The ecology of reintroduced lions on the Welgevonden Private Game Reserve, Waterberg

by

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Dedicated to my parents for their love, support and encouragement throughout my life, and for providing me with the opportunity to fulfil my dreams.

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Supervisor: Prof. J. du P. Bothma

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ABSTRACT

Five lions were reintroduced to the Welgevonden Private Game Reserve in 1998. These lions were studied to increase the limited knowledge of the ecology of reintroduced lions on small wildlife reserves, and to provide baseline data to the reserve management from which to develop management decisions.

In the past, reintroduction attempts of felids have often failed because the animals failed to establish ranges in the new environment. During the current study, homing behaviour and range establishment of the reintroduced lions were studied and used as an indication of the success of the reintroduction attempt. The ease with which lions

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on Welgevonden established ranges indicated that they did not experience problems with adapting to their new environment

The population dynamics of the reintroduced lion population were investigated. The population grew rapidly due to early breeding and short inter-litter intervals. The collected data were used to model the lion population using VORTEX population modelling software. Various potential management strategies to reduce the population growth were also modelled and discussed.

The feeding ecology and predation patterns of the reintroduced lions were investigated to give an indication of the predator-prey relationships on Welgevonden. These data were used in a model that investigated the effect of lion predation on the various prey populations of Welgevonden. The model was also used to test the influence of other factors on the prey populations, as well as the number of killing lions that can be supported by the prey population.

The study has shown that reintroduction can be used successfully to establish a lion population on a small game reserve, but that certain management actions will increase the chances of success. However, continual monitoring and management will be necessary to ensure the long-term viability of the lion and prey populations.

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CHAPTER 1

INTRODUCTION

The lion *Panthera leo* (Linnaeus, 1758) is the largest predator in Africa (Skinner & Smithers 1990) and usually occupies the top position in the African food chain. Although large clans of the spotted hyaena *Crocuta crocuta* can sometimes dominate small lion prides, the lion is the dominant predator of the larger prey species in many parts of Africa.

Several species of the genus *Panthera* once ranged over four continents and were more widely distributed than any other mammal. The African lion was probably one of the most fearsome beasts that roamed the African plains (Bothma & Walker 1998). Because of the recent increase in the human population in Africa, more and more land that was inhabited by humans was cleared and was used for agriculture. Pastoralists inhabited large parts of the range previously used by lions. This led to conflict between lions and pastoralists, and many lions and other large predators were destroyed (Schaller 1972; Anderson 1981; Stander 1990). The result was that the range of distribution of the lion shrunk more than that of any other cat species in Africa. Although they still occur in sparsely populated areas, lions are mainly restricted to national parks, private and official wildlife reserves and wildlife ranches where they are one of the greatest tourist attractions in Africa.

The development of the ecotourism industry in southern Africa and the creation of new wildlife ranches and reserves have led to a demand for large predator introductions. The wide habitat tolerance and wide range of prey types of the lion make it an animal that is well suited for reintroduction (Van Dyk 1997). When considering the area and population that is required to maintain a self-sustaining and viable lion population, and given the limited size of most wildlife reserves and ranches in southern Africa, few of these areas are large enough to support self-sustaining lion populations. However, to do so, intensive and continual management of these reintroduced lion populations will be necessary (Van Dyk 1997).

The management of large predators remains a controversial and highly emotional issue all over the world. This can largely be ascribed to a lack of knowledge of the basic factors that influence predator and prey populations (Smuts 1978a), despite much research on lions having been done in the past. Published information of research done all over Africa on all aspects of lion ecology are available (e.g.: Wright 1960; Mitchell, Shenton & Uys 1965; Kruuk & Turner 1967; Hirst 1969; Makacha & Schaller 1969; Pienaar 1969; Schaller 1972; Bertram 1973; Eloff 1973a; Rudnai 1974; Caraco & Wolf 1975; Bryden 1976; Smuts 1978a; Smuts, Hanks & Whyte 1978; Saba 1979; Smuts 1979; Anderson 1981; Berry 1981; Van Orsdol 1982, Packer & Pusey 1983; Eloff 1984; Pusey & Packer 1987; Cooper 1991; Scheel & Packer 1991; Stander 1991a, Stander 1991b; Dunham 1992; Mills & Schenk 1992; Stander 1992; Van Schalkwyk 1994; Van Valkenburg 1996; Viljoen 1997). However, the majority of the above studies were done in reserves larger than 1000 km^2, where lions occur under natural circumstances. There is precious little information on reintroduced lions in areas smaller than 1000 km^2.

The failure of several reintroduction attempts in the past has led authors to believe that relocation cannot be used successfully to establish large carnivores in areas from which they have become extinct. Mills (1991) states that translocation and reintroduction of large carnivores are complicated practices and are rarely successful. Failures generally occurred because the way in which the animals reacted to translocation was poorly understood. Translocation of lions is now a well-practised technique to establish a population in an area from which they have become extinct. There is, however, still little information available on how lions will react to an introduction. There are few documented studies on the post-release behaviour of large African predators, despite the fact that post-release monitoring is essential in determining whether an introduction was successful or not (Van Dyk 1997). Mills (1991) states that only after an adequate number of studies have been carried out will we be in a position to judge whether drastic conservation measures like introductions should be embarked upon.

Welgevonden Private Game Reserve is a recently established, small wildlife reserve and the demand for the introduction of the Big Five was also present there. This has led to lions being introduced to the reserve in 1998. Nobody knew what to expect from such an introduction, and the owners and management of Welgevonden wanted to know what would happen to the lions after they were introduced. Most importantly, knowledge was required on the effect that they will have on the prey populations of Welgevonden. It was important to gather sufficient data that could assist in future management decisions. This presented a perfect opportunity to launch a research project on post-release behaviour of lions to increase the available knowledge on lion introductions on small wildlife reserves, as well as to answer the questions of the owners and managers of Welgevonden. Most importantly, it provided the opportunity to test the hypothesis that it was feasible to reintroduce lions successfully to small wildlife reserves, if managed correctly. To test this hypothesis, the following key questions were researched:

1. What will happen to the lions after reintroduction?
2. Will the lion establish ranges in the reserve, how large will they be and where will they be established?
3. Will the lions breed successfully after reintroduction?
4. What prey will be utilised?
5. What effect will the lions have on the prey-populations?

These five key questions were used as a basis for this study, and answers to these questions are explored in the relevant chapters. To do so, these key questions were briefly addressed in the various chapters that follow.

The post-release movements of reintroduced lions have not been documented well in the past. Hunter (1998) gives a detailed description of how the introduced lions in Phinda Resource Reserve reacted to their introduction, and the movements of these lions after release were well documented. The current study provided a further opportunity to determine the post-release movements of lions, and to relate them to the project success (Chapter 5). Large carnivores, especially felids, have a tendency to return to their capture sites (Hunter 1998). One of objectives of this part of the study was to test whether the lions that were reintroduced into Welgevonden showed any homing behaviour. The immediate movements after release, and the way in which the lions dispersed over the reserve after release, are also described. This should serve to increase the knowledge on how lions react to reintroduction, and could serve as an indication to other reserves of what to expect when they plan a lion introduction in the future.

Although the spatial patterns of lions have been well studied in natural and established populations, this has not happened yet in relocated and reintroduced populations (Hunter 1998). Little data are available on range use and territory characteristics of reintroduced felids. The introduction of lions into Welgevonden offered opportunities to study the range establishment of lions in an area where there are no large competitors at present, and which has an abundance of prey. It therefore offered the opportunity to the lions to choose the area in which they wanted to establish ranges without major interference from competitors of the same or different species, like the spotted hyaena. The study was an attempt to explore the processes and patterns of range use and establishment after introduction (Chapter 6). The study also attempted to explore the habitat selection of lions on Welgevonden, and to correlate that with factors that might affect this selection. The distribution of ranges and the way in which they are affected by an event such as the removal of a fence was investigated. This was important, especially in the light of the current process of fence removal between Marakele National Park and Welgevonden Private Game Reserve (Chapter 2). Possible management actions and the way in which they could affect range use patterns were also discussed.

Population dynamics and demography (Chapter 7) should be central in any study with the objective of determining the success of a reintroduction attempt. Reproduction and population growth are crucial factors in understanding the population dynamics of an animal population. Successful breeding is a reliable indicator of the success of a

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reintroduction attempt (Linnell, Odden, Smith, Aanes & Swenson 1997). One of the objectives of the study was to determine the rate with which lions colonised the reserve after introduction. The patterns of reproduction were investigated and compared with what was known from elsewhere. Demography and population characteristics were determined, and were used as an indication of the success of the introduction. The above data were used to model the lion population and to investigate the effects of various management practices on the population over the next 100 years. It will hopefully assist in providing baseline data for future lion introduction efforts in other areas.

Although lion predation has been well studied in many areas, it is still a controversial subject. Moreover, results cannot be extrapolated from one area to another and each situation is unique. The owners of Welgevonden wanted to know which prey animals were killed and what was the dominant prey of the lions on Welgevonden. This provided the opportunity to collect kill data (Chapter 8) and to compare those data with lion predation studies in other, larger areas. The habitat types in which the kills were made, were determined and compared with the habitat selection of lions and their prey. The relationship between lion group size and the type of prey killed was investigated and discussed against the backdrop of how this might affect future management decisions. This study should serve as indication to other reserves of what to expect when lions are introduced there.

A lack of space on small reserves usually limits prey from migrating to escape predation. The potential for considerable impact by predators on the prey population is therefore a real threat, and should be always be kept in mind when making

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management decisions. In Chapter 9, predator-prey relationships are investigated with the use of a model that predicts the impact of the lions on the prey population of Welgevonden. Predator-prey relationships are difficult to measure accurately. Models are intended to give an indication of what could happen in a population before it actually happens, based on the available knowledge. It could therefore serve to indicate and eliminate possible problems before they actually occur. Although such models cannot accurately simulate the actual situation, it can serve as an important management tool if applied correctly and circumspectly.

CHAPTER 2

STUDY AREA

Location

Welgevonden Private Game Reserve, hereafter referred to as Welgevonden, is located in the Limpopo province (formerly the Northern Province) of South Africa at latitudes 24° 10' to 24° 25' South and longitudes 27° 45'to 27° 56' East. Welgevonden falls in what is known as the Waterberg region. The Waterberg region stretches from Bela-Bela (formerly Warmbaths) in the south to Lephalale (formerly Ellisras) in the north, and from Thabazimbi in the west to Mokopane (formerly Potgietersrus) in the east (Figure 2.1).

Welgevonden lies 20 km west of the town of Meetshetshela (formerly Vaalwater), on the way north to Lephalale. It currently covers an area of 330 km^2 at an altitude of from 1200 m to 1500 m above sea level. Eighty percent of the reserve is mountainous, with numerous deep valleys. There are two perennial rivers that flow through the reserve. They are the Malmanies River and the Sterkstroom River. Welgevonden also serves as a catchment area for two other perennial streams because both the Taaibosspruit and the Platbosspruit have their headwaters in Welgevonden. All four of the above rivers and streams eventually flow into the Mogol River, which in turn serves as an important feeder to the Limpopo River. As the name Waterberg would suggest, Welgevonden is criss-crossed by little streams, with water flowing out of every little crevice in wet years. Seventeen man-made dams dating from earlier farming still exist on Welgevonden. Some of them serve as important waterholes for wildlife in areas without perennial water.

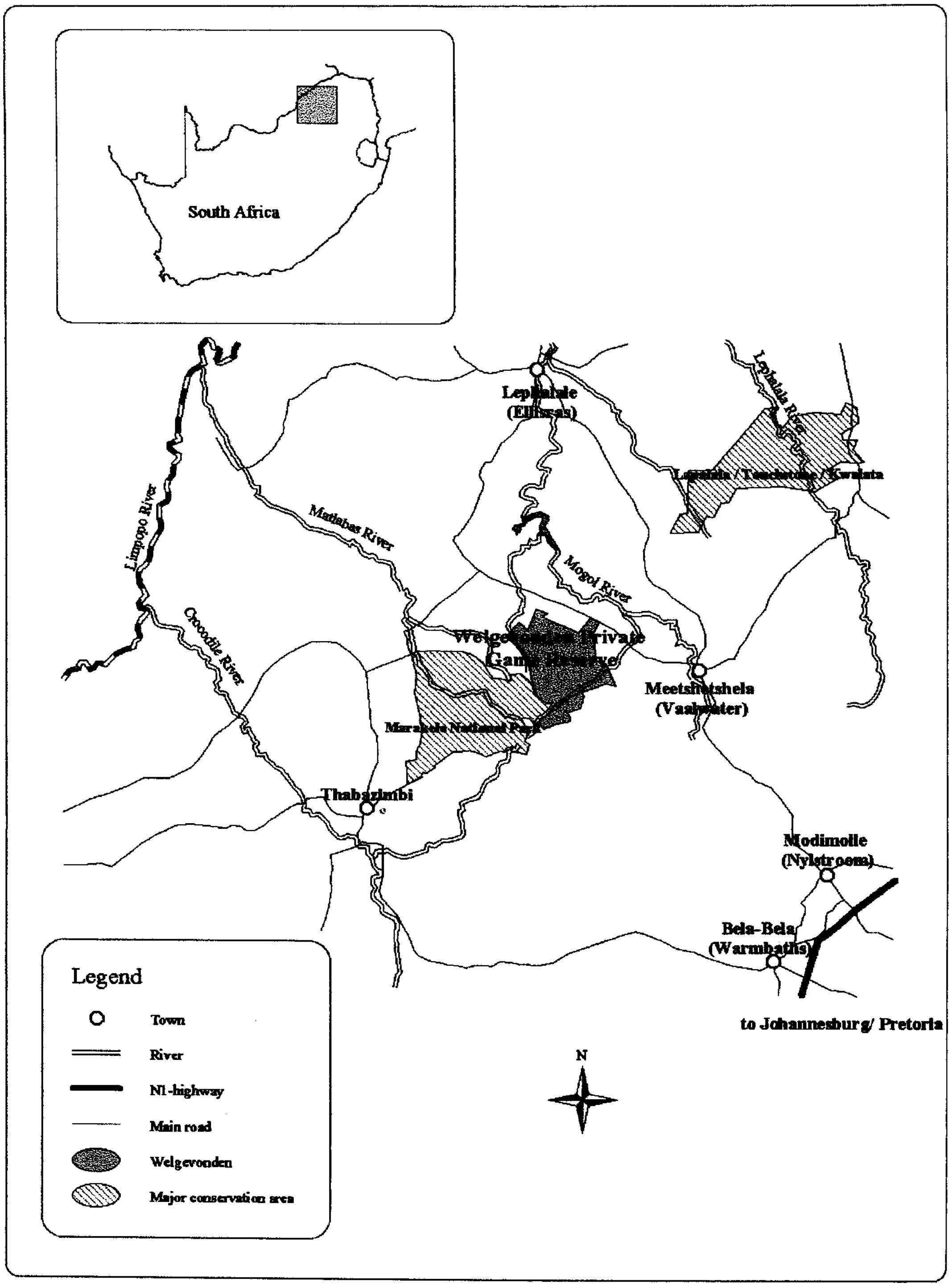

Figure 2.1. The location of the Welgevonden Private Game Reserve in the Waterberg region of the Limpopo province, South Africa.

