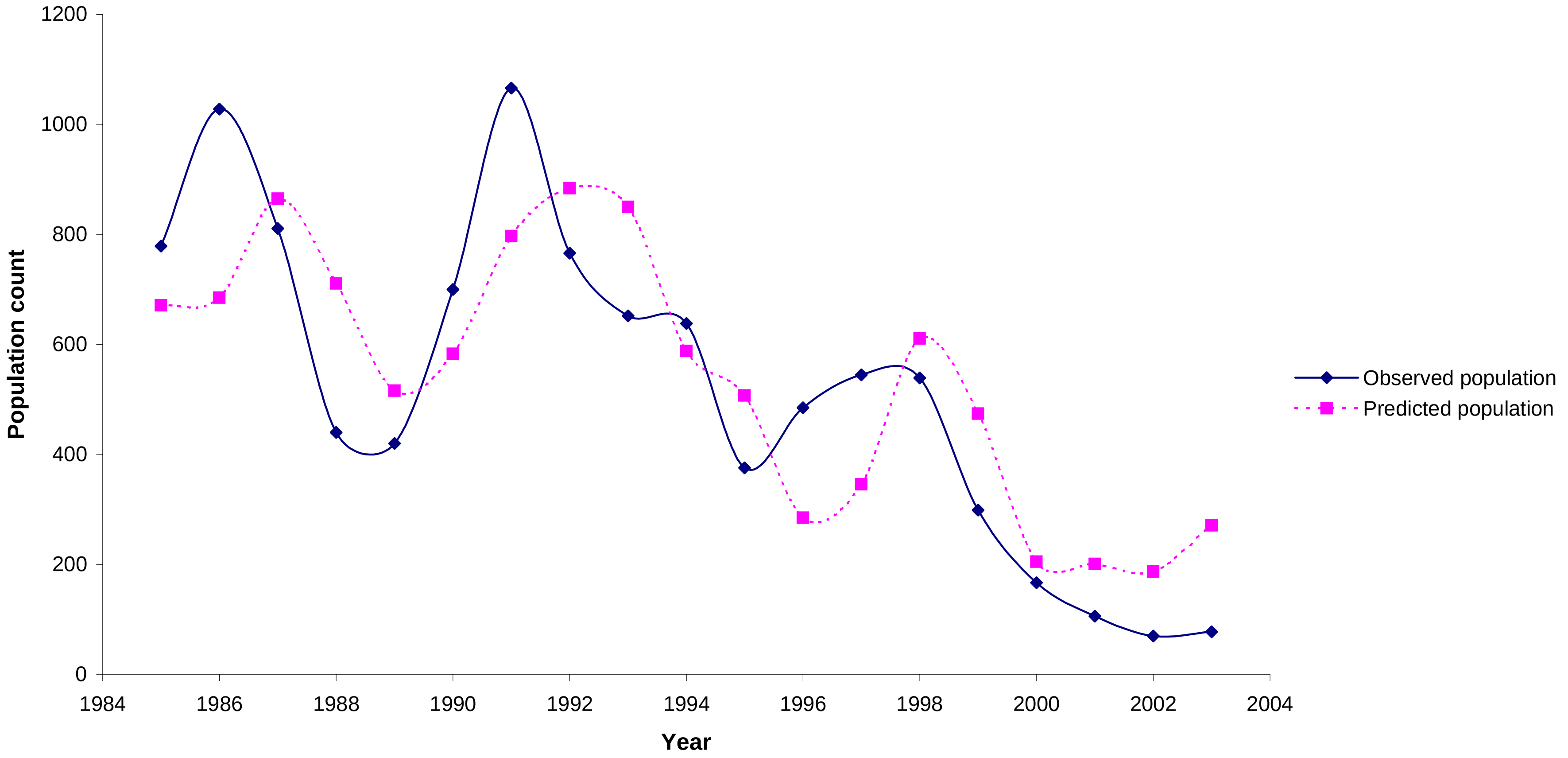


**Figure 8.5:** Observed and predicted population trends for the blue wildebeest in the Klaserie Private Nature Reserve from 1985 to 2003 when using a three-parameter model generated using general linear modelling for the relationship between population size, lion kill proportion and seasonal rainfall as shown in Table 8.8 (Mills, Biggs & Whyte 1995)

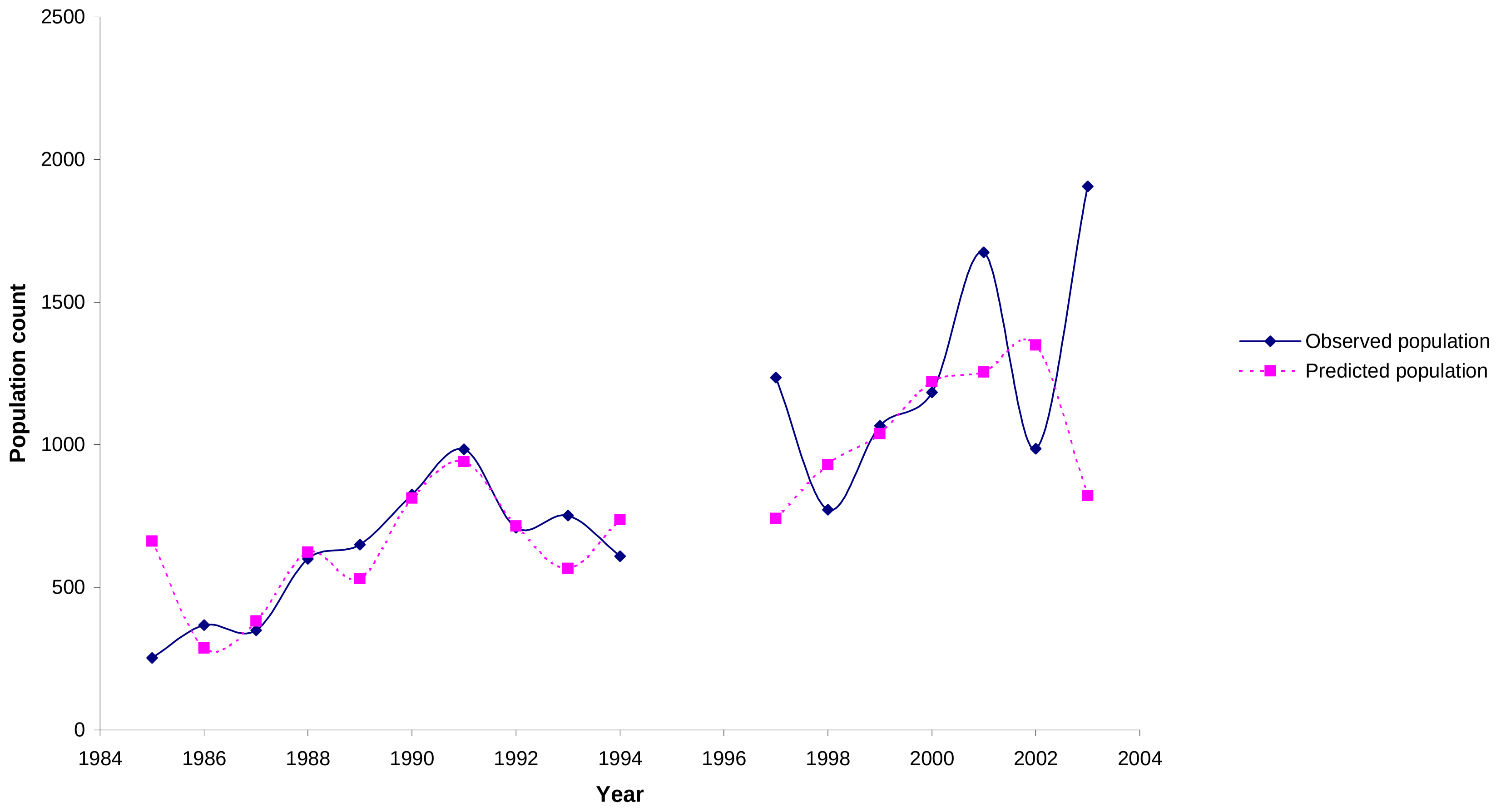


**Figure 8.6:** Observed and predicted population trends for the buffalo in the Klaserie Private Nature Reserve from 1985 to  2003 when using a three-parameter model generated from general linear modelling for the relationship between population size, lion kill proportion and seasonal rainfall as shown in Table 8.8 (Mills, Biggs & Whyte 1995). No data were available for 1995 and 1996.

giraffe ($\chi^2$ = 397.876; df = 19; P > 0.05) (Figure 8.4), the blue wildebeest ($\chi^2$ = 1128.203; df = 19; P > 0.05) (Figure 8.5) and the buffalo ($\chi^2$ = 2547.684; df = 19; P > 0.05) (Figure 8.6). The population models can therefore not be extrapolated to make future predictions.

