LIONS ON SMALL RESERVES: AN EVALUATION OF ECOLOGICAL IMPACT AND FINANCIAL VIABILITY.

by

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SUMMARY

A founder population of lion (*Panthera Leo*) was introduced into a 70 km² privately–owned, wildlife reserve in the Waterberg area of South Africa. The lion and prey species' populations were monitored between 2001 and 2004. In this period, 452 kills were recorded at a mean kill rate of one kill every 2.43 days. The lions killed 11 common prey species. Eland, warthog, kudu, wildebeest and zebra comprised 75 % of the lion's diet. The lions consumed an average of 8 % of the available common prey species population per annum. Initially, the mean ungulate population growth rate was 30.9 %, but this rate declined to –0.8 % during the study period. Significantly more animals were killed in open habitats than in closed habitats. The loss in game value for the study period was over one million Rand. A formula was compiled to quantify the cost versus return aspects of introducing lion.

Key words: Lion, financial viability, kill rate, biomass, population growth.

CHAPTER 1
INTRODUCTION

1.1 Literature review

Reintroduction of large carnivores is a controversial subject. Although large carnivores are frequently the focus of reintroduction efforts, previous post-release monitoring of such attempts has been poor (Hunter, 1998) and, in general, the success of such projects has been limited (Childes, 1988; Hamilton, 1981; Kruger, 1988; Pettifer, 1981; Mills, 1991; Linnell, *et al.* 1997). Such failures have led many authors to conclude that the factors affecting success are not understood well enough to justify relocation as a method for conserving and monitoring large carnivores (Panwar & Rogers, 1986; Wemmer & Sunquist, 1988; Mills, 1991). These failures can be attributed to a number of factors including the following: long-term monitoring programmes are costly and are often abandoned before sufficient data is collected. In many cases, subject lions escape from the reserve or farm and are destroyed. In addition, and perhaps a more common disruption to such studies are the landowners who come to realise the lions' negative impact on prey populations and have them removed/destroyed. Furthermore, few studies have been able to determine viable population sizes for large predators, probably as a consequence of the inherent complexity of such studies, since the persistence of these predators is intrinsically linked to the availability of their prey species.

1.2 Lion evolution and taxonomy

The genus name *Panthera* (in *Panthera leo*) originates from the East Asian word *Panthera* meaning the yellowish animal, or according to folklore the combination of *pan* (Greek) meaning all and *ther* (Greek) meaning beast (Wozencraft, 2005). The meaning of the species name *leo* is unclear but is derived from the French/ Greek words *leon*, later simplified to *leo*. The taxonomic name *Panthera*

leo was first attributed to a North African (Algerian) specimen by the taxonomist Carolus Linnaeus in 1758. Lions are the largest of all African cats. Smithers (1982) weighed and measured 344 individuals of all ages in the Kruger National Park (South Africa) and found that their average mass was greater than those distributed further north in Africa (Skinner & Smithers, 1990). Lions grow rapidly for the first three years; subsequently, their growth into adulthood slows down. Male lions reach an average mass of 225 kg with a shoulder height of up to 1.25 m, with adult females weighing an average of 126 kg (Skinner & Smithers, 1990).

The male lion develops a mane usually evident late in his first year. Mane hair differs in length, density and colour between individuals and range from short or longhaired yellow manes to very dense and impressively long black manes. Pelage also differs in hue from dark tan with lighter rosette markings (particularly on the lower limbs) to a much lighter colour as in some individuals, sometimes referred to as white lions. These white lions represent one of two possible mutations known as chinchilla or acromelanic albinism, which, like albinism, are known to arise from the same gene locus in the individual's chromosomes (Skinner & Smithers, 1990).

1.3 Lion distribution

Lions historically occurred throughout much of Europe and the whole of Africa even as far south as South Africa's Cape Point. The modern day free-range distribution of lions, however, reveals that they have become extinct in Europe (since AD 100), North Africa (since 1920) as well as much of their Southern African range, and are now restricted to national parks and as isolated, re-introduced island populations where they are offered a level of sanctuary (Skinner & Smithers, 1990). Lions are currently protected by the South African Department of Environmental Affairs and Tourism as being

a "specially protected species" – a directive from CITES (Convention for the International Trade on Endangered Species). The implication of this status means that no one may hunt, capture or relocate this species without special written consent being granted by the Government of South Africa. See Figure 1 below for lion distribution.
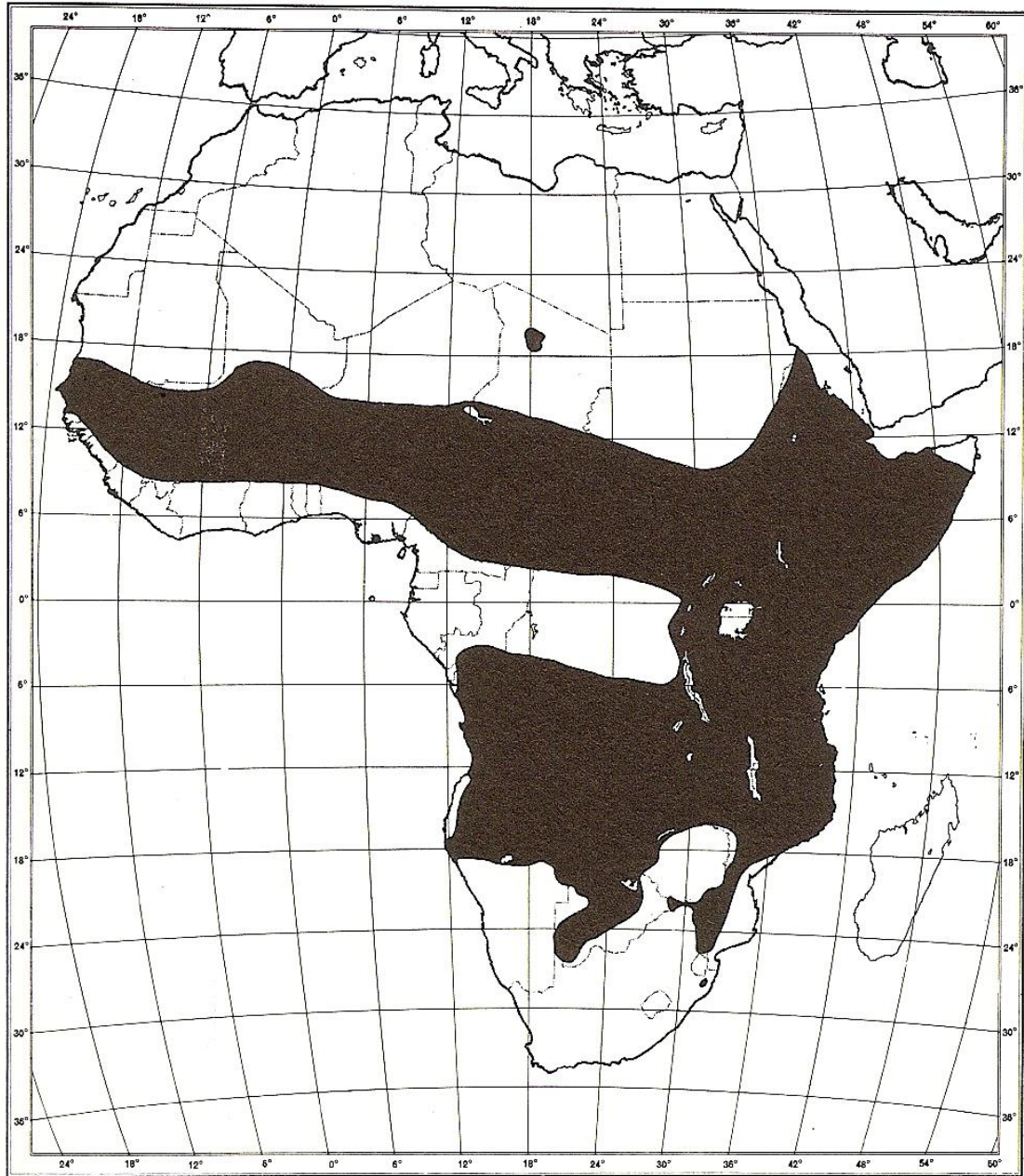
Figure 1. Lion distribution in Africa (Skinner & Smithers, 1990).

1.4 Previous lion studies

Lions are regarded as high profile animals by the eco-tourism industry and are a sought-after species by local and international tourists alike. In an effort to be more competitive in the tourism market, landowners often agree to establish lions in their game reserves. However, the consequences of lion introduction on the age and sex structure ratios of prey species are less often considered, despite the large potential influence on their population structure and growth rate. Prey mortality could become greater than net recruitment and/or the herd structure may become skewed through prey selection. For example, selection skewed towards females reduces growth rate, while selection towards males may increase growth rates, assuming that an efficient ungulate breeding system naturally contains fewer males than females.

According to Viljoen (1996), lionesses require a mean of 5 kg of edible biomass per day while male lions require 7 kg and are able to consume 20-25 % of their own body weight in just a few hours. Generally, a pride seldom makes more than one kill every two to three days, but the frequency of kills varies according to the number of lions in the group, prey availability and the sex and age of the prey species. Bothma (1996), in a study of large predators in the Serengeti (East Africa), showed that there was a trend to catch the most expendable segment of the population, namely old animals as well as those in poor condition.

Whilst lions have been intensively studied in numerous established populations, little formal scientific data is available on their response to relocation. Numerous predator-prey relationship studies concentrating on behavioural and feeding ecology of lions have been published. Mills and Shenk (1992) conducted a study in the Kruger National Park (KNP) from 1990 to 1992. In a study

area of 235 km², they concluded that lion predation did not have a negative effect on the population growth rate of Burchell's zebra (*Equus burchellii)* and blue wildebeest (*Connochaetes taurinus)*, two of the most commonly selected prey species. Hunter (1998) concluded that in the Phinda Resource Reserve (170 km²), lions generally preyed on male and female (as well as sub-adult and adult age class) ungulate species at a similar frequency to their occurrence. Based on a three-year study in the greater Makalali Conservancy (140 km²), Slotow, *et al.* (2004) found that approximately 20 lions were sustained on up to 3.1 % of the available biomass per annum, and each lion killed up to 3.2 kg of live biomass per day.

Lions have a significantly greater impact on prey species in smaller areas. An informal case study conducted by Entabeni Game Reserve (Limpopo Province) showed that, in 2000, four lions, enclosed within 15 km², killed an average of 25 kg of biomass each per day (Dixon, Pers. Comm., 2001). Eight lions at Mabula Game Reserve (also enclosed in 15 km²) killed less biomass (Power 2002). However, prey was killed at five to six times their availability at both sites respectively and had, therefore, to be replenished artificially on an annual basis. Factors that may have influenced the high kill rate are as follows: a high (albeit initial) concentration of prey species, and prey species that are unfamiliar with lion and can, therefore, be cornered at boundary fences. Physiological stress associated with game capture (capture myopathy) and relocation, which may debilitate game animals, could be an additional contributing factor.

Another possible but less explored cause of prey depletion is the conceptual affect of Minimal Viable Population (MVP). According to Shaffer (1981), a population is considered viable when it is able to exist regardless of the four main uncertainties that confront populations namely:

- *Demographic stochasticity,* which arises from chance events in the survival and reproductive success of a finite number of individuals,

- *Environmental stochasticity,* due to the temporal variation of habitat parameters and the populations of competitors, predators, parasites and diseases,

- *Natural catastrophes,* such as floods, fires, droughts, and so forth, which may occur at random intervals through time and,

- *Genetic stochasticity,* resulting from changes in gene frequencies due to the founder effect, random fixation and inbreeding.

Little is, however, known about the role of any of these factors in any specific case of extinction. Because all of these factors increase in importance with decreasing population size, assessing the relative importance of each will always prove difficult (Shaffer, 1981).

In 2001, a founder population of three lions was introduced to Touchstone Game Ranch (TGR). TGR was deemed large enough to support lion on the basis of studies done by Smithers and Smuts (1982) and Patterson (1988), who found that lion prides range over a 2 500 ha area in the Kruger Nation Park (K.N.P) and 7 200 ha in Mashatu (Botswana), respectively. The lions reintroduced to TGR roamed the entire 7 000 ha study area. Three cubs were bred to a single mother in 2002 (September), bringing the 2004 population to six lions.

It was not known at TGR which animals would be susceptible to MVP, that is, should there be more concern for the low number of introduced lion or a concern for some prey species population numbers. Six lions were introduced to Phinda (which is considerably larger than TGR) and within a few short years, the pride was stabilised at about 30 individuals. In fact, the lion breeding was so successful there that surplus lions were regularly relocated to reserves elsewhere (Hunter, 1998). In this instance and therefore probable with the introduction at TGR, the lions would be successful because there were no other lions/competitors at the site and that TGR was relatively densely

stocked with prey species. Over time however, concern for the existence of some prey species populations was raised.

The prey species population at TGR was considered adequate to sustain the lion introduction, with prey numbers estimated at a density of 1 Large Animal Unit equivalent (LAU) per 9 hectares in 2000/ 2001. At the time of permit application for the introduction of lions, the South African Department of Environmental Affairs and Tourism (DEAT) suggested that the prey species game population should occur at a density of not less than 1 LAU per 14 hectares. Thus, in enclosed areas, a minimum requirement of suitable prey species quantity to fulfil the lion's feeding ecology must exist.

The LAU equivalent is, according to van Hoven (Bothma 1996), a guideline method to determine the metabolizable energy requirements and probable food intake of game animals compared to one large-animal stock unit (bovine) of 450 kg whose mass increases by 500 g per day on grassland with a mean energy digestibility of 55 %. For example, 1 zebra = 0.66 LAU (or 1.51 animals per LAU); 1 impala = 0.19 LAU (5.2 animals per LAU); 1 eland = 1.08 LAU (0.92 animals per LAU); 1 blue wildebeest = 0.50 LAU (2 animals per LAU), 1 warthog = 0.25 LAU (4.04 animals per LAU).

The ecological and financial viability of introducing free-range lion into a game ranching and tourist enterprises as well as their long-term sustainability had to be taken into account. In other words, would the lions cost more than what they were worth to TGR? This factor was of concern to management prior to the lion introduction. At the time of writing, no other studies were found to answer this question. This study was, therefore, initiated as an attempt to overcome the lack of published information on predator-prey relationships among reintroduced lions. More specifically, the question to be answered was what costs implications could be associated with such introduction projects. The aims of this study, therefore, were to determine:

1.4.1 Distance traversed and interval between kills.

By monitoring the distance traversed, field guides could use this information to predict approximately how far the lions would be from their previous sighting, which would help improve the tourists' chances of regular viewings. In other words, telemetry could be started near the area where they were encountered previously. Similarly, if it were known when the lions last fed, this information could be used to predict when they would next hunt providing for a more memorable tourism experience. From a more analytical point of view, the inter-kill interval and overall kill frequency data could be compared with other lion populations to see if the TGR lions were behaving within normal predatory rates. Also, it could be determined whether there was a correlation between the distance traversed and the kill rate. One could assume that lions would travel less distances if their prey density was high, or conversely, they would have to traverse further with a lower concentration of prey. In addition, if the latter were true, the question could be asked whether the lions would be able to maintain their kill rate despite the further distance they had to cover to find prey.

1.4.2 Prey availability and demographics.

To investigate the potential effects of lion on prey populations, quantitative assessments of the availability of prey in terms of both species and their quantity as well as population structure (male: female and adult: sub–adults ratios) would be compared before and after lion reintroduction.

Numerous questions needed to be answered in this connection. Could TGR sustain a viable lion population as well as a viable prey species population? Better still, could the current game population continue to increase to surplus proportions with lower live-game sales targets still being

met? Lastly, would the lions have an impact on prey species age and/or sex structure, given that a stable population and its growth relied on the intrinsic balance of sub-adult recruitment and adult breeding as well as the correct male: female ratio?

1.4.3   Prey species population growth.

The ungulate population growth prior to the lion introduction was determined using data from previous aerial censuses. The growth was monitored and a comparison was drawn between the before and after growth rates. Knowledge of a change in growth would help management plan in advance if either more game needed to be introduced, or if game could be harvested. Or in fact, would the current population mix be able sustain the lion introduction project?

1.4.4   Biomass consumption.

This analysis was aimed at determining the quantity of ungulate biomass consumed at TGR compared to lion populations in other reserves/parks. The edible biomass portion could otherwise provide an income through the venison market. We, therefore, could test whether there would be a greater financial reward through venison harvesting or photographic exposure through lion-based tourism.

1.4.5   Prey species selectivity.

The number of kills per species would be determined to test whether the lions preferentially targeted certain species. Nyala, for example, are expensive (three times the cost of a blue wildebeest yet perhaps one third of the size). They rely solely on camouflage for defence and can easily become prey. With their population numbers already under pressure from other predators, nyala could face

population depletion. Lion are also expert warthog killers. Warthogs lay-up in burrows at night, and lions are known for their prowess in digging them out. Would they also suffer a drop in numbers? Impala, blue wildebeest, eland and zebra, all common lion prey species, were according to the aerial census data plentiful, and their selectivity was not viewed as a concern at the time. There was concern, however, for warthog, bushpig, nyala, ostrich, red hartebeest and waterbuck should the lions display a trend to selecting these species. Financially, these species are either very expensive to purchase and/or fail to habituate well after introduction. Furthermore, viable population sizes would need to be introduced for populations to re-establish themselves, which in the case of warthog and bushpig for example would be impractical.

1.4.6   Seasonal influences.

In this instance, the prediction that more kills would be made during summer, when there was an abundance of calves/sub–adults, than in winter, would be tested.

1.4.7   Habitat influences.

The number of kills per different habitat/vegetation unit should be skewed toward habitats with greater cover. Lions are generally regarded to lack stealth and endurance and, therefore, are assumed to employ ambush hunting tactics. The TGR lions originated from a woodland/savannah habitat in the Mpumalanga lowveld, similar in many respects to their new habitat. The topography at TGR is however very different in that boulders and pebble scree, especially at higher elevations, dominate the landscape and although these areas were inhabited by a variety of game animals, it was doubtful whether the lions would actually pursue their quarry into these areas. Lowland flat valleys intersect slope and plateau regions, and it was believed that this is where most lion hunting activity would take place.

1.4.8 Financial viability.

Apart from the pleasurable aesthetics of managing lions, their financial viability is less often considered. For this purpose, a financial model based on all the cost elements associated with the TGR lions would be summarised into an original formula into which variables specifically suited to the introduction site could be substituted.