Welgevonden shares 14 km of its western boundary with the 610 km^2 Marakele National Park, hereafter referred to as Marakele. Marakele was declared a national park in 1994. The Welgevonden Land Owners Association and South African National Parks are currently finalising the agreement for the removal of the fence between Welgevonden and Marakele to create a larger contiguous conservation area.

Welgevonden also forms part of the Waterberg Biosphere Reserve that was declared in 2001 by UNESCO. This biosphere reserve currently covers an area in excess of 4000 km^2 in the Waterberg region (Collinson & Brett 2001), with new areas continuously being investigated to be added as core areas. Current core areas include Welgevonden Private Game Reserve, Marakele National Park, Wonderkop Nature Reserve, Masebe Nature Reserve, the Moepel farms, Lapalala Game Reserve, Touchstone Game Reserve, Kwalata Game Reserve and Mokolo Dam Nature Reserve.

Climate

The climate of the Waterberg region is classified as warm and temperate, with summer rainfall. There are distinct wet and dry seasons, stretching from October to March and April to September respectively. The mean annual rainfall at the Elandshoek Weather Station south of the reserve was 670 mm from 1924 to 1993. The Vaalwater Weather Station, 10 km east of Welgevonden, recorded a mean annual rainfall of 613 mm from 1924 to 1999. The mean annual maximum temperature at the Vaalwater Weather Station is 26.5 °C and the mean annual minimum temperature is 11 °C, with a mean annual temperature of 18.8 °C. The mean frost season lasts 51 days, and a moderate frost is experienced in 91.7% of all the years.

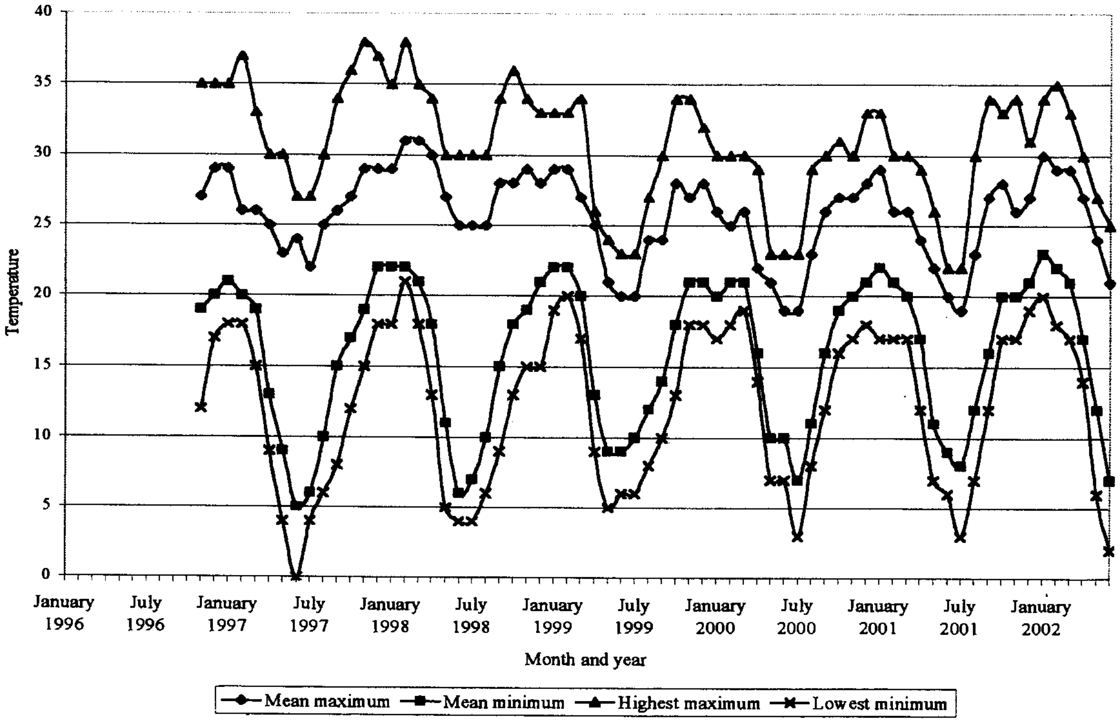

Figure 2.2. Mean monthly temperatures (°C) for the period November 1996 to June 2002 as recorded at the offices of the Welgevonden Private Game Reserve in the Waterberg region of South Africa. There are no temperature data available before November 1996.

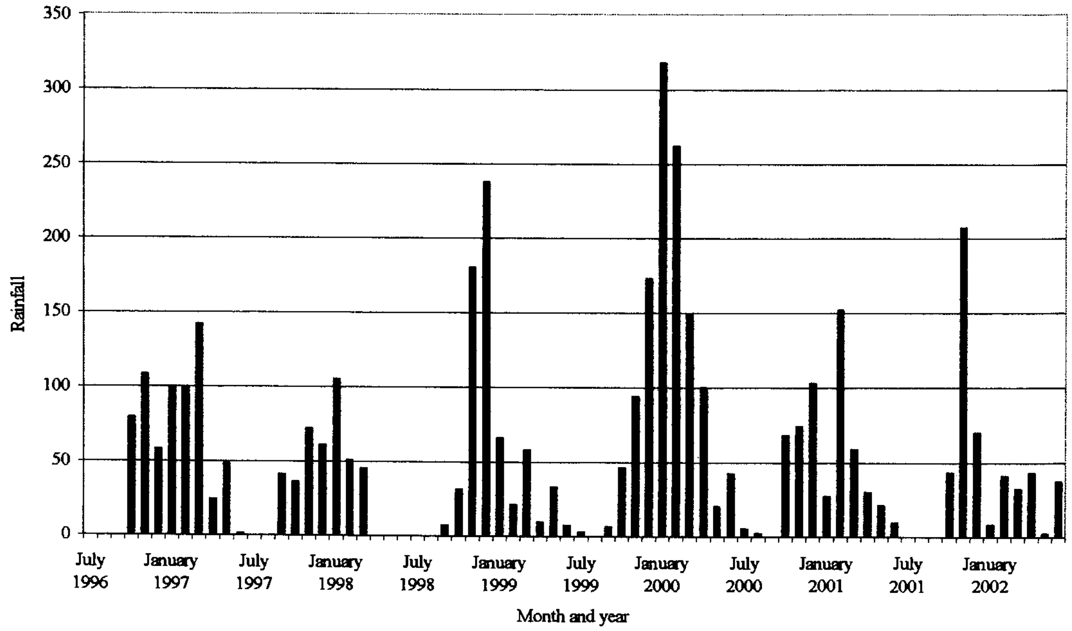

Figure 2.3. Monthly rainfall (mm) for the period July 1996 to June 2002 as recorded at the offices of the Welgevonden Private Game Reserve in the Waterberg region of South Africa. Where there are no data for a specific month, it indicates that there was no rainfall during that month.

Geology, geomorphology and soils

Welgevonden forms part of an undulating plateau that rises to 1000 m above the surrounding lowlands, and consists of ancient sandstone of the Kransberg Subgroup of the Waterberg Group. The Waterberg strata form a rugged topography with some striking cliffs. The Waterberg Group consists of a succession of coarse, clastic, sedimentary rocks (Callaghan 1987). The soils are dystrophic (markedly leached and nutrient poor) to mesotrophic (moderately leached) yellow-brown apedal coarse sands, and medium to coarse sandy loams and apedal grey loamy coarse sands (Collinson & Brett 2001). The clay content of the soil is low, and ranges from 1.7% to 2.9% clay, creating the leached and nutrient poor soils. The absence of lime causes a high soil acidity, ranging in pH from 3.82 to 4.26.

The leached, acidic, sandy soils give rise to nutrient-poor, low quality sour veld that cannot support large numbers of herbivores. Grazing animals are especially affected as the sour veld causes low quality, unedible grass species to dominate the grass layer. The ability of the veld to support large numbers of grazers is further decreased by up to 60% rock cover in certain areas.

Vegetation

Welgevonden falls within two different vegetation types as classified by Acocks (1988). The Sour Bushveld: Veld Type 20 covers the largest part of Welgevonden, and the Mixed Bushveld: Veld Type 18 stretches into Veld Type 20 on various places in Welgevonden. Low & Rebelo (1996) classified both these veld types as a single veld type, the Waterberg Moist Mountain Bushveld: Type 12. Typical tree species of the Sour Bushveld: Veld Type 20 are *Faurea saligna, Burkea africana, Protea caffra,* *Englerophytum magalismontanum, Dombeya rotundifolia, Lannea discolor, Combretum molle, Combretum zeyheri, Gardenia volkensii, Diplorhynchus condylocarpum, Kirkia wilmsii, Ficus thonningii, Ochna pulcra, Strychnos pungens, Elephantorrhiza burkei, Nuxia congesta, Dovyalis zeyheri, Pseudolachnostylis maprouneifolia, Euclea crispa,* and *Grewia* spp.. In the Mixed Bushveld: Veld Type 18, the following species are commonly found on Welgevonden: *Terminalia sericea, Pterocarpus rotundifolia, Peltophorum africanum, Ziziphus mucronata, Ozoroa paniculosa, Mundelea sericea,* and *Syzygium cordatum.* A number of trees that are common to the region occur in limited numbers elsewhere, including *Pavetta zeyheri, Canthium spinosum, Canthium gilfillanii, Combretum nelsonii, Kirkia wilmsii, Rhus engleri, Rhus zeyheri, Widdringtonia nodiflora, Vitex pooara* and *Vitex zeyheri* (Collinson & Brett 2001).

Acocks (1988) described the grassveld constituent as "*a rich one floristically, even if peculiarly useless for grazing.*" The common grass species are all indicative of sour veld and they include: *Schizachyrium sanguineum, Schizachyrium jeffreysii, Elionurus muticus, Loudetia simplex, Diheteropogon amplectans, Hyperthelia dissoluta, Trachypogon spicatus, Panicum natalense, Brachiara nigropedata, Eragrostis curvula, Eragrostis superba, Themeda triandra, Sporobolus pectinatus, Heterpogon contortus, Aristida* spp., *Pogonarthia squarrosa, Melinis repens* and *Urelytrum agropyroides.*

Farming activities, but particularly commercial and subsistence crop production, have altered parts of the reserve. In the past, commercial dryland cultivation of maize and groundnuts, and irrigated orchards of oranges and pecan nuts were practised (Roets *pers. comm.*[1]), but because of erratic rainfall and nutrient-poor soils, there has been a considerable decline in these farming practises. This has resulted in a large number of old lands that are currently in various states of recovery on Welgevonden. These old lands are predominantly covered in *Cynodon dactylon* and they support a large number of grazers.

Habitat types

Although a detailed vegetation map for Welgevonden is still in preparation, four broad habitat types were identified for use in this study. They are: old lands, plateaux, valley bottoms and hill slopes (Figure 2.4). These habitat types were defined by plant species and structure, as well as landscape structure, and were mapped using ArcView version 3.1. The old lands are flat, open grasslands with little rock cover. This habitat type supports a large number of different types of grazer like the blue wildebeest *Connochaetes taurinus*, red hartebeest *Alcelaphus buselaphus*, eland *Taurotragus oryx*, zebra *Equus burchellii*, white rhinoceros *Ceratotherium simum* and tsessebe *Damaliscus lunatus lunatus*. Plateaux are relatively flat areas with various degrees of rock cover. The vegetation there is relatively open, with larger trees like *Burkea africana* and *Combretum zeyheri*. The hill slopes are steep and rocky, with a dense tree and shrub cover. The valley bottoms have deep soils, little rock cover, and tall trees such as *Faurea saligna* and *Syzygium cordatum* dominate the tree layer.

History of the reserve

Welgevonden is a privately owned wildlife reserve that became a conservation area in 1993. Before this, the land comprised mostly of private farms with cattle ranching the

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[1] Roets, H.J: Operations Manager, Wel P.O. Box 433, Vaalwater, 0530.

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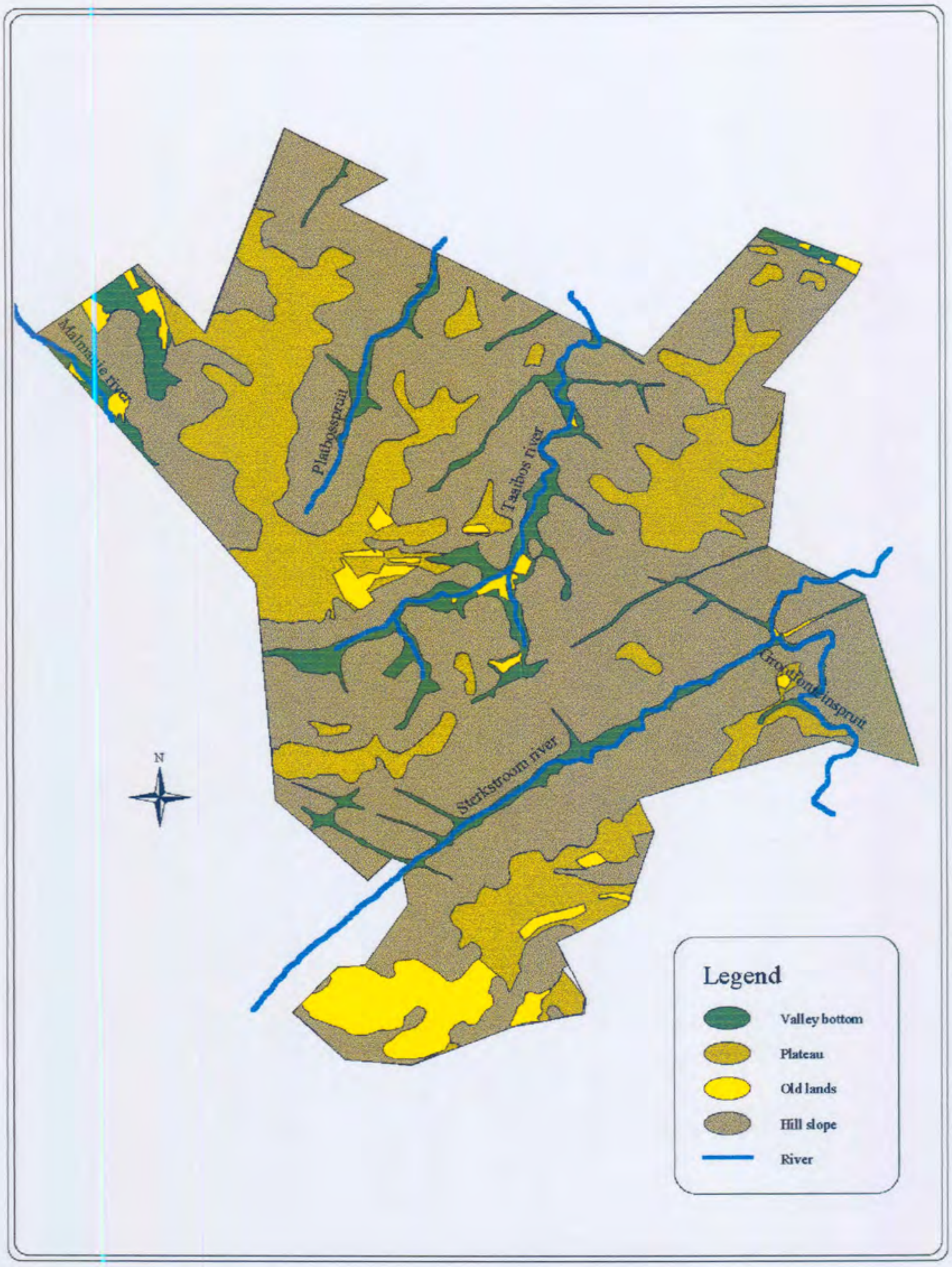

Figure 2.4. The four broad habitat types and rivers occurring on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

dominant form of land-use. Maize, groundnuts and fruit trees were planted in the valleys and flat plateaux. These agricultural practices stopped before and during the development of the reserve. The fruit trees were removed and the old lands were reclaimed, some of them by re-seeding them with grasses like *Digitaria eriantha*. Originally, Welgevonden also consisted of some small wildlife ranches with few large, wild animals. The Rand Merchant Bank originally developed Welgevonden, buying up the land, fencing the reserve, removing the internal fences and introducing the wildlife. The whole reserve was then divided into unfenced 500 ha units that were sold separately under free-hold title to the current owners. Each owner has traversing rights over the whole reserve and is allowed to build a maximum 10-bed lodge on his 500 ha subdivision, but does not have managing rights of his property. Collectively, the owners form the Welgevonden Land Owners Association, from which a Board of Trustees is elected that decides on the business management of the reserve. The Welgevonden Land Owners Association appoints the executive management staff that manages the day to day running of the reserve, including the ecological management.