## DISCUSSION

The ecological parameters in predator-prey models are difficult to measure and the field data obtained are only crude measurements of these parameters. The aerial counting data are order of magnitude assessments and do not have confidence limits (Mills, Biggs & Whyte 1995). The change in the aerial counting method from a helicopter count to a fixed-wing one may also have skewed these data. However, the greater proportion of the aerial counts were helicopter counts that were performed consistently from 1985 to 1992 and from 1997 to 2003. The use of moving means for the aerial counts reduced the effect of the change in counting method on the prey population trends. Management actions such as the culling, or selling of wildlife, ration shooting and habitat manipulation were not taken into account in the models. Reliable data relating to these management actions were not available at the time of this study. The models produced satisfactory results in terms of understanding the ecological processes during the historical time series, but the confidence limits were broad and therefore the results cannot be extrapolated accurately (Mills, Biggs & Whyte 1995). The objective of using computer modelling in this study was, however, not to make future predictions but to determine the most important current predictors of the population size for the most abundant lion prey in the Klaserie Private Nature Reserve.

The models predicted the effect of fluctuations in rainfall and lion predation trends on prey populations from 1985 to 2002. Annual changes in prey population do not have to be correlated strongly with population size (Mills, Biggs & Whyte 1995). The linear regression models provided an approach to gauge the importance of the effect of the previous year's population size on the current population size for a given year. Although this relationship seems self-explanatory, the previous year's population size was considered an important predictor in the present study because it fluctuated inconsistently when the eastern boundary fence of the Klaserie Private Nature Reserve was removed, and when the aerial counting method changed. The removal of the eastern boundary fence of the Klaserie Private Nature Reserve in 1993, and the change in the aerial counting method from 1992 to 1996, were therefore included in the models as predictors. The eastern boundary fence between the Klaserie Private Nature Reserve and the Timbavati and Umbabat Private Nature Reserves was removed in 1993, as was the boundary fence between the Kruger National Park and the Timbavati and Umbabat Private Nature Reserves. These boundary fences previously prevented the seasonal movement of the blue wildebeest and Burchell's zebra within the Associated Private Nature Reserves and between the Associated Private Nature Reserves and the Kruger National Park.

Modelling based on predator-prey data recorded over an extended period allows the determination of shifts in predator-prey dynamics, such as a switch in prey selection. Although the lion kill proportions were biased towards larger prey, the focus of this study was the larger ungulate species. The model that was used in the present study did not account for age and sex selection. This aspect of lion predation was, however, studied in detail in Chapter 7.

## Ecological relationships

The final models suggest several important ecological relationships that affect the predator-prey dynamics in the Klaserie Private Nature Reserve. The previous year's population size was a significant predictor of the population size of the most abundant prey animals, except the waterbuck. The buffalo was the only prey animal that increased in number from 1985 to 2002. The populations of the other types of prey appear not to have recovered from the decline during the droughts in 1981, 1991 and 1997 (Kruger 1988; Weaver 1995) (Chapter 4). The increased abundance of certain prey animals and the decrease in the numbers of others caused the predation pressure by lions in the Klaserie Private Nature Reserve to shift (Pienaar 1969; Kruger 1988; Weaver 1995). The killing frequency of the blue wildebeest, giraffe and Burchell's zebra by lions was greater than their relative abundance as prey (Chapter 7), and their populations therefore continued to decrease after the droughts in 1981, 1991 and 1997 (Peel 2003). The buffalo population increased after the removal of the eastern boundary fence in 1993, due to the movement of buffalo into the Associated Private Nature Reserves from the Kruger National Park (Weaver 1995). The impala population recovered due to their high reproductive rate (Kruger 1988) and the low frequency with which lions killed them (Figure 8.3).

Although the giraffe was not the least abundant prey animal in the Klaserie Private Nature Reserve, the predator-prey model indicates that it was the most sensitive to the parameters tested. The population size of the giraffe for a given year was correlated with the previous year's population size, the lion kill proportion and mean rainfall. The continued decline of the giraffe population and its susceptibility to both lion predation and climatic change is evidence of the vulnerability of the giraffe population in the Klaserie Private Nature Reserve.

The most significant predictor of the size of the blue wildebeest population for a given year was the previous year's population size. No significant correlation was found between mean rainfall and the lion kill proportion or the population size, for the blue wildebeest in the Klaserie Private Nature Reserve. This contrasts with the findings of studies done on lion predation in the Central District of the Kruger National Park (Whyte & Joubert 1988; Mills & Shenk 1992; Mills, Biggs & Whyte 1993; Funston 1999). Although rainfall was not a significant predictor of the population size of the blue wildebeest in the present study, a drought that occurred in 1981 caused the blue wildebeest population in the Klaserie Private Nature Reserve to decrease by 94% (Kruger 1988; Weaver 1995). After a major population decline blue wildebeest numbers may be so low that the net recruitment rate is lower than the rate of lion predation and the blue wildebeest population may continue to decline (Hilborn & Sinclair 1979). Although the lions in the Associated Private Nature Reserves shifted their prey selection from a declining blue wildebeest and Burchell's zebra population, to the more abundant impala, and the larger buffalo and giraffe, the populations of these preferred blue wildebeest and Burchell's zebra continued to decline because the predation pressure was greater than their relative abundance (Chapter 6).

### The population models for the lion prey

Population models can be used to predict future demographic trends and may therefore be an invaluable tool for conservation managers (Nicolls *et al.* 1996). The population models for the seven most abundant types of lion prey showed that lion predation is not the major factor that has affected the population size of the large ungulates in the Klaserie Private Nature Reserve. For each of the lion prey, the effect of the various ecological parameters is discussed in relation to historical population trends and the results of other studies. The population models for the giraffe, buffalo and blue wildebeest are discussed separately from the models for the Burchell's zebra, impala, greater kudu and waterbuck, because the final regression models were only significant for the aforementioned animals.

### ***Giraffe, buffalo and blue wildebeest***

The three-parameter regression models that were used for the giraffe, buffalo and the blue wildebeest were statistically meaningful because mean rainfall and lion kill proportion were uncorrelated (Table 8.3) (Mills, Biggs & Whyte 1995). These models also have the advantage over two-parameter models in that the combined effects of mean rainfall and kill proportion can be interpreted unambiguously.

#### *Giraffe*

The population size of the giraffe for a given year was determined by the previous year's population size, the lion kill proportion and mean rainfall. The decline of the giraffe population under the influence of these ecological conditions is evidence of the vulnerability of the giraffe population to starvation and lion predation in the Klaserie Private Nature Reserve. In contrast to the results of the present study, Mills *et al.* (1995) concluded that giraffe in the Kruger National Park were not susceptible to drought or lion predation. The giraffe in the Klaserie Private Nature Reserve were more susceptible during a dry than a wet cycle to starvation and lion predation (Hirst 1969; Kruger 1988). The adult female and juvenile giraffe in the study area were particularly vulnerable to lion predation during a period of above mean rainfall (Chapter 7). However, the lion predation rate for the giraffe was consistently greater than its relative abundance in the prey population from 1985 to 2002 (Figure 8.4) (Kruger 1988). The droughts in 1981, 1991 and 1997 appear to have been major limiting factors of the giraffe population (Kruger 1988; Weaver 1995; Peel 2003) (Chapter 4). Lion predation becomes a regulating factor when the predation pressure shifts from the blue wildebeest and the

Burchell's zebra to the giraffe and the buffalo. The shift in prey selection to the giraffe is likely to have been caused by a decrease in the relative abundance of the preferred prey of lions (Pienaar 1969) (Chapter 7). Despite the stability in the number of giraffe occurring in the Klaserie Private Nature Reserve from 2000 to 2003, evidence from this study suggests that the giraffe population will decrease in any new dry cycle.