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CHAPTER 2

STUDY AREA

2.1 Location and size

TGR is a 70 km² (7 000 ha) wildlife reserve situated within the Waterberg Nature Conservancy (approximately 1 200 km²) (23°50` south; 28° 22`east) and forms part of the greater Waterberg Biosphere Reserve (approximately 14 500 km² in extent) in the Limpopo Province, South Africa.
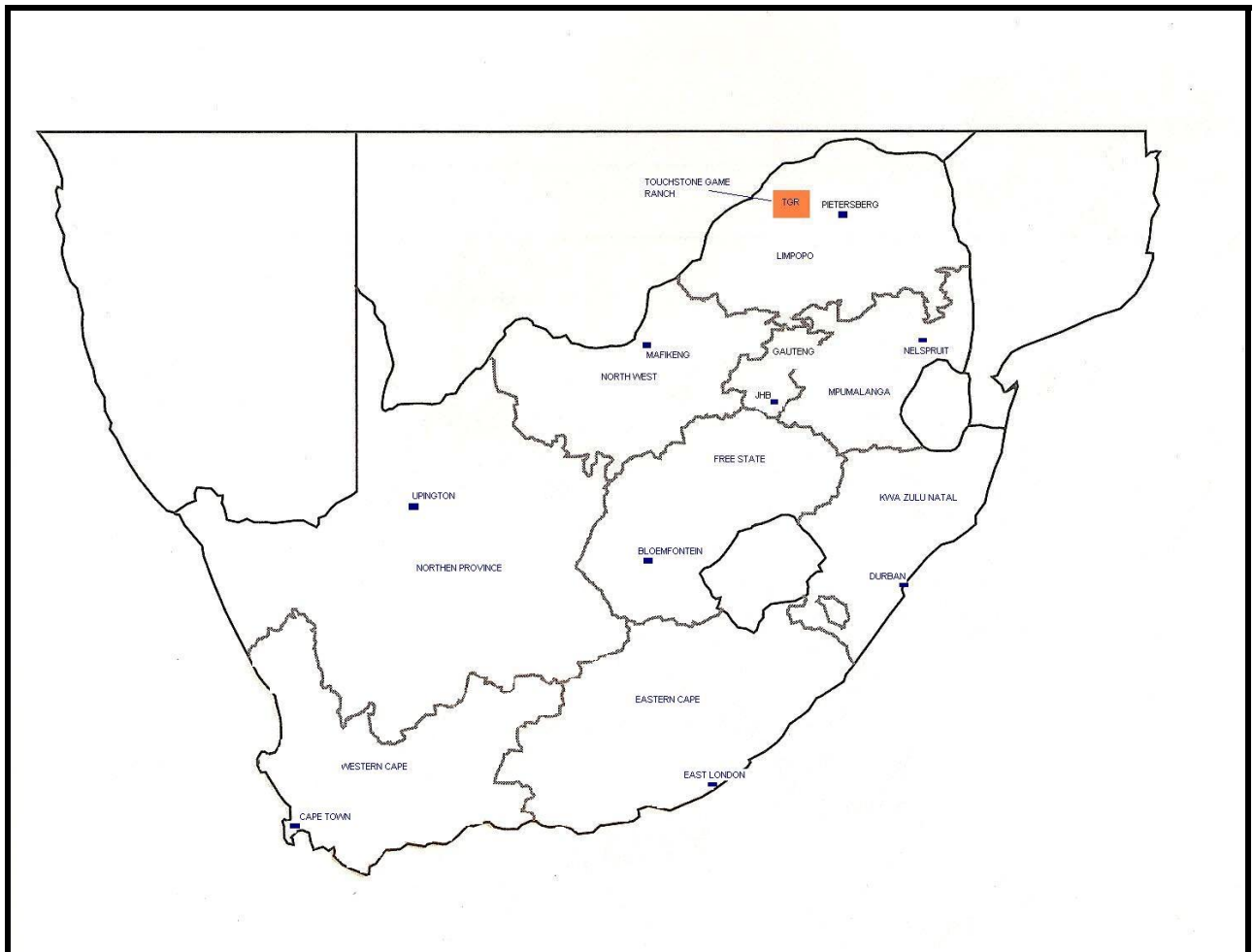
Figure 2. Outline map of South Africa and geographical position of TGR.

2.2 Topography

The altitude at TGR varies between 980 m to 1 310 m above sea level. The study area forms part of the visually striking Waterberg mountain range complex that extends from Nylstroom (Modimolle) and Warmbaths (Bela-Bela) in the south, to Ellisras (Lephelale) in the west and to Potgietersrus (Mokopane) and Naboomspruit (Mookgopong) to the east. TGR is situated roughly 15 km south of the northern escarpment where 300 m sheer laminated sandstone cliffs give way to the sweet arid thornveld commonly associated with the Limpopo river low-lands. The many streams and tributaries that drain from the Waterberg give rise to the three prominent rivers of the region, namely the Mogol, Mogalakwena and Lephelale Rivers. The Lephelale River, in particular, is responsible for cutting a deep groove in the exposed sandstone cliffs bisecting the vast and unpopulated highlands of the central Waterberg Nature Conservancy.
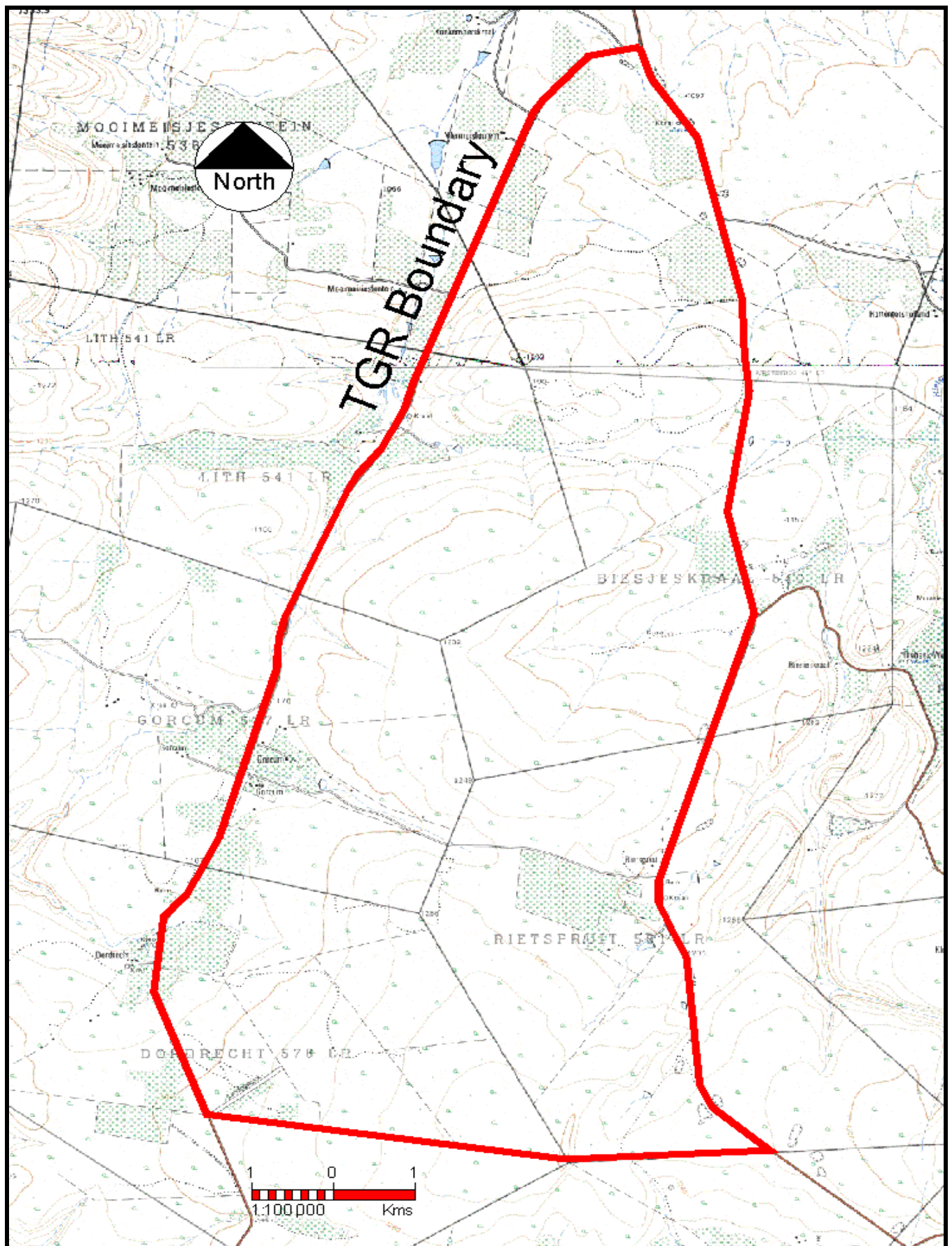
Figure 3. TGR boundary and topographical map. Scale 1:100 000.

2.3 Rainfall

Rainfall is infrequent and highly variable; precipitation is only expected between late November and April with the bulk of the rain falling between December and February. The period prior to the onset of the rainy season is characterised by extremely high temperatures with many consecutive days reaching 38 °C (Table 1; Figure 5). At times like these, soil and forage moisture content is at its lowest. Seeplines, streams and rock pools nourished from the previous season's rainfall have dried up. Dam water levels are reduced to not much more than mud wallows, and game animals seem to dehydrate themselves further by having to travel increasing distances to reach their now-preferred artificial watering points.

In contrast to the Waterberg's harsh winter landscape, average and above average rainfall periods transforms the bushveld into wet and saturated areas. The conditions are such that 4x4 game drives vehicles cannot access many areas, making vehicle-borne game viewing almost impossible. Many freshwater springs develop from rock fissures on the high plateau areas. Seep-lines release water from their *Terminalia* fringes into adjacent wetlands that generate water flow into streams, rivulets and earthen dams.

During periods of good rainfall (> 600 mm per annum), surface seep water is abundant and persists late into the dry period with some of the fresh-water springs generating flows until the onset of the following rain season. This valuable natural water resource is especially well utilised by elephants and eventually forms compacted water-filled depressions from the continuous bathing, thus providing drinking and wallowing ponds for all passing game animals.

There are at least eleven permanent (for above average rainfall seasons) watering sources at TGR; roughly one water resource existed per every 640 ha. These watering sources were reduced to seven,

which provides one drinking point per 1000 ha during drier periods. Impoundments are not always ideally situated, since dams were originally constructed for domestic livestock watering where the criterion for placement was to optimise water run-off and catchment so as to keep the dams as full as naturally possible. Due to the land shape at TGR, however, run-off is either to the extreme west or east passing through the property boundary. Consequently, during the development phase, additional artificial watering points were constructed deeper into the property to reduce game animal concentrations, especially elephant, close to the boundary fencing. See Figure 4 below for the aerial image of the water resource distribution at TGR

Dry electric storms are common from late October through November and can be responsible for numerous wild fires. Within a week or two, these burnt areas flush without requiring rain and provide new nutritious sustenance for weary game animals having survived for months on dry unpalatable forage.

The highest rainfall recorded at Melkrivier station was 1 370 mm for the 1999/2000 period and was followed by the lowest recorded rainfall (220 mm) two seasons later during the 2001/2002 season. The twenty-year mean annual rainfall is 620 mm (+/- 671 mm). Rainfall typically presents itself as a result of strong thunderstorm activity from the north (thundershowers of 60 mm or more are not uncommon) and to a lesser extent; more gentle and prolonged orographic and frontal rain from the south. Winter rainfall occurs but is uncommon and is only associated with cold front weather systems which would typically yield less than 10 mm of rainfall per season.

Figure 4. TGR water resource. Scale: 1:80 000.	
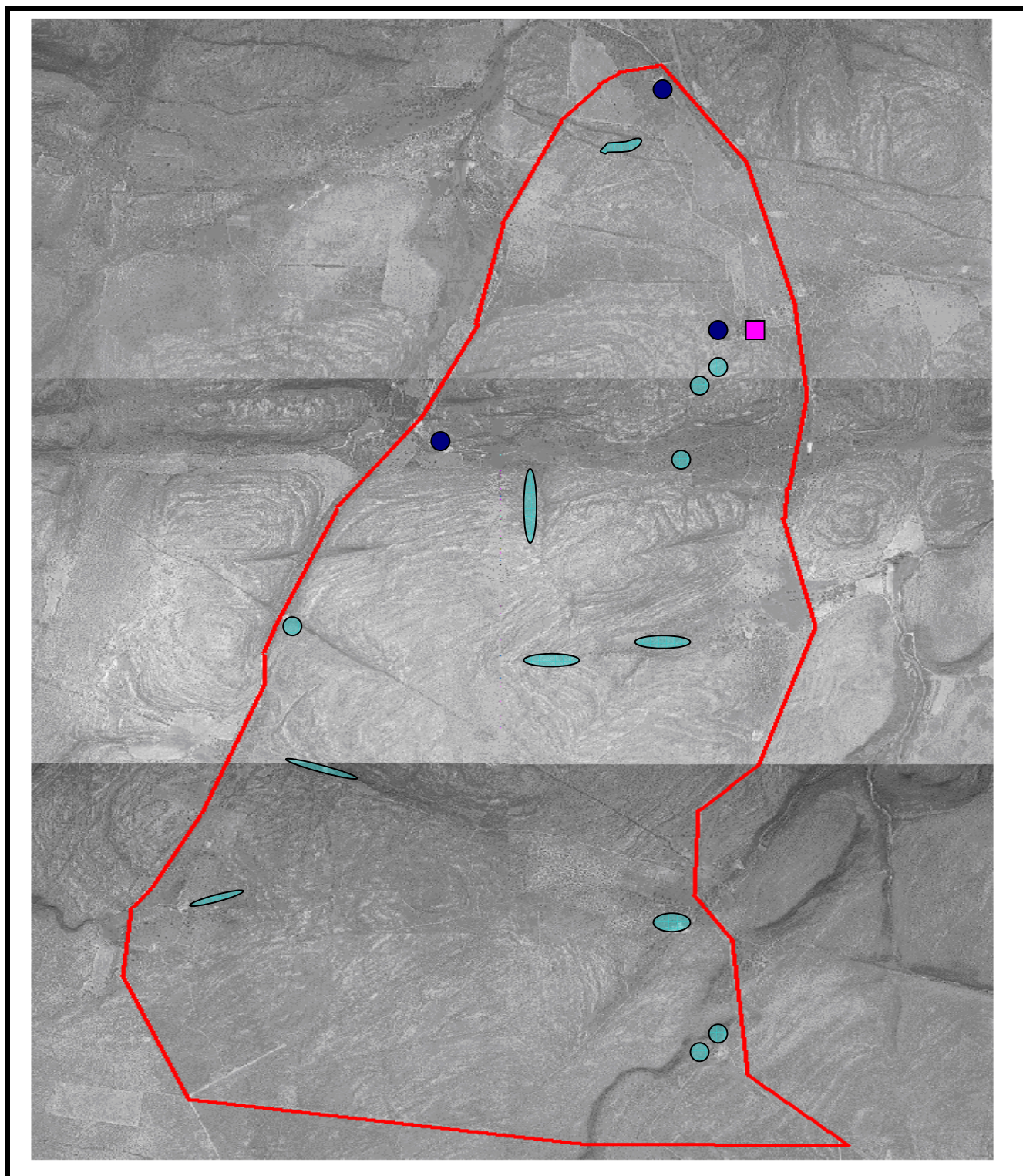
	Tourist lodge
	Permanent water
	Seasonal water
	TGR boundary

2.4 Temperature

The climate is sub-tropical. The winter climate is characterised by a long autumn (April, May and June) and a short, but often chilly, winter (July and August). During winter (from March through August) temperatures range between –8 °C (coldest recorded) and 21 °C but usually average at a low of 3 °C and high of 28 °C (highest recorded). Occasional winter cold snaps are associated with high-pressure frontal weather systems that usually persist for two to three days. Winter frost commonly occurs in low-lying areas. By contrast, summers (from September through February) are hot, often attaining temperatures of up to 40 °C with the relative humidity, sometimes in excess of 80 %. Typical summer temperatures average between a night time low of 18 °C and a daytime high of 32 °C. (Table 1 and Figure 4).

Table 1. Climate summary at TGR for the period 2000 to 2004.

MONTH	TEMPERATURE (Degrees Celsius)				PRECIPITATION		
	Highest Recorded Temperature (Celsius)	Average Daily Maximum (Celsius)	Average Daily Minimum (Celsius)	Lowest Recorded (Celsius)	Average Monthly (mm)	Average No. Of Days with >=1mm	Highest 24 hour Rainfall (mm)
January	40	30	17	9	120	12	77
February	37	29	17	10	84	9	102
March	37	28	15	3	74	9	65
April	34	26	12	2	37	6	37
May	32	24	7	-2	7	2	22
June	28	21	3	-8	6	1	30
July	28	21	3	-6	2	1	14
August	33	24	6	-6	5	1	26
September	37	28	10	-3	16	2	41
October	38	29	14	3	58	8	84
November	38	29	15	6	101	11	88
December	39	30	16	7	124	13	82
	40	**27**	**11**	**-8**	**634**	**75**	**102**
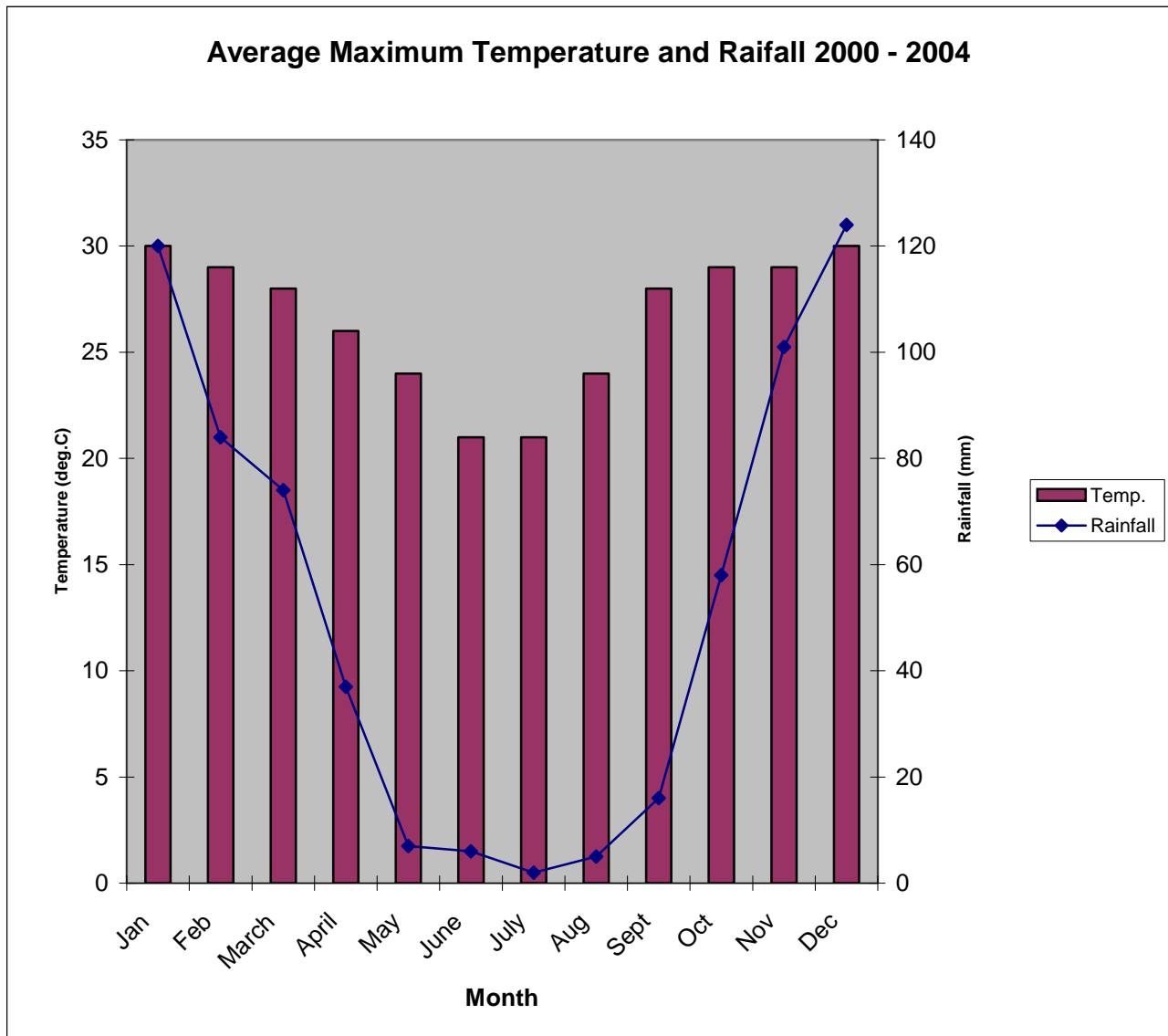
Figure 5. Average temperature and rainfall data at TGR for the period 2000 to 2004.

2.5 Geology

The main mass of the Waterberg consists of sedimentary rock and is bounded by escarpments to the north, south and east with the central portion forming the Palala Plateaux. These sediments are completely detritus and consist of sandstones, mudstones, shales, conglomerates and lenses of grits (Truswell, 1977; SACS, 1980). However, the Waterberg Group of Sandstones is almost entirely limited to the area occupied by the Waterberg Biosphere Reserve. The Bushveld Igneous Complex, the bedrock of the Waterberg Mountains, was formed +- 1 954 million years ago while the Waterberg System or Super Group was formed some 1 790 million years ago following an extensive period of levelling due to the erosion of the Bushveld Igneous Complex (Truswell, 1977; SACS, 1980). The local geology, dominated by the sedimentary Waterberg Group of the Mogalakwena Conglomerate Formation (Brandle, 1993), is represented by coarsely grained boulder and boulder conglomerate strewn maintain terraces, which level off to plateau regions. Low-lying seep-lines and ex-agricultural lands separate the plateau systems.