History of the lion introduction.

When the reserve was started in 1993, it was decided to develop the reserve as a Big Five wildlife reserve. Leopard *Panthera pardus* occurred naturally in the area, but elephant *Loxodonta africana*, white rhinoceros, buffalo *Syncerus caffer* and lion were reintroduced. One male and two female lions were introduced from Pilanesberg National Park and one male and a female lion from Madikwe Game Reserve. The details of the various lions that were introduced are shown in Table 2.1.

Table 2.1. Genders, origin and ages at reintroduction of the lions that were reintroduced into the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

LION	GENDER	ORIGIN	RELATIONSHIP WITH OTHER LIONS	AGE IN MONTHS AT INTRODUCTION
WLG 1	Male	Pilanesberg National Park	Brother of WLG 3	36
WLG 2	Male	Madikwe Game Reserve	Unrelated	35
WLG 3	Female	Pilanesberg National Park	Sister of WLG 1	36
WLG 4	Female	Madikwe Game Reserve	Unrelated	34
WLG 5	Female	Pilanesberg National Park	Unrelated	43

All five lions arrived together on Welgevonden and were first released into a holding boma of 50 x 50 m. The holding boma was fenced with a 2.8 m high Bonnox® fence, with an additional four strands of electrified wire at heights of 0.3 m, 0.6 m, 1.5m and 2.3 m from the ground. A further electrified strand, 0.15 m high and 0.5 m away from the main fence, was added to prevent animals from burrowing under the main fence. The lions were fed with a complete blue wildebeest carcass once a week, or more regularly when it appeared that they were losing condition (Burger *pers. comm.*[2]). Because of the limited size of the boma and the associated lack of exercise, it was attempted not to overfeed them so as to prevent them from becoming obese and lazy while in the boma (Burger *pers. comm.*[2]). The food was delivered into the boma by the use of a pulley-system in which it was first hoisted onto a tower, and then slid into the boma with a pulley on an overhead cable. The carcass was dropped when it reached the end of the cable in the middle of the boma. The boma was screened on the side from which the lions were fed to prevent them from seeing humans and associating them with the food.

The lions were kept in the boma for three months before they were released. The lions were not fed during the week before their release. Once the gate was opened, the lions were allowed to leave the boma on their own accord, although an impala carcass was provided outside the gate to entice them to move out. The events after release are described in detail in Chapter 4.

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CHAPTER 3

GENERAL METHODS

In this chapter, the general methods that were used during the study are described. The specific methods used in determining the different aspects of the study are described under Methods in each relevant Chapter.

Radio telemetry

Four lions were fitted with radio-collars. These radio collars each consisted of a MMK4 transmitter from Telonics^{TM} (Mesa, Arizona, USA) in the 148 to 151 MHz wavelength. The transmitter and a lithium battery was encased in dental acrylic and attached to a collar made from conveyer belting. The collar was fitted onto the animal and secured by pop-rivets. A Yaesu FT 290RII receiver and a four-element Yagi antenna were used to locate the radio signals from the collars. The distance from which the signal could be received ranged from 300 m in mountainous areas, to 3 to 4 km in higher-lying or flat areas. The radio-collars were replaced on two occasions when their battery life expired, or when they became too tight, especially on the male lions.

Monitoring the lions

Each lion could be recognised individually during the study period that lasted from January 1998 to February 2002. It was only possible to do long-term, continual monitoring of the lions up to October 1999, during which data were collected primarily to study the movements, prey use and breeding behaviour of the lions after release. Time restraints prevented continual observation during the latter part of the study. Since October 1999, the data collected were mostly on births and other factors affecting population dynamics, although kills were still recorded when observed or found. Being based full-time on Welgevonden, it was possible to collect all the data on births and other aspects of population dynamics as the events occurred.

The lions were monitored extensively after they were released. Monitoring usually started in the late afternoon when the lions first became active, usually just before sunset. It lasted until they became inactive or made a kill, often until just after sunrise. The lions became habituated to the vehicle quickly and it was possible, where the terrain allowed, to follow them for extended periods without disturbing them. A spotlight was used to maintain visual contact when the lions had to be followed at night. A red filter was initially used on the spotlight, but it appeared that the lions did not react differently to whether a white or a red light was used. A normal white spotlight was therefore used during the latter part of the study.

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CHAPTER 4

SOCIAL BEHAVIOUR AFTER REINTRODUCTION

INTRODUCTION

Reintroduction is an increasingly popular option to establish lions in areas from which they have become extinct. Although behaviour and social ecology of lions have been widely studied in natural lion populations (Schaller 1972; Bertram 1979; Cooper 1991; Stander 1992; Bosman & Hall-Martin 1997; Packer & Pusey 1997), less information is available on how the reintroduction of lions will affect their social behaviour.

Although it is often believed that lion prides are prime examples of sociality in predators, it may not be altogether true (Packer & Pusey 1997, Bothma & Walker 1999). Lions usually stay together in prides, and although some females are nomadic, it is usually the males who become nomadic after puberty. However, a nomad may become a pride resident, and vice versa. Nomadism and pride membership are therefore not mutually exclusive (Bothma & Walker 1999).

The females in a pride are usually interrelated, as are the males, but the males and females are usually not related (Bertram 1979). Females and their young are the focus of the pride (Bosman & Hall-Martin 1997), and female cubs born to pride lionesses usually remain in their natal pride for life (Bothma & Walker 1999).

The observations presented here is a detailed case history of the events and behaviour of the lions after they were reintroduced into the Welgevonden Private Game Reserve.

METHODS

The methods used during the study were described in Chapter 3. Upon their release, the lions were monitored extensively with the aid of visual observations and radio tracking equipment

RESULTS

After capture, the lions were first released and kept together in a boma on Madikwe before they were translocated to the Welgevonden holding boma. The lions settled into the boma without any confrontation between the individuals. The lions from the two different reserves interacted without any serious aggression, and there was soon playful interaction between members of the different groups. At the time of release, it was clear that the lions had established bonds and formed a single, cohesive group.

The lions were released on the morning of 16 January 1998. An impala carcass was provided outside the gate to attract the lions out of the boma. The gate was opened, and after initial hesitance the lions went out and started to feed on the carcass. They then went back into the boma after feeding and rested inside the boma for the remainder of the day, before leaving the boma again at 18:20 to move into the reserve. At 21:15, Female 3 broke away from the group and moved away on her own, while the rest of the lions stayed within 2 km of the boma. Female 3 was located the following morning about 6 km from the boma, where she had killed a bushpig. On the 21 January 1998, she was located after killing another bushpig. A wound was noted on her back, probably sustained while killing the bushpig. She was seen again on 28 January 1998. The wound on her back was now infested with maggots and she was weak. She was darted the following morning, the wound was treated and she was returned to the boma to recover. As follow-up treatment of the wound was necessary, the lioness was kept in the boma for another month. In this period the other lions had settled on the plains near the boma, staying within 3 to 4 km of the boma. However, they were never observed to approach the boma since their release, and had no known visual contact with Female 3 inside the boma before the events described below. They appeared to have bonded well and no signs of aggression were seen between the different lions, the group now consisting of two males and two females. It also appeared that they had settled in their new surroundings.

On the morning of 6 March 1998, they approached the boma for the first time after their release and appeared to be interested in the female inside. By now the wound on the back of Female 3 had recovered well and it was decided to release her from the boma while the other lions were in the immediate area. The other lions immediately approached her after she moved out of the boma. She was aggressive towards the two males, not allowing them to approach her. All five lions rested under the trees next to the boma for the rest of the day, with Female 3 lying a short distance away from the others. Whenever the males moved closer to her during the day, she became aggressive and growled at them. This situation continued for the following two days. She only allowed Female 2 to come close to her, and they even played with and rubbed against each other. Female 1 appeared unconcerned with the events around her and did not attempt to make any contact with Female 3, although Female 3 never showed any aggression towards her. It appeared that the continued aggression of Female 3 irritated the males, and they started to return the aggression.

In the late afternoon of the second day after the second release of Female 3, the two males again moved closer to her. When she growled at them, they attacked her. When the two males attacked Female 3, Female 1 suddenly joined them in the attack. Female 2 then joined the skirmish, but instead attacked the two males and Female 1, and chased them off. This happened twice more during the evening. During the night, Females 2 and 3 broke away from the other three lions and moved away together. They rejoined them three days later. When the two groups came together, Female 2 went to greet them with the normal greeting behaviour of rubbing, smelling and rolling. However, there were still signs of aggression between the males and Female 3. Female 2 intervened every time that the two males showed any aggression or moved towards Female 3, snarling at them and chasing them off. Females 2 and 3 broke away again the following day. During the following 2.5 months, the two groups rejoined on five different occasions, but the situation described above repeated itself every time. They would only stay together for a day or two before going their separate ways again.

On joining the group again on 25 May 1998, Female 3 was in oestrus. The previous aggression between her and the two males suddenly disappeared and Male 1 mated with her over a period of three days. However, Female 1 did not show any interest in Female 3 and avoided her as far as possible. While Male 1 mated with Female 3, Female 1 suddenly broke away from the group and moved away on her own to

Elandshoek in the southern section of the reserve, about 15 km away from the release boma. When she came into oestrus, she moved back to the central part of the reserve, apparently searching for the males. She joined Male 1 for two days while they mated, but returned alone to Elandshoek afterwards. She had her first litter of four cubs and managed to raise them on her own. She mated a second time, but this time Male 1 went looking for her on Elandshoek. He returned to the central part of the reserve after they had mated, and she had her second litter of four cubs on Elandshoek. She stayed with her offspring on Elandshoek until the end of the study and still does so today. However, Male 1 has now joined her permanently on Elandshoek. Male 2 and Females 2 and 3 are still in the central and western parts of the reserve with their offspring.

DISCUSSION

It has been observed previously that reintroduced lions tend to stay close to their release site after their release (Hunter 1998), but that a lack of social stability in a population results in increased mortality and movement (Stander 1990). Although it appeared as if a cohesive social bond had developed between all the lions while they were in the boma in the present study, it was not permanent enough to prevent later disintegration.

The lions were still young when they were originally captured. Female 3 was about 2.5 years old, while the others were barely two years old. Female 3, being older, would have gained more experience than the others before they were captured. She was also the one that initially broke away from the group after they were released, perhaps as a result of being more experienced.

The observed aggression between the lions after Female 3 was released was unexpected. Initially after her release from the boma, the males appeared to be interested in her, but did not show any visible signs of aggression towards her. The males only became aggressive towards her after her continued aggression towards them whenever they approached her. It possibly was a defence reaction, as she might have felt vulnerable because of her injury.

The behaviour of Female 2 in attacking the males after they had attacked Female 3 was considered strange for the following reasons:

- Female 2 and 3 originated from different prides in Pilanesberg
- Female 2 attacked the males with whom she had been familiar with since release
- Female 2 previously did not show any aggression towards the males
- Female 2 broke away from the pride with Female 3 after her attacks on the males
- Female 2 remained friendly with the males whenever they came together for short periods, but she still did not allow them to come close to Female 3. Later, when Female 3 came into oestrus and was joined by the males and Female 1, there was no aggression from either Female 2 or 3 towards the males, or from either of the males towards Female 3.

When Females 2 and 3 were still with the original group, Female 1 kept her distance and only once joined a skirmish between the males and Female 3. She eventually left the pride, as was described above. It is known that female lions can be nomadic

(Bothma 1998) and that they sometimes stay on their own, but this is not common. It is interesting to note that Female 1, who was associated with a group, became nomadic for a while after the other two females had joined the group. She left the group without any apparent reason and moved to the southern parts of the reserve. After that, she never sought the company of any of the other lions, except when she was in oestrus and wanted to mate.

CONCLUSION

The events described above reveal interesting aspects of lion social behaviour. No references of similar behaviour by lions could be found in the literature. The strange behaviour could likely have been caused the fact that no pride structure existed when the lions were first released into the reserve. As they were still young lions when they were captured, they had possibly never learned how to operate in a pride, as there were no older lions present at their release site to stabilize the pride structures. It is speculated that this behaviour is therefore more likely to occur in populations of young, introduced lions in an area vacant of older, resident lions. It will be interesting to see whether this is an isolated case, or whether similar behaviour will be observed in other reserves that introduce young lions.

CHAPTER 5

POST-RELEASE MOVEMENTS

INTRODUCTION

Translocation is now a well-known technique for the management of large carnivores. Early attempts of translocation were mainly done to remove problem animals that came into contact with humans and killed livestock (Van der Meulen 1977; Anderson 1981; Stander 1990). Translocation was used as an alternative to killing these problem animals. Translocation is currently often used to reintroduce animals into areas from which they have become extinct, or to create populations in new reserves or parks.

In the past, attempts at the translocation of large carnivores had mixed successes. Failures mainly occurred because of the poor understanding of the way in which the animals reacted to translocation. The lack of understanding was often created because there was little or no long-term post-release monitoring of the translocated animals (Van Dyk 1997). Stander (1990) stated that the success of a predator translocation programme depends heavily on such a long-term monitoring programme.