### *Buffalo*

The most significant predictors of the population size of the buffalo were the removal of the eastern boundary fence and the size of the buffalo population in the previous year. The buffalo population increased when the boundary fences of the Associated Private Nature Reserves were removed in 1993 and allowed the movement of buffalo into these reserves from the Kruger National Park (Weaver 1995). Although the present study found no significant relationship between rainfall and the size of the buffalo population from 1985 to 2002, this contrasted with the observations of Kruger (1988). A population decrease of 92% was recorded for the buffalo in the Klaserie Private Nature Reserve after the drought in 1981 (Kruger 1988). The cause of the population decrease was starvation due to insufficient grazing. Mills *et al.* (1995) had similar findings for the buffalo in the Kruger National Park. The reserve management should be aware of the vulnerability of the buffalo with the probable approach of a new dry cycle in the Associated Private Nature Reserves (Peel 2003).

The present study found no relationship between lion kill proportion and the size of the buffalo population. This contradicts the findings of Mills *et al.* (1995) for buffalo in the Kruger National Park. Although the lion kill proportion for buffalo in the Klaserie Private Nature Reserve increased from 2% in 1983 to 30% in 2003 (Chapter 7), this was consistent with the increase in the relative abundance of the buffalo in the study area from 3% in 1983 to 20% in 2003

(Chapter 7). The combined effect of a drought and a high killing frequency by lions could, however, limit the buffalo population in the future.

*Blue wildebeest*

The major decrease in the blue wildebeest population of the Klaserie Private Nature Reserve occurred in 1981 when 94% of the population died from starvation, during a period of drought (Kruger 1988). The eastern boundary fence between the Klaserie Private Nature Reserve and the Timbavati and Umbabat Private Nature Reserves, and the eastern boundary fence between the Timbavati Private Nature Reserve and the Kruger National Park, prevented the seasonal movements of the blue wildebeest to and from the areas of better grazing (Hirst 1969; Kruger 1988). The blue wildebeest population failed to recover to its former numbers despite the removal of the fences in 1993. The most significant predictor for the population trends of the blue wildebeest was the previous year's population size. Identifying the most significant predictors of the population trend in the blue wildebeest is particularly important at the time of the present study when only an estimated 78 blue wildebeest remain in the Klaserie Private Nature Reserve (Chapter 4).

Several studies have found that the most significant factor regulating the blue wildebeest population was predation by lions during a period of rainfall that is above the long-term mean (Hirst 1969; Smuts 1982; Kruger 1988; Whyte & Joubert 1988; Mills & Shenk 1992; Funston 1999). The present study did not find a significant correlation between the size of the blue wildebeest population and lion kill proportion or fluctuations in rainfall. The blue wildebeest was the preferred prey of the lions in the Kruger National Park and the Timbavati and Klaserie Private Nature Reserves (Pienaar 1969; Hirst 1969; Kruger 1988; Mills & Shenk 1992; Funston 1999). The lion kill proportion was greater than the relative abundance of the blue wildebeest in the Klaserie Private Nature Reserve from 1983 to 2003 (Figure 8.3) (Chapter 7). This was due to the vulnerability of the blue wildebeest after the drought in 1981. However, the decrease in the availability of this preferred prey has caused the lions to switch their prey selection to the larger and more abundant giraffe and buffalo (Table 7.11). A similar trend has been observed for the lions in the Kruger National Park (Pienaar 1969). Provided that there is sufficient suitable habitat available for the blue wildebeest in the Klaserie Private Nature Reserve, there should be an annual influx of blue wildebeest from the Timbavati Private Nature Reserve and the Kruger National Park during the spring and summer months (October to March), when the conditions for grazing are most favourable. Although these animals were the preferred prey of the lions in the study area, the predation rate is likely to decrease during any new dry cycle (Kruger 1988; Mills & Shenk 1992), and the blue wildebeest population in the Klaserie Private Nature Reserve should ultimately recover.

### *Burchell's zebra, impala, greater kudu and waterbuck*

The population sizes of the Burchell's zebra, impala, greater kudu and waterbuck in the Klaserie Private Nature Reserves were not affected by lion kill proportion or mean rainfall. The removal of the eastern boundary fence of the Klaserie Private Nature Reserve was a significant predictor of the population sizes of the Burchell's zebra, impala and greater kudu, and the change in the aerial counting method was correlated with the observed population sizes of the impala and the greater kudu.

#### *Burchell's zebra*

The present study disagrees with the results of earlier studies that showed the Burchell's zebra population in the Klaserie Private Nature Reserve was regulated by lion predation and not by starvation mortalities after a drought (Kruger 1988; Weaver 1995). The Burchell's zebra population decreased by 31% in 1983 and by 41% in 1985, following droughts (Kruger 1988). Furthermore, other studies have shown that the Burchell's zebra is a preferred prey of the lions in the Klaserie and Timbavati Private Nature Reserves and the Kruger National Park, and that lion predation during a period of above mean rainfall regulates the Burchell's zebra population in these areas (Hirst 1969; Kruger 1988; Funston 1999). Although the lion killing frequency for the Burchell's zebra was greater than their relative abundance from 1985 to 2002, the major decrease in the population was after the drought in 1981 and 1983. When the relative abundance of the Burchell's zebra decreased, the lions switched their prey selection to the larger giraffe and the more abundant buffalo (Chapter 7). Any new dry cycle in the Klaserie Private Nature Reserve should cause the lion predation rate on the Burchell's zebra to decrease and allow the population to recover.

### *Impala*

The size of the impala population and rainfall were not correlated, but there is evidence in the mortality records that contradicts this. The drought that occurred in the Klaserie Private Nature Reserve in 1991 caused the impala population to decrease by 32% (Chapter 4). The studies of Kruger (1988) and Hirst (1969) showed similar results for the impala in the Klaserie and the Timbavati Private Nature Reserves during a period of drought. Mills *et al.* (1995) excluded impala from their study in the Kruger National Park. However, Engelbrecht (1986) concluded that impala in the Kruger National Park are water-dependent and that their distribution is restricted by the distance that they occur from permanent water.

The kill proportion of the impala in the Klaserie Private Nature Reserve was less than its relative abundance and the population therefore could recover after a drought (Kruger 1988). The population size of the impala decreased after the removal of the eastern boundary fence in 1993 and when the aerial counting method changed from 1992 to 1996. The change in the aerial counting method coincided with the removal of the eastern boundary fence and therefore distorted the population trends of the impala. According to the count data obtained before and after the change in the aerial counting methods from 1992 to 1996, the impala population decreased. The decrease in the impala population was, however, exaggerated by the change in the counting method from 1992 to 1996.

The size of the impala population before the boundary fence was removed was significantly greater than after it was removed (Table 8.6). The impala population decreased after the drought in 1991 and failed to recover to its former numbers after the boundary fence was removed (Kruger 1988; Weaver 1995). However, the impala has a high reproductive rate (Skinner & Smithers 1990), allowing the impala population in the Klaserie Private Nature Reserve to stabilise from 2000 to 2002 and to increase in 2003 (Chapter 4).

*Waterbuck*

The linear regression models for the waterbuck showed no correlation between population size and mean rainfall or lion kill proportion. This contrasts with the results of Kruger (1988) which showed the waterbuck population was regulated by lion predation and starvation mortalities during the dry season. Although Mills *et al.* (1995) found in their study that waterbuck in the Kruger National Park were sensitive to climatic fluctuations, they did not find a relationship between lion kill proportion and the annual change in the waterbuck population. In the present study, however, the kill data may have been distorted by the difficulty in counting waterbuck from the air and of locating carcasses in the dense vegetation of their preferred habitat. Similar difficulties were experienced by Hirst (1969) whilst studying the waterbuck in the Timbavati Private Nature Reserve. The killing frequency of the waterbuck by the lions in the Klaserie Private Nature Reserve was greater than its relative abundance in the prey population (Chapter 7). Therefore, lion predation may regulate the waterbuck population in the Klaserie Private Nature Reserve, as was found for the waterbuck in the Kruger National Park (Pienaar 1969).

*Greater kudu*

The size of the greater kudu population was significantly correlated with the previous year's population size. Although Mills *et al.* (1995) found that the greater kudu population in the Kruger National Park decreased during a dry cycle, the present study found no relationship between the size of the greater kudu population and lion kill proportion or mean rainfall. However, the decrease in the population size of the greater kudu in the Klaserie Private Nature Reserve was correlated with the change in the aerial counting method from 1992 to 1996. The change in the aerial counting method followed the drought in 1991, distorting the count data for that period. This suggests that the greater kudu population in the Klaserie Private Nature Reserve may be more sensitive to the ecological parameters than was concluded from the models (Figure 8.1).