2.6 Soils

Due to the domination of quartzitic sandstone, the nature of the soil is predominantly sandy. Sandy soils are very leached because of the relatively high rainfall and are, therefore, mostly of a distrophic nature (De Klerk, 2003). As a result of the predominantly hilly and mountainous terrain, a large portion of the soils is very shallow and rocky (Low and Rebello, 1996) and can, therefore, be classified according to the South African soil classification system of McVicar, *et al.* (1997) as being of the Glenrosa and Mispah soil forms. Dominant soils found on the flat areas, such as plateau and low-lying plains, are of the Clovelly and Avalon forms. Although these forms are also found in the valleys and drainage lines; other soil forms with a higher clay and nutrient content and generally

with a better-developed structure are more common. The following soil forms also occur frequently in the region: Hutton, Dundee, Oakleaf, Katspruit, Westleigh, Champagne, Cartref, Inanda, Kranskop, Magwa, Griffin, Longlands, and Fernwood (Land Type Survey Staff, 1988).

2.7 Vegetation

The World Network of Biosphere Reserve Map classifies the vegetation area as savannah (De Klerk, 2003). The Waterberg Biosphere represents a considerable area of the savannah biome of Southern Africa. Although the conservation status of savannah is principally good, less than 5 % of the biome is formally protected (Rutherford and Westfall, 1986). Savannah vegetation types are inadequately conserved within formally proclaimed nature reserves.

The Waterberg has the largest portion of the Sour Bushveld veld type, which characterises mountainous savannah areas. A large diversity of habitat types can be found in the Waterberg plateau, valleys, cliffs and slopes (Henning, 2002). Deep sandy soils alternated by shallow and rocky soils occur on the flats and plateau, while in the valleys the vegetation changes from riparian vegetation (among others, riparian woodlands and near-forests, reed beds and marshes/vleis) to the predominantly thornveld on the loamy alluvial valley floors. The grassveld is particularly rich floristically, while the woody component is diverse. Apart from the termitaria patches on the slopes, where near-forests develop, there is a great wealth of forb and bushy plants, including stragglers with affinity to the southern (fynbos) flora. The savannah biome is home to a wide variety of large herbivores, which together with fire, play a decisive role in ecosystem processes and the maintenance of plant species diversity (Henning, 2002).

The Mixed Bushveld type is found at lower elevations than the Sour Mixed Bushveld and occurs as a maze of variations and transitions. They vary from rather dense short savannah to tall, sparser savannah and generally provide better grazing for the large herbivores than the Sour Bushveld (De Klerk, 2003).

According to Acocks (1988), five different veld types are represented in the biosphere reserve; two of which are commonly represented in the study area, i.e. Sour Bushveld (veld type 20) and Mixed Bushveld (veld type 18), both typical savannah vegetation types. The clear gradient in the vegetation, from sour in the south and on higher elevations to sweet in the north on lower elevations, is linked to the variation in annual precipitation as determined by elevation and latitude (more moist in the south and drier in the north).

The previous classification of the study area, Sour/ Sourish and Mixed Bushveld (Acocks, 1988), has more recently been redefined as Mixed Bushveld (Van Rooyen & Bredenkamp, 1996). On the basis of these descriptions, the researcher identified five vegetation units in the study area (Figure 6).

2.7.1 *Terminalia* sandveld.

This relatively homogenous unit comprises 7 % of the study area and is characterised by a well-developed canopy and understory. Crown cover is high (approximately 75 %) with between 2 500 and 3 500 woody individuals per hectare of which many individuals attain a height of over 5 m. Grass cover varies between 60 % and 70 %. The soils are generally deep, fine-grained and well-leached sand. This unit occurs only at low elevations between 980 m and 1 000 m.

The most common woody species occurring in this vegetation unit is the indicator species *Terminalia sericea* (silver-leaf Terminalia). The following other woody species are also well

represented: *Burkea africana* (red syringa), *Cassine transvaalensis* (Transvaal saffronwood), *Combretum apiculatum* (red bushwillow), *Dombeya rotundifolia* (round leaf pear), sumach *Elephantorrhiza burkei* (sumach bean), *Faurea saligna* (beachwood), *Grewia flava* (brandybush), *Peltophorum africanum* (weeping wattle), *Protea caffra* (highveld protea) *Rhoicissus revoilii* (bushveld grape), *Securidaca longipeduniculata* (violet tree), *Dichrostachys cinerea* (sickle bush).

Grass species occurring in this unit include *Aristida congesta* subsp. *congesta, Setaria ustilata, Aristida diffusa, Sporobolus pyramidalis, Aristida meridionalis, Sporobolus stapfianus, Aristida rhiniochloa, Stipagrostis uniplumis, Brachiaria deflexa, Trichoneura grandiglumis, Cynodon dactylon, Eragrostis biflora, Eragrostis chloromelas, Eragrostis lehmanniana, Eragrostis pallens, Eragrostis racemosa, Eragrostis rigidior, Heteropogon contortus, Melinis repens, Panicum maximum, Panicum natalense, Perotis patens, Pogonarthria, squarrosa, Setaria sphacelata.*

2.7.2 *Combretum apiculatum - Burkea africana* mixed Bushveld.

This vast heterogeneous unit comprises 37 % of the study area, occurring mostly at elevations between 1 000 m and 1 200 m. Crown cover is moderate, estimated at between 65 % and 70 %. The majority of woody individuals are between 2 m and 5 m with some *Burkea* trees exceeding 5 m. Woody individuals number 1 500 to 2 000 per hectare, typical of "open" woodland. Grass cover is relatively low, estimated at 50 % to 60 %. The soils in this unit are course–grained and generally shallow.

Woody species occurring in this unit include *Acacia caffra* (common hook-thorn), *Rhus pyroides* (common taaibos), *Acacia galpinii* (monkey thorn), *Schotia brachypetala* (weeping boer bean),

Englerophytum magalismontanum (stamvrug), *Vangueria infausta* (wild medlar), *Burkea africana* (red syringa), *Vitex rehmanni* (pipe-stem tree), *Cassine transvaalensis* (Transvaal saffronwood), *Ziziphus mucrunata* (buffalo thorn), *Combretum apiculatum* (red bushwillow), *Combretum molle* (velvet bushwillow), *Croton gratissimus* (lavender croton), *Dombeya rotundifolia* (round-leafed pear), *Ehretia rigida* (puzzle bush), *Euclea crispa* (blue guarri), *Faurea saligna*(beachwood), *Ficus thonningii* (common wild fig), *Grewia flava* (brandybush), *Kirkia wilmsii* (mountain syringa), *Lannea discolor* (live-long), *Pappea capensis* (jacket plum), *Ochna pulchra* (peeling plane), *Olea europaea* subsp. *africana* (wild olive), *Ozoroa paniculosa* (common resin tree), *Albizia tanganycensis* (paperbark albizia), *Commiphora africana* (poison–grub commiphora), *Commiphora marlothii* (paperbark commiphora).

Grass species occurring in this unit include *Andropogon chinensis*, *Aristida adscensionis*, *Aristida congesta* subsp. *congesta*, *Aristida diffusa*, *Aristida meridionalis*, *Brachiaria deflexa*, *Cynodon dactylon*, *Digitaria eriantha*, *Digitaria diagonalis*, *Diheteropogon amplectens*, *Eragrostis chloromelas*, *Eragrostis curvula*, *Eragrostis gummiflua*, *Eragrostis lehmanniana*, *Eragrostis rigidior*, *Heteropogon contortus*, *Loudetia simplex*, *Melinis repens*, *Panicum maximum*, *Perotis patens*, *Pogonarthria squarrosa*, *Setaria incrassata*, *Sporobolus ioclados*.

2.7.3 *Combretum zeyheri* - C. *molle* mixed Bushveld.

This unit comprises 43 % of the study area and dominates the higher elevations from 1 200 m to 1 300 m. The unit is characterised by a sparse canopy, which covers approximately 50 % of the unit. Most woody individuals are below 4 m in height (although some *Kirkia* spp. attain heights of > 6 m) and at a density of 1 800 to 2 300 individuals per hectare. Grass cover is relatively low, ranging between 40 % and 50 %. The soils are shallow, coarse-grained, pebble and boulder strewn.

Woody and grass species for this unit are relatively consistent with that of the *Combretum apiculatum – Burkea africana* (2.7.2 above) mixed bushveld unit but vary with the dominance of the key indicator species, such as *Combretum zeyheri* (large-fruited bushwillow) and *Combretum molle* (velvet bushwillow), and include *Acacia caffra* (common hook thorn), *Rhus lancea* (karee), *Acacia galpinii* (monkey thorn), *Schotia brachypetala* (weeping boer bean), *Englerophytum magalismontanum* (stamvrug), *Vangueria infausta* (wild medlar), *Burkea africana* (red syringa), *Vitex rehmanni* (pipe-stem tree), *Cassine transvaalensis* (Transvaal saffronwood), *Ziziphus mucronata* (buffalo thorn), *Combretum apiculatum* (red bushwillow), *Combretum molle* (velvet bushwillow), *Croton gratissimus* (lavender croton), *Dombeya rotundifolia* (round-leafed pear), *Ehretia rigida* (puzzle bush), *Euclea crispa* (blue guarri), *Faurea saligna* (beachwood), *Ficus thonningii* (common wild fig), *Grewia flava* (brandybush), *Kirkia wilmsii* (mountain syringa), *Kirkia acuminata* (white syringa), *Lannea discolor* (live-long), *Pappea capensis* (jacket plum), *Olea europaea* subsp. *africana* (wild olive), *Ozoroa paniculosa* (common resin tree), *Commiphora mollis* (velvet commiphora), *Commiphora pyracanthoides* (common commiphora).

2.7.4 *Sclerocarya birrea - Acacia* woodland.

This vegetation unit comprises 9 % of the study area and is dominated by *Sclerocarya birrea* and *Acacia* spp., namely *A. robusta*, *A. burkei* and *A. karroo*. Crown cover is high (>70%) with a well- developed understory. Woody species occur at > 3 000 individuals per hectare, typical of "closed" woodland. Grass cover is low (< 40 %). This vegetation unit occurs only at low elevations on lineaments and diabase dyke extrusions. The soils are deep, humous-rich, fine-grained fertile red sand-loam.

Woody species that occur in this unit include *Sclerocarya birrea* (marula), *Acacia caffra* (common hook-thorn), *Acacia erubescens* (blue thorn), *Acacia galpinii* (monkey thorn), *Acacia gerrardii* (red thorn), *Acacia karroo* (sweet thorn), *Acacia nigrescens* (knob-thorn), *Acacia nilotica* (scented thorn), *Acacia robusta* (splendid acacia), *Acacia tortilis* (umbrella thorn), *Dichrostachys cinerea* (sickle bush), *Grewia spp.*, *Strychnos madagascariensis* (black monkey orange), *Gardenia volkensii* (savannah gardenia), *Ehretia rigida* (puzzle bush), *Peltophorum africanum* (round-leafed teak), *Diospyros lycoides* (bluebush), *Cussonia paniculata* (mountain cabbage tree).

Grass species common associated with this unit include *Panicum maximum*, *Digitaria eriantha*, *Cynodon dactylon*, *Cenchrus ciliaris*, *Aristida congesta*, *Setaria verticillata*, *Schmidtia pappophoroides*, *Eragrostis rigidior*, *Eragrostis lehmanniana*, *Eragrostis curvula*, *Sporobolus panicoides*, *Sporobolus ioclados*, *Brachiaria deflexa*, *Dactyloctenium aegyptium*, *Diheteropogon amplectens*, *Brachiaria brizantha*, *Heteropogon contortus*.

2.7.5 Wetlands.

The wetlands comprise nearly 2 % of the study area and are characterised by dense grass cover (> 90 %) with no tree cover. The soils are deep, dark and clayey and mottled with oxides. Woody species rarely occur in the wetland areas; however, a few individuals of *Peltophorum africanum* (weeping wattle) and *Terminalia sericea* (silver leaf Terminalia) do occur. Although perhaps a vegetation unit, isolated woody stands associated with termitaria commonly occur in the wetlands. These often-huge termite mounds (mounds sometimes > 2 m high with trees well over 6 m high) host several woody species and include most conspicuously the *Mimusops*

zeyheri (Transvaal red milkwood), *Sprirostachys africana* (tamboti), *Ficus natalensis* (Natal fig), *Carissa bispinosa* (num-num) and *Euphorbia ingens* (candelabra tree).

Common wetland grass species include *Aristida junciformis*, *Acroceras macrum*, *Andropogon appendiculatus*, *Bothriochloa bladhii*, *Brachiaria serrata*, *Cynodon dactylon*, *Digitaria diagonalis*, *Diplachne fusca*, *Echinochloa colona*, *Eragrostis capensis*, *Imperata cylindrical*, *Miscanthus junceus.*
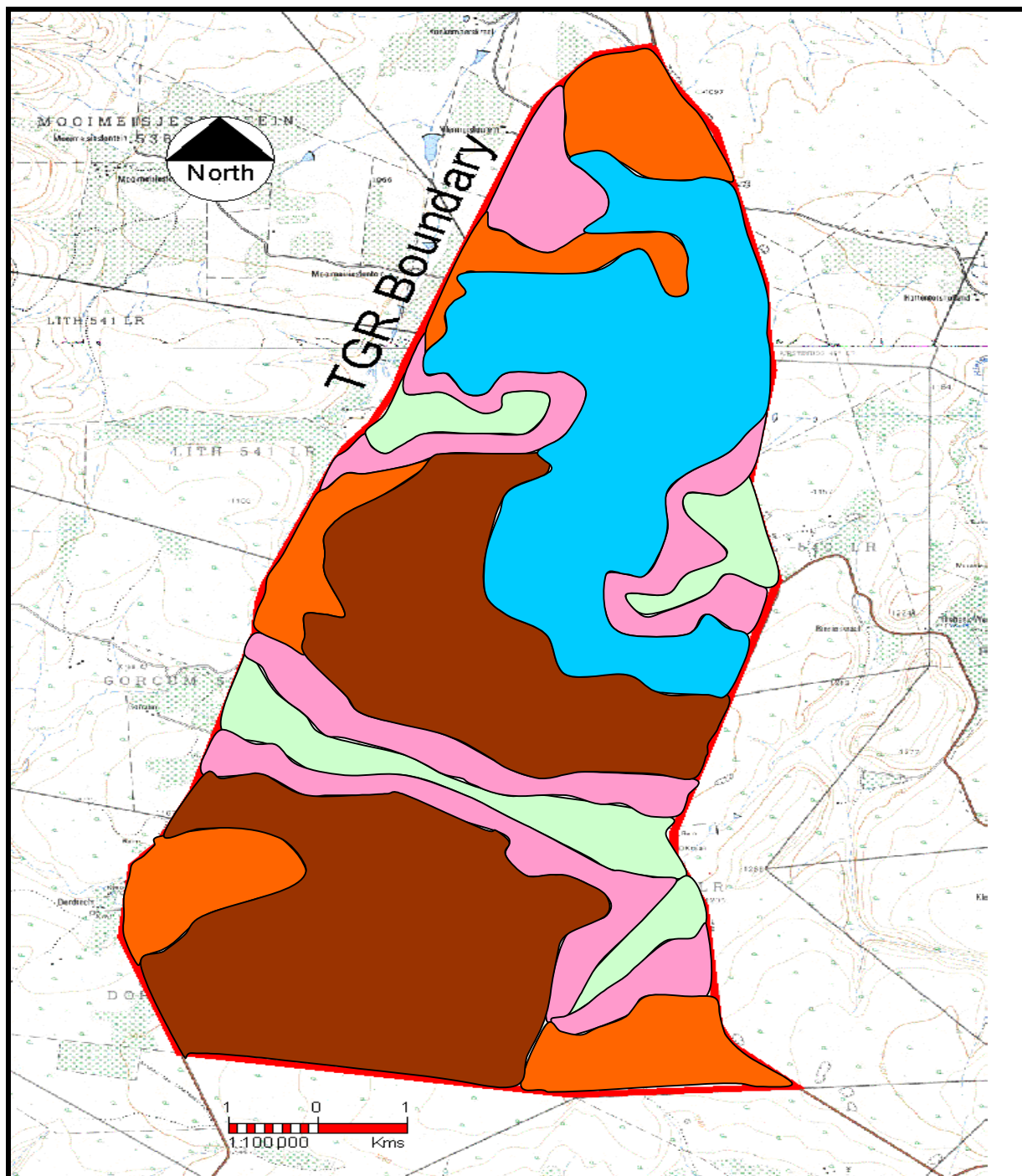
Key to TGR vegetation units.

	Combretum apiculatum/ Burkea africana mixed bushveld
	Combretum zeyheri/ C. molle mixed bushveld
	Sclerocarya birrea/ Acacia woodland
	Terminalia sandveld
	Wetland
———	TGR boundary

Figure 6. TGR vegetation map.

2.8 Land use - Waterberg

The Waterberg has a long history of human occupation and has been inhabited by a succession of people over the past hundreds of thousands of years. If the remains of early Hominids are included, its history spans more than a million years (De Klerk, 2003). Excavations at the Olieboompoort Shelter in the north-western part of the Waterberg have yielded tools, which display a large degree of specialization and skills in stone working and are representative of the Middle Stone Age (Woodhouse, 1987). The people of the Late Stone Age included the San (Bushmen), who were indigenous hunter-gatherers, as well as the KhoiKhoi herders who came from eastern Africa with their sheep, cattle and goats and preferred the wetter coastal areas. Some material remains of the KhoiKhoi may be found on the inland plateau (Palala), since they may even have passed through the Waterberg, where paintings of fat-tailed sheep occur. Within the last two thousand years, however, the San were displaced when the first Iron Age people moved into the area (Van der Ryst, 1996). These people owned cattle and practised subsistence farming on the fertile deep red soils (diabase dyke extrusions) that surface along the river valleys and lineaments.

It was at this time that the Agro-Pastoralists from the lowlands moved into the Waterberg. Auckema (1991) is of the opinion that this move was prompted by the spread of the tsetse fly into the lowveld areas where these farmers had lived for centuries. Their farming in the Waterberg seemed successful and they moved their cattle between patches of sweetveld, eventually causing overgrazing that resulted in encroachment by pioneer thorn bushes. According to Auckema (1991), the Waterberg plateau was also inhabited by another group who were Nguni-speaking and who selected hilltop sites for settlement. The ancestors of the northern Transvaal Ndebele, who now live further to the east, may have built these settlements. Boersema (1996) states these northern Ndebele people have lived in the Mokopane (Potgietersrus) area since approximately 1750.

The remote and inaccessible Waterberg was one of the last regions in the geographical area formally known as the Transvaal (now Limpopo Province) to be permanently occupied by white farmers (Van der Ryst, 1996). Although the first Voortrekker farmers moved into the Waterberg in the 1850s, the region has been increasingly occupied on a regular basis only since the early part of the twentieth century (Van der Ryst, 1996).

2.9 Land use - TGR

In more recent history, prior to 1989, the study area comprised mainly homogenous land-use efforts. Much of the deep-sand, lowland areas were cleared, ploughed and planted with groundnuts, dry land maize, and, in earlier times, tobacco. Areas that could not be cultivated were set aside for animal husbandry in the form of cattle ranching. However, the erratic rainfall, well-leached nutrient-poor soils supporting sour vegetation of a low-carrying capacity and bush encroachment, proved that intensive ranching on relatively small properties was unsustainable. Competition between crop pests and cash-crop farmers also took its toll, forcing many farmers to concentrate entirely on beef production.

With the recent deregulation (mid-1990s) of the beef supply industry from a quota-based system to a free-market system as well as a cut in government farming aid to farmers in the form of subsidies, many beef producers found they were unable to adapt to new marketing procedures and contracts. The local beef market became over-supplied, forcing prices and the producer's profit margin down. During this period of destabilisation, many farmers took to a combination of ranching cattle and game simultaneously. Advantages of game ranching over cattle are numerous. Whilst cattle need to be dipped for parasites at an increasing cost, game animals occur naturally and are generally resistant to parasitic infestations and the associated infections. Game can also be hunted, thus earning additional income through hunting tourism and venison sales.

Game animals can also be bred up to levels where excess animals can be harvested through live capture and sold. Game animals are a great attraction for photographers, thus appealing to yet another set of tourists. Lodges and tourist facilities can be developed to accommodate these tourists, and so the focus on land-use in the area has gradually shifted to a point where every ex-cattle rancher has, at least, some diversification into the wildlife industry.