The fact that large carnivores, especially cats, are highly territorial (Schaller 1972; Smuts 1976, 1978b; Funston and Mills 1997; Hunter 1998; Bothma and Walker 1999) often causes low success rates in translocation projects involving these carnivores. Large carnivores tend to return to their capture site after reintroduction into the new area in

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what is known as homing behaviour (Hunter 1998). Hunter (1998) also mentioned that most of the previous efforts at large felid translocation were hard-releases in which the animals were freed at the release site as soon as possible after translocation, and did not have time to adapt to their new environment before their release. This resulted in low project successes because the animals returned to the capture sites more often than not. In contrast, the lions that were introduced into Phinda Resource Reserve in KwaZulu-Natal were released with a soft-release method after having been kept in a boma for several weeks to acclimatise first. The post-release movements and behaviour of most of the lions introduced into Phinda suggested that they did not experience the historical problem of homing behaviour that is often seen with carnivore translocations. Only two groups showed homing behaviour, and these groups were either males or were male-dominated (Hunter 1998).

Another factor that can influence the success of a translocation is competition with resident animals of the same or different species in the release area. Animals may leave reserves or parks because there is no space for them in the resident population (Hunter 1998). On Welgevonden there were none of the above factors present that could have influenced the success of the reintroduction attempt with lions. There were no other lions or large carnivore competitors like spotted hyaenas present on the reserve. The environment is controlled, and the reserve is fenced with electrified fencing that limited the chances of the lions escaping and returning to their capture sites. As in Phinda, the Welgevonden lions were first kept in a boma for an extended period, which gave them a chance to get used to their surroundings. Therefore, the lion introduction on

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Welgevonden presented a perfect opportunity to test the homing behaviour of lions after they were released from a boma where they had been kept for an extended period.

The objectives of this part of the study were to test whether the introduced lions showed any homing behaviour and to use it as an indication of the success of the reintroduction. The immediate movements after release, as well as the way in which the lions dispersed over the reserve after their release, were determined. The various management actions that could have influenced the post-release movements, and the way in which they could have influenced the success of the reintroduction attempt, are also discussed.

METHODS

The general methods that were used during the study have been described in Chapter 3. After the lions were released, they were monitored extensively. Their movements were recorded primarily by direct observations as far as the terrain allowed. Where it was impossible to follow the lions in inaccessible areas like hills, their location was determined by triangulation by using the radio-collar signals (Amlaner & Macdonald 1980). In doing so, the geographical position of the observer, where the first radio signal from the collar is received, is determined by GPS and noted on a map. The observer then takes a compass reading of the direction of the signal. The compass reading is then used to draw a straight line from the position of the observer to the origin of the signal. By repeating this procedure from a second or more points in quick succession, the estimated location of the lion is at the point where the drawn lines intersect.

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A daily location of the lions was determined for the first three months. Because there was at least one collared animal in each group of lions on the reserve during the first three months, it was possible to determine the daily positions of all the lion groups. The data were analysed separately for each lion, because the structures of the groups changed during the first three months after release. In cases where the individual lions stayed together for the first three months (for example lions 1, 2 and 3), the data for these lions were pooled. The direction and distance of travel, and the subsequent dispersal from the release boma were determined by using the Animal Movement Analysis Extension for ArcView GIS software (Hooge & Eichenlaub 1997).

The location data for the first three months after release were used to determine the direction of movement. To test whether the lions showed any homing behaviour, the direction of movement relative to the direction of the capture site was determined. The Rayleigh test was used to test whether the direction of movement was uniform or randomly distributed around a circle. The Rayleigh test is a one-sample test for mean angles (Zar 1984) and was used to determine significance of direction of travel (Hooge & Eichenlaub 1997). It uses the *r*-value (angular concentration) to determine the confidence intervals of whether the population's mean angle of movement over a period is equal to a specified value, in this case the direction of home (capture site). The mean angle of movement was determined by the Animal Movement Analysis Extension for ArcView GIS software (Hooge & Eichenlaub 1997). It uses the daily direction of movement over a given period to determine a mean bearing of movement for the whole period

RESULTS

Lions 1,2 and 3 stayed together for the first three months after their release on Welgevonden, and the data of their dispersal for that period were therefore pooled. Lioness 4 was with lions 1, 2 and 3 for the first 1.5 months after release, and with lioness 5 during the second 1.5 months. Therefore, the dispersal of lioness 4 is the same as that of lions 1,2 and 3 for month 1, and the same as that of lioness 5 for month 3. Therefore, although lioness 4 was never alone, it was necessary to show her dispersal separately from the rest in all the figures and tables that follow. The way in which the lion groups broke up and dispersed is described in detail in Chapter 4.

Dispersal after release

Except for lioness 5 who broke away alone, the lions stayed within the vicinity of the boma for the first month after their release, and then slowly dispersed into the rest of the reserve. Figures 5.1 to 5.3 illustrate the dispersal of the lions for the first three months after release. The concentric circles indicate equal distances away from the release boma, and each circle represents 1 km on the ground. From Figures 5.1 to 5.3 it is clear that, except for lioness 5 who broke away from the rest just after her release, the lions rarely moved more than 4 km away from the boma during the first three months after release.

The mean distance that the lions moved from the boma in the first three months after their release is shown in Table 5.1. It ranged from 2.38 ± 0.93 km to 6.06 ± 1.26 km in various lions. The longest movement of 6.06 km away from the boma involved lioness 5 just after she broke away from the rest of the group. The maximum distance moved away from the boma during the first three months after release was 8.4 km for lions 1, 2 and 3 during month 3. There was a significant increase in the mean distance that all the lion groups moved away from the boma during the first three months after their release, showing increasing dispersal with time.

Daily distance moved after release

There also was a significant increase in the mean daily distance moved by two of the lion groups during the first three months after their release (Table 5.2). The mean distance moved for the first three months ranged from 3.10 ± 1.30 km to 5.22 ± 3.60 km. The number of radio fixes of lioness 5 for months 1 and 2 was smaller than the number of radio fixes for the other lions during the same period. This happened because she was put back into the boma for almost four weeks after she sustained injuries when killing a bushpig (Chapter 4). The maximum recorded distance travelled per day for the first three months was 16.15 km. This was done by a male after he broke away from the group (lion 1,2 and 3) for six days. This was also the maximum recorded distance travelled by any lion for the whole study period.

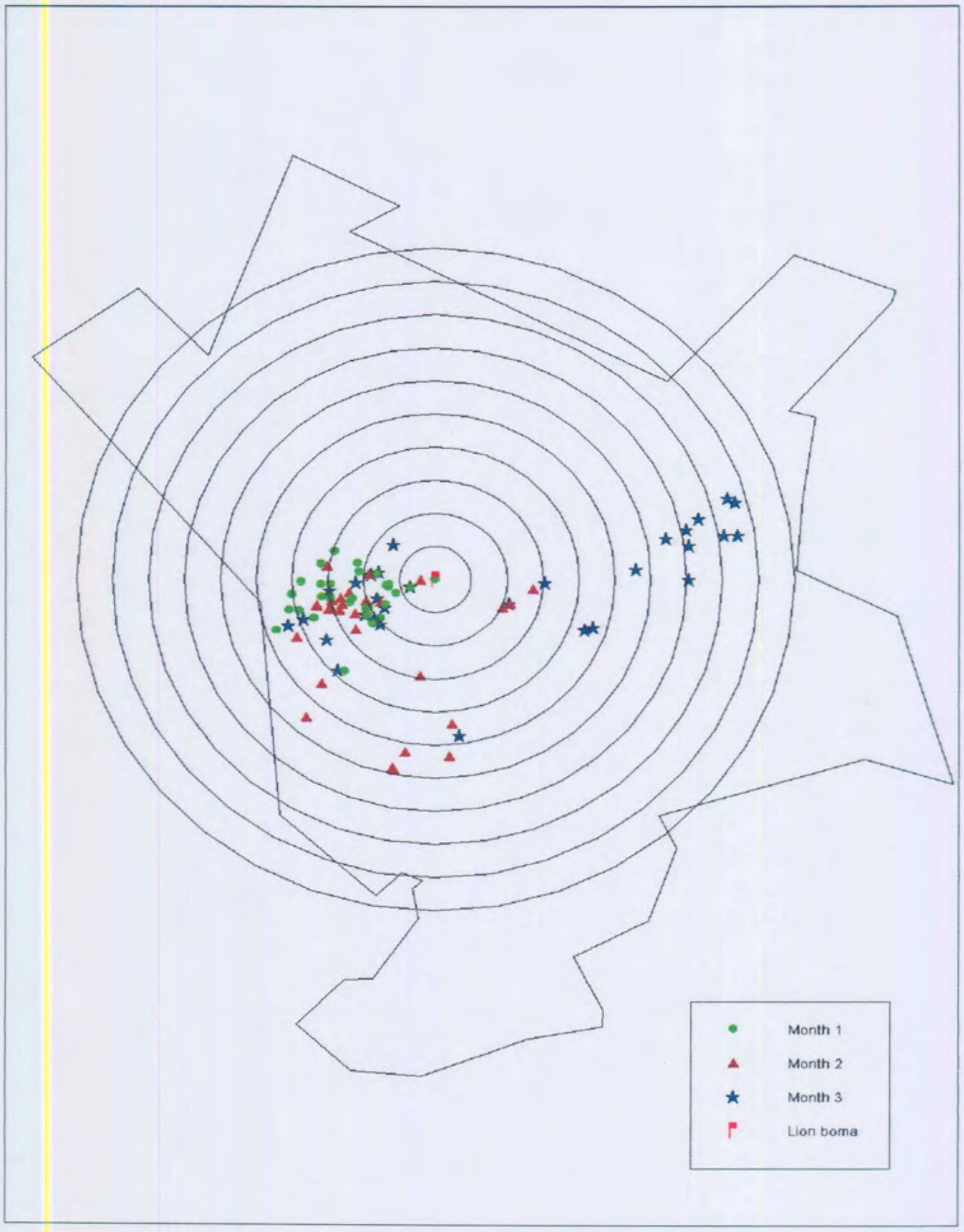

Figure 5.1. The dispersal of lions 1, 2 and 3 to show the increasing distance that they moved away from the boma during the first three months after their release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa. Each circle represents 1 km on the ground.

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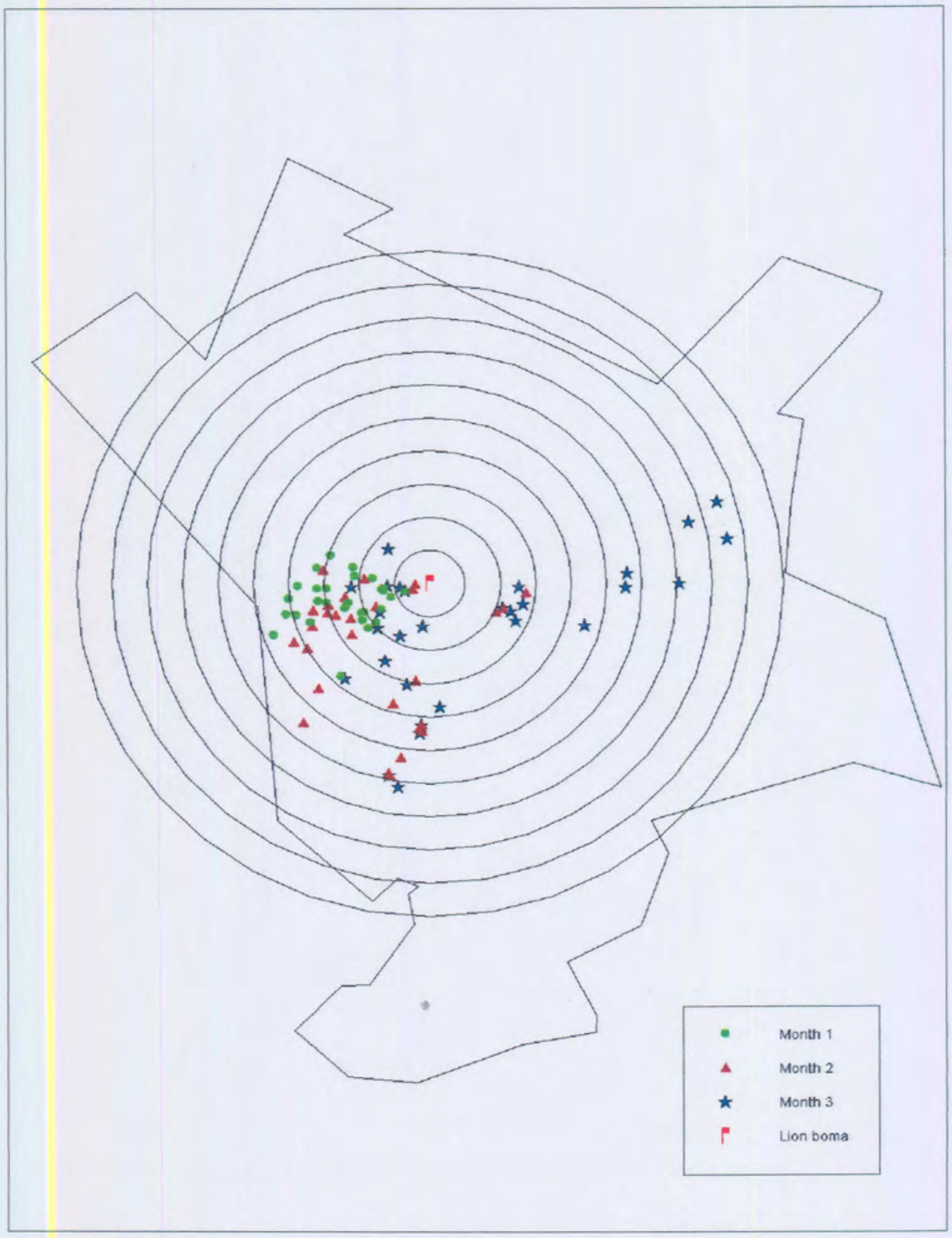

Figure 5.2. The dispersal of lioness 4 to show the increasing distance that she moved away from the boma during the first three months after her release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa. Each circle represents 1 km on the ground.