The greater kudu were less susceptible to starvation during periods of drought than the other major prey types (Kruger 1988). However, Hirst (1969) concluded that the adult greater kudu in the Timbavati Private Nature Reserve were limited by lion predation and starvation. A further cause of the fluctuation in the greater kudu population was the irregular immigration and emigration of the greater kudu bulls to and from the areas adjacent to the Klaserie Private Nature Reserve. This movement of greater kudu bulls was due to their far-ranging habits and disregard for fences (Hirst 1969; Kruger 1988).

### Observed and predicted prey population trends

The predicted population trends for the giraffe, blue wildebeest and buffalo generally followed the observed ones, especially when considering the free-floating nature of the models that were used in the sequential time series (Mills, Biggs & Whyte 1995). The distortion of the aerial counting data from 1992 to 1996 is evident in Figs. 4, 5 and 6, with the predicted population trend diverging from the observed one. The final model for the giraffe was the most statistically significant of all the models, and the observed and predicted population trends were the most closely related. The deviation of the predicted population trend from the observed trend in the giraffe, blue wildebeest and buffalo from 2000 to 2003 reflects the broad confidence limits of these models, which can therefore not be extrapolated to make future predictions.

## CONCLUSIONS

Ecological modelling was used to better understand the interrelationship between rainfall, prey population trends and lion predation in the Klaserie Private Nature Reserve. According to the predator-prey models the previous year's population size was a significant predictor of the population size for the prey animals studied, except the waterbuck. Lion predation was a significant predictor of the population size of the giraffe only. Buffalo, blue wildebeest and giraffe were killed more frequently by lions when they were more abundant. The giraffe population was the most sensitive to the ecological parameters tested, and it was limited by lion predation and starvation during the dry cycle. There was no relationship between mean rainfall and the population size of any of the prey that were studied. It appears that there may be a correlation between the population size of the blue wildebeest and mean rainfall that was not shown in the present study because certain of the count data were distorted. The population sizes of the most abundant prey animals, except the waterbuck and the buffalo, decreased after the removal of the boundary fence of the Klaserie Private Nature Reserve with the Timbavati and Umbabat Private Nature Reserves, and the removal of the western boundary fence of the Kruger National Park with the Timbavati Private Nature Reserve in 1993. After the removal of these boundary fences animals such as the blue wildebeest and Burchell's zebra may have moved from the Associated Private Nature Reserves to the Kruger National Park in search of better grazing. The population sizes of the impala, greater kudu and the giraffe decreased when the aerial counting method changed from 1992 to 1996. The removal of the boundary fence and the change in the aerial counting method coincided with a period of drought hence distorting the population data for that period. Whyte & Joubert (1988) had a similar difficulty in their study of the blue wildebeest population trends in the Kruger National Park. The present study emphasizes the importance of consistency in the aerial counting methods used, and the caution required when applying management actions based on inadequate ecological records.

The populations of the most abundant types of lion prey, except for the impala and the buffalo, decreased from 1983 to 2003. The greatest decrease in the prey populations occurred after the drought in 1981. The lion predation rate for the blue wildebeest, Burchell's zebra, giraffe, greater kudu and the waterbuck was greater than their relative abundance as prey during the period of study. Impala were not a preferred prey of the lions. The buffalo population increased despite the increase in the predation rate by lions from 1998 to 2002. The lions changed their prey selection as the abundance of their major prey animals changed, switching from blue wildebeest and Burchell's zebra to giraffe and buffalo.

In the present study, the inconsistency in the population data caused by the change in the aerial counting method distorted the model predictions. Although the models did not indicate that mean annual rainfall was the driving force in the ecosystem, as was found by Mills *et al.* (1995), the major decrease in the prey populations occurred during the period of drought in 1983. An important factor that was not taken into account in these models, was the change in the habitat of the Klaserie Private Nature Reserve from 1985 to 2002. The habitat became less suitable for grazing animals, such as the blue wildebeest, and more suitable for mixed feeders, such as the impala (Kruger 1988; Weaver 1995) (Chapter 4). As in the study of Mills *et al.* (1995), the models produced satisfactory results in terms of understanding the ecological processes during the period of study. However, the confidence limits for the estimates from the models were broad due to the inconsistent data, and therefore the results cannot be accurately extrapolated. The objective of using computer modelling in this study, however, was not to make future predictions but to determine the most important predictors of the population size of the most abundant prey of the lions in the Klaserie Private Nature Reserve, historically and at the time of this study. The results of the present study support the hypothesis that the decrease in the large ungulate populations in the Associated Private Nature Reserves from 1980 to 2003 is due to a combination of lion predation, climatic fluctuations, the change in habitat over time, the removal of the boundary fences between the Associated Private Nature Reserves and the Kruger National Park, and the change in the aerial counting method from 1992 to 1996.

# CHAPTER 9

# GENERAL DISCUSSION

The present study was proposed by the landowners in the Associated Private Nature Reserves because of a concern over the continual decline in the large ungulate populations in these reserves. The perception also existed amongst certain landowners that there was an overpopulation of lions and that the solution to curbing the decline in the prey populations was to implement a lion removal programme. The aims of this study were therefore to determine the impact of lion predation on the large ungulate populations in the Associated Private Nature Reserves and to identify any other factors that may have an influence on the decline in the large ungulate populations in this area. This study therefore tested the hypothesis that the decrease in the large ungulate populations in the Associated Private Nature Reserves from 1980 to 2003 was due to a combination of lion predation, climatic fluctuations, the change in habitat over time, the removal of the boundary fences between the Associated Private Nature Reserves and the Kruger National Park, and the change in the aerial counting method from 1992 to 1996. To test this hypothesis it was necessary to divide the study into five major components:

- prey population dynamics
- ungulate-habitat dynamics
- lion population dynamics
- ranging dynamics of the lions
- lion predation, climatic fluctuations and large ungulate population trends

## Prey population dynamics

The determination of prey population trends and their spatial distribution in relation to predator habitats are imperative to the success of any wildlife management programme and, in particular, the study of predator-prey relationships (Ogutu & Dublin 2004). A combination of aerial counting and road strip censusing methods produced the best results for determining the prey population dynamics in a dense bushveld area such as the Associated Private Nature Reserves (Weaver 1995; Bothma 2002).

Despite the inconsistency of the aerial counting methods used in the Associated Private Nature Reserves from 1991 to 2003, the broad population trends of the ungulates in the Timbavati, Klaserie and the Umbabat Private Nature Reserves were similar (Peel 2003). The results confirmed the continual decline in the population size of the most abundant large ungulates in the study area, except for the buffalo, from 1991 to 2003. The buffalo population increased from 1991 to 2003. As was concluded in earlier studies by Kruger (1988) and Weaver (1995), these population decreases were a consequence of starvation mortalities during the extreme droughts in 1981, 1991 and 1997, and the regulation of the already low prey populations by lion predation. The total biomass of animals in the Associated Private Nature Reserves was, however, greater than the maximum expected biomass from 2001 to 2003, and the available prey biomass for lions in these combined reserves from 2001 to 2003 was greater than the minimum expected guideline for the sustainable management of that area (Coe *et al.* 1976; Peel 2003). The prey biomass therefore increased during the period of study, despite the effects of lion predation, climatic changes and habitat factors.

### *Feeding class proportions*

Although the available prey biomass may be sufficient to sustain a lion population, an imbalance in the proportion of prey in the four feeding classes may cause the competitive exclusion of a prey species by another one, and eventually cause habitat degradation (Collinson & Goodman 1982). This was indeed the case in the Associated Private Nature Reserves during the present study. The proportions of bulk grazers, selective feeders, mixed feeders and browsers in the study area differed from the recommended proportion of

45:20:20:15 (Collinson & Goodman 1982) for these feeding classes. The proportion of bulk grazers and mixed feeders in the Associated Private Nature Reserves was greater than the recommended proportions, whilst the proportion of selective feeders and browsers in the study area was lower than the recommended proportions for these feeding classes (Peel 2003). The proportion of bulk grazers increased above the recommended proportion when the boundary fences were removed between the Associated Private Nature Reserves and the Kruger National Park in 1993 and a large number of buffalo, white rhinoceros and elephant moved into this area from the Kruger National Park. Because buffalo, white rhinoceros and elephant are water-dependent, the availability of water in artificial waterholes in the study area probably assisted the movement of these animals from the Kruger National Park to the Associated Private Nature Reserves.