Since TGR was also previously used for beef and cash-crop production, much time, effort and funds were used to restore the degraded environment. Human activity and agricultural practices had resulted in the veld being trampled and overgrazed. Bush encroachment had reduced the grazing capacity and forage quality. Derelict internal fencing dividing cattle camps, scrap wire and refuse of all description as well as disused buildings and old cattle-handling facilities littered the property. Earth dams had long since silted up and burst their walls. Drinking troughs were in disrepair and the pipelines feeding them leaked at the joints. Borehole pumps were either unserviceable or their machinery outdated. Signs of previous farming hardship abounded.

The restoration/development project started with the upgrade of the external perimeter fence into what was recognised locally as the best electrified game fence in the region. It was originally constructed with the view to containing not only a variety of plains game species, but also elephant, white rhino, and buffalo. Prior to the lion introduction, the perimeter fence was again upgraded and boasted features in accordance with the stringent requirements as set out by the Department for Environmental Affairs and Tourism (DEAT) for the containment of lions. These features included a minimum of 24-strand steel wire 2.4 m high fence, 2.4 m fence-reinforcing droppers spaced at 1.5 m intervals, hanging posts spaced at 50 m intervals with straining posts at every 200 m.

The electrification component comprised five vertically spaced, double offset brackets, each with one earth and one live wire. Offset brackets where installed at 10 m intervals, often closer, to follow the

contour of uneven terrain. An electrified trip wire was attached to ground-driven stays (10 m intervals), 300 mm above ground level and 600 mm inside the fence to deter the lions from crawling or digging their way out underneath the fence. Another DEAT requirement was that the electrical component be operational at all times, meaning that provision for power back up was necessary. To overcome the sometimes-erratic power supply from the state-run utility ESKOM, 12-volt Stafix B18 battery-operated energizers were used. These energisers are capable of powering up to a distance of 15 km and under no-fault conditions produce 8000 v (at termination) with an 18 Joule energy output. Five energiser stations were installed, roughly 12 km apart. ESKOM supplied electricity was used to power battery chargers that kept the batteries fully charged, and in the event of a power failure, the energisers would run on reserve battery power for up to 20 hours. Each station included one energiser, one battery charger, and one 105 aH (ampere hour) deep-cycle battery.

The fence electrification was very effective for containing lions, and whilst the lions often traversed the electrified boundary, they were never seen attempting to pass through it. This lack was probably as a result of the lions' lengthy period of habituation in their release camp where some respect for the electrified fence would have been acquired. Some creatures that did try to pass through the fence were found electrocuted between the earth of the fence and the ground and the electrified trip wire. These animals comprised mostly large leopard tortoises, bushpig, warthog, pangolin, porcupine, and jackal.

All the internal fencing and scrap wire were collected and removed. Old buildings, unsuitable cattle drinking troughs, and handling facilities were levelled and buried. Teams of workers from the rural communities were employed for various bush-clearing projects. Dams were re-excavated and repaired. An extensive road network of some 400 km was developed in anticipation of its use by game drive vehicles. Areas damaged by erosion were ripped up, rock-terraced, seeded and brush-packed. These projects, including the development of several tourist lodges, absorbed a work force of up to 220 people over a period of six years.

2.10 Fauna at TGR

The following mammal species occurred at TGR (the * symbol denotes rare species, [1] denotes species introduced during development):

Order Primata

Chacma baboon (*Papio ursinus*)

Vervet monkey (*Cercopithecus aethiops*)

Order Lagomorha

Scrub hare (*Lepus saxatilis*)

Jameson's red rock rabbit* (*Pronolagus randensis*)

Order Rodentia

Cape porcupine (*Hystrix africaeaustralis*)

Springhare (*Pedetes capensis*)

Woodland dormouse (*Graphiurus murinus*)

Tree squirrel (*Paraxerus cepapi*)

Greater canerat (*Thryonomys swinderianus*)

Order Pholidota

Pangolin* (*Manis temminckii*)- perhaps locally extinct

Order Tubilendata

Aardvark (*Orycteropus afer*)

Order Carnivora

African wild dog* (*Lycaon pictus*) - vagrant

Black-backed jackal (*Canis mesomelas*)

Cape clawless otter* (*Ursus arctos*) - vagrant

Honey badger* (*Mellivora capensis*)

Striped polecat* (*Ictonyx striatus*)

Genet, large spotted (*Genetta tigrina*)

Genet, small spotted (*Genetta genetta*)

Mongoose, banded (*Mungos mungo*)

Mongoose, dwarf (*Helogale parvula*)

Mongoose, slender (*Galerella sanguinea*)

Mongoose, white-tailed* (*Ichneumia albicauda*)

Mongoose, Selous' (*Paracynictis selousi*)

Mongoose, yellow (*Cynictis, penicillata*)

Cheetah* (*Acinonyx jubatus*) - vagrant

Caracal (*Felis caracal*)

Serval* (*Felis serval*)

African wildcat (*Felis lybica*)

Leopard (*Panthera pardus*)

Lion (*Panthera leo*) [1]

Hyaena, brown* (*Hyaena brunnea*)

Aardwolf* (*Proteles cristatus*)

Fox, bat-eared* (*Otocyon megalotis*)

Order Proboscidia

African elephant (*Loxodonta africana*) [1]

Order Perissodactyla

Zebra, Burchell's (*Equus burchellii*) [1]

Rhinoceros, white (*Ceratotherium simum*) [1]

Order Artiodactyla

Hippopotamus* (*Hippopotamus amphibious*) [1] – locally extinct

Bushpig* (*Potamochoerus porcus*)

Warthog (*Phacochoerus aethiopicus*)

Giraffe (*Giraffa cameloparadalis*) [1]

Wildebeest, blue (*Connochaetes taurinus*) [1]

Hartebeest, red (*Alcelaphus buselaphus*) [1]

Blesbok (*Damaliscus dorcas phillipsi*) [1] – locally extinct

Tsessebe (*Damaliscus lunatus*) [1] – locally extinct

Duiker, common (*Sylvicapra grimmia*)

Klipspringer* (*Oreotragus oreotragus*)

Steenbok (*Raphicerus campestris*)

Sharpe's grysbok* (*Raphicerus sharpie*)

Impala (*Aepyceros melampus*) [1]

Reedbuck, mountain* (*Redunca fulvorufula*) [1]

Reedbuck, common (*Redunca arundinum*) [1] – locally extinct

Roan (*Hippotragus equines*) [1] – locally extinct

Sable (*Hippotragus niger*) [1] – locally extinct

Gemsbok (*Oryx gazella*) [1] – locally extinct

Buffalo (*Syncerus caffer*) [1]

Kudu (*Tragelaphus strepsiceros*) [1]

Nyala (*Tragelaphus angasii*) [1]

Bushbuck* (*Tragelaphus scriptus*)

Eland (*Taurotragus oryx*) [1]

Waterbuck (*Kobus ellipsiprymnus*) [1]

Three hundred and four bird species were recorded as sighted on TGR. Some of the common raptor species include Gymnogene (*Polyboroides typus*), Brown snake eagle (*Circaetus cinereus*), Blackbreasted snake eagle (*Circaetus gallicus*), Steppe eagle (*Aquila nipalensis*), Black eagle (*Aquila verreauxii*) and Wahlberg's eagle (*Aquila wahlbergi*). Vultures did occur but were infrequently sighted and included Lappetfaced vulture (*Torgos tracheliotus*) and Whitebacked vulture (*Gyps africanus*).

Other woodland bird species include members from the following families: herons (*Ardeidae*), grebes (*Podicipedidae*), hammerkop (*Scopidae*), storks (*Ciconiidae*), ibises (*Plataleidae*), ducks and geese (*Anatidae*), buzzards (*Accipitridae*), francolins quails and buttonquails (*Phasianidae*), bustards (*Otididae*), dikkops (*Burhinidae*), coursers (*Glareolidae*), sandgrouse (*Pteroclididae*), pigeons and doves (*Columbidae*), cuckoos and coucals (*Cuculidae*), owls (*Tytonidae* and *Strgidae*), nightjars (*Caprimulgidae*), swifts (*Apodidae*), kingfishers (*Halcyonidae*), bee-eaters (*Meropidae*), rollers (*Coraciidae*), woodhoopoes and hoopoes (*Phoeniculidae*), hornbills (*Bucerotidae*), barbets (*Capitonidae*), honeyguides (*Indicatoridae*), woodpeckers (*Picidae*), larks (*Alaudidae*), swallows (*Hirundinidae*), cockooshrikes (*Campephagidae*), drongos (*Dicrurudae*), orioles (*Oriolidae*), tits (*Paridae*), babblers (*Timaliidae*), bulbuls (*Pycnonotidae*), thrushes (*Turdidae*), warblers (*Sylviidae*), flycatchers (*Muscicapidae*), wagtails and pipits (*Motacillidae*), shrikes bushshrikes and helmetshrikes (*Laniidae*, *Malaconontidae* and *Prionopidae*), starlings (*Sturnidae*), oxpeckers (*Buphagidae*), sunbirds (*Nectariniidae*), white-eyes (*Zosteropidae*), weavers (*Ploceidae*), waxbills (*Estrildidae*), whydahs (*Viduidae*), finches canaries and buntings (*Fringillidae*).

Snakes are common, including the highly venomous black mamba (*Dendroaspis polyleps*), Mozambique spitting cobra (*Naja mossambica*), Egyptian cobra (*Naja haje*), boomslang (*Dispholidus typus*), twig snake (*Thelotornis capensis*), sand snakes as well as many other asp, skink and lizard families, including the memorable giant-plated lizard *Gerrhosaurus validus*.

During the developmental period, numerous game species populations were introduced. In addition to the later introduction of lion, other large predators, such as brown hyena and leopard, occurred naturally on TGR. Cheetah and wild dog were sighted infrequently and are considered rare vagrants. Although some small game occurred naturally in the study area, much game was introduced in the formative years including herds of kudu, zebra, blue wildebeest, red hartebeest, nyala, giraffe, eland, hippo, elephant, white rhino and buffalo. Roan antelope, sable and gemsbuck were also introduced, albeit unsuccessfully, due possibly to unrefined game capture and relocation techniques or, in some cases, the habitat simply did not suit the species. The latter probably having an impact on gemsbok, roan, sable and tsessebe.

Although the conservation-style land use for TGR remained a priority since inception, management has sought and experimented with various options to optimise income in this relatively new concept of game farming. The recipe to achieve a satisfactory income included a combination of game- and nature-related activities that have shifted in focus since 1989 and include in order of priority 1.) Passive photographic tourism together with income generated from lodge accommodation, game drives/nature walks, and the exploitation of restaurant and bar facilities; 2.) The breeding and live sale of surplus valuable and plains game species; 3.) Trophy hunting and catering for the international adventure tourist.

The mid-1990s, however, saw a boom in the tourism-related game ranching industry. This boom, perceived as a generous income potential from the hospitality trade, saw many cattle ranchers converting to game until almost every second farm in the Waterberg had something to do with tourism. Larger farms, however, require a better-developed infrastructure. Consequently, as more maintenance and, of course, the need for more experienced staff and expenditure increased, so too did the need to earn additional income. These factors resulted in a shift in the income-generating priorities. Game capture on TGR became more frequent as did trophy hunting. The lodge operations continued offering various promotions and cut-rates to attract a broader market.

While selective trophy hunting is sustainable, large-scale game capture is not, and in late 1999, the decision to introduce lion (which had not occurred naturally in the area within recent history) was taken. TGR could now be marketed as a Big Five game reserve; something that could only be claimed by various establishments far to the east in the Mpumalanga lowveld.

The rationale behind the decision was based on the premise that the lions' presence would attract more local and, especially, foreign visitors. Since TGR is situated as a three-hour drive from the Gauteng metropolis, their introduction would succeed in improving tourism income. Once again, tourism-based revenue was prioritised, while trophy hunting continued and game capture ceased.

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CHAPTER 3

METHODOLOGY

3.1 Study lions

Three lions from Thornybush Game Reserve (Mpumalanga lowveld, South Africa) were introduced to a release camp facility on TGR in March 2001. They were released ten weeks later, after a period of habituation, into the 7 000 ha study area. The original capture lion plan called for four lions (two male and two female) to be immobilised. A pride of eleven lions were lured to bait at night, where three were successfully darted with the immobilising drug Zoletil® at a dosage rate of 5,0 mg/kg. The anaesthetic was administered from 5 ml Pneu-darts® fired from a CO_2 – charged dart gun at a distance of roughly 20 m, made accurate with a night vision scope and infrared locater bead. Effects of the drug were visible within several minutes with full immobilisation taking effect within twelve minutes. With the safety of the drugged lions a priority and to avoid the harassment of these lions by other pride members, the decision was taken to recover the darted lions and immobilize a second male lion at a later stage. Further capture was, however, abandoned.

The group comprised one sub-adult male (2 ½ years) and two adult females. Initially, one female was contracepted, while the second was allowed to breed. Both females were, thereafter, contracepted (one lioness for the second time) after the first litter of three cubs (one male: two females) were born in September 2002. All six lions survived throughout the study period.

3.2 Lion data collection

Prior to release, the male and one female were radio-collared. The lions were located primarily by using radio telemetry (Telonix ProTrack 150 MHz receiver). Other traditional methods for location were used when telemetry proved unreliable and included tracking on foot (following spoor), presence of vultures (or other scavengers) and vocalization (roaring). Although the receiver had a line-of-sight signal detection capability of approximately 5 km, the mountainous terrain often restricted its effectiveness. After trial and error, the researcher found it simpler to travel to the highest point on the reserve (1 310 m) and begin telemetric tracking from there. If no signal were audible, the researcher would zigzag the lower lying areas starting from north moving southwards. It would sometimes happen that the equipment was found to be faulty; the culprit usually being the connecting co-axial cable between the antenna and the receiver meaning that several spare cables had to be carried in the event of failure. When the equipment was faulty and no signal could be found, cables were changed and the process of finding the lions was re-started.

Whenever possible, the lions were located up to three times per day. Early morning locations (between 6 am and 8 am) were generally the most effective for discovering fresh kills. Late afternoon locations showed their typical resting habits, while late night locations (after 10 pm) often found the lions hunting. Direct observations amounted to 2 200 hours averaging over two hours per day. Many more hours were spent attempting to locate them. Once located, the field guides would arrive with their guests after which they would report their additional observations. Apart from general behaviour, the lions were observed for any obvious signs that a kill had been made, e.g. the presence of a carcass, engorged bellies or bloodstains, in which case attempts would be made to locate the prey.

Because of the often-difficult terrain and vehicle inaccessibility, perhaps as many as 40 % of telemetric findings did not yield a sighting. Due to the dangers involved (lions are known to charge if surprised or

harassed) tracking on foot was not always the most intelligent option. If it happened that the lions were signalled to be in approximately the same location consecutively, it was probable that a kill had been made. The researcher would venture on foot into the area once the lions had departed. Often though, the researcher found kill sites but no carcass material remained as he had been beaten to the scene by scavengers. Similarly, the researcher was of the opinion that an indeterminable number of small-sized prey (calves, small antelope, etc.) were killed but could be recorded because of a lack of data. On numerous instances, it was obvious to see that a kill had been made, but the prey had probably been ingested in a few mouthfuls leaving no evidence of a kill site.

3.3 Distance moved and interval between kills

The average daily distance walked by the lions between observations was measured as a straight line, and expressed as a mean km/day traversed. Within months after release, the lions seemed to settle into a predictable destination routine using well-developed game trails established mainly by the elephants and rhinos. This pattern of movement included water points, areas of dense cover as well as areas high elevation where they would sometimes lie-up for the day. The researcher used a Garmin Global Positioning System (GPS), *E*Trex Vista hand-held device to co-ordinate daily sightings that calculated the distances traversed between sightings.

 The researcher used the one-way ANOVA to test significance for the difference in the annual distances traversed during the study period. The inter-kill period was calculated by dividing the number of days by the number of kills for each year, expressed as a kill frequency, i.e. 1 kill: x days. The Chi-square test (SPSS) was used to test for significance in the difference of the number of kills per year. The inverse of this value provides an estimate of kill rate (i.e., the number of days between each kill).

3.4 Prey availability and demography

Game founder populations were established on TGR between 1989 and 1994 and have since been monitored for growth rate and population age and sex structure. Aerial censuses (ten in total since 1989, two of which were conducted during the study period) were used to determine the year-on-year population growth, which is the difference from successive counts represented as a percentage, as well relative species composition. This method of counting game has several shortcomings; therefore, the data described in this study should be seen as illustrative rather than conclusive and can only indicate potential trends.

Typical pitfalls of this method include 1.) Time of year: counts are only effective with minimal (or no) canopy cover, 2.) Repeatability: where possible, the same experienced air and counting/recording crew should be used for consecutive surveys, 3.) Air speed, altitude, strip width and counting area need to be consistent, 4.) Countability of game: the use of correction factors for post-count game numbers must be consistent, or avoided altogether depending on the crew's level of expertise. It is extremely difficult to obtain accurate figures on the size of any game population (Bothma, 1996). Unfortunately, no alternative feasible method exists for counting game populations on properties of this size.

During the same period, ground counts were used to sample the male: female and sub-adult: adult cohorts. From these counts, prey availability and prey population structure were determined as well as relative ungulate density expressed as LAU per ha, prior to lion introduction.

3.5 Biomass consumption

The mass of each prey carcass (Bothma 1996) was estimated to calculate the biomass consumption and pooled into total and edible biomass after Viljoen (1993). These aspects are described fully in the Results section under the heading Biomass Consumption below. The total biomass consumption was divided by the number of lions present to give biomass consumption per lion and divided again by 365 (number of days in the year) for the daily consumption rate.

3.6 Prey species selection

Each prey carcass was classified according to species, sex and age, i.e. sub-adult or adult (see Prey species selection under the Results section below for assessment criteria). Old animal carcasses were identified by either horn or teeth wear. Ivlev's Electivity Index method (Krebs, 1989) was used to assess whether species were killed randomly, selected or avoided in proportion to their availability. Selection was calculated using the formula:

$$\mathbf{I = \frac{(\% \ U - \%A)}{(\%U + \%A)}}$$

Where **I** = Index;
       U = Percentage utilized
       A = Percentage available

A result which is near + or − 0 (zero) is considered random. A result closer to +1 indicates selected. A result closer to −1 indicates that the species is avoided as prey.

3.7 Seasonal influences

All kill data was divided into the summer or winter seasons in which they occurred. The summer season includes all kills recorded from September through February, and the winter season includes those kills recorded from March through August. The summer season assumes the inclusion of spring, and winter includes autumn - a total of six months in each period. Kills were represented as a percentage of total prey species population.

3.8 Habitat influences

A 1:50 000 map of the study area was divided into equal blocks of 20 ha each and numbered from 1 to 350. Each kill was referenced according to block number, which was then referenced to the vegetation unit type in which the kill had occurred. Each kill site was given a GPS co-ordinate using the *E*Trex Vista device and referenced to a digitised topographical map (supplied by The Chief Directorate – Surveys and Mapping, map numbers 2328 CB and 2338 CD) using MapMaker® software.

Again, Ivlev's Electivity Index was used to test whether the lions preferred specific habitats in which to hunt or if kills occurred randomly irrespective of the habitat type.

3.9 Financial model

Few wildlife managers, in a South African private reserve context, would manage wildlife unless there was some financial reward to be gained. The critical question, therefore, for would-be lion-owners is: Can lions pay for themselves? To answer this question, the researcher developed a formula, which after pooling all the financial events associated with the lions, can be used to determine the cost per lion per year based on the expenses experienced at TGR. The formula is as follows:

$$\mathbf{R_{pa} = [(N_i * C_v) + (N_{rpa} * C_v)]}$$

Where:

$\mathbf{R_{pa}}$ = Rands cost per annum.

$\mathbf{N_{rpa}}$ = Natural lion growth rate per annum (calculated as a percentage but expressed as a number e.g. 30% = 0.3).

$\mathbf{N_i}$ = Number of lions introduced.

$\mathbf{C_v}$ = Cost variable. This is a summary of the actual cost (per lion), calculated by adding the different costs (e.g. a = fencing, b = value of game lost, c = monitoring etc) then dividing this result by the number of lion for that year i.e.

$$C_v = \frac{(a + b + c + \ldots\ldots)}{N_L}$$

Although these costs were calculated as a cost variable for TGR, they may not be a variable for other introductions; inflation needs to factored into the equation and, almost certainly, each introduction will have different (although similar) costs. This cost experienced by TGR is dealt with in more detail in the Results section below.