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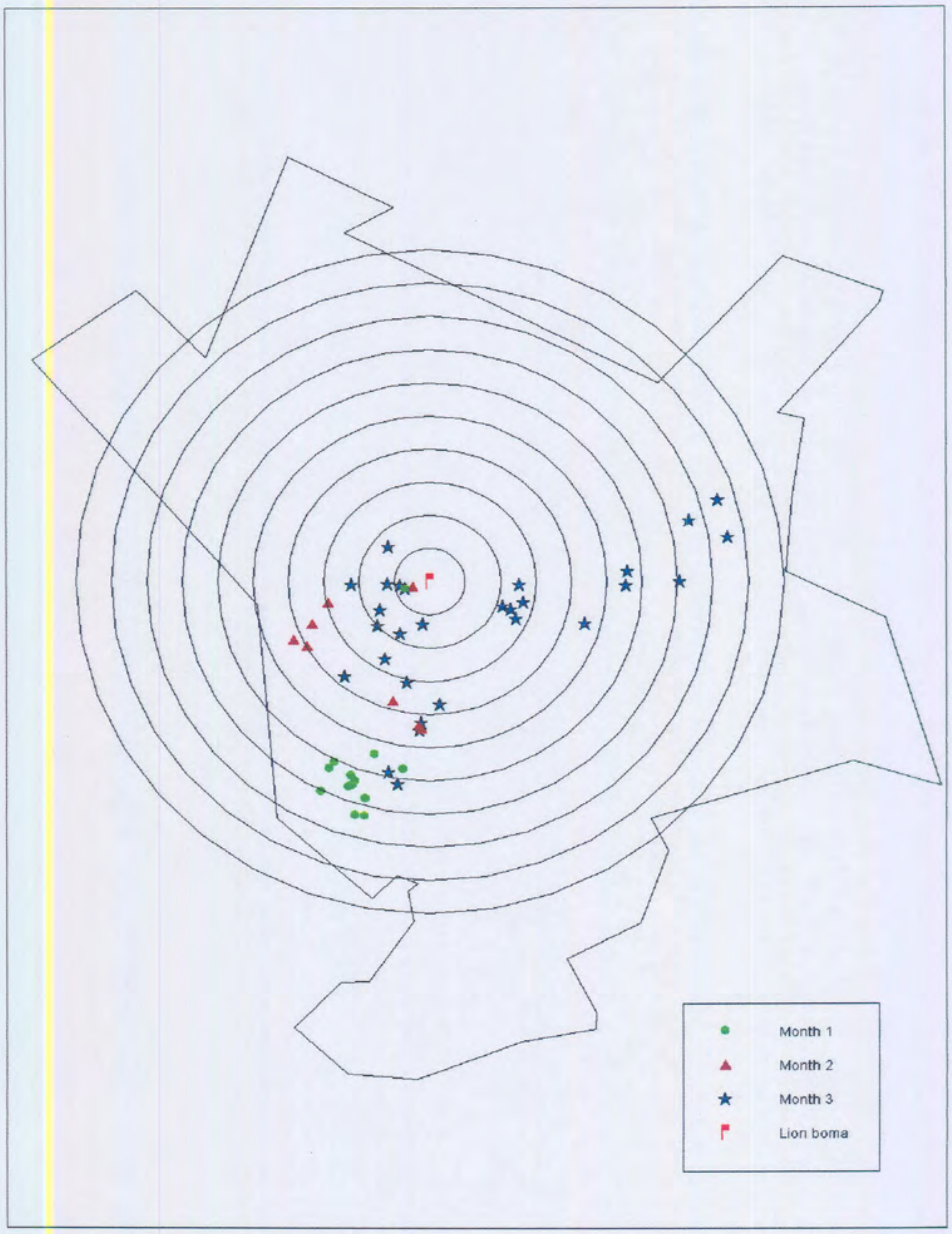

Figure 5.3. The dispersal of lioness 5 to show the increasing distance that she moved away from the boma during the first three months after her release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa. Each circle represents 1 km on the ground.

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Table 5.1: The mean, standard deviation and ANOVA results of the distance (km) that the introduced lions moved from the boma during the first three months after their release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

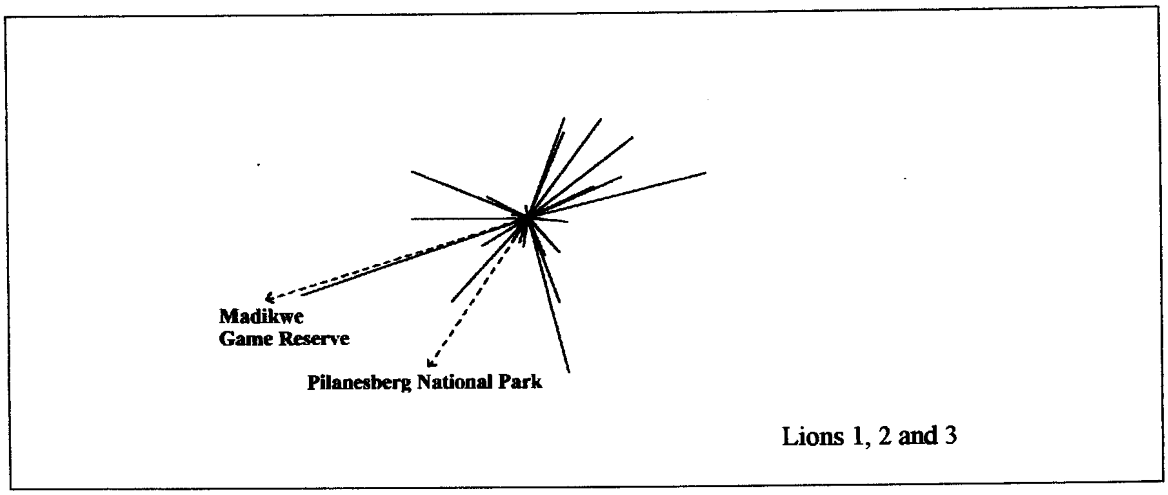
LION NUMBER	**DISTANCE MOVED**			**ANOVA**		
	Month 1	**Month 2**	**Month 3**	**F-value**	**P-value**	**df**
1,2 and 3	2.38 ± 0.93	3.18 ± 1.42	4.01 ± 2.33	7.37	0.001	2
4	2.38 ± 0.93	3.20 ± 1.45	3.52 ± 2.15	4.15	0.02	2
5	6.06 ± 1.26	3.32 ± 1.28	3.52 ± 2.15	9.44	0.0003	2

Table 5.2: The mean, standard deviation and ANOVA result of the daily distance (km) that the introduced lions moved during the first three months after their release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

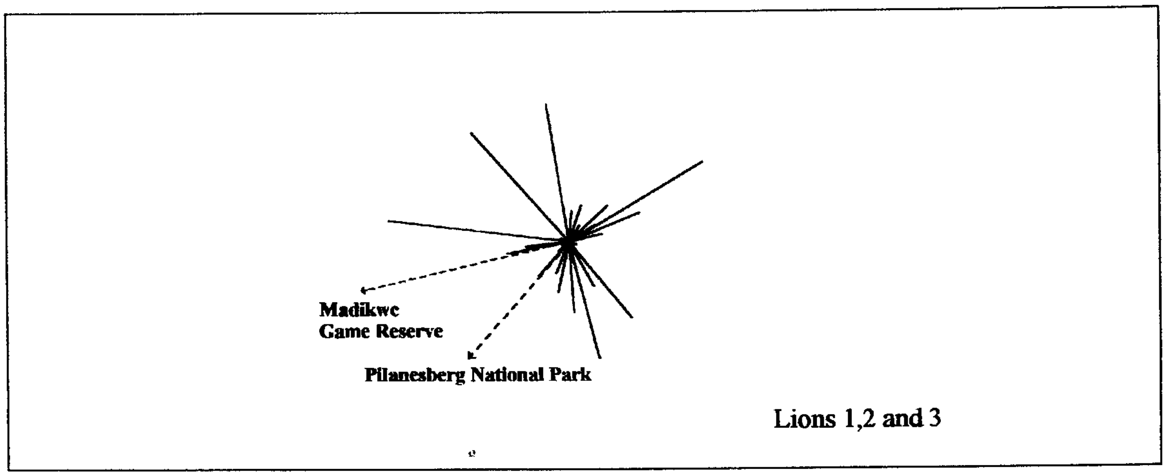
LION NUMBER	**DISTANCE MOVED**			**ANOVA**		
	Month 1	**Month 2**	**Month 3**	**F-value**	**P-value**	**df**
1,2 and 3	3.10 ± 1.30	3.89 ± 1.93	5.22 ± 3.60	5.50	0.006	2
4	3.10 ± 1.30	4.0 ± 1.68	3.67 ± 2.11	1.90	0.16	2
5	1.72 ± 1.99	4.61 ± 1.86	3.67 ± 2.11	5.59	0.007	2

Table 5.3. The results of circular statistical analysis of the direction of movement data, to test whether the released lions showed any significant movement towards their original capture sites (homing) during the first three months after their release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

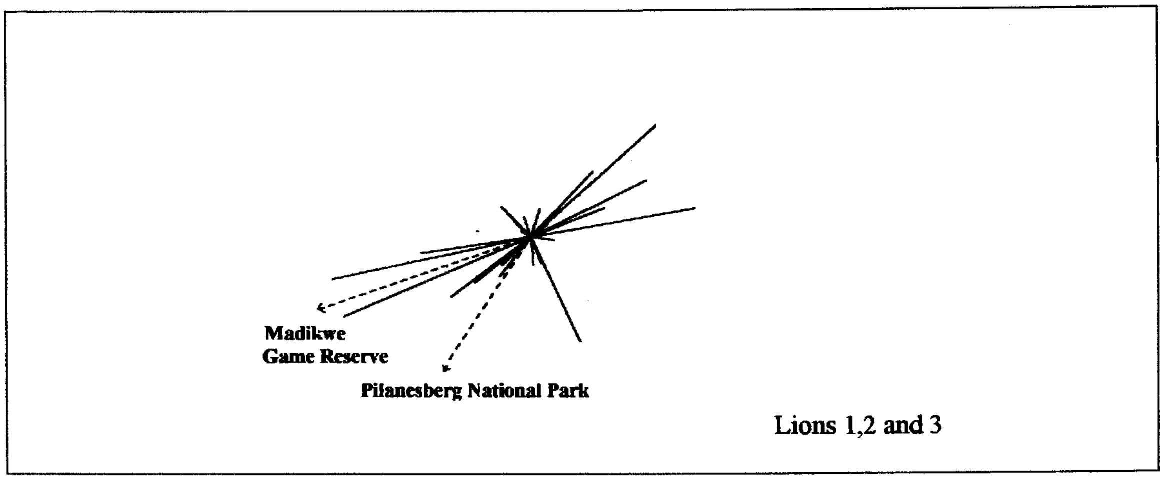
	LION 1,2 AND 3			**LIONESS 4**			**LIONESS 5**		
	Month 1	**Month 2**	**Month 3**	**Month 1**	**Month 2**	**Month 3**	**Month 1**	**Month 2**	**Month 3**
Mean bearing in degrees	128.75	264.67	30.45	128.75	146.27	180.50	209.25	46.51	180.50
Angular deviation (s)	131.69	123.94	126.02	131.69	127.50	115.59	95.26	131.27	115.59
Angular concentration (*r*)	0.07	0.10	0.09	0.07	0.08	0.13	0.25	0.07	0.13
Rayleigh's z-value	0.15	0.25	0.23	0.15	0.19	0.48	0.76	0.03	0.48
Number of bearings	30	27	29	30	27	28	12	7	28
Homing behaviour	Negative	Negative	Negative	Negative	Negative	Negative	Negative	Negative	Negative



Month 1

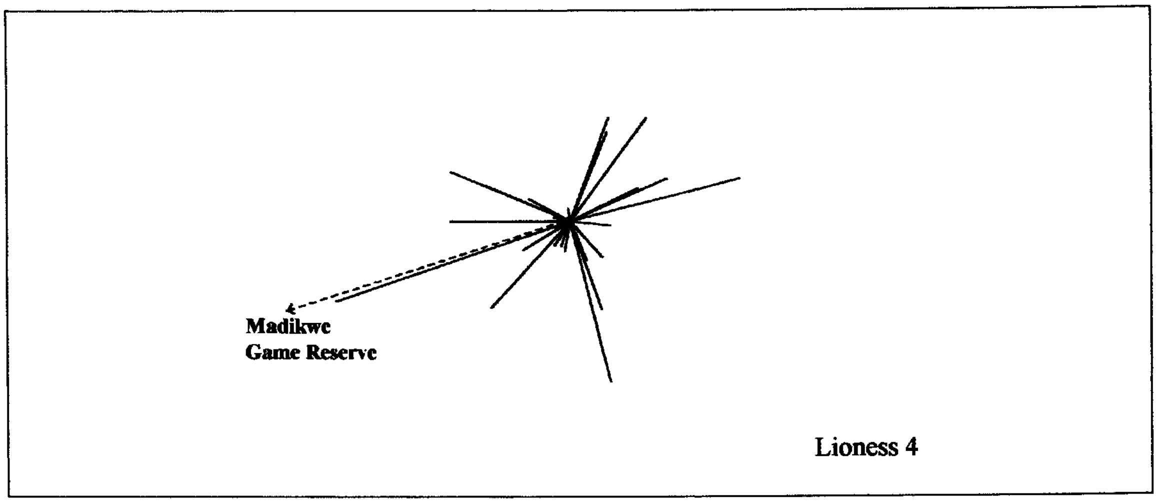


Month 2

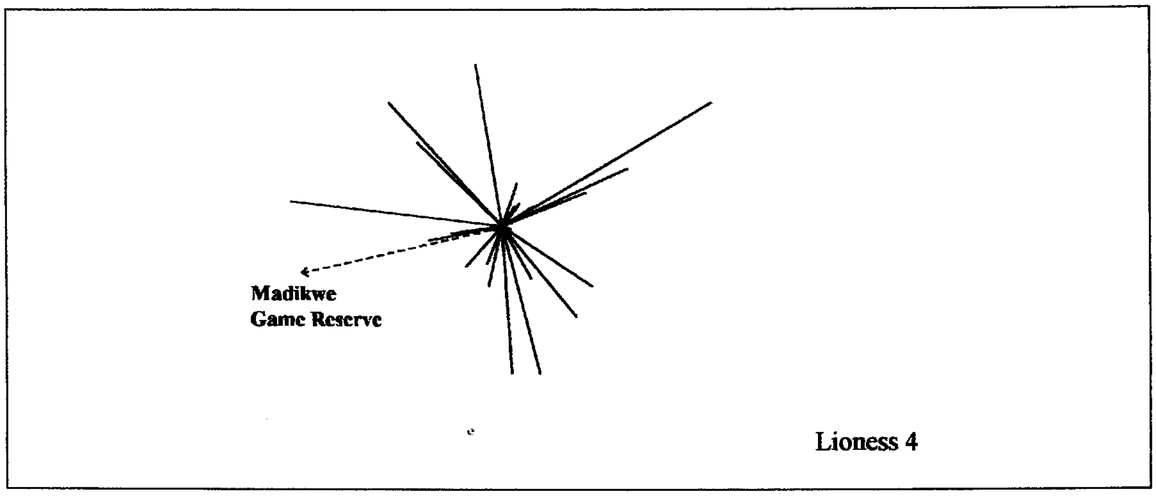


Month 3

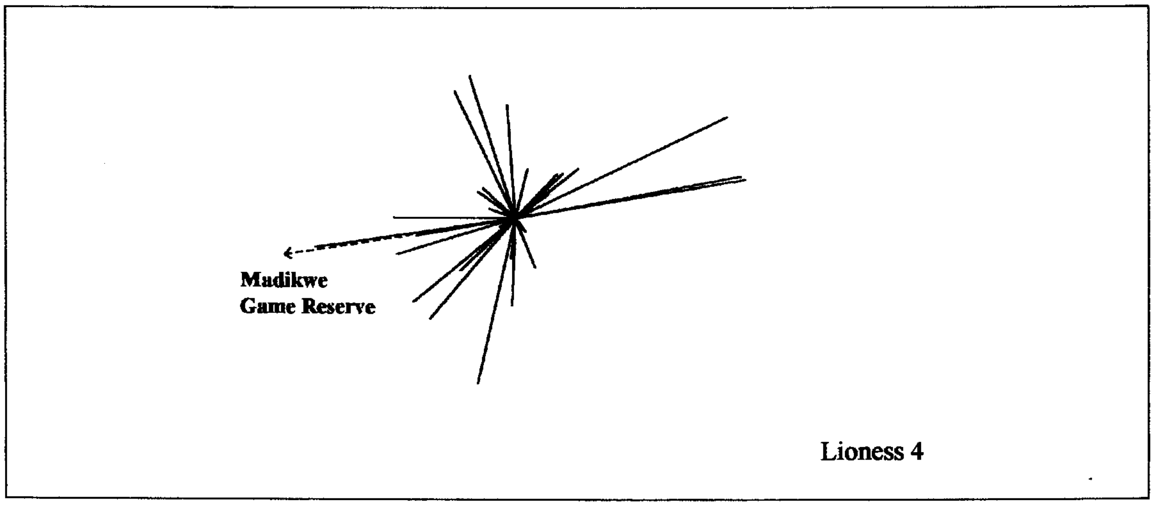
Figure 5.4. The daily direction of movement of lions 1, 2 and 3 for the first three months after their release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa. The dotted lines indicate the direction to the original capture sites.