Relative to the recommended feeding class proportions of Collinson & Goodman (1982), the proportion of selective feeders and browsers in the study area has decreased over time as a consequence of starvation mortalities after a series of droughts in 1981, 1991 and 1997 (Kruger 1988; Weaver 1995; Peel 2003). The blue wildebeest and warthog populations, in particular, both decreased by 94% after the drought in 1981. Similar drought-related mortalities were observed in the Timbavati Private Nature Reserve (Hirst 1969), Kruger National Park (Pienaar 1969; Whyte & Joubert 1988) and the Serengeti (Mduma *et al.* 1999). Because the rainfall that occurs in the Lowveld of South Africa is cyclical, the abundance of ungulate populations in this region has fluctuated in accordance with these natural cycles (Whyte & Joubert 1988), and it is expected that these populations will continue to do so.

### *Age structure, sex ratio and seasonal abundance*

The road strip censusing method was used to determine the age and sex structure, and the seasonal abundance of ungulate populations in the Associated Private Nature Reserves. In most ungulate populations the population structure should be biased towards adult females, and 30 to 40% of the population should consist of young animals to ensure productivity and therefore population growth (Kruger 1988; Bothma 2002). The age and sex structure of the buffalo, impala, greater kudu, warthog and waterbuck in the Associated Private Nature Reserves were consistent with that of ungulate populations elsewhere in the African savannas. The proportion of juveniles relative to adults in the populations of the giraffe, Burchell's zebra and the blue wildebeest was, however, lower than the recommended 30 to 40% of Bothma 2002. Previous studies have suggested that a decreasing population trend in these ungulates was because either insufficient progeny were being produced or there was a high mortality rate among the young because of poor habitat conditions or shortages of food (Kruger 1988; Weaver 1995). Taking this further, Peel (2003) determined through faecal analyses that there was a dietary deficiency in phosphorus and nitrogen in the available grass and browse, and that this may have caused the low reproductive rate of these ungulate populations during the present study. Further faecal analyses recorded over an extended period of time will show whether this is indeed the case.

The prey abundance in the Associated Private Nature Reserves increased and decreased in accordance with the seasonal and cyclical climatic changes that occur in this region. As expected the prey abundance was greater in the wet than the dry season because the primary plant production in the Associated Private Nature Reserves, and other African savannas, is greater in the summer rainfall (wet) season than the winter rainfall (dry) season (Coe *et al.* 1976; Hirst 1969; Dunham 1992; Campbell & Hofer 1995; Weaver 1995; Peel 2003). It follows from this that the prey abundance in the Associated Private Nature Reserves increased during a wet climatic cycle and decreased during a dry one. These wet and dry climatic cycles generally conform to a 20-year oscillation consisting of 10 years of above mean rainfall, followed by 10 years below it (Tyson & Dyer 1975; Gertenbach 1980). The most drastic decline in the prey populations of the Klaserie Private Nature Reserve occurred after the drought in 1981, when there was a 94% decrease in both the blue wildebeest and warthog populations and a 64% decrease in the impala population (Kruger 1988).

## Ungulate-habitat dynamics

The vegetation in the Associated Private Nature Reserves has changed over time from an open savanna to a dense woodland as a result of herbivore impact, artificial water provision and a lack of systematic burning (Hirst 1969; Porter 1970; Kruger 1988; Weaver 1995). The grass standing crop fluctuated annually in synchrony with changes in rainfall, whereas the tree density remained constant from 1996 to 2002. The observed decrease in the available grazing habitat was of concern because of the continual decrease in the number of selective grazers in the Associated Private Nature Reserves (Hirst 1969; Kruger 1988; Weaver 1995; Peel 2003). Because ungulates have specific habitat requirements (Thompson 1986), any change in the vegetation types in the Associated Private Nature Reserves will affect the prey communities found there. The habitat preferences of the eight most abundant types of lion prey were similar to the preferences found for these prey in other areas of southern Africa. However, a current trend away from the suitable habitat for certain of these prey types appears to have contributed to the continual decrease in the size of their populations.

### *Blue wildebeest, Burchell's zebra, giraffe and waterbuck*

For the blue wildebeest, Burchell's zebra, giraffe and waterbuck in the study area, the proportion of preferred habitat that was available to them was considerably lower than the proportion that was being utilized by them. The present study strongly agreed with that of Weaver (1995), in that the continual decline in these ungulate populations is most likely because of a major change in habitat over recent time.

### *Warthog and greater kudu*

The warthog and greater kudu in the Associated Private Nature Reserves had a broad habitat tolerance, utilizing at least eight of the 12 available vegetation types. The habitat requirements of the warthog and greater kudu in the present study therefore appeared to have been met and the continual decline in their populations was most probably a consequence of starvation mortalities during the drought in 1981, 1991 and 1997 (Kruger 1988) (Chapter 8).

*Buffalo*

In the present study, the broad habitat tolerance of the buffalo for habitat varying from open bushveld to dense riverine vegetation suggested that their habitat requirements were being met. Buffalo are water-dependent (Skinner & Smithers 1990) and large numbers of these animals therefore moved from the Kruger National Park into the Associated Private Nature Reserves following the removal of the boundary fence in 1993, because there is an abundance of artificial waterholes in the Associated Private Nature Reserves (Weaver 1995). The buffalo population therefore increased after the removal of this fence, and continued to increase over time.

*Impala*

The impala in the study area showed distinct habitat preferences by utilizing only four of the 12 available vegetation types. Nevertheless, the impala population in the Associated Private Nature Reserves has continued to increase over time, suggesting that its habitat requirements are being met or that the change in habitat over time may be favouring them.

### Lion population dynamics

The present study was the first attempt to describe the population dynamics of the lions in the entire Associated Private Nature Reserves. The call-in counting method is a reliable technique for estimating lion population size and may be employed to effectively monitor carnivore populations in the long term (Ogutu & Dublin 1998). A modified call-in counting technique was therefore used in the present study to survey the lion population in the

Timbavati, Klaserie and Umbabat Private Nature Reserves in November 2000 and 2001. This counting method provided minimum estimates of the lion population size and density in the Associated Private Nature Reserves that were validated by the results of the independent study by Funston (2004). The lion population estimates from the study by Funston (2004) were similar to those found in the present study, although the survey that Funston did was based on a different methodology. The reserve management staff, field guides at the lodges, and the landowners provided the necessary information on the lion prides in the Associated Private Nature Reserves, from which Funston (2004) estimated the total population size.

Based on a similar mean pride size, total population size, and number of lion prides in 2000 and 2001, the lion population was considered stable during the present study. When compared with lions in other African savanna woodland habitats, the lions in the Associated Private Nature Reserves were found to be at intermediate densities and pride sizes. Because these private nature reserves form an open ecosystem with the Kruger National Park it was not surprising that the lion population dynamics there were similar to those in the Park. In contrast to the Kruger National Park and most other areas in Africa, however, a greater proportion of the subadults and cubs in the Associated Private Nature Reserves was males rather than females. It was concluded that this skewed sex ratio may be due to the male-biased litters that result from trophy hunting of lions in the Associated Private Nature Reserves. This assertion is supported by evidence from studies done on the effect of trophy hunting on the social organization of lions in the Kruger National Park (Smuts 1976; Starfield *et al.* 1981), the Luangwa Valley in Zambia (Yamazaki 1996), the Selous Game Reserve in Tanzania (Creel & Creel 1997), and in the Ngorongoro Crater and Serengeti National Parks in northern Tanzania (Whitman *et al.* 2004). All these lion studies found a skewed sex ratio in favour of males in the subadults and cubs in the lion populations that were studied. .

### Range size, distribution and habitat selection

It is important to determine an animal's range size and shape, and patterns of habitat utilization for most ecological and behavioural studies (Harris *et al.* 1990). The range use and habitat selection of the lions in the Associated Private Nature Reserves had not previously been studied. Because these private nature reserves are an open system with the Kruger National Park, it was of particular interest to compare the range dynamics of the lions in these private nature reserves with that of lions in the Kruger National Park. As was expected, the range sizes of the lions in the Associated Private Nature Reserves were similar to those of lions in the Kruger National Park, but smaller than those of lions in arid, probably prey-poor, savannas, and greater than those in more mesic, prey-rich savannas. Although the range use patterns of male lions was not determined conclusively in the present study because of the small sample size, the range size of male coalition N was similar to that of male lions in the Kruger National Park.