Using the formula result on the cost of maintaining lions, the researcher modelled an income scenario based specifically on TGR's potential to earn revenue and compared this income to the expenses that the lions had incurred. For the income model, it was possible to calculate what occupancy rate (i.e. the number of guests required to stay at the tourist lodge) was needed to recover the lions to break-even point. For further comparison, the researcher calculated what the occupancy rate should be to recover (again to break–even point) the entire ranching operation, including the lions cost as well as the overall cost for maintaining the operation's components.

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CHAPTER 4

RESULTS

4.1 Distance traversed and intervals between kills

In year 1, the lions traversed a mean of 2.3 km per day (+/- 2.49) calculated from 278 sightings. In year 2, the mean distance calculated from 275 sightings was 2.6 km per day (+/- 2.5) and 3.1 km per day (+/- 2.54) in year 3 after 289 sightings. The researcher used the one-way ANOVA statistic (SPSS) to test if there were significant differences in the distances traversed year-on-year, and if so, which year specifically was more significant compared to the others, resulting in $F_{2, 33} = 60.489$, P<0.001. The *post-hoc* Tukey H+/- test showed that all three years' distances differed significantly from one another. The difference in the distance traversed for year 3 differed most significantly from year 1, with the least significant difference being year 2 compared with year 1.

There was a total of 452 recorded kills in three years. The kills per year were: 142, 158 and 152 for 2001, 2002 and 2003 respectively at a mean kill rate of 1 kill: 2.47 days (+/- 0.13) or 0.411 kills per day^{-1}. Alternatively, the kill rate was summarised as 1:2.57 days (2001/2), 1:2.31 days (2002/3) and 1 kill: 2.42 days for 2003/4. There was no significant difference in the number of kills per year during the study period: (Chi-square) $x^2 = 0.867$, P= 0.648 df=2.

4.2 Prey availability and demography

Eleven ungulate species were identified as being targeted as prey, namely bushpig (*Potamochoerus porcus*), eland (*Taurotragus oryx*), red hartebeest (*Alcelaphus buselaphus*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), warthog (*Phacochoerus aethiopicus*), waterbuck (*Kobus ellipsiprymnus*), blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus burchellii*) and although ostrich (*Struthio camelus*) is not an ungulate, the species was represented by several kills.

Game census techniques have been discussed in detail under Methods above and were included to highlight possible shortcomings in game data collection. No game census data is entirely accurate (unless for known numbers); therefore, comparative results based on game numbers should be assumed as illustrative rather than conclusive. Count data for three species in particular, warthog, bushpig and nyala, are and will always be questionable. Warthog and bushpig, for example, are not usually counted during aerial censuses because of their poor countability. Nyala, however, are counted, but due to their skulking habits in dense vegetation, their numbers cannot be accurately recorded and are generally underestimated.

See Table 2 below for ungulate population numbers on TGR from 1995 to 2004.

Table 2. Ungulate population numbers on TGR from 1995 to 2004.

SPECIES	1995/6	1996/7	1997/8	1998/9	1999/2000	2000/1	2001/2	2002/3	2003/4
Bushpig	14	14	14	14	14	14	40	9	4
Eland	30	35	39	47	75	100	126	84	97
Hartebeest	59	63	69	71	80	74	98	133	140
Impala	103	149	171	223	254	482	607	413	460
Kudu	64	85	109	130	241	305	319	285	305
Nyala	6	17	23	23	39	24	32	47	38
Ostrich	16	21	30	48	23	24	16	8	5
Warthog	63	76	85	93	179	145	143	191	215
Waterbuck	16	32	59	120	94	90	79	76	67
Wildebeest	135	148	143	146	298	341	438	254	280
Zebra	52	62	68	85	208	228	271	169	188
TOTAL	**693**	**848**	**966**	**1172**	**1694**	**1974**	**2169**	**1669**	**1799**

Prior to 2001, TGR managed its game population numbers using live mass capture. The lions were introduced in early 2001 (see vertical red arrow, Figures 7 to 16 below), after which no further ungulates were harvested. During the five-year period prior to introduction, the overall mean growth rate was 30.9 % (+/- 17.3 %). Although the decline in numbers of some species e.g. eland, impala, kudu, wildebeest and zebra can be attributed to the game capture of 2001, the overall population growth rate during the three-year study period was markedly slower than the previous five–year period with the mean annual growth rate being –0.8 % (+/-3 %). See figures 7 through 16 below for the individual population growth rates. No accurate growth rate data exists for bushpig; they were, therefore, excluded from this section. Aerial censuses were conducted in 2001 and 2003 with the value for 2002 calculated as an estimate based on ground count data using individual/ herd recognition. Although the count data for 2002/3 showed some sharp falls compared with 2001/2002, the aerial census for 2003/4 reversed these declines to show a modest gain in population numbers.

Figure 7. Eland population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), eland experienced a population growth of 27.9 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was −6.8 % although count data from the 2003 census indicated that the population was increasing. The average growth rate since 1995 was 10.5 %.

Figure 8. Hartebeest population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), red hartebeest experienced a population growth of 9.5 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was 14.28 %. The average growth rate since 1995 was 11.8 %.
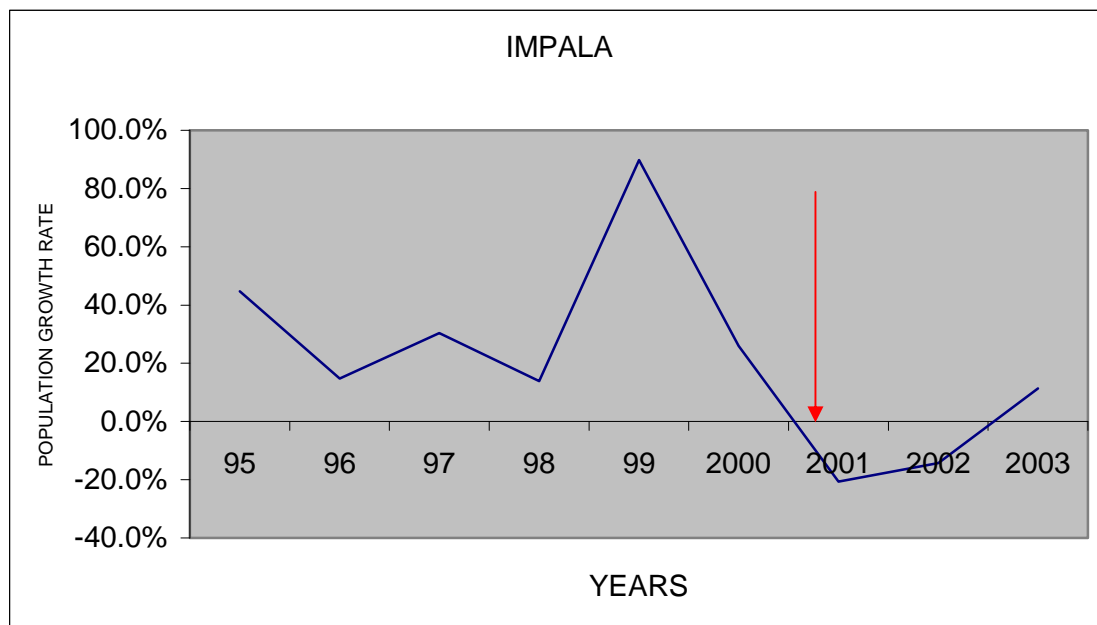
Figure 9. Impala population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), impala experienced a population growth of 36.6 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was -7.8 %. The average growth rate since 1995 was 14.8 %.
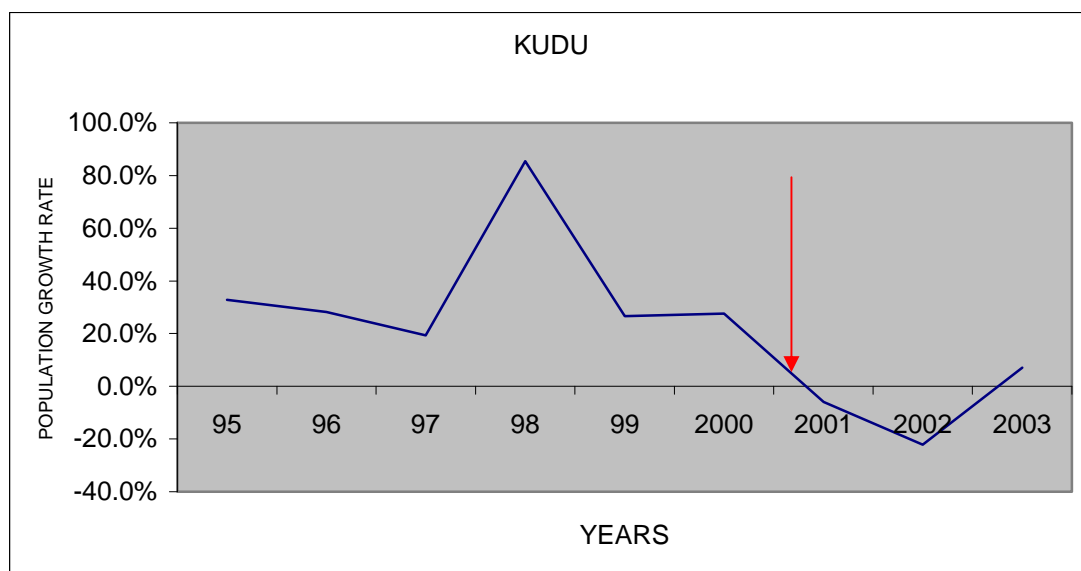
 Figure 10. Kudu population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), kudu experienced a population growth of 36.6 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was -7.0 %. The average growth rate since 1995 was 14.8 %.
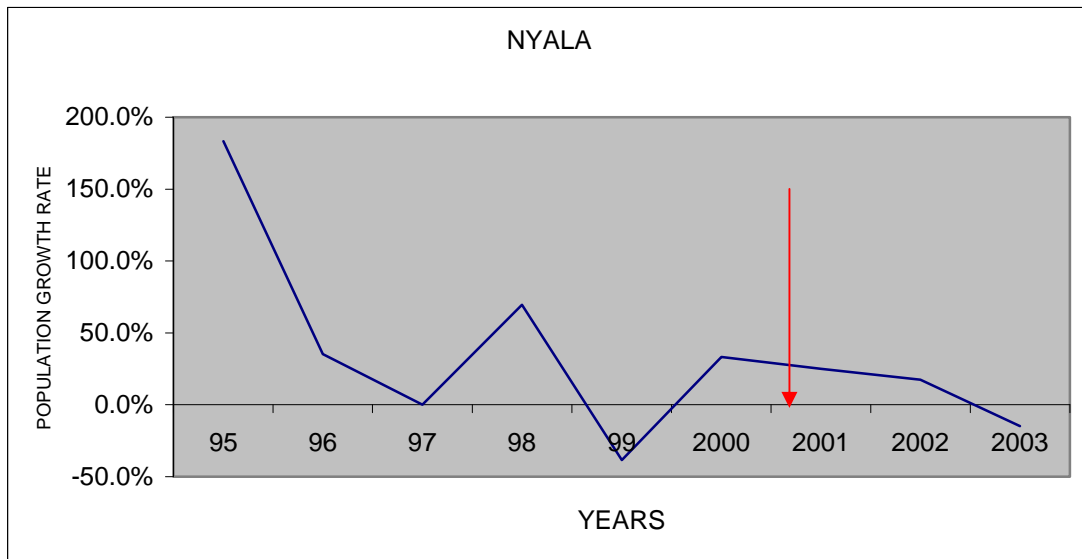
Figure 11. Nyala population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), nyala experienced a population growth of 47.2 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was 9.2 %. The average growth rate since 1995 was 28.2 %.
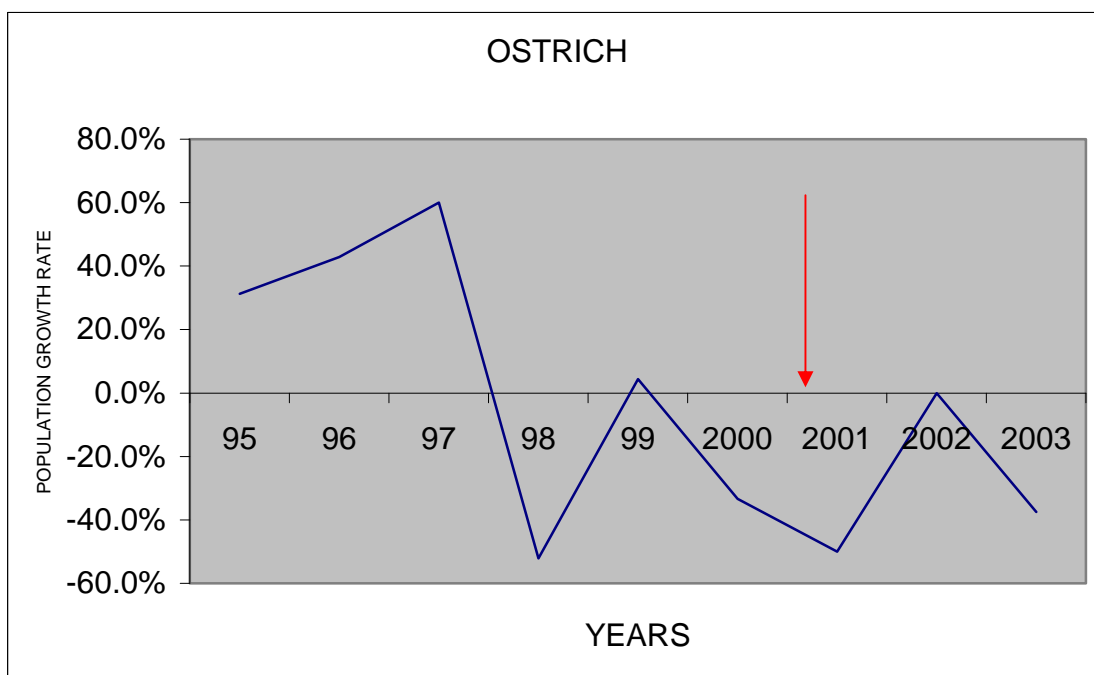
Figure 12. Ostrich population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), ostrich experienced a population growth of 8.8 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was –29.2 %. The average growth rate since 1995 was –10.2 %.
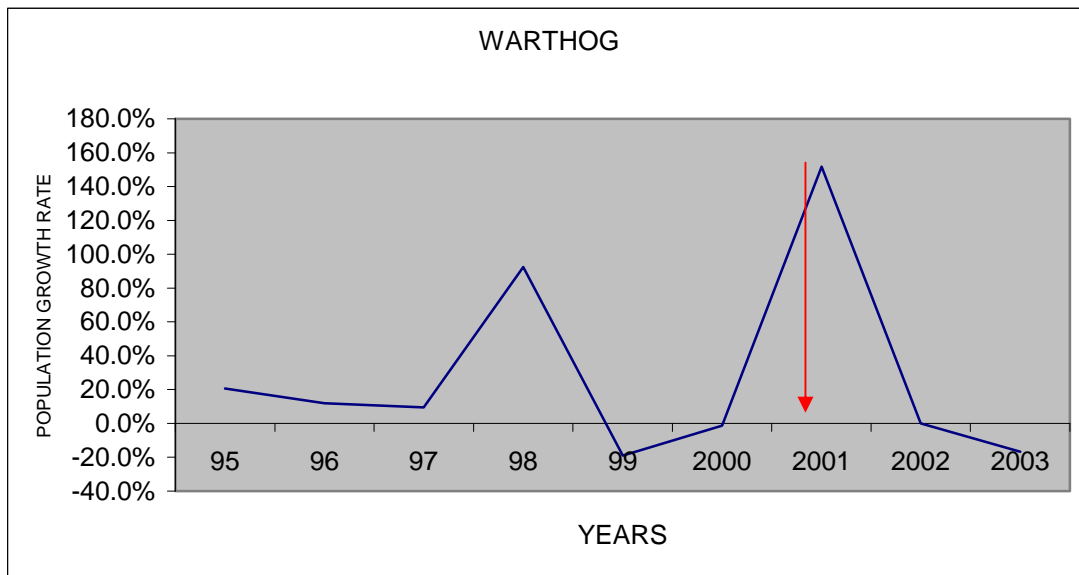
Figure 13. Warthog population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), warthog experienced a population growth of 19 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was 45 %. The average growth rate since 1995 was 32 %.
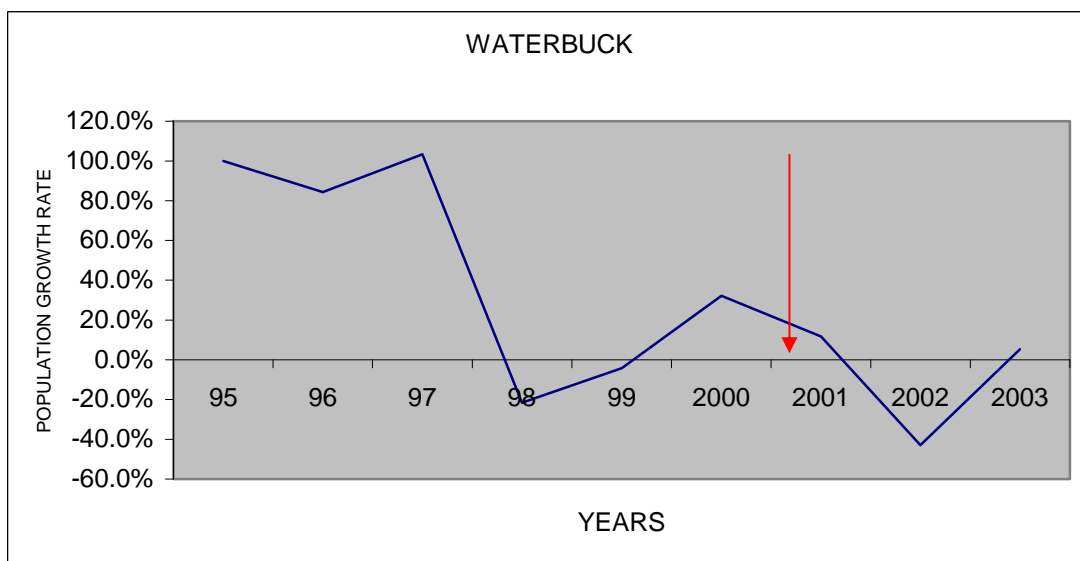
Figure 14. Waterbuck population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), waterbuck experienced a population growth of 49 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was –8.6 %. The average growth rate since 1995 was 20.2 %.
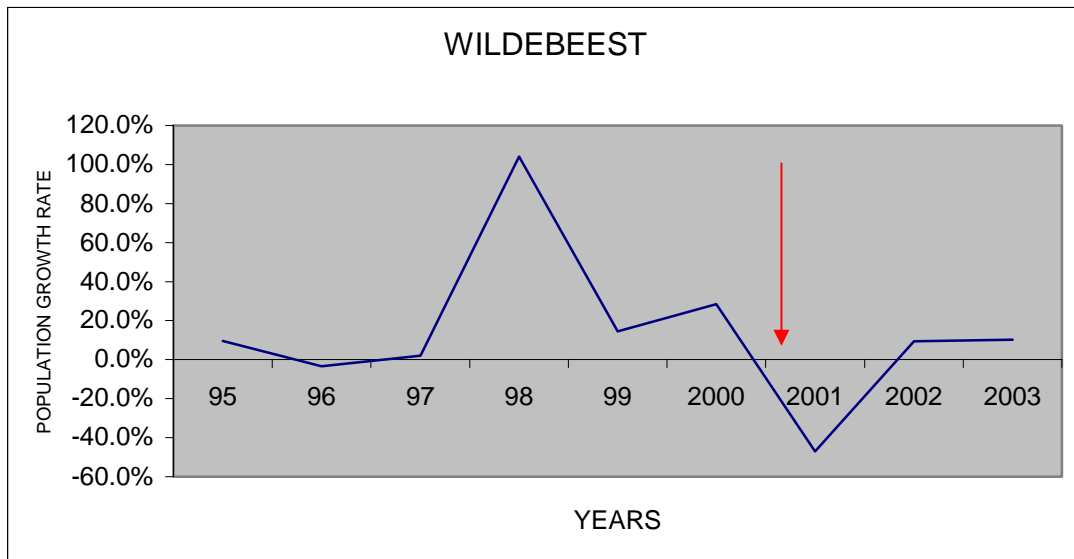
Figure 15. Wildebeest population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), wildebeest experienced a population growth of 25.9 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was −9.1 %. The average growth rate since 1995 was 8.4 %.
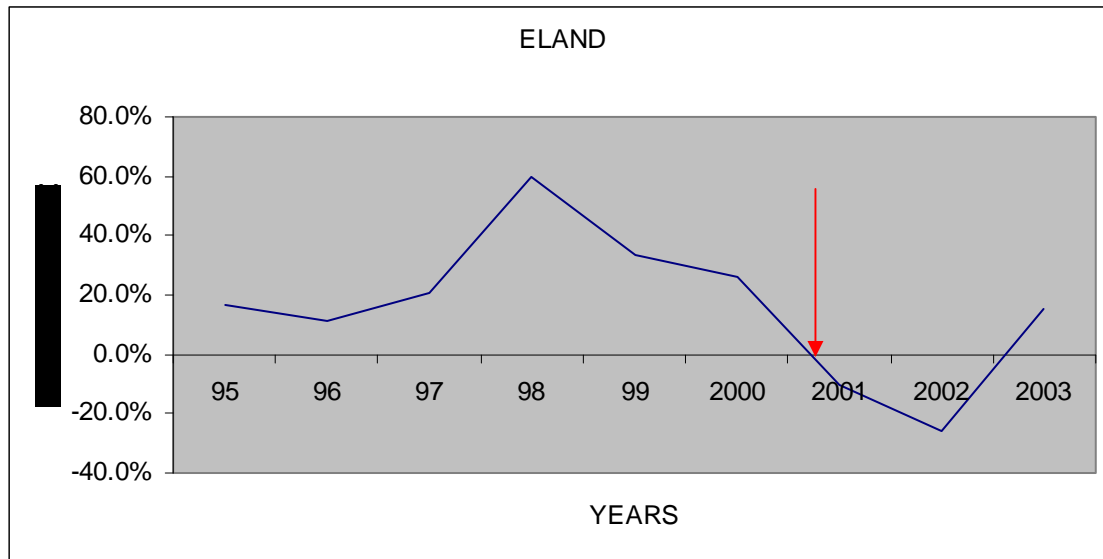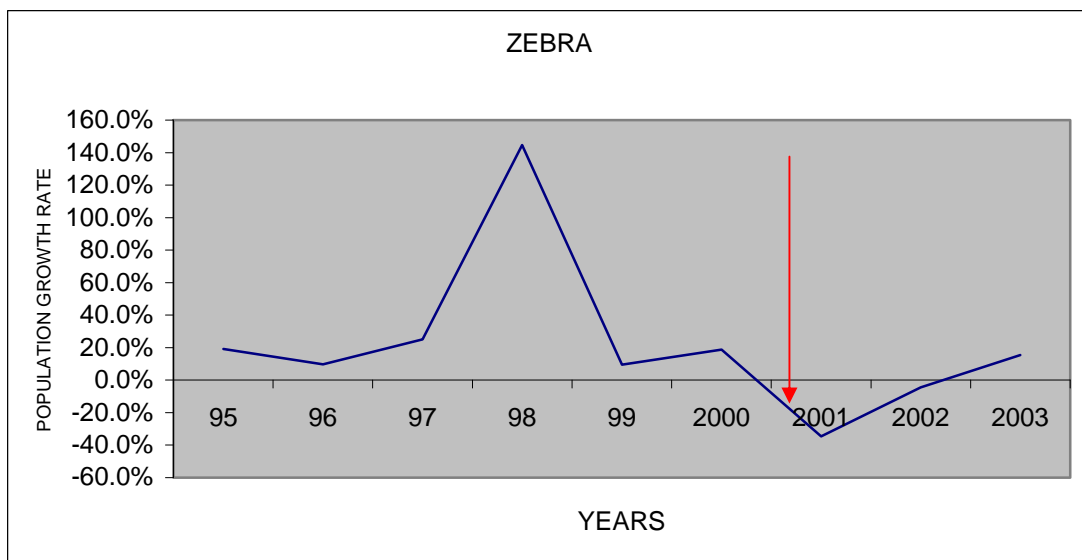