Month 1



Month 2



Month 3

Figure 5.5. The daily direction of movement of lioness 4 for the first three months after her release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa. The dotted line indicates the direction to her original capture site.

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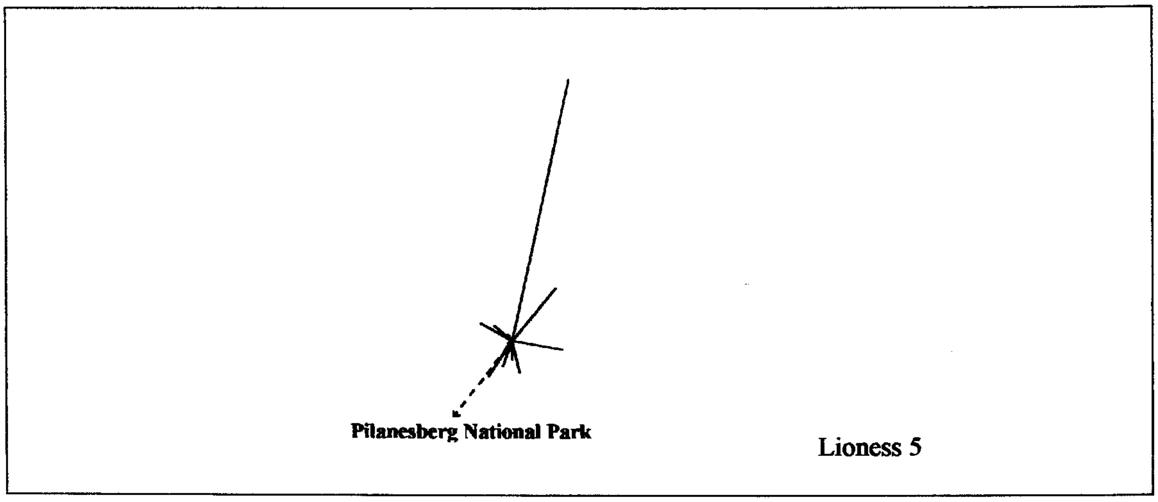
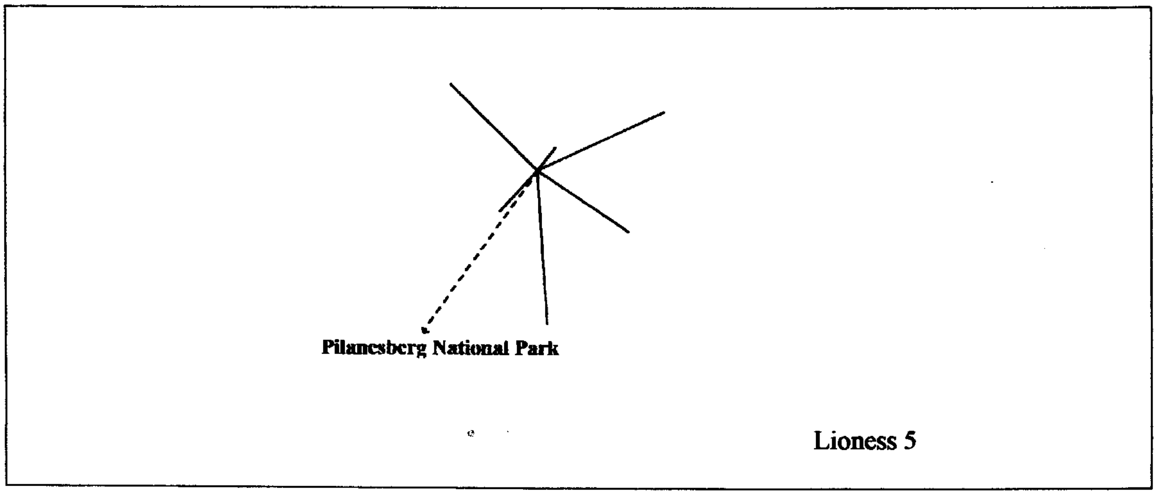
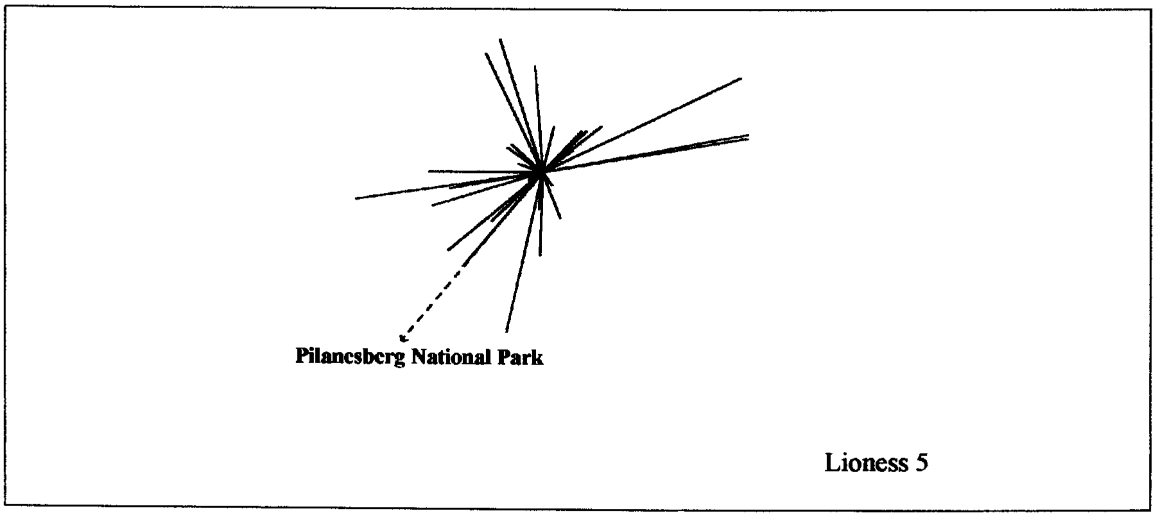


Month 1



Month 2



Month 3

Figure 5.6. The daily direction of movement of lioness 5 for the first three months after her release on the Welgevonden Private Game Reserve in the Waterberg Region of South Africa. The dotted line indicates the direction to her original capture site.

Direction of movement after release

The direction of movement was randomly distributed around the release point for all the lions. Figures 5.4 to 5.6 show the spider diagrammes that indicate the daily direction of movement for the different lions during the first three months after their release. The dotted lines indicate the directions to the sites where the lions were captured originally (Madikwe and/or Pilanesberg). The results of the statistical analysis of the direction of movement data as depicted in the spider diagrammes in Figures 5.4 to 5.6 appear in Table 5.3. Indicated in the results are the mean directions of movement, *r*-values (angular concentration), s-values (angular deviation), Rayleigh's z-values, and the number of bearings that were used in the analysis. The *r*-values were too small to determine confidence intervals. This indicates that there was no significant direction of orientation of the data (Zar 1984).

DISCUSSION

The objectives of a reintroduction attempt for any species will determine whether the reintroduction was successful or not. One of the factors that will determine success is whether the animals stayed in the area where they were released, or whether they moved out of this area into neighbouring areas, or back home. It is known that carnivores, especially felids, have a marked ability to return to their place of capture, even as far as several hundred kilometres away (Linnell, Odden, Smith, Aanes & Swenson 1997). This has often made people question whether such reintroductions are viable methods of establishing felids in new areas. Several successful lion reintroductions have been done in the recent past in various reserves, and the available knowledge on the management of such reintroductions has increased. The factors affecting such reintroductions are now better understood. and every reintroduction in the future will only increase the existing volume of knowledge on the reintroduction of carnivores.

The reintroduction of lions into Welgevonden was successful, and the reintroduced lions soon established ranges (Chapter 5) and bred (Chapter 6) without any apparent difficulties. The movements of the reintroduced lions on Welgevonden suggested that they did not experience the problems that are often associated with carnivore reintroductions.

Dispersal and daily distance moved after release

The reintroduced lions showed increasing dispersal with time after they were released on Welgevonden. Except for lioness 5, who broke away from the rest on the first day after her release, the lions stayed within 2 km of the boma for the first three days after their release. Over the following three months they showed an increase in the distance that they moved away from the boma. The increase in distance with time that they moved away from the boma coincided with the increase in distance that they moved per day. Hunter (1998) made similar observations on released lions in Phinda Resource Reserve. It appears as if this is a general trend with reintroduced lions because similar patterns were also observed with other reintroductions (Van Dyk, *pers. comm.*[1]).

Direction of travel and homing behaviour

The released animals did not show any obvious homing movements. The angular distribution or *r*-values were too small to determine confidence intervals for the data. This indicates that there was no significant direction of orientation of the data (Zar

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1984), which means that the lions did not show any significant movement into any particular direction, including the direction of the original capture sites.

However, the movements of lioness 5 might be an exception. It appears as if her initial movement on the day of release was back towards her capture site, but this was for one day only before she encountered the fence and changed her direction. As this was a single day's movement only, it may not be a significant movement towards her capture site. The fact that she encountered the fence which caused her to change direction, indicates that she could have left the reserve at that time, but whether she would have gone all the way back to the capture site are impossible to tell.

The above case highlights a difficulty that will be experienced with similar studies on other small reserves. It will be difficult to prove on small reserves that lions do not show homing behaviour, even if statistical tests indicate that there were no significant movements towards the capture site. Sustained movements in the direction of the capture site are prevented by the presence of fences on small reserves, while it will be possible for lions introduced into large or unfenced areas to make sustained movements towards home. The release site on Welgevonden, as would be the case in most other small reserves, was close to the boundary fence, and lions are therefore likely to encounter a fence if successive movements in the same direction are made.

Various other factors will have an effect on the initial movements of lions after their release. The availability of suitable habitat and/or areas with high concentrations of prey will influence the lions' decision on the direction in which they will move (Caro 1994). The release boma on Welgevonden was on the north-eastern side of a plain, which stretched in a V-shape towards the west and south, incidentally also in the

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direction of the original capture sites. The lions used this plain, with its high concentrations of prey, extensively for the first two months following their release. Hunter (1998) used a method that uses the angles of direction of each movement from the release site to indicate homing behaviour. Using this method with the data collected on Welgevonden for the first two months after their release indicated some homing behaviour. Normally, this homing behaviour would have been interpreted as an attempt at returning to the capture site. However, it appeared that in this particular case it also indicated the direction of the plains that were mentioned earlier, and not merely a movement towards home. This motivated the use of the mean direction of movement as used in this study as an indicator of homing behaviour, rather than the method used by Hunter (1998).

The method used in this study determines the mean direction of movement by using the direction of each location point from the previous location point, rather than from the release site as used by Hunter (1998). The method used with this study appeared to give a better estimate of homing behaviour, because even if the availability of prey or suitable habitat influenced single movements, the mean direction of movement would have been towards home if the lions did show any homing behaviour. The different results shown by the two different methods serve as a good example of the caution needed when choosing methods to analyse homing behaviour, and the caution needed when the results are interpreted. When determining homing behaviour, all the possible factors that can influence initial movements should be considered before conclusions on homing behaviour are made.

Although they cannot be tested statistically, other observations on the movements of the lions just after their release [illegible]s no homing behaviour. If

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the lions had any intention to go back home, one would have expected them to attempt to cross the fence or to stay next to the fence closest to their capture sites for extended periods. The fact that this did not happen indicates that there was no real urge to go back to the capture sites. Although the lions came across the fence on several occasions, no attempts at escape were observed during the study period. Considering these observations and the results of the mean direction of movement method used earlier, it can probably be assumed that the lions on Welgevonden did not show any homing behaviour.

Contribution of management actions to the success of a reintroduction

The fact that no attempts to escape were observed, can largely be attributed to the value of some management actions such as boma training in ensuring project success. Van Dyk (1997) advocates the necessity of boma training to increase project success. Keeping lions in a boma for extended periods, and exposing them to electrified fencing is a valuable tool to increase the chances of project success. After some exposure to the electrified fence, the lions soon learn to stay clear of it. Clear examples of them avoiding the fence were observed on two occasions during the study period. On both occasions, cattle grazed on neighbouring properties within view of the lions. Although the lions showed an interest in the cattle and walked up to the fence, they stayed clear of it without making any attempt at crossing the fence. The lessons learned in the boma were obviously still remembered. A lion escaped from Welgevonden on only one occasion, but that was after the study period. This incident involved a subadult male that was born on Welgevonden, and therefore was not boma-trained and was unfamiliar with the fence. He followed a prey animal that he was chasing through the fence. However, whether there was a correlation between the lion breaking out and the fact that the lion that broke out was unfamiliar with the fence, is unknown and is not applicable to this study.

The age at which lions are translocated can possibly also influence whether they will return to their capture site or not. Lions that are translocated at an age at which they would normally start dispersing are more likely to settle in a new area than lions that have already established themselves in an area or in a pride at the original capture site. The Welgevonden lions, except lioness 5, were still young (22 to 24 months old) and at an age when they would normally have dispersed from their natal prides when they were captured. They were probably not yet established in prides by the time that they were captured, and would therefore possibly have settled in a new area elsewhere anyway had they not been translocated. The fact that lioness 5 was older (30 months old) than the rest when she was captured, could possibly explain her breaking away from the pride just after release. Although it can be speculated that she had already established herself in a pride at Pilanesberg and wanted to return there, no data are available to support this.

The period in a holding boma should be long enough for the animals to settle down, and to get to know the electrified fences and each other (Van Dyk 1997). It often happens that lions from different prides, and even from different reserves, are introduced into the same reserve. The time that they spend together is valuable for establishing bonds, relationships and prides. Through boma training, unrelated and unfamiliar animals can be encouraged to form a stable social group or pride. Even unrelated males can be bonded in this way (Van Dyk *pers. comm*[1]). The Welgevonden lions stayed in the boma for 3.5 months, and although they came from different reserves, four of the li [illegible] ediately after their release.