The habitat selection of the lions in the Associated Private Nature Reserves reflected that of their preferred prey. This is in accordance with the general pattern for lions in African savanna woodlands. As was observed for the lions in the Kruger National Park (Mills & Gorman 1997), prey distribution appeared to be the main determinant of habitat selection by the lions in the Associated Private Nature Reserves. Kilian (2003) made similar observations for the lions on the Welgevonden Private Game Reserve, in the Limpopo province of South Africa. The habitat types that were utilized most frequently by the lions on this reserve were in areas where there was a high concentration of prey. Because the habitat selection of lions is not dependent on the type of vegetation, and because lions show a wide habitat tolerance (Schaller 1972), the existing habitat dynamics in the study area appeared to have met the lions' habitat requirements of sufficient suitable prey, denning sites and drinking water.

### Lion predation, climatic fluctuations and large ungulate populations

Ecological modelling was used to better understand the interrelationship between rainfall, prey population trends and lion predation in the Associated Private Nature Reserves. As in the study of Mills *et al.* (1985), the models produced satisfactory results in terms of understanding the ecological processes during the period of study despite the trends being distorted by the inconsistency of the aerial counting data. The confidence limits for the estimates were therefore broad and the results cannot be accurately extrapolated. The overall conclusions of the ecological modeling were, however, in accordance with the findings of the present study that was done on lion predation in the Associated Private Nature Reserves.

The present study concluded that lion predation had only become a regulating factor of the blue wildebeest and Burchell's zebra populations, in particular, in the Associated Private Nature Reserves after these prey populations had declined because of certain factors other than lion predation:

1. A major decline occurred in the blue wildebeest (94%) and Burchell's zebra (31%) populations in the Klaserie Private Nature Reserve due to starvation after the severe drought in 1981 (Kruger 1988). Population decreases were also recorded for impala, warthog, greater kudu, giraffe and waterbuck after the droughts in 1991 and 1997.
2. The habitat in the Associated Private Nature Reserves became less suitable for plain's animals because of a lack of systematic burning, overstocking with large ungulates, and artificial water provision (Hirst 1969; Porter 1970; Kruger 1988; Weaver 1995).
3. After the removal of the boundary fences between the Associated Private Nature Reserves and the Kruger National Park, some of the blue wildebeest in the study area may have moved to better grazing in the Kruger National Park.

The results of the present study are therefore in agreement with the general contention that predators cannot regulate prey populations in natural areas, unless those prey populations are already low in number (Bothma & Walker 1999). For example, in the Nairobi National Park and the Kruger National Park lion predation also caused the decline or continuation of a decline in the blue wildebeest populations in these areas, after man had interfered by putting in fences and by changing the grass-burning regime (Foster & Kearney 1967; Rudnai 1974; Smuts 1978).

The prey selection of the lions in the Associated Private Nature Reserves was determined by using a combination of short-term continual predation observations and historical lion kill data that were obtained from the reserve management staff and the field guides from the lodges. Although lions in different areas of the Associated Private Nature Reserves showed particular prey preferences, the general pattern of lion predation was consistent for the entire study area. The major prey animals of the lions at the time of the present study were the impala, blue wildebeest, buffalo and giraffe. The non-territorial male lions selected larger prey and killed prey more frequently than the pride females. Predation by male lions was high on the buffalo and giraffe in the study area. Lion prides in the present study had a broader prey species selection for medium-sized prey (101 to 300 kg in mass) (Mills & Shenk 1992; Mills & Biggs 1993).

The buffalo was the only lion prey in the present study that increased in number from 1985 to 2002. The buffalo population increased after the removal of the eastern boundary fence of the Associated Private Nature Reserves in 1993, because of movement of buffalo into this reserve from the adjacent Kruger National Park (Weaver 1995). The killing frequency of the blue wildebeest, giraffe and Burchell’s zebra by lions was greater than their relative abundance as prey (Chapter 7), and their populations therefore continued to decrease after the droughts in 1981, 1991 and 1997 (Peel 2003). The impala population recovered due to their high reproductive rate (Kruger 1988; Skinner & Smithers 1990) and the low frequency with which lions killed them. The increased abundance of certain prey animals and the decrease in the numbers of preferred prey caused the predation pressure by lions in the Associated Private Nature Reserve to shift (Pienaar 1969; Kruger 1988; Weaver 1995). The lions in the Associated Private Nature Reserves therefore switched their selection from the formerly preferred blue wildebeest and Burchell’s zebra to the more abundant impala, and the larger buffalo and giraffe.

Similar to lions in other African savannas, the focal lions showed a preference for blue wildebeest and Burchell’s zebra in the wet season, and buffalo and giraffe in the dry season. Lions kill blue wildebeest and Burchell’s zebra more easily during the wet season, when tall grass conditions and a tendency for herds to fragment increases the vulnerability of these prey animals to lion predation (Whyte & Joubert 1988; Mills & Shenk 1992; Mills, Biggs & Whyte 1995). The lions in the Associated Private Nature Reserves selected juvenile and female giraffe because these population categories are more easily killed and are therefore vulnerable to lion predation. Also, the males of the larger ungulates were selected by the lions in preference to the females, particularly during the mating season when the physical condition of the adult male ungulates is poor and they are easy to hunt (Schaller 1972).

The killing and consumption rates of the lion groups in the present study were similar to the predation rates of lions in the Kruger National Park (Smuts 1976; Funston 1999). The current impact of lion predation on the total prey population of the Associated Private Nature Reserves was sustainable, although the population size of certain prey animals continued to decline during this study.

# CHAPTER 10

# MANAGEMENT RECOMMENDATIONS

The present study was the first attempt to determine the ungulate-habitat and predator-prey dynamics in the entire Associated Private Nature Reserves. The aim of this study was to develop more realistic management decisions within the economical and ecological objectives of the Associated Private Nature Reserves in conjunction with the guidelines of the Kruger National Park Master Plan which also act as ecological management guidelines for the Associated Private Nature Reserves.

After the removal of the fences between the Associated Private Nature Reserves and the Kruger National Park in 1993, a joint management objective was outlined for this open system. It aims to promote "*The conservation or preservation of the intrinsic values of the open system consisting of the Kruger National Park and the Associated Private Nature Reserves, by limiting managerial involvement to those aspects where man-induced influences or changes due to catastrophic natural pressures have led to deviations in the ecological composition and / or structure, or to the natural processes, due to the spatial limitations imposed on that open system. Where such deviations have been identified, remedial measures will be aimed at achieving the closest possible simulation of the pristine state"* (Joubert 1997)

With this management objective in mind, and based on the results of the present study and earlier studies that were done in the Timbavati and Klaserie Private Nature Reserves, a number of management recommendations are therefore suggested:

### Aerial counting techniques and record keeping

- The present study would have been more conclusive if the mortality records kept by the reserve management staff and the aerial counting techniques used were more consistent in style and timing. In a study such as the present one, the value of consistent data that were recorded over an extended period of time cannot be over-emphasized. This is shown by the consistency of the data collection for the comprehensive studies that were conducted on lions in the Serengeti National Park (e.g: Schaller 1972; Bertram 1979; Packer & Pusey 1984; Hopcraft *et al.* 2005), the Rwenzori National Park (e.g: Van Orsdol 1981; Van Orsdol *et al.* 1985), and the Kruger National Park (e.g: Pienaar 1969; Smuts 1976; Mills & Shenk 1992; Funston 1999).

### Habitat dynamics

- The expected dry cycle in the Associated Private Nature Reserves (Peel 2003) and the continual decline of the plain's animals there suggest that there is an imperative for the reserve management to protect or improve the available grazing habitats. This may be achieved by mechanical vegetation removal techniques, systematic burning, and by restricting herbivore access to areas being improved by rotating water availability in artificial waterholes (Weaver 1995).

Mechanical vegetation removal has been implemented in certain areas of the Timbavati, Klaserie and Umbabat Private Nature Reserves, and a systematic burning programme was put into practice in 1996. The rotation of water availability in the large number of artificial waterholes has not, however, been successfully executed. Many of the landowners, and particularly lodge owners, have not complied with this management proposal because they are of the opinion that the presence of waterholes will ensure better viewing of animals. The overgrazing and trampling that occurs in the vicinity of the waterholes by herds of large ungulates such as buffalo, has caused bush encroachment and habitat degradation.