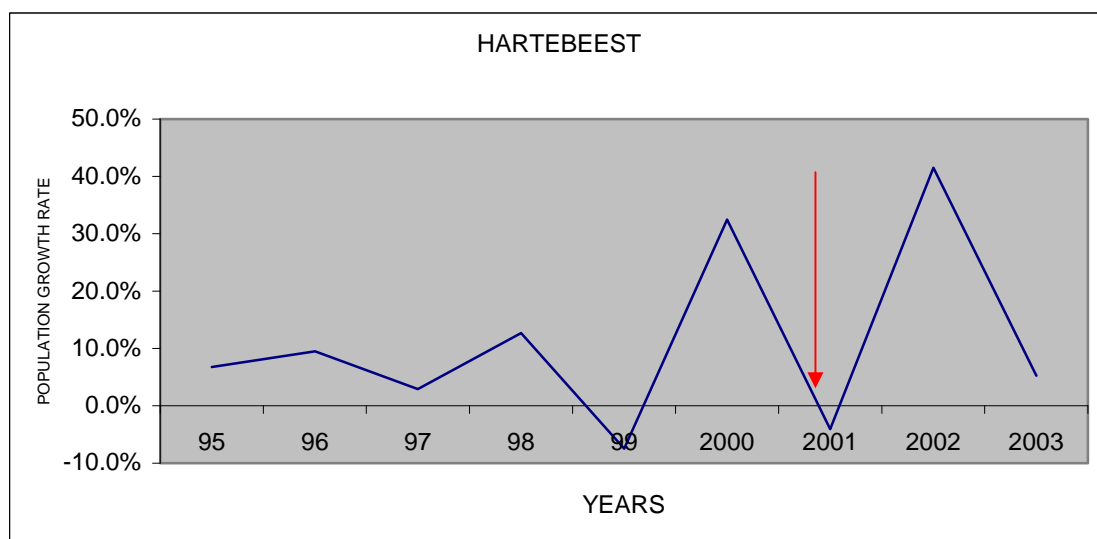**Figure 16.** Zebra population growth from 1995 to 2004.

Between 1995 and 2000 (inclusive), zebra experienced a population growth of 37.8 %. For the period of 2001 to end 2003, since lion introduction, the growth rate was 25.2 %. The average growth rate since 1995 was 31.5 %.

According to the aerial census data, the population growth trends for eland, impala, kudu, waterbuck and zebra all showed a marked decline from 2001 but began to recover thereafter. After a similar decline in 2001, wildebeest growth remained constant from 2002 onwards. Although erratic, hartebeest growth experienced a sharp decline from 2002 to 2003. Nyala and ostrich showed a constant decline during the same period. The warthog population crashed after 2001 and still showed a decline in growth after 2003.

The population age structure varied insignificantly during the study period, Chi-square: χ^2=0.802, P=0.976 df=5. Ground-based sample censuses for the periods showed that; in 2001/2002, adults accounted for 63.4 % of the population and sub-adults 36.6 %. In 2002/2003, adults accounted for 68.7 % and sub-adults 31.3 %. In 2003/2004, adult numbers increased to 74.5 % and sub-adults decreased to 25.5 %. Unlike the population age structure, the sex structure experienced significant change in the sex ratio i.e. males to females, Chi-square: χ^2=556.31, P<0.0001 df=5 meaning that more males than females were likely to be selected as prey.

4.3 Prey availability and Demography – the Lau aspect

The game ranching industry assesses animal density in terms of 1 unit (i.e. large animal unit - LAU) per x hectares. As part of the management plan of wildlife areas, managers must calculate the ecological carrying capacity (k) of the area which provides a guideline as to how many LAU's can be accommodated without negatively impacting on the habitat's ecological viability. The wildlife area would be considered balanced with k being utilized to its optimum potential. The converse applies when the area is either over- or under–stocked, where over time, the habitat ecology modifies itself to the detriment of the species that live in it. Although not a perfect science, this optimal level is generally accepted by the industry as being between 50 % and 70 % of k taking into account the

often-extreme variations in the amount of rainfall experienced. The introduction of large predators, such as lion onto small reserves, could understandably cause a change to the amount of standing LAU's and, *inter alia,* the ecology of the area, thereby highlighting the importance of both monitoring and managing predator - prey relationships.

However, no significant change was experienced in LAU density before introduction (2000) and at the end of the study in 2004 that is, x^2 = 0.0984, P ≥ 1 df = 1. For the year ending 2000, the 11 common prey species amounted to 821 LAU equivalents or a prey species density of 1LAU: 9.6 ha. The LAU density was higher for 2001, i.e. 1LAU: 7.64 ha (870), but had been reduced after mass capture (2001), declining to 1LAU: 9.5 ha in 2002 (642) and further to 1LAU: 10.5 ha ending 2003 (694), with perhaps a more acceptable level, albeit as a result of the lion introduction.

Table 3. Little or no significant change in the relative LAU's contribution occurred for the period preceding lion introduction up until the end of the study period.

SPECIES	Relative LAU contribution before i.e. 2000	Relative LAU contribution after i.e. 2004
Bushpig	0.4%	0.1%
Eland	10.8%	12.6%
Hartebeest	6.4%	10.1%
Impala	6.5%	10.6%
Kudu	15.5%	17.6%
Nyala	1.6%	1.4%
Ostrich	0.9%	0.2%
Warthog	3.7%	4.0%
Waterbuck	6.8%	4.3%
Wildebeest	23.9%	20.2%
Zebra	23.4%	18.9%
TOTAL	**100.0%**	**100.0%**

The ecological carrying capacity for TGR was assumed to remain constant at 1LAU: 10 ha. See figure 17 below for the variation in stocking density in relation to carrying capacity over time. The red vertical arrow indicates the lion introduction during 2001.
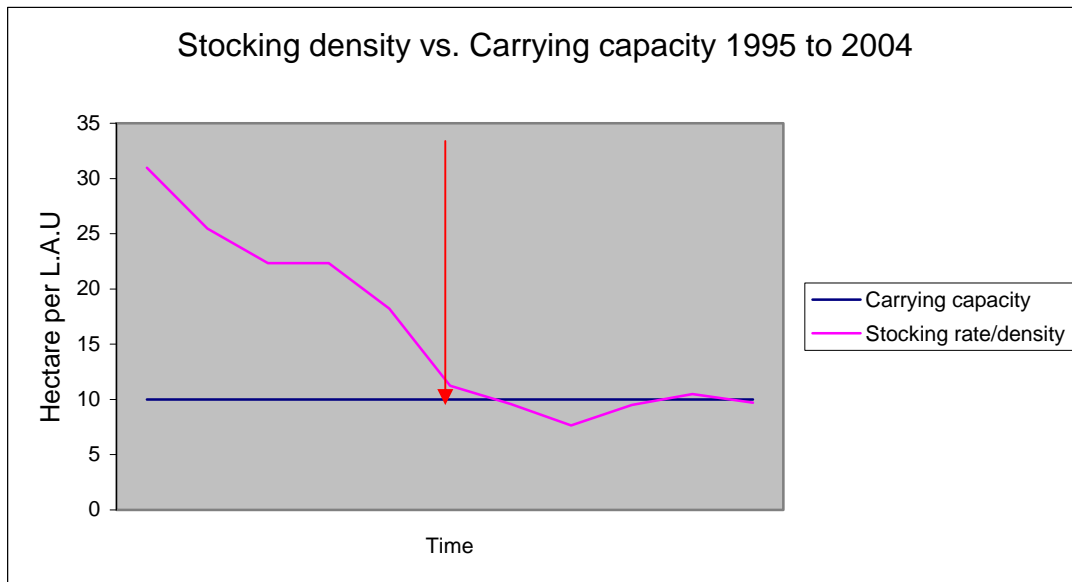
Figure 17. The carrying capacity is estimated at 1LAU: 10 ha. The stocking rate/density remained relatively constant since the lion introduction in 2001.

According to the aerial census count data, there was an overall decline in prey species numbers when comparing before (i.e. 2000) and after (i.e. 2004) figures, those marked with (*) being the most significant. Although there was some increase in population numbers for red hartebeest, nyala and warthog, these increases (particularly with regard to warthog and nyala) may be due to counting errors. Warthog, for example, were possibly undercounted (Type I error) in 2000, whilst the count for 2004 seems more realistic and *visa versa* (Type I I error) with the nyala. With an overall population growth rate prior to lion introduction at 30.1 % per annum, the figures below (Table 4) for after should have shown at least some natural increase had there been no lions.

Table 4. Chi-square significance in population decline marked with *.

SPECIES	Population end 2000 (before)	Population end 2004 (after)	Chi – square
Bushpig	40	4	$x^2 = 23.1064$, P< 0.001 df = 1 *
Eland	126	97	$x^2 = 0.2885$, P =1 df = 1
Hartebeest	98	140	-
Impala	607	460	$x^2 = 1.6846$, P = 0.20 df = 1
Kudu	319	305	$x^2 = 2.7226$, P= 0.10 df = 1
Nyala	32	38	-
Ostrich	16	5	$x^2 = 3.9082$, P < 0.05 df = 1 *
Warthog	143	215	-
Waterbuck	79	67	$x^2 = 0.0173$, P= 1 df = 1
Wildebeest	438	280	$x^2 = 9.9025$, P < 0.01 df = 1 *
Zebra	271	188	$x^2 = 3.1891$, P= 0.10 df = 1
TOTAL	2 169	1 799	

4.4 Biomass consumption

Table 5 below lists the number of kills and estimated live biomass recorded. These figures show that, with a total of 26 kills, eland contributed to 7 805 kg of live biomass consumed by lions. Warthogs, with 174 kills, accounted for an estimated live-kill biomass of 6 585 kg. These species, together with three other species, kudu (6 110 kg), wildebeest (5 484 kg) and zebra (4 515 kg), contributed 75 % of the lions' diet. The minimum live biomass removed by the lions during the study period was 40 491 kg, with the edible portion being 31 353 kg. Edible biomass, described by Viljoen (1993), varies by percentage according to the mass of the prey viz. < 50 kg = 80 % edible, 50-150 kg = 75 %, 151-250 kg = 70 % and 251-500 kg = 65 %. The mean rate of live biomass

consumption was 7.76 kg per lion per day. The edible portion amounted to 6.03 kg per lion per day.

The lions consumed a mean of 8 % (+/- 1.5) per annum of the available prey population.

Table 5. The number of kills and live biomass from 2001 to 2004.

SPECIES	2001/2002		2002/2003		2003/2004	
	Number of Kills	Kill biomass (Kg)	Number of Kills	Kill biomass (Kg)	Number of Kills	Kill biomass (Kg)
Bushpig	7	275	8	290	0	0
Eland	6	1 010	10	3 245	10	3 550
Hartebeest	9	790	11	1 240	7	750
Impala	12	615	10	248	21	575
Kudu	14	1 560	11	1 590	20	2 960
Nyala	9	663	12	740	10	565
Ostrich	3	310	2	200	0	0
Warthog	55	2 165	71	2 030	48	2 390
Waterbuck	5	700	5	770	6	1 260
Wildebeest	9	970	10	1 440	24	3 075
Zebra	13	1 375	8	1 690	6	1 450
TOTAL	**142**	**10 433**	**158**	**13 483**	**152**	**16 575**

Although the differences in the number of kills per year were non-significant: Chi-square χ^2= 4.534, P= 0.1036 df=2, the actual biomass killed during the period increased significantly χ^2 = 6.339, P= 0.0420 df=2. See Table 6 below for the number of kills and kilogram biomass killed across years.

Table 6. Chi-square significance in biomass killed marked with *.

Year	Number of kills	Biomass killed (Kg.)
2001/02	142	10 433
2002/03	158	13 483
2003/04	152	16 575*

4.5 Prey species selection

Warthog were the most frequently killed species, 174 or 37 % of the total contribution of the various species, which made up the lions' diet. See Figure 18 below for the relative prey species kill composition. Old animals accounted for 17.7 % of all kills.

Prey Species Kill Composition 2001 to 2004

Y-axis: **% Contribution** (0% to 45%)

X-axis: **Prey Species**

Legend:
- Bushpig
- Eland
- Hartebeest
- Impala
- Kudu
- Nyala
- Ostrich
- Warthog
- Waterbuck
- Wildebeest
- Zebra
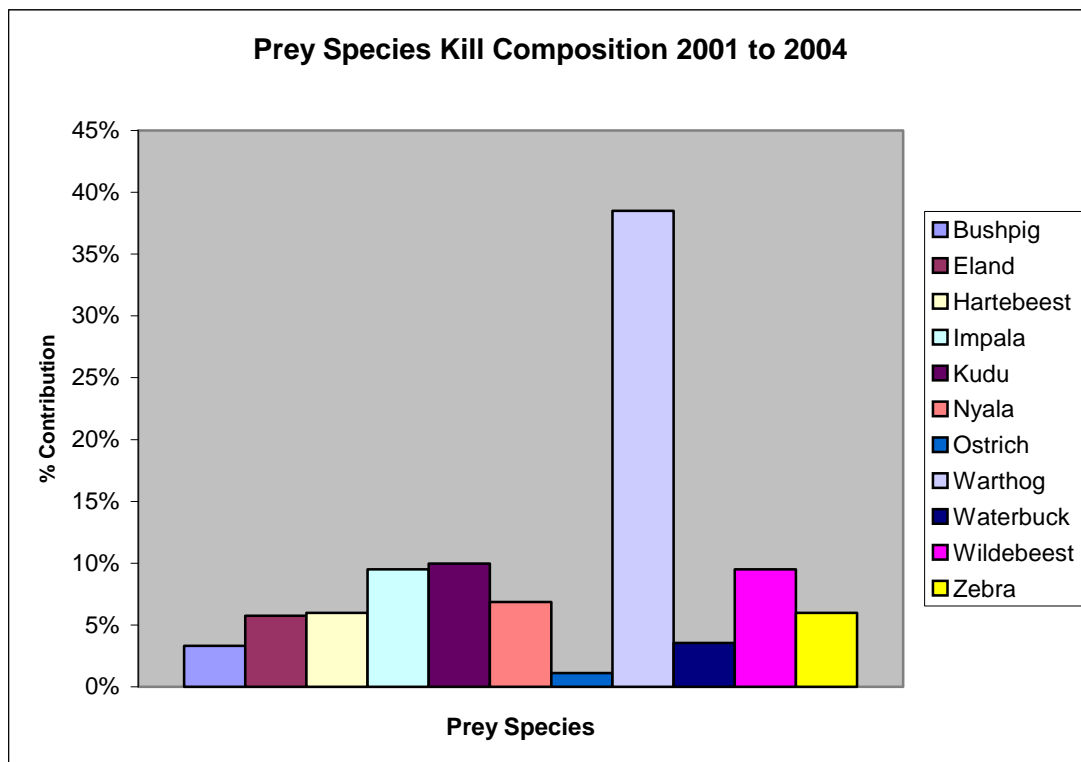
Figure 18. The percentage contribution of various species to the lions' diet.

The researcher used Ivlev's Electivity Index to determine the level of kill species selectivity for each year during the study period (see coloured key below for random, selected or avoided), where a value closer to +1 = selected (i.e. +0.5 to +1), closer to 0 = random (i.e. –0.49 to +0.49) and closer to –1 (i.e. –0.5 to –1) = avoided.

Selection Index key	Level of selectivity
-0.49 to +0.49	Random
+0.5 to +1	Selected
-0.5 to -1	Avoided

In 2001/2002, eland, hartebeest, kudu, waterbuck and zebra were killed randomly. Bushpig, nyala, ostrich and warthog were selected. Impala and wildebeest were avoided (see Table 7 below).

Table 7. Ivlev's Electivity Index for 2001/2. Marked * = selected.