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Although the bonds and social organisation of the lions on Welgevonden have changed over the years since introduction, the bonding of the lions in the boma undoubtedly contributed to the success of the project.

The results of this and other projects (Hunter 1998) indicate that reintroduced lions that are habituated in a boma tend to stay in the vicinity of the boma for the first month or two after release, and then slowly disperse into the rest of the reserve. The placement of the boma can therefore have a significant influence on the short-term project success. The boma should be placed in an area with a high concentration of potential prey animals, as well as a suitable habitat. This could be crucial for project success, because the lions are likely to stay in the vicinity of the boma area after their release. If the boma is located in a suitable area, the newly introduced lions will have an area in which to settle down before they disperse to establish territories in the rest of the reserve.

CONCLUSIONS

The success of this and other lion reintroductions indicates that reintroduction can be a viable method of establishing lions in reserves from which they have become extinct. Although there are numerous factors, like homing behaviour, that could cause the failure of such reintroduction attempts, it has been shown more than once that certain management techniques, like boma training, can serve as valuable tools to increase the chances of project success. The knowledge and experience gained with this and other similar reintroduction attempts will prove to be valuable aids to increase the chances of project success for future reintroductions elsewhere. However, continued research and monitoring will be necessary to increase the available

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knowledge on the reintroduction, translocation and behaviour of lions after a reintroduction

CHAPTER 6

RANGE ESTABLISHMENT, USE AND HABITAT SELECTION

INTRODUCTION

During historic times the lion ranged throughout the continent of Africa, as well as through much of Europe and Asia (Bothma & Walker 1999). They are now mostly restricted to isolated populations in national parks and private game reserves. More and more lions are being introduced into new, small reserves or wildlife ranches. Most of these areas are so small that the long-term viability of lions in these areas is uncertain. Although various introductions have already taken place, the scientific knowledge on how lions react to such introductions is limited. Range establishment by wild lions in large areas has been studied in detail, but it is still largely unknown for introduced lions in small reserves, except that the size of the ranges in small reserves will obviously be influenced by the size of the area and the available habitat.

The availability of resources appears to be the major factor in determining the spatial characteristics of felid ranges (Sandell 1989; Mizutani & Jewell 1998). The size of the ranges of females is largely determined by the availability and distribution of prey (Sandell 1989; Bothma, Knight, Le Riche & Van Hensbergen 1997), while the establishment of ranges of males is heavily influenced by the availability of mating opportunities (Schenkel 1966; Sandell 1989; Bothma 1998).

The fact that lions are social animals (Bothma 1998) has important implications for their ranging dynamics. They show complex patterns of territoriality that influence the social behaviour of the population. Prides occupy defended ranges or territories, whereas nomads have undefended ranges (Bothma & Walker 1999). Females, most often related, live in stable social groups and may occupy the same ranges for generations (Hanby, Bygott & Packer 1995). Coalitions of males associate with females and have exclusive ranges that can include more than one pride of females (Sunquist & Sunquist 1989; Bothma 1998). Pride lions, especially males, patrol their territories regularly, often to the exclusion of all else at the expense of large amounts of energy (Bosman & Hall-Martin 1997; Funston & Mills 1997). When neighbouring prides meet, they will more often than not only approach each other, and then withdraw (Bosman & Hall-Martin 1997). This is usually not the case with intruding males, and fights between males are fierce, sometimes causing fatal wounds (Bothma & Walker 1999).

The territorial system of lions is dynamic and fluctuates depending on the reigning environmental conditions (Schenkel 1996; Bothma & Walker 1999). The size of the range of lions is largely dependent on the resource abundance and availability (Bothma 1998), as well as the size of the pride (Stander 1991a). Considerable variations in range size have been observed. The ranges of lions on the Serengeti Plains, where prey and lair-sites are scattered, are five times larger than in the Ngorongoro Crater, where prey and lair-sites are more evenly distributed (Hanby *et al.* 1995). Range size in the arid Etosha National Park may be as large as 2 075 km^2, presumably due to migratory movements and a low density of prey (Stander 1991a). Range size of lions in Uganda underwent a reduction in size when there was an increase in the lean season biomass of prey in good years (Van Orsdol 1982; Van Orsdol, Hanby & Bygott 1985). During droughts, the size of the range can expand considerably. In the central Kalahari, the range size of one pride increased from 702 m^2 to 3 900km^2 in response to prey dispersion during a drought (Owens & Owens 1984). In times of extreme hardship, the territorial system of lions in the Serengeti may even break up (Scheel & Packer 1995). Lions from different prides may also share the same areas during times of extreme drought and hardship (Eloff 1973a; Bothma & Walker 1999). Range size of females may also decrease dramatically when there are small cubs to care for (Bothma & Walker 1999).

Lions occur in various habitat types all over Africa, ranging from semi-arid landscapes in Etosha National Park and the southern and central Kalahari (Eloff 1973a; Mills, Wolff, Le Riche & Meyers 1978; Owens & Owens 1984; Stander 1992, 1997; Bothma 1998), to arid savannas like Kruger National Park and Chobe National Park (Smuts 1978c, 1982; Viljoen 1997), the grasslands of the Masai steppe (Mills *et al.* 1978; Saba 1979), the mesic savannas of the Serengeti and the Ngorongoro Crater (Wright 1960; Schaller 1972; Bertram 1979; Van Orsdol 1982; Hanby *et al.* 1995) and the mesic savannas and subtropical areas of Kwazulu-Natal (Anderson 1981; Hunter 1998). The lions of Welgevonden were introduced into a habitat type unlike any of the above, namely the Waterberg Mountain Bushveld. This is a semi-arid mountainous savanna, requiring the lions to adapt to it in a different way than elsewhere.

The spatial patterns of lions have been well studied in natural and established populations in Africa, but little in relocated and reintroduced populations (Hunter 1998). Little data are available on range use and territory characteristics for reintroduced felids. Ruth, Logan, Sweanor, Smith & Temple (1993) studied three translocated mountain lions *Puma concolor* and mention that ranges were established, but do not give additional details. Lynx *Lynx lynx* populations have been re-established in several European countries (Breitenmoser & Breitenmoser-Wursten 1990; Yalden 1993), but limited data on range establishment are given. Hunter (1998) did a detailed study on the behavioural ecology of reintroduced lions and cheetahs *Acinonyx jubatus* in the Phinda Resource Reserve, and gives detailed descriptions of the range establishment and use of these felids. The present project is a further attempt to determine the range establishment and use of reintroduced lions, but in a totally different environment than any of the other introductions mentioned above.

The reintroduction of lions into Welgevonden offered opportunities to study the range establishment and range use of lions in an area where there are no competitors present, and which has an abundance of prey. It therefore offers the opportunity to the lions to choose the area in which they want to establish a range without the interference from competitors of the same or different species. The fact that there were no other lions present on the reserve gave the reintroduced lions the opportunity to establish ranges that only had to contend with the limits of the natural resources and the reserve boundary. Because of the limited size of the reserve, the prey population is non-migratory. This allows the lions to hunt throughout the year.

In this chapter it is attempted to give a better picture of how the lions established their ranges after reintroduction into an area without competitors. Details of range establishment and range use are given for the first three months after reintroduction, as well as the final home range establishment three years after reintroduction. Seasonal ranges and the ranges of females with small cubs are also presented. An internal fence was removed during the study period, giving the opportunity to determine how the lions dispersed into a new area after they had settled down initially after their reintroduction. Habitat selection by the reintroduced lions was also determined, and was correlated with the dispersion of the lions after reintroduction.

METHODS

Radio telemetry

Radio telemetry was used to locate the radio-collared lions. This was done daily when possible, but at times the interval ranged to once every third day. Tri-angulation, as described in Chapter 5, was often used to determine the position of a lion in inaccessible terrain. In order to determine the range of the lioness without a radio collar, opportunistic sightings or reports from guides were used.

Range use analysis

In order to determine the range use of the lions during the study period, the time interval between fixes was taken as a minimum of one day. This was done to prevent auto-correlation of the data (Swihart & Slade 1985). Independence between successive observations is an implicit assumption in statistical analysis of animal movements. Auto-correlation of data occurs when an animal's position in its range at time $t+k$ is not a function of its position at time t (Swihart & Slade 1985). Because frequent successive observations will tend to be positively correlated, sample variances will be underestimates of the true values, and statistical estimates of range size will underestimate the true size of the range. Non-statistical range size measurements, like the minimum convex polygon, are not affected by dependent data in this manner. Hunter (1998) used a simple way of overcoming this problem. The time to independence between successive locations is the time it that takes an animal to move through its range (Harris, Cresswell, Forde, Trewhella, Woollard & Wray 1990). Lions on Welgevonden could easily, and often did, traverse their ranges within a day. Therefore, intervals of a day will be sufficient to establish the range sizes correctly. When lions were stationary for more than one day, those locations were removed and only the first location was used in the analysis. Daily locations have previously been used in other studies and produced meaningful results (Hunter 1998; Mizutani & Jewell 1998).

Various methods exist to calculate range size of animals. Two methods were used for this study, the minimum convex polygon method and the kernel utilisation distribution. Although one of the earliest and simplest techniques for range size analysis, the minimum convex polygon method is still used most frequently. It is the only method that is strictly comparable between studies, and its inclusion as one of two or more methods of range calculation is therefore valuable (Harris *et al.* 1990). In order to compare the size of the various ranges found in this study with those of other studies, the minimum convex polygon method was therefore included with the kernel method. The kernel method is a probabilistic method of range size and use analysis that attempts to assess an animal's probability of occurrence at each point in space. It is commonly referred to as the utilisation distribution (Van Winkle 1975). It determines the range size and use in terms of the relative amount of time that an animal spends in different areas of the range (Worton 1987, 1989; Seaman & Powell 1996). Kernel methods give a good indication of the patterns of range use (Worton 1995), range size, and the internal structure of the range (Harris *et al.* 1990). Kernel methods are increasingly being used in range size and use analysis because of its advantages over more traditional methods. It has, for example, recently been used in other studies of the range use patterns of large carnivores in South Africa (Bothma *et al.* 1997; Hunter 1998).

The distribution points as determined through telemetry fixes were plotted and analysed by using Geographical Information Systems (GIS) software (ArcView version 3.1). The *Spatial Analyst* extension for ArcView and a new extension that was developed specifically for animal movements, *Animal Movement Analysis for ArcView* (Hooge & Eichenlaub 1998), were used to perform the range use analysis. Although this extension gives the choice of several different methods of range use analysis, the minimum convex polygon and kernel methods were adopted for this study. Range sizes were determined separately for the male coalition (lions 1 and 2), the female group (lionesses 4 and 5) and the single lioness (lioness 3). The range size of the single lioness was determined only for the time after she broke away from the pride. The period before she broke away from the other lions was not included when her total range was determined, because it only lasted for the first five months after her release, and was still an investigative period of expanding range use. Thereafter a shift in the area of use occurred. Including this period would not have given a true reflection of the location and size of her range. The 50%, 75% and 95% utilisation distributions were calculated for each group. The 50% utilisation distribution is considered to be a reliable estimate of an animal's centre of activity or core area of use of its range, while the 95% utilisation distribution is an estimate of the total range size, excluding outlier distribution points (Mizutani & Jewell 1998).

Range establishment

Little is known on how introduced lions establish their range, except that they tend to first stay in the area where they were released, and then disperse slowly into other areas (Hunter 1998, Hofmeyr, *pers. comm.*[1], Van Dyk, *pers. comm*[2]). Hunter (1998) studied an introduced lion population in Phinda, but no details of how the lions expanded their ranges were given. Range establishment and the expansion of the range after introduction were studied for the lions of Welgevonden. The size of the range for months 1 to 3 was determined separately for each month to test for the expansion of the range of the introduced lions. The range

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establishment and range expansion were determined for one group (lions 1, 2, 3 and 4) for month 1, and then for two groups (lions 1, 2 and 3, and lionesses 4 and 5) for month 2 and month 3. The range establishment of lioness 5 could not be determined for the first month, because she was in the boma for most of this period.

The influence of other factors on range size

Several factors that could have influenced the size of the ranges were also investigated. Lionesses are known to decrease their range sizes when they have small cubs (Bothma & Walker 1999). The ranges of lionesses with cubs younger than three months old were therefore determined separately, and were then compared with those of the same females when they did not have cubs. The interval of three months was chosen because cubs older than three months are able to follow their mothers to the furthest end of their ranges (*pers. obs*).

Van Orsdol *et al.* (1985) showed that in Uganda the ranges of lions tend to decrease in the winter when prey animals were more concentrated than in the summer. This was not expected to happen on Welgevonden because of its limited size and therefore limited seasonal concentration of prey, but it was nevertheless decided to test it on Welgevonden. The range size for the dry winter months (May to September) were compared with that for the wet summer months (October to April). Seasonal range use was determined separately for the coalition of males and for the group of females, but not enough data were available to determine seasonal ranges for the single lioness.

The removal of an internal fence also provided an opportunity to test how lions disperse into a new area. The fence was removed eight months after the release of the lions, which gave them enough time to have settled down in their new ranges before the fence was removed. It also gave them enough time to get to know the fence, and therefore the boundary of the area that they could utilise. It therefore provided the opportunity to study the way in which lions would expand their original range when one of the factors that limited the size of their range, was removed. The size of their ranges before and after the fence was removed was determined separately, and was then compared to each other.

Habitat selection

An estimation of the habitat selection of the reintroduced lions was also made. The lion density in each habitat type was determined and chi-square analysis was done to compare these data with a random distribution. Hunter (1998) adopted a method whereby the expected habitat use was determined separately for each lion, rather than using the total distribution of the habitat types over the entire reserve. A minimum convex polygon was derived that encompassed every location point, including all excursions, for each individual lion, and the surface area of each habitat type was then determined. This was done to exclude the areas that the lions had never visited before. Therefore it ensured that the lions at least had some knowledge of the areas that they did not use by preference.

RESULTS

Radio-telemetry

Because lioness 3 was not collared, it was necessary to rely on reports by rangers or chance sightings to get a fix of her position. Therefore, only 161 fixes were used to determine the size of her range, compared to 620 fixes for lions 1 and 2, and 719 fixes for lionesses 4 and

5. Lions 1, 2, 4 and 5 were all collared and it was possible to use radio-telemetry fixes for their respective positions.

Range establishment and use

The range size estimates for the different lions that were monitored are given in Figures 6.1 – 6.3. The range size for the study period (95% utilisation distribution) varied from 60.03 km^2 for the single lioness (lioness 3) to 103.32 km^2 for the two-male coalition (lions 1 and 2). The size of the core area (50% utilisation distribution) varied from 5.02 km^2 for the lioness group (lionesses 4 and 5) to 14.02 km^2 for the single lioness (lioness 3) (Table 6.1). The mean range size for female lions on Welgevonden was 70.03 km^2 (SE = 14.14 km^2, n = 2). Figures 6.4 and 6.5 show the kernel estimates of the change in range size as the lions established themselves in their new environment. This is described in detail in Table 6.3. The range size for lions 1,2 and 3 was 8.47 km^2 in month 1 compared to 33.55 km^2 in month 3, and that for lionesses 4 and 5 was 8.47 km^2 in month 1 compared to 35.57 km^2 in month 3.