- The proposal to introduce from 500 to 1000 blue wildebeest to the Associated Private Nature Reserves is believed to be futile without sufficient suitable habitat for these animals and because lion predation is high on this type of prey. Evidence in support of this assertion is the continual decline of the blue wildebeest in the Sabi Sand Game Reserve despite the introduction of 600 of these animals in 2003 and 2004 respectively. The Sabi Sand Game Reserve has a similar history and vegetation as the Associated Private Nature Reserves, and it is also an open system with the Kruger National Park. Two years after their initial introduction the blue wildebeest population in the Sabi Sand Game Reserve had decreased by 80%, but predation accounted for only 20% of that decline (Gavin Hullett pers. comm.)[1]. Because there is insufficient suitable habitat in the Sabie Sand Game Reserve for blue wildebeest it is likely that many of these animals moved to areas with better grazing in the Kruger National Park. The continual decline of the blue wildebeest population in the Sabie Sand Game Reserve and the prevalence of dense vegetation caused the blue wildebeest to disperse into small groups which are more vulnerable to lion predation than large herds. A similar scenario would be expected to occur in the Associated Private Nature Reserves if blue wildebeest were to be introduced.

### Lion population dynamics

- The present study concluded that there is not an overpopulation of lions in the Associated Private Nature Reserves and that a lion removal programme should not be implemented. Following a lion removal programme in the Kruger National Park, Smuts (1978) concluded that the removal of lions in that area was of questionable value in terms of increasing the prey population. Despite the decrease in the size of the lion population, the blue wildebeest and Burchell's zebra populations in the Central District continued to decline. The lion population in the Central District of the Kruger National Park returned to its former numbers

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[1] Mr G. Hullett. Warden, Sabi Sand Game Reserve, Private bag X105, Skukuza 1350.

within 18 months after the lion removal programme had been terminated (Smuts 1978). Because the Associated Private Nature Reserves form an open system with the Kruger National Park, the vacant areas would be recolonised by nomadic lions from the Kruger National Park. Furthermore, the present study has shown that the lion density in the Associated Private Nature Reserves is similar to that of the Kruger National Park and that the current level of lion predation is sustainable. A lion removal programme should therefore not be implemented in the Associated Private Nature Reserves.

- Because the Associated Private Nature Reserves allow trophy hunting of lions, it is important that the lion population dynamics in this area are determined so that a sustainable lion quota can be determined for ecological and economical reasons. An accurate estimate of the number of male lions that are either nomadic or past their prime is therefore essential for establishing a hunting quota for lions in these private nature reserves.

- For the purpose of identifying and selecting an appropriate male lion that may be trophy hunted, an on-going photographic record of particularly the facial patterns of the male lions in these reserves should be kept. As was determined in the present study, this can easily be done with the assistance of the field guides from the lodges, the reserve management staff and landowners in the Associated Private Nature Reserves. By involving all of the interested and affected parties in these private nature reserves, decisions taken by the reserve management staff with regard to lion hunting will be better supported by scientific information. This photographic archive for male lions will also be of assistance to any future studies that are done on the predator-prey dynamics in the Associated Private Nature Reserves.

- It is also suggested that the simple non-invasive technique of estimating lion age by using nose colour patterns (Whitman *et al*. 2004) be considered for aging male lions in the

Associated Private Nature Reserves. This technique provided a reliable estimate of the age of lions in the Serengeti and Ngorongoro Crater National Parks, and Whitman *et al.* (2004) have suggested that hunting quotas would be unnecessary in any male-only trophy species where age determination could be reliably implemented.

### Range use dynamics

- The range use patterns of male lions in the Associated Private Nature Reserves was not determined conclusively in this study because of the small sample size. Moreover, the high impact that male lion predation had on the buffalo and giraffe populations, in particular, and the fact that these reserves do allow trophy hunting of male lions, make it advisable to conduct a more detailed survey of the male lions in the Associated Private Nature Reserves.

### Feeding ecology

- Although the general pattern of lion predation was similar for the Timbavati and Klaserie Private Nature Reserves, there were differences in prey selection and lion predation rates. Future predator-prey studies in the Associated Private Nature Reserves should focus more closely on a greater sampling of the lion prides in each of the private nature reserves.

### Recent expansion of the Associated Private Nature Reserves

- As part of the open system with the Associated Private Nature Reserves, the predator-prey and ungulate-habitat dynamics of the Balule and Olifants River Private Nature Reserves have to be studied too. At the time of completing the present study in September 2005 the fences have been removed between the Klaserie Private Nature Reserve, and the Balule and Olifants River Private Nature Reserves. The entire Associated Private Nature Reserves is now approximately 1800 km$^2$ in size, and the predator-prey dynamics in the Balule and Olifants River Private Nature Reserves have not been assessed to date. The increased size of the open system with the Kruger National Park is in keeping with the current paradigm of increasing the size of conservation areas, and is of benefit to the seasonal movement patterns of the blue wildebeest and elephant populations in particular. Ecological monitoring does take place in both the Balule and Olifants River Private Nature Reserves and these reserves are governed by the management principles of the Associated Private Nature Reserves and the Kruger National Park Masterplan. The present study was, however, focused on the Timbavati, Klaserie and Umbabat Private Nature Reserves and the management recommendations cannot be applied to these other reserves without determining the predator-prey and habitat dynamics there. The present study can therefore only be used as a guideline for the management of the Balule and Olifants River Nature Reserves.

# CHAPTER 11

# CONCLUSIONS

The overall conclusion reached from this study supports the hypothesis that the decrease in the large ungulate populations in the Associated Private Nature Reserves from 1980 to 2003 was due to a combination of lion predation, climatic fluctuations, the change in habitat over time, the removal of the boundary fences between the Associated Private Nature Reserves and the Kruger National Park, and the change in the aerial counting method from 1992 to 1996. Because the lion density and range sizes of the lions in the Associated Private Nature Reserves were similar to that of lions in the Kruger National Park, and the lion predation rate was sustainable in the present study, it is concluded that a lion removal programme should not be implemented in the Associated Private Nature Reserves. This is further supported by the findings of Smuts (1978) that a lion removal programme in an open system such as the Kruger National Park was of questionable value in terms of increasing the prey population.

# The impact of lion predation on the large ungulates of the Associated Private Nature Reserves, South Africa.

by

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## SUMMARY

A predator-prey study was undertaken to determine the impact of lion *Panthera leo* predation on the declining populations of large ungulates in the Associated Private Nature Reserves, an open system with the Kruger National Park.

The determination of prey population trends and their spatial distribution in relation to predator habitats are imperative to the success of any wildlife management programme and particularly the study of predator-prey relationships. A combination of aerial counting and road strip censusing techniques produced the best results for determining the prey

population trends in a dense bushveld area such as the Associated Private Nature Reserves. The age structure, sex ratio, seasonal abundance and habitat selection of the most abundant lion prey were determined and compared with those of large ungulates in other African savannas. The age and sex structure of the buffalo, impala, greater kudu, warthog and waterbuck were consistent with that of ungulate populations elsewhere in African savannas. The proportion of juveniles relative to adults in the populations of the giraffe, Burchell's zebra and the blue wildebeest was lower than the recommended ratio of 30 to 40%. As expected, the prey abundance in the study area increased and decreased in accordance with the seasonal and cyclical climatic and habitat changes in this region. However, a current trend away from the suitable habitat for certain types of lion prey appears to have contributed to the continual decline in the size of these prey populations.

A reliable estimate of the density of lions in an area is fundamental to lion conservation and management. The population dynamics of the lions in the Associated Private Nature Reserves were investigated by using the call-in counting technique. This counting method was reliable for estimating the minimum population size and density of the lions in the Associated Private Nature Reserves. The total population size in November 2000 and November 2001 was 156 lions and 148 lions, respectively. These population estimates were similar to the one of 172 lions determined in an independent survey that was done in 2004. The mean pride size was 10 and the mean lion density was 8.0 lions per 100 km$^2$. When compared with lions in other African savanna woodland habitats, the lions in the Associated Private Nature Reserves were found to be present at intermediate densities and pride sizes. The age and sex structure of the adult lions in the study area were consistent with that of other areas in Africa, where adults contribute >50% to the population and the number of adult females outnumber adult males. In contrast, however, a greater proportion of the subadults and cubs in the Associated Private Nature Reserves were males than females. This skewed sex ratio may be due to the male-biased litters that result from trophy hunting of lions in the Associated Private Nature Reserves.