Species	Population	Number Of kills	Percentage Proportion	Proportion of Population	Proportion of Kills	Electivity Index
Bushpig	40	7	17.5 %	1.8 %	4.9 %	0.5*
Eland	126	6	4.8 %	5.8 %	4.2 %	-0.2
Hartebeest	98	9	9.2 %	4.5 %	6.3 %	0.2
Impala	607	12	2.0 %	28.0 %	8.5 %	-0.5
Kudu	319	14	4.4 %	14.7 %	9.9 %	-0.2
Nyala	32	9	28.1 %	1.5 %	6.3 %	0.6*
Ostrich	16	3	18.8 %	0.7 %	2.1 %	0.5*
Warthog	143	55	38.5 %	6.6 %	38.7 %	0.7*
Waterbuck	79	5	6.3 %	3.6 %	3.5 %	0.1
Wildebeest	438	9	2.1 %	20.2 %	6.3 %	-0.5
Zebra	271	13	4.8 %	12.5 %	9.2 %	-0.2
TOTALS	**2 169**	**142**		**100.0 %**	**100.0 %**	

Table 8 below shows that, in 2002/2003, eland, hartebeest, kudu, ostrich, waterbuck, wildebeest, and zebra were all killed randomly. As with the previous year, bushpig, nyala and warthog were selected. Impala were again avoided.

Table 8. Ivlev's Electivity Index for 2002/3. Marked * = selected.

Species	Population	Number of Kills	Percentage Proportion	Proportion of Population	Proportion of Kills	Electivity Index
Bushpig	9	8	88.9 %	0.5 %	5.1 %	0.8*
Eland	84	10	11.9 %	5.0 %	6.3 %	0.1
Hartebeest	133	11	8.3 %	8.0 %	7.0 %	-0.1
Impala	413	10	2.4 %	24.7 %	6.3 %	-0.6
Kudu	285	11	3.9 %	17.1 %	7.0 %	-0.4
Nyala	47	12	25.5 %	2.8 %	7.6 %	0.5*
Ostrich	8	2	25.0 %	0.5 %	1.3 %	0.4
Warthog	191	71	37.2 %	11.4 %	44.9 %	0.6*
Waterbuck	76	5	6.6 %	4.6 %	3.2 %	-0.2
Wildebeest	254	10	3.9 %	15.2 %	6.3 %	-0.4
Zebra	169	8	4.7 %	10.1 %	5.1 %	-0.3
TOTALS	**1 669**	**158**		**100.0 %**	**100.0 %**	

Table 9 below shows that, in 2003/2004, eland, hartebeest, impala, kudu, waterbuck, and wildebeest were killed randomly. Nyala and warthog were selected for the third consecutive year. Zebra were avoided, as were bushpig and ostrich; this avoidance was probably due to their low numbers (no kills were, in fact, recorded for these two species).

Table 9. Ivlev's Electivity Index for 2003/4. Marked * = selected.

Species	Population	Number of Kills	Percentage Proportion	Proportion of Population	Proportion of Kills	Electivity Index
Bushpig	4	0	0.0 %	0.2 %	0.0 %	-1
Eland	97	10	10.3 %	5.4 %	6.6 %	0.1
Hartebeest	140	7	5.0 %	7.8 %	4.6 %	-0.3
Impala	460	21	4.6 %	25.6 %	13.8 %	-0.3
Kudu	305	20	6.6 %	17.0 %	13.2 %	-0.1
Nyala	38	10	26.3 %	2.1 %	6.6 %	0.5*
Ostrich	5	0	0.0 %	0.3 %	0.0 %	-1
Warthog	215	48	22.3 %	12.0 %	31.6 %	0.5*
Waterbuck	67	6	9.0 %	3.7 %	3.9 %	0.3
Wildebeest	280	24	8.6 %	15.6 %	15.8 %	0.1
Zebra	188	6	3.2 %	10.5 %	3.9 %	-0.5
TOTALS	**1 799**	**152**		**100.0 %**	**100.0 %**	

Of the eleven prey species studied, six are categorised as large–framed (>100 kg) and included eland, hartebeest, kudu, waterbuck, wildebeest and zebra. Five are considered as small–framed (< 100 kg) and include; bushpig, impala, nyala, ostrich and warthog (Table 10). The researcher performed a 2-way ANOVA to investigate whether there were any differences in electivity indices between years and weight classes. There was no significant difference across years i.e. $F_{2,27} = 1.498$, $P>0.05$.

There was also no significant interaction between year and weight class i.e. $F_{2,27} = 2.131$, $P>0.05$. There was, however, a marginally significant difference between weight classes $F_{2,27} = 4.155$, $P = 0.051$, demonstrating a trend to kill more large-framed and fewer small-framed prey in the third year.

Table 10. The number of large and small-framed animals killed across years.

		Number of kills		
	Species	**2001/2002**	**2002/2003**	**2003/2004**
Large - framed	Eland	6	10	10
	Hartebeest	9	11	7
	Kudu	14	11	20
	Waterbuck	5	5	6
	Wildebeest	9	10	24
	Zebra	13	8	6
	TOTAL	**56**	**55**	**73**
Small-framed	Bushpig	7	8	0
	Impala	12	10	21
	Nyala	9	12	10
	Ostrich	3	2	0
	Warthog	55	71	48
	TOTAL	**86**	**103**	**79**

4.6 Seasonal influences

There was no significant difference in the number of sub–adult prey species killed in winter compared to those killed in summer (54 % were killed in summer). Similarly, there was also no significant difference in the number of adult prey killed in winter compared with those killed in summer (55 % adults were killed in winter). Adults and sub–adults were also killed randomly across the winter and summer seasons.

4.7 Habitat influences

At 120ha in extent, wetlands contribute only 1.7 % of the study area, yet fifty-five kills (12.2 %) were recorded in this vegetation unit. Ivlev's Electivity Index value for this vegetation unit, with the least woody component was 0.8, showing a high degree of selectivity. With the exception of the Terminalia sandveld community, all the other vegetation units were selected against (i.e., had negative values). The vegetation unit with the densest woody component, *Sclerocarya birrea* / *Acacia* woodland was most strongly avoided. See Table 11 below.

Key to the vegetation unit abbreviations in Table 11.

- Ts = *Terminalia* sandveld

- CaBb = *Combretum apiculatum*/*Burkea* bushveld

- Cz/mb = *Combretum zeyheri*/*molle* bushveld

- SbAw = *Sclerocarya birrea*/*Acacia* woodland

- Wet = wetland

Table 11. Habitat influences on kill sights. More kills than expected occurred in wetlands and fewer kills than expected were recorded in *Sclerocarya/ Acacia* woodland.

Vegetation unit type	No. Kills per vegetation unit	Relative proportion of kills per vegetation unit	Vegetation unit area (Ha.)	Contribution of vegetation unit	Electivity Index
Ts	67	14.8 %	540	7.7 %	0.3
CaBb	152	33.6 %	2 650	37.9 %	-0.1
Cz/mb	153	33.8 %	3 050	43.6 %	-0.1
SbAw	25	5.5 %	640	9.1 %	-0.2
Wet	55	12.2 %	120	1.7 %	0.8
TOTAL	**452**	**100 %**	**7 000**	**100.0 %**	

The above kills are represented in the topographical map, Figure 19 below. It is inevitable that prey species congregate around drinking points, some of which are situated in close proximity to the boundary (see Figure 3 above) and as a result, some 15 kills involved (perhaps) the tactic of cornering game into the fence. The oblique-angled southeast corner was a particular concern where, on at least one occasion, a herd of eland escaped into the neighbouring property after being hunted by the lions. On this occasion the lions did indeed fence an eland and consumed it once it was entangled in the fencing wire. This neighbouring property was a stud cattle ranch and any losses sustained, as the result of escaped lions would have amounted to thousands of Rands. Similarly, three kills involving the fence occurred in the southern to southwest boundary corner, opposite a disease-free buffalo breeding project with each animal valued upward of R120 000.00. Consequently, any kills involving the fence could cause escaping game animals to create a large enough exit path for the lions to penetrate putting their own and human safety at risk.

As can be seen in figure 19 below, the lions made use of the entire property judging by the scattered distribution of kills. Some kill concentrations were observed in the vicinity of the permanent water near the tourist lodge, other permanent earth dams and drinking troughs, the level plateau regions and the low–lying valley areas as well as along water courses and tree–lined thickets. The least kill concentrations were in the southern central region following a lower game concentration because of the absence of permanent drinking water. Fewer kills also occurred on the rugged terrace slopes northwest of the central plateau where the terrain and dense vegetation deters the hunting effort.
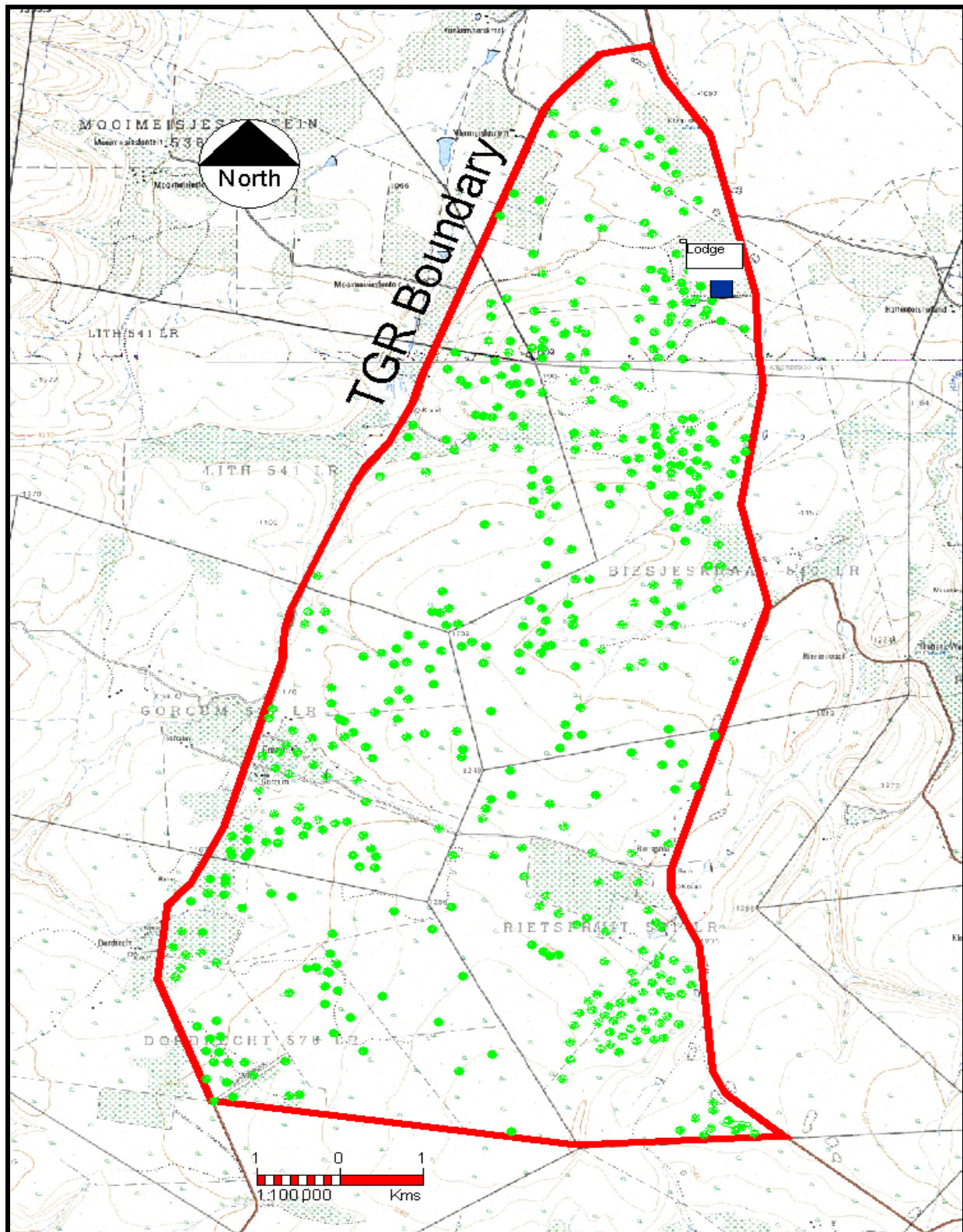
Figure 19. Kill distribution at TGR.

4.8 Financial model

Capital-employed, fixed once-off (asset) costs were incurred for the introduction of the lions in 2001. These costs totalled R501 572.00 and included the following cost centres: fencing upgrades (perimeter and release boma), administration, game relocation (disease-free buffalo were re-located), radio telemetry and the interest on expenditure. As these costs will vary due to the unique circumstances at different introduction sites, they have not been included in the formulation below. If required, this amount can be added as one of the factors with the other cost variables in the formula.

The running costs were the variable expenses and represented the year-on-year costs of maintaining a lion population. These costs included the purchase costs of lions, marketing, fence maintenance, cost of escaped game, cost of killed game, lion monitoring, veterinary consultation and interest lost because of expenditure of cash that would otherwise have earned interest.

The most significant cost of maintaining lion was the loss of game value through lion kills. In 2001/2002, the three lions killed 142 animals with a market value of R292 595.00. In 2002/2003, the three hunting lions (with three cubs) killed 158 animals with a market value of R377 459.00. In 2003/2004, the six lions killed 152 animals with a market value of R389 791.00. Although the number of animals killed (year–on–year) was not significantly different, the value of the game increased as more expensive large–framed antelope were being killed from 2002 to 2004. The total value of game lost to lion kills was (at least) R1, 060 m. Game market values remained relatively constant throughout the period.

The Cost variable (C_v) per annum of R121 865.00 was calculated by dividing the variable expenses by the number of lions per annum, during the period i.e. year one = 3 lions, year two = 6 lions (3

adults and 3 cubs) and year three = 6 lions (3 adults and 3 sub–adults). No doubt the number of lions would have increased further had contraception not been used. Three lions were introduced and doubled to six in year two but remained at six for the third year – an effective growth rate of 33% per annum. An interest rate of 8 % (for lost earnings on expenditure), compounded per annum, multiplied by the number of periods (3) was also factored into the C_v.

The above variables (except for capital employed), were substituted into the formula below where R_{pa} equals the total Rands per annum cost of maintaining lion:

$$R_{pa} = [(N_i * C_v) + (N_{rpa} * C_v)]$$

For this study:

N_i (Number of lions introduced) = 3,

N_{rpa} (Natural reproductive rate per annum) = 33 %

C_v = R121, 865.00

Therefore, Rands per annum cost:

R_{pa} = [(3 x R121 865.00)+(0.33 x R121 865.00)]

R_{pa} = R405 810.00

Or roughly R1, 2 million over the three–year study period. Add to this the one–off capital expenditure of R501 572.00 that would amount to a new total cost of the lions, for a three-year period, to R1, 7 million. This formula is adaptable to any other lion introduction scenario – the only variables being the N_i (number of lion introduced) and the lion growth rate (in this case 33 %),

which can be changed in the formula providing different results based on different circumstances. The cost variables would be typical of those experienced elsewhere and need not be changed.

To gauge the financial viability of introducing lion, the researcher converted the costs of maintaining lion into a required occupancy rate (to break–even point only), which the tourist lodge (now the only source of income) would have to achieve. The tourist infrastructure comprises a 40-bed lodge with daily rates that varied from: R650.00 per person per night (pp/pn) in 2001/2, R750.00 pp/pn in 2002/3 and R900.00 pp/pn in 2003/4.

To recover TGR's lion cost to balance, a tourist occupancy rate of 5.86 % (or 856 guests) would be required for year 1. Occupancy of 5.02 % (or 733 guests) would be required for year 2 and an occupancy rate of 4.04 % (or 590 guests) would be required for year 3. However, to recover the costs of the entire operation (including the cost of lion as well as capital employed i.e. other operational costs), the following occupancy rate would have to be achieved: 37.7 % (or 5504 guests) for year 1; 24.74 % (or 3 612 guests) for year 2 and 17.74 % (or 2 590 guests) for year 3. At best, TGR only attracted a full–rate average occupancy of up to 13 %. The income produced from such a low occupancy rate could not compete with the combined operational and lion costs (Figure 20).

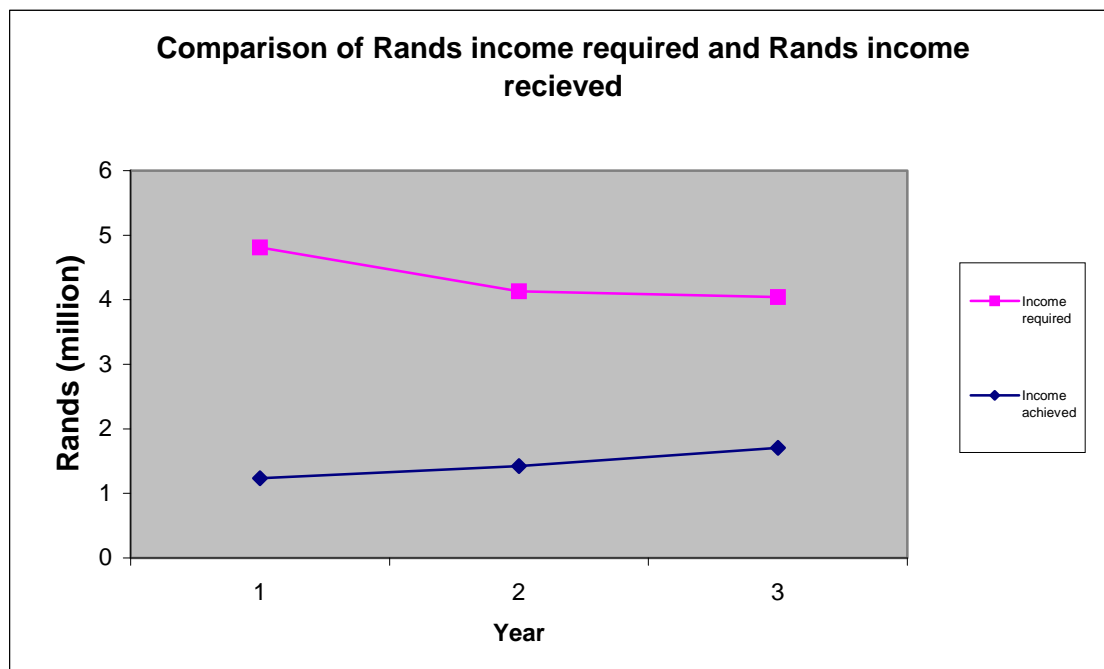**Comparison of Rands income required and Rands income recieved**

Figure 20. The representation of the income amount of Rands required Compared with the actual income achieved for three years.

References

VILJOEN, P.C. 1993. The effects of changes in prey availability on lion predation in a natural ecosystem in northern Botswana. *Symp. Zool. Soc. London*. 65:193-213.

CHAPTER 5

DISCUSSION

The introduction of lions onto small reserves requires careful consideration by landowners if the reason for doing so is to improve their eco-tourism earning potential. The smaller the reserve, the more intensive the efforts needed to effectively manage a lion population, in terms of both labour and economic costs (Anderson 1981; Van Schalkwyk 1994; Bothma 1996; Viljoen 1996; Van Dyke 1997). Lion can have a profound effect on prey species populations in small reserves and, according Van Schalkwyk (1994) and Viljoen (1996) should only be introduced as a normal pride size and structure.

Many scientists recognise the Minimum Viable Population concept (MVP) and the mechanisms that lead to species population depletion and ultimate extinction. In view of this, only three lions were introduced to TGR; their small number raised questions about their survival. In the short term for example, it was not unlikely for instance, for the male to be accidentally killed as a result of a hunt. Such a loss would have meant that no further breeding could take place because only two females would remain. Similarly, should one of the two females have died; it would mean that a co-operative hunting bond involving the surviving lioness would be lost. Furthermore, it has been well documented that females play the major role in hunting. The question arises of how would a one-male/ one female coalition fare? It is plausible to say that so few individuals are not likely to survive because their exposure to environmental risk increases as their numbers decrease. The lions would, therefore, have to adapt (initially at least) by selecting small-framed prey species - those that are easily overcome. Consequently, the population numbers of small-framed species may also decline perhaps to levels where they are also at risk of the factors associated with the MVP concept.

In the long term, it is possible that a small population at risk of MVP could be exposed to inbreeding depression, which tends to produce homozygous stocks (Storer *et al*. 1979) and the loss of heterozygosity due to the limited gene pool of the founder population. The effects of this may result in a number of consequences including high birth mortality, lowered fecundity and general loss of reproductive vigour. Soule (1980), Lacey (1987) and Yalden (1993) in Hunter (1998) suggest that 50 is the minimum number of individuals necessary to maintain genetic variance. Without this and combined with possible catastrophic events, a population will be forced into extinction.   It so happened that no lions were injured or killed during the study period and had bred successfully to six individuals by the end of the study period and had increased to nine individuals the following year.