The range use and habitat utilization of an animal are important in most ecological and behavioural studies. The range dynamics and habitat selection of four focal lion groups in the Associated Private Nature Reserves were studied. The C, S and M prides had the largest pride size, and the N coalition consisted of the largest group of nomadic males in the study area. The selected lion groups were lured to capture sites and the focal lions were then immobilised. An adult lioness from each of the C, S and M prides, and an adult male from the N coalition were then fitted with radio-collars. The ranges of the focal lion groups were based on plots of all radio-locations for the collared animal in each group. As was expected, the range sizes of the lions in the study area were similar to that of lions in the Kruger National Park, smaller than the range sizes of lions in arid, probably prey-poor, savannas but greater than in more mesic, prey-rich savannas. The habitat selection of the lions in the Associated Private Nature Reserves concurred with that of their preferred prey. This is in accordance with the general pattern for lions in African savanna woodlands. The existing habitat dynamics in the study area appeared to have met the lions' habitat requirements of sufficient suitable prey, denning sites and drinking water.

Ecological modelling was used to better understand the interrelationship between rainfall, prey population trends and lion predation in the Associated Private Nature Reserves. The models produced satisfactory results in terms of understanding the ecological processes during the period of study, despite the trends being distorted by the inconsistency of the aerial counting data. The confidence limits for the estimates were therefore broad and the results cannot be accurately extrapolated. The overall conclusions of the ecological modelling were, however, in accordance with the results of a separate lion predation study that was done in the Associated Private Nature Reserves from 2000 to 2002.

The predation rate and prey selection of the lions in the Associated Private Nature Reserves was determined by using a combination of short-term continual predation observations for the focal lions, and historical lion kill data that were obtained from the reserve management staff and the field guides from the lodges. Although lions in different areas of the Associated Private Nature Reserves showed particular prey preferences, the general pattern of lion predation was consistent for the entire study area. The major prey animals of the lions at the time of the present study were the impala, blue wildebeest, buffalo and giraffe. The non-territorial male lions selected larger prey and killed prey more frequently than the pride females. Predation by male lions was high on the buffalo and the giraffe populations in the study area. Lion prides in this study had a broad species selection for medium-sized prey (101 to 300 kg in mass).

The buffalo was the only lion prey in this study that increased in number from 1985 to 2002. The buffalo population increased after the removal of the eastern boundary fence in 1993, because of the movement of buffalo into the Associated Private Nature Reserves from the Kruger National Park. The killing frequency of the blue wildebeest, giraffe and Burchell's zebra by lions was greater than their relative abundance as prey, and their populations therefore continued to decrease after the droughts in 1981, 1991 and 1997. The impala population recovered from these droughts due to their high reproductive rate and the low frequency with which lions killed them. The increased abundance of certain prey animals and the decrease in the numbers of previously preferred prey caused the predation pressure by lions in the Associated Private Nature Reserve to shift from the preferred blue wildebeest and Burchell's zebra to the more abundant impala, and the larger buffalo and giraffe.

Similar to lions in other African savannas, the focal lions showed a preference for blue wildebeest and Burchell's zebra in the wet season, and the buffalo and giraffe in the dry season. Lions kill blue wildebeest and Burchell's zebra more easily in the tall grass conditions that result during a period of rainfall that is above the long-term mean. The lions in the Associated Private Nature Reserves selected juvenile and female giraffe because these categories are more easily killed and are therefore vulnerable to lion predation. Also, the males of the larger ungulates were selected by the lions in preference to the females, particularly during the mating season when the physical condition of the adult male ungulates is poor and they are easy to hunt.

The predation study concluded that lion predation only became a regulating factor of the large ungulate populations in the Associated Private Nature Reserves after these prey populations had declined severly because of starvation after a drought in 1981, the lack of suitable habitat, and the movement of certain ungulate species to better grazing in the Kruger National Park after the boundary fences were removed. The results of the present study were therefore in agreement with the general contention that predators cannot regulate prey populations in natural areas, unless those prey populations are already low in number. The killing and consumption rates of the lion groups in the present study were similar to the predation rates of lions in the Kruger National Park. The current impact of lion predation on the total prey population of the Associated Private Nature Reserves was sustainable, although the population size of certain prey animals continued to decline during this study.

The overall conclusion reached from this study supports the hypothesis that the apparent decrease in the large ungulate populations in the Associated Private Nature Reserves from 1980 to 2003 was due to a combination of lion predation, climatic fluctuation, the change in habitat over time, the removal of the boundary fences between the Associated Private Nature Reserves and the Kruger National Park, and the change in the aerial counting method from 1992 to 1996. Because the lion density and range sizes of the lions in the Associated Private Nature Reserves were similar to that of lions in the Kruger National Park, and the lion predation rate was sustainable in the present study, it is finally concluded that a lion removal programme should not be implemented in the Associated Private Nature Reserves.

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# APPENDIX A

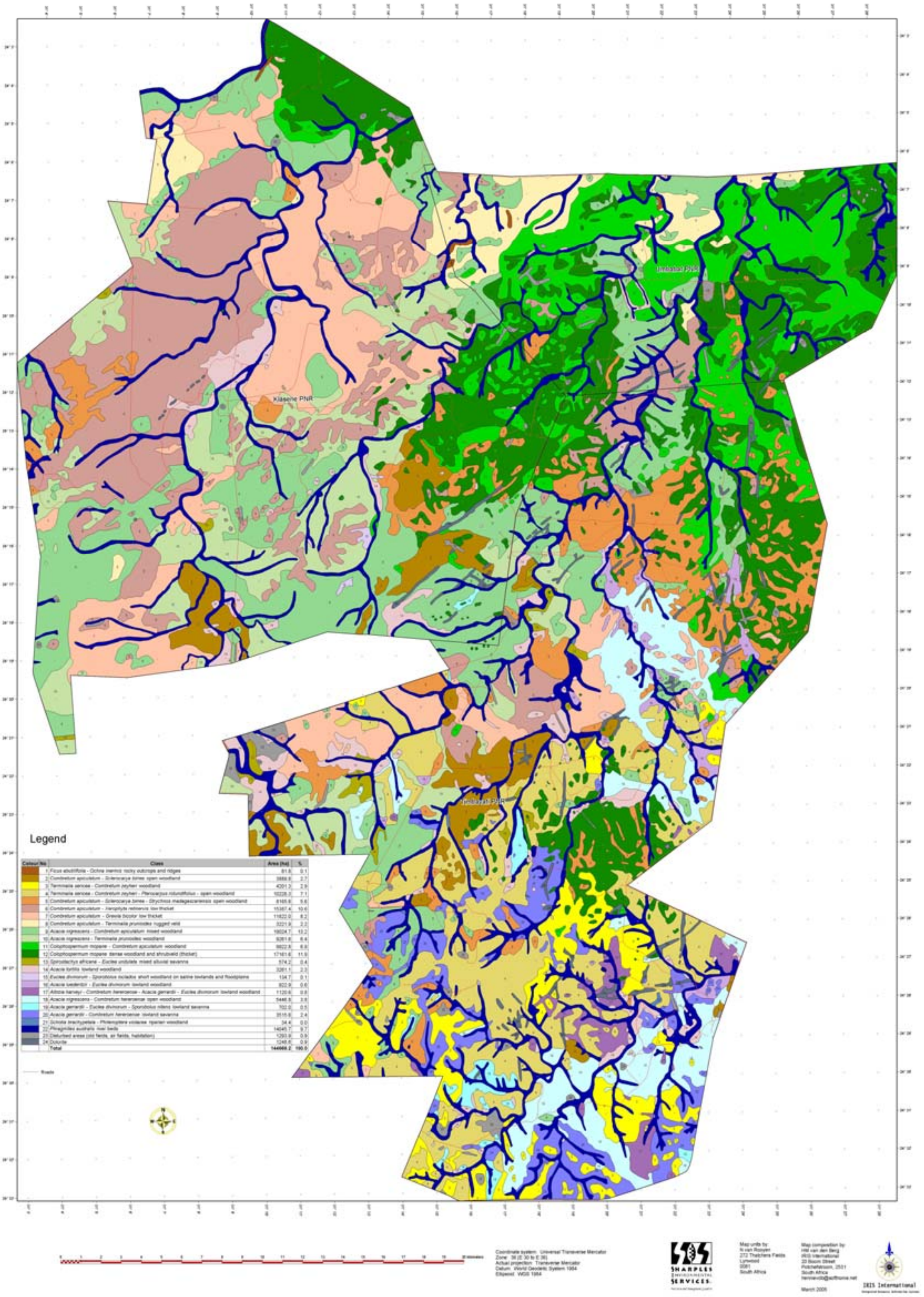

**Figure A:** The total vegetation map of the Associated Private Nature Reserves showing the 24 plant communities identified by Van Rooyen, Van Rooyen & Purchase (2005)