Lions are highly social, group-living animals that live in prides numbering, on average, between 11.8 and 12.5 individuals up to 30 individuals (Smuts 1982; Stander 1991). According to Power (2002), a pride of this size (on small reserves of < 20 km²) will result in prey species declines to the extent that management will have to replenish prey stocks on an annual basis. The issue here is that a large enough founder population of inter-familiar individuals should be introduced simultaneously. The larger the population, the less like it is to succumb to the factors governing MVP. Axiomatically, the larger the lion population, the greater the impact it will have on the prey species population.

Power (2002) also calculated (using the MSY- Maximum Sustainable Yield method) that 1 Lion Feeding Unit (LFU) or 6.7 LFU's/100 km² would be sustained on a continual basis by removing prey at a rate at which they seek to increase it. In other words, population growth will be zero and will be attributed to the lion's hunting activities. Similarly, during this study period, TGR had up to six lions at a relative density of 1 Lion: 1 166 ha or 6 LFU's per 100 km² and also experienced an approximate zero percent overall growth rate for the prey species population.

5.1 Lions on other reserves

Early studies of lion predation indicated that lion prey preference was dictated by the availability of species (Berry 1981). In a more recent study at GMC, Slotow, *et al.* (2004), showed that many species, including warthog, wildebeest and waterbuck, were consistently killed at a frequency greater than would be expected based on their occurrence. Hunter (1998) also found that lion tend to kill warthog and wildebeest with a greater frequency than their occurrence. This study at TGR found that bushpig, warthog and nyala were consistently killed more frequently than predicted by their occurrence in the habitat. By the third study year at TGR, eland were also killed more frequently than expected on the basis of their representation in the population. Waterbuck, hartebeest and kudu were generally killed at a rate equal to their availability. Zebra and impala were mostly avoided, as were wildebeest during the first two study years. Old animals accounted for 17.7 % of all kills.

5.2 Distance traversed and kill rate

In year 3, the lions frequently split into three loose associations rather than occurring as one pride; this created a problem with telemetric observations because only the collared female could readily be located. Consequently, many more kills made by the other two associations could have gone unobserved, and so the estimates given here are conservative. These associations included; two males (one adult and one sub-adult), two sub-adult females and two adult females (one collared). The mean kill rate was 0.411 kills per day^{-1} (+/- 0.13). The lions roamed the entire 70 km² reserve and traversed 2.3 km per 24-hour period during the first year and up to 3.1 km per 24-hour period in the third year.

The reason for the lions having to traverse significantly greater distances during the third year was inconclusive but might have been that either as a result of the ungulate population had, since the lion introduction, becoming more vigilant towards their predation and, therefore, becoming increasingly difficult to kill or more likely that the overall ungulate population had decreased causing the lions to traverse greater distances to find prey.

Towards the end of 2003/4, the group regularly split into three two-individual coalitions. The researcher followed mainly the two adult females (one of which was collared). The other two groups consisted of two younger females and the father/ son coalitions. These two groups (males and younger females) generally lived off of the hunting successes of the two older females and would regularly be found at kill sites that it was assumed they had not initiated. Although the distance traversed increased, the kill rate remained constant. This fact meant that the lions were able to maintain the kill rate even though they had to travel further to find prey.

5.3 Prey species population growth

TGR's ungulate population (for the five-year period prior to the lion introduction) grew at an overall average rate of 30.9 % (+/- 17.3) per annum, declining significantly to –0.8 % (+/- 3) by the end of the study period. Although the methods employed to conduct censuses provided data that should be interpreted to produce trends only, the growth trend had historically been 30 % per annum.

Since the lion's introduction, growth per annum was more or less 0 %. No natural catastrophe or environmental change had occurred during the period nor was there any game capture. Therefore, the drop in ungulate growth can be attributed to the presence of lion. It was unlikely that there could

have been an increase in population of other competitor carnivore species causing a decline in growth since several individuals each of cheetah (three), leopard (two), hyena (five) as well as jackal (six) were assumed to have been killed by the lions. These species (excluding jackal) were encountered so seldom that it should be assumed that their population numbers were naturally low on a small reserve the size of TGR. According to sightings, tracks and kill activities, the researcher estimated that only one (or perhaps two) leopard were resident at TGR or at least encompass large parts of TGR as a home range, with a third individual appearing from time to time. Population numbers for the shy and nomadic brown hyena were more difficult to ascertain, but the researcher estimated that there were probably fewer hyena than leopard considering the amount of spoor activity. Cheetahs were not resident at TGR and were able to (as were leopard and hyena) pass under the electrified fence where, due to their bigger size, lions could not.

According to the aerial census conducted at the end of 2003/4, all eleven common prey species showed a decline in population size except for warthog, nyala and red hartebeest. The researcher considered the count data for red hartebeest to be accurate because they were easily counted. The count data for both nyala and warthog were not, however, deduced to be accurate. Both nyala and warthog have poor countability, and perhaps their previous counts were overestimated inflating their actual population size. As a result of the absence of consistently accurate count data; no conclusion could be made on the growth performance of these two species. Red hartebeest were only represented by 27 kills possibly avoiding a heavier toll by herding closely and keeping to rocky, high lying mountain terraces where the lions did not frequently hunt. Bushpig, ostrich and blue wildebeest experienced the most significant decline in population growth. No doubt the remaining common prey species would begin to show statistically significant population declines given continued longer-term study.

5.4 Prey species selection

The relative contribution of each species to the population remained fairly constant. Warthog numbers revealed a substantial and inexplicable (perhaps an under-count error) decline in population for the year ending 2002, but subsequently showed some recovery. Impala, although contributing to 25.6 % (2003/4) of the prey species population, constituted only 9.5 % of kills, whereas warthog, which represented only 12 % (2003/4) of the population constituted 38.5 % of all kills. Similarly, at GMC, Slotow, *et al.* (2004) also found that impala were the most abundant species but contributed to only 7 % of the observed kill carcasses. This trend applies to studies done in Malilangwe, Zimbabwe (Cotterill 1995) and in South Africa in the Phinda Resource Reserve (Hunter 1998) as well as in the KNP (Funsten 1999).

In year 1, only small-framed species were selected as prey, including bushpig, nyala, ostrich and warthog. The nimble impala and far tougher and bulkier blue wildebeest were avoided. Eland, red hartebeest, kudu, waterbuck and zebra were killed randomly. In year 2, again, only small-framed prey was selected, namely, bushpig, nyala and warthog. Ostrich numbers had already been reduced making them only randomly killed. Impala were again avoided. Eland, red hartebeest, kudu, waterbuck, wildebeest and zebra were killed randomly. By year 3, nyala and warthog continued to be selected. The lions had little chance of encountering bushpig or ostrich because of their low numbers, and these were, therefore, avoided. Year 3, however, showed a trend for the lions to randomly kill more of the larger framed prey, such as kudu, waterbuck and wildebeest than in the previous years. For the very large-framed eland, kills for year 3 remained constant with kills for year 2, but both years 2 and 3 showed an increase in kills compared with year 1.

5.5 Prey species, age and sex structure

Significantly more males were killed than females, probably because of their herding nature. Males, being young or old evictees from breeding groups, were seen at TGR to form loosely associated bachelor herds whilst breeding herds were more tightly associated – this tighter association being achieved by the dominant herd bulls/rams collecting straying individuals, forcing a compacted herd structure. In doing so, fewer prey from breeding groups (mostly females and calves) were selected. The disadvantage for the bachelor herds was that there was reduced vigilance behaviour as aspiring males were often involved in sparring and unaware of predators. In addition, lone or separated males did not have the benefit of co-operative vigilance. In particular, in the case of blue wildebeest, territorial bulls going about their routine of latrine marking become vulnerable in their solitude and were frequently hunted. Waterbuck, red hartebeest, eland and kudu bulls became victims in this way, as were impala rams.

The population age structure showed a decline in the proportion of sub-adults compared to adults, although more kills were recorded on adults. For 2001/2, the overall population age proportion was recorded as 63.4 % adult and 36.6 % sub-adult or at a ratio of 1:1.7 (1sub-adult: 1.7 adults). However at the end of the study period, ground count data showed that this ratio had changed to 74.5 % adult and 25.5 % sub-adult or 1:2.9 (1sub-adult: 2.9 adults). Although this shift in ratio was statistically insignificant, there had been some measure of change bringing to a reasonable assumption that there would perhaps be significance given a longer-term study. A decline in the sub-adult population would (without intervention), reduce net recruitment resulting in fewer adults in the long term to continue breeding putting the population at risk of MVP.

5.6 Lion density, prey availability and carrying capacity

The carrying capacity (K) at TGR was estimated to be 1 LAU equivalent: 10 ha. The pre-lion prey species density was 1 LAU: 9.6 ha which was reduced only marginally to 1LSU: 10.5 ha in 2003/4. The relative prey species LAU contribution also remained mostly unchanged, with only a slight decline in wildebeest and zebra LAU's, but an increase in kudu, hartebeest and impala LAU equivalents. According to Caughley and Sinclair (1994), reducing population numbers to ½K will place those populations in a growth phase. Although TGR's population had mostly experienced zero growth (-0.8 %; +/- 3%), since the initial decline in 2001, the lion population could be allowed to increase beyond 7.1/100 km² up to such point were ½K can be sustained i.e. 1LAU: 20 ha. Theoretically this would result in a reduced kill rate because fewer kills would be randomly made due to prey abundance. Alternatively, prey species could be harvested to achieve ½K, and the lion numbers could be maintained at the current level. Power (2002) determined, however, that 13.3 lions/100 km² could be sustained – this, of course, would be determined by the factors governing K.

Prey species were considered abundant at TGR with 0.25 individuals per hectare^{-1} (2003/4). During the same period in the KNP, there existed 0.06 individuals per hectare^{-1} with a lion density of 0.0006 per hectare^{-1}. Lion density at TGR was similar but lower at 0.0008 per hectare^{-1}. The decline in game numbers at TGR during 2000/1 was attributed to game capture for the purpose of reducing game numbers to within the limits of K. Some of these were high value species (e.g., nyala and waterbuck), which may have otherwise been lost through lion predation.

5.7 Lion biomass consumption

The biomass consumption of TGR's lions complemented the findings of Viljoen (1996) who calculated that male lions consume on average up to 7 kg live biomass daily and females 5 kg biomass daily (or alternatively 6 kg on average between the male and female sexes). TGR's lions consumed 40 491 kg of live biomass in the three-year study period of which 31 353 kg was considered edible. This amounted to 7.76 kg of live biomass per lion per day and 6.03 kg edible biomass per lion per day, nearly 2 kg per day more per lion (on average) as the findings by Viljoen (1996). These masses accounted for the minimum quantity of biomass killed because many kills were unrecorded due to inaccessible kill locations or the speed at which small prey were devoured and should, therefore, be interpreted as conservative. Due to a lack of input data, kills that occurred under these circumstances were not recorded.

The total number of recorded kills (452) represented a lion-related harvest of 8 %(+/- 1.5 %) of the available prey population per annum. Eland, warthog, kudu, wildebeest and zebra contributed to 75% of the lions' diet. As the lion numbers increased from two hunting lions (two adult females plus one sub-adult male) at year 1 to six hunting lions at year 3, there was a trend to kill a heavier weight class prey rather than small-framed animals.

5.8 Seasonal kill variations

Sub-adults and adults were equally likely to be killed in summer or winter, since there was no significant difference in the numbers of kills across seasons. Similarly, there was no significant difference in the seasonal association of male and female kills. It was predicted that, statistically speaking, more sub-adults (these include new-born calves) would be selected during the summer season because of their vulnerability. However, the recorded kill data did not show this to be the case. We should, however, assume this to be inaccurate because of the speed and efficiency in which the lions can dispatch of several young individuals in a very short time. In one instance, three lionesses were witnessed to dig out and consume six warthog piglets in a frenzy that lasted only seconds. Whilst lying up in thickets waiting for lactating mothers to return, kudu calves were regularly seen to be sought out by the lions and swiftly dispatched. Furthermore, because small prey kill sites leave little or no remains, many kills would have gone unrecorded.

5.9 Habitat selection

Of the five vegetation units represented, the wetland vegetation unit was proportionately the most frequently selected habitat for lion kills. This unit type represented only nearly 2 % of the study surface area but was the location of 12.2 % of all kills. Slotow, *et al.* (2004) found a similar trend for lions to kill more frequently in open woodland and grassland at GMC. Similarly, Hunter (1998) in Phinda found that lions made most of their kills in grassland and open mixed bushveld.

The lions were frequently found to make use of the densely vegetated termitaria often found in and on the wetland margins. These wooded outcrops provided ideal cover from which to launch attacks.

The lions would wait for prey to approach and would dart out some 40 m to 50 m into the adjacent open grassland. In most instances, the kill would be dragged back into the shade of the outcrop.

The *Terminalia* sandveld vegetation unit was the second most frequently selected unit. Here the lions enjoyed the relatively high, fairly closed canopy, shade and dappled light, medium to tall height grasses and a low density of undergrowth with good vision – ideal conditions for co-operative hunting. The *Terminalia* units are most frequently associated with neighbouring wetland habitats and, because of their easy accessibility; palatable forage and open line-of-sight, are favoured by game species. They, therefore, attract the highest concentration of prey species.

The *Sclerocarya birrea*/ *Acacia* woodland vegetation unit being the most densely wooded vegetation unit predictably attracted the least number of kills, not because few of the game utilised it (kudu and nyala especially thrived in it) but hunting co-operation was probably less effective in the dense cover.

An equal amount of kills were made in both of the more extensive vegetation units, *Combretum apiculatum*/ *Burkea* bushveld and *Combretum zeyheri*/*C. molle* bushveld. Both units simply described as open woodland/ bushveld units were equally randomly selected.

Statistically, no vegetation units at TGR were avoided; some just being selected more frequently than others. The lions made full use of TGR's 7 000 ha, and although some kills were made on the inaccessible high-lying terrace slopes, these areas were selected less frequently. The proximity to water did not seem to be a criterion as to where the lions would make a kill. If water was not freely available nearby, the lions were seen to readily walk 2 km to water after a bout of feeding and return to consume the carcass.

5.10 Financial costs

The cost of maintaining a lion population can be considerable; yet little or no formal data is available on this aspect of lion management. The costs of lions should not only be assessed as financial cost, but also in terms of their ecological impact. During the study period at TGR, many non-target species succumbed apparently to the lion's intolerance of competition, e.g. cheetah, leopard and brown hyena – all of which were represented by several kills. Aardvark, black-backed jackal, honey badger and civet were also killed (but not consumed). Sadly, and perhaps also as a result of the lion, bat-eared foxes are now considered to be extinct at TGR. White rhino and hippo have also been attacked, and the lions killed at least one elephant calf. Ostrich, bushpig and nyala numbers became critically low, and their continued existence as viable populations became questionable. In view of these observations, it seems reasonable to conclude that lion may only contribute to species biodiversity at the expense of other species, which raises the question of whether they represent a net gain or, in fact, a net loss to biodiversity in a given area.

The cost of lion in financial terms was not commensurate with the expected revenue that they could generate for TGR. A formula to assess the financial impact of the lions was developed and used to provide an estimate of costs, using TGR as the benchmark. The value of game killed by the lions was R1 054 324.00 during the study period. According to the actual and required income earnings during the study period, this short-term study shows that whilst the photographic presence of the lions could not stimulate enough the earnings to recover the entire operation, there was a trend showing a reduction in the deficit. Again, given time, with more effective marketing and closer budgetary control, this trend could favour their existence.

Perhaps some of the financial successes shown by other Big 5 reserves can be attributed to the fact that (in recent years) land-owners have consolidated their properties into conservancies where game

becomes common property and with an increase in land area, game populations enjoy all the advantages of being free-range. Free-range lions, according to DEAT, are those lions that are introduced into an area of no less than 1 000 ha and lions in a smaller area are considered to be captive bred, being subject to a different legal requirement from DEAT. As a result of this study, it is the writer's opinion that, having witnessed the impact of lion on 7 000 ha, this regulation should be subject to review on grounds of lion and prey species questionable sustainability.

An appropriate example of free-range (in the modern context of South African conservation) are the successes of the state-owned Kruger National Park, which in the early 1990s began incorporating numerous private game reserves into what is now known as the Greater Kruger National Park. Whilst these (ex) private landowners still enjoy the privacy of their own land, much of its land management is conducted co-operatively through the state authority. The advantage of this is two-fold. Landowners can concentrate their efforts solely on tourism generation whilst benefiting from the reduction in the reserve's running costs. Similarly, some conservancies are structured as co-operative ownerships where levies are paid to independent contractors for the infrastructure upkeep, relieving the burden on one single landowner. Fence-line maintenance, for example, is a major contributing cost. At TGR, four workers (amounting to nearly 11 000 man hours in three years) and one vehicle was dedicated to this task.

Another major cost centre is road maintenance. TGR developed a road network of some 400 km primarily to give access to tourist vehicles, but due to the uneven rocky terrain and varying topography, many roads were considerably damaged after heavy rainfall periods. The repair and maintenance of these roads meant that heavy machinery, such as a 4-wheel drive front-end loader; self-propelled grader, tractors and an aggregate tipper were constantly in operation. Concrete storm-water drains and causeways had to be built to divert water run-off – all at considerable expense.

Game populations in large reserves require less management than those in small reserves and larger game populations are more viable than smaller ones, and although predator populations increase and decrease with the availability of prey populations, the natural balance shifts to self-sustainability require little or no human interference.

No new game had been introduced at TGR prior to (or during) this study because the game numbers remained close to *K*. There was, however, evidently some scope to harvest prey species so that *K* was reduced to ½K, provided that the number of lion remained constant. In this way, some of the value of the game loss could be recouped. From 2001 to 2004, the lions consumed game to the value of ± R351 000.00 per annum. This game could be considered surplus and harvested for sale, rather than lost to lions. Alternatively, capturing and selling this game could have had an income potential of ±R50/ ha. Escaped game lost through the fencing amounted to a further cost of ±R150 000.00 for the study period, bringing a total estimated loss of game species to R71/ ha per annum. In comparison, a neighbouring reserve, which harvested and sold game during the same period achieved an average net income of approximately R46/ ha per annum.

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CHAPTER 6

CONCLUSION

From an eco-tourism perspective, lions are probably the most captivating and charismatic of all the large predators. Given their complex social structure, they can be highly affectionate, attentive and cooperative – all of which is, at times, traded for violent aggression and seemingly near-death skirmishes. They inspire a sense of rapacious power and command, yet no other species has suffered more through range contraction than the lion.

Unfortunately, as a result of experimental introductions based on assumptions of trial-and-error within the privately–owned wildlife areas, many custodians gauged the success in their meaningful repatriation of this high–profile species by the profit which (it was hoped) the lions could return. Tragically, lions often sealed their own fate by being too good at what they do. They compete with landowners over resources (game animals), which would otherwise contribute to income revenue. They cause fleeing prey to damage and escape through fencing. There is also constant concern that the lions could escape into neighbouring populated areas. They require constant management and regular contraception to keep their numbers in check. Often, in the long term, lions over-stay their welcome and, in a wildlife market where there are more lion sellers than lion buyers and where state authorities resist the movement of lions, they are often disposed of unethically resulting in even further contraction of their range.

The ecological and financial viability of game farming in the presence of lion on small reserves is questionable. This study showed that whilst the lion population increased successfully (even with the use of contraception) no growth in the prey species population was experienced. Lion killed rare and endangered non-target species. Significantly more males were killed than females, resulting in a skewed male/female sex ratio possibly causing future population growth declines. Significantly more adults were killed than sub-adults meaning that fewer individuals were able to breed in the future. The lions were relentless; they managed (in a diminishing prey population) to maintain their kill rate even though they had to traverse significantly greater distances to do it. As their population increased and matured, they showed a tendency to successfully hunt larger prey. Generally, larger game is more expensive. The lions caused many prey to crash into and escape through damaged fencing. Although the tourist income revenue was adequate to recover the lions' expenses, it was not (at the time of writing) enough to recover the costs of the entire operation, as had been hoped. In 2003/4 a trend emerged that the tourist lodge would increase its lion-based earnings. A long-term study would perhaps verify this aspect.

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