The influence of other factors on range size

Kernel estimations of the seasonal ranges appear in Table 6.4. No range sizes were determined for the summer of 1998 when the lions were released and still exploring their new environment. The seasonal range of lioness 3 was also not determined because not enough data were available to do a seasonal analysis of her range use. The mean range size (95% utilisation distribution) of lionesses 4 and 5 was 105.99 km^2 in the summer, compared to a mean range size of 69.65 km^2 for the winter. The difference was not significant (t = -1.38, p = 0.30, df = 2). For lions 1 and 2 the mean range size (95% utilisation distribution) in the summer was 183.81 km^2, compared to a mean range size of 83.48 km^2 in the winter. This difference was significant (t = -8.08, p = 0.02, df = 2). The mean core area (50% utilisation distribution) for lions 1 and 2 during the summer was 12.29 km^2 compared to 8.84 km^2 in the winter ($t = -1.34$, $p = 0.31$, $df = 2$). The core area for lionesses 4 and 5 during the summer was 6.54 km^2 compared to 5.53 km^2 in the winter ($t = -1.59$, $p = 0.25$, $df = 2$).

The range sizes of lionesses with cubs were determined for only one litter each. The period when the second litters were born was outside the study period and not enough data on the movement of the lionesses during this period were available for analysis.

The mean (95% utilisation distribution) range size for the lionesses with cubs was 41.68 ± 9.25 km^2, and the mean core area for use for lionesses with cubs was 4.06 ± 0.78 km^2 (Table 6.5). The data are for one litter per lioness only, and therefore no statistical analysis of the range size of each lioness with and without cubs could be done. However, there was no significant decrease in the mean range size for lionesses when they had cubs ($t = -3.38$, $p = 0.18$, $df = 1$).

The movements of the lions before and after the removal of an internal fence appear in Figures 6.10 and 6.11. The removal of the fence added another 60 km^2 to area of the reserve. The total (95% utilisation distribution) range size of lions 1 and 2 before the removal of the fence was 52.06 km^2, compared with 115.86 km^2 after the fence was removed. For lionesses 4 and 5, the total range size before the removal of the fence was 49.91 km^2 and 80.27 km^2 after the fence was removed. The core area of use of lions 1 and 2 was 4.37 km^2 before the fence was removed and 6.58 km^2 after the fence was removed. The size of the core area of use of lionesses 4 and 5 was 4.10 km^2 before the fence was removed and 5.13 km^2 after the fence was removed. Although the ranges appear to have increased, no statistical analysis of the data sets could be done due to a lack of variance in the data sets.

Table 6.1. The range sizes (km^2) of the reintroduced lions on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to May 2000.

TYPE OF ANALYSIS	RANGE SIZE		
	Lions 1 and 2 *n* = 620	**Lionesses 4 and 5** *n* = 719	**Lioness 3** *n* = 161
Kernel estimation			
• 95% utilisation distribution	103.32	80.03	60.03
• 75% utilisation distribution	9.72	10.73	25.18
• 50% utilisation distribution	6.00	5.02	14.02
Minimum convex polygon estimation	251.42	232.49	101.23

Table 6.2. Range sizes (km^2) of lions in various parts of Africa compared to that of lions on the Welgevonden Private Game Reserve in the Waterberg region of South Africa, as determined with minimum convex polygon analysis.

CONSERVATION AREA	RANGE SIZE	SOURCE
Central Kalahari	702 – 3900	Owens & Owens 1984
Etosha National Park	150 – 2 075	Stander 1991a
Kaudom Game Reserve	1 055 – 1745	Stander 1997
Lake Manyara National Park	20	Schaller 1972
Ngorongoro Crater	45	Hanby *et al.* 1995
Savuti Marsh	300	McBride 1990
Serengeti National Park	40 – 400	Schaller 1972
Serengeti National Park	200	Hanby *et al.* 1995
Welgevonden Private Game Reserve	101.23 – 251.42	This study

Table 6.3. The increase in the size (km^2) of the ranges of the reintroduced lions over the first three months after release on Welgevonden Private Game Reserve in the Waterberg region of South Africa.

TYPE OF ANALYSIS	**LION 1,2,3 AND 4**	**LION 1,2 AND 3**		**LIONESSES 4 AND 5**	
	Month 1	**Month 2**	**Month 3**	**Month 2**	**Month 3**
	n = 30	n = 27	n = 29	n = 27	n = 28
Kernel estimation					
• 95% utilisation distribution	8.47	18.02	33.55	21.47	35.57
• 75% utilisation distribution	4.63	5.46	8.14	6.98	10.51
• 50% utilisation distribution	1.76	2.73	4.15	3.58	4.35
Minimum convex polygon estimation	5.96	25.10	47.31	22.29	46.78

Figure 6.1. Kernel estimation (95%, 75% and 50% utilisation distribution) of the range of lions 1 and 2 on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to M

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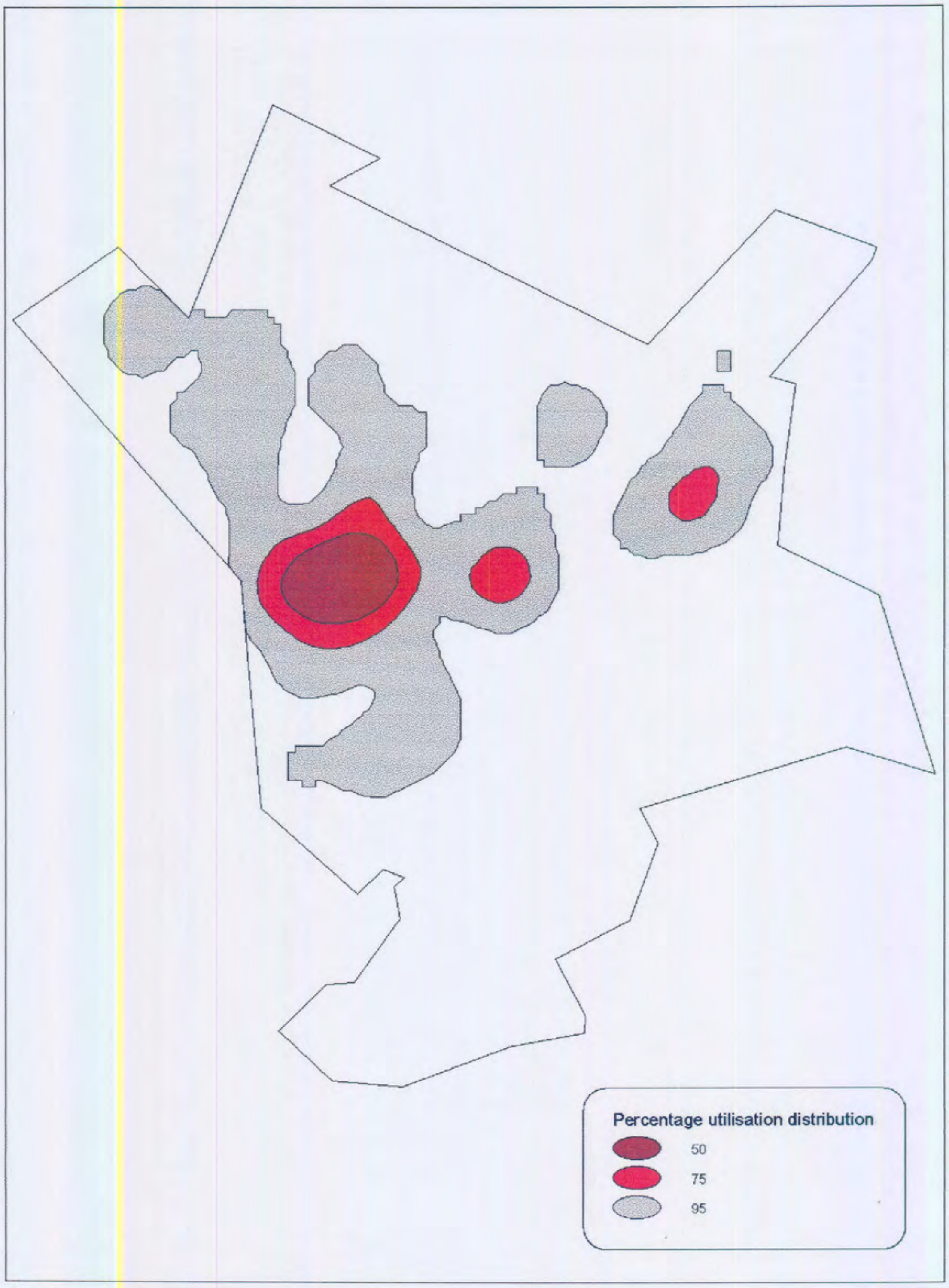

Figure 6.2. Kernel estimation (95%, 75% and 50% utilisation distribution) of the range of lionesses 4 and 5 on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to

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Figure 6.3. Kernel estimation (95%, 75% and 50% utilisation distribution) of the range of lioness 3 on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to May 2(

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Figure 6.4. Kernel estimation (95%, 75% and 50% utilisation distribution) of the ranges of lions 1,2 and 3 for the first three months after their introduction into the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

Month 1 Month 2 Month 3

Lioness 4 only Lionesses 4 and 5 Lionesses 4 and 5

Figure 6.5. Kernel estimation (95%, 75% and 50% utilisation distribution) of the ranges of lionesses 4 and 5 for the first three months after their introduction into the Welgevonden Private Game Reserve in the Waterberg region of South Africa. The range of lioness 5 during month 1 was not determined as she was in the boma recovering from an injury (Chapter 2)

Table 6.4. Seasonal kernel range size estimates (km^2) of the different lions for the first 2 years after release on the Welgevonden Private Game Reserve in the Waterberg region of South Africa, to show the difference in the size of the ranges used in the summer and the winter.

ANIMALS	WINTER 1998	SUMMER 1998/99	WINTER 1999	SUMMER 1999/00
LIONS 1 AND 2				
Sample size	119	219	118	196
95% utilisation distribution	87.89	172.21	79.06	195.41
75% utilisation distribution	30.97	56.18	14.58	48.79
50% utilisation distribution	10.22	14.46	7.45	10.11
LIONESSES 4 AND 5				
Sample size	125	221	118	195
95% utilisation distribution	75.62	80.37	63.68	131.61
75% utilisation distribution	14.14	15.44	11.41	23.85
50% utilisation distribution	5.32	5.94	5.74	7.13

Table 6.5. Range size (km^2) of lionesses when they had cubs, compared to the total range size for the same lionesses during the whole study period from January 1998 to May 2000 on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

LIONESS	SAMPLE SIZE	NUMBER OF LITTERS	TOTAL AREA (95%)	CORE AREA (50%)
Total range	763	-	80.02	5.02
Lioness 4 with cubs	92	1	35.14	3.51
Lioness 5 with cubs	89	1	48.22	4.61

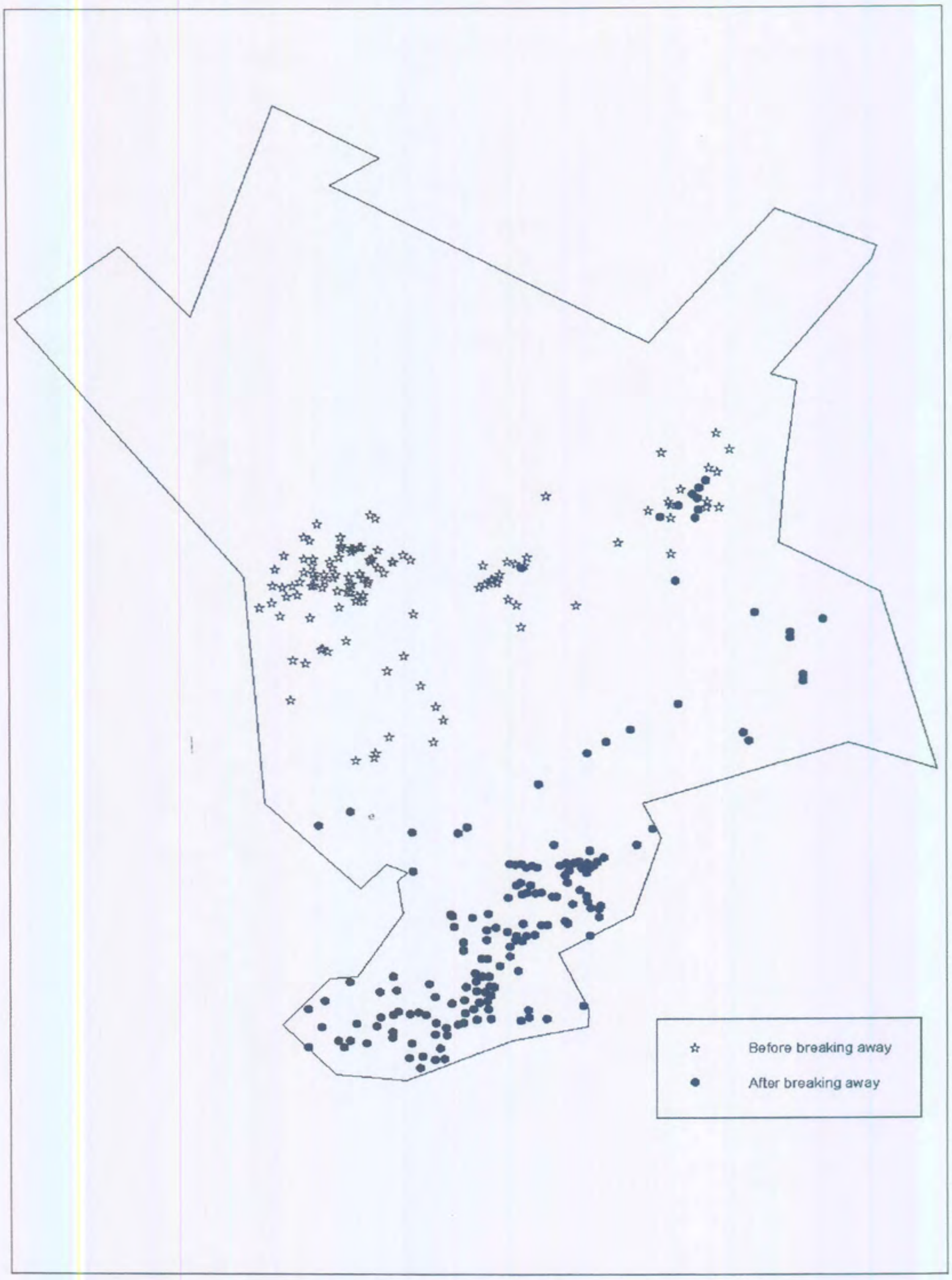

Figure 6.9. The distribution of lioness 3 before and after she broke away from the other lions during the study period form January 1998 to May 2000 on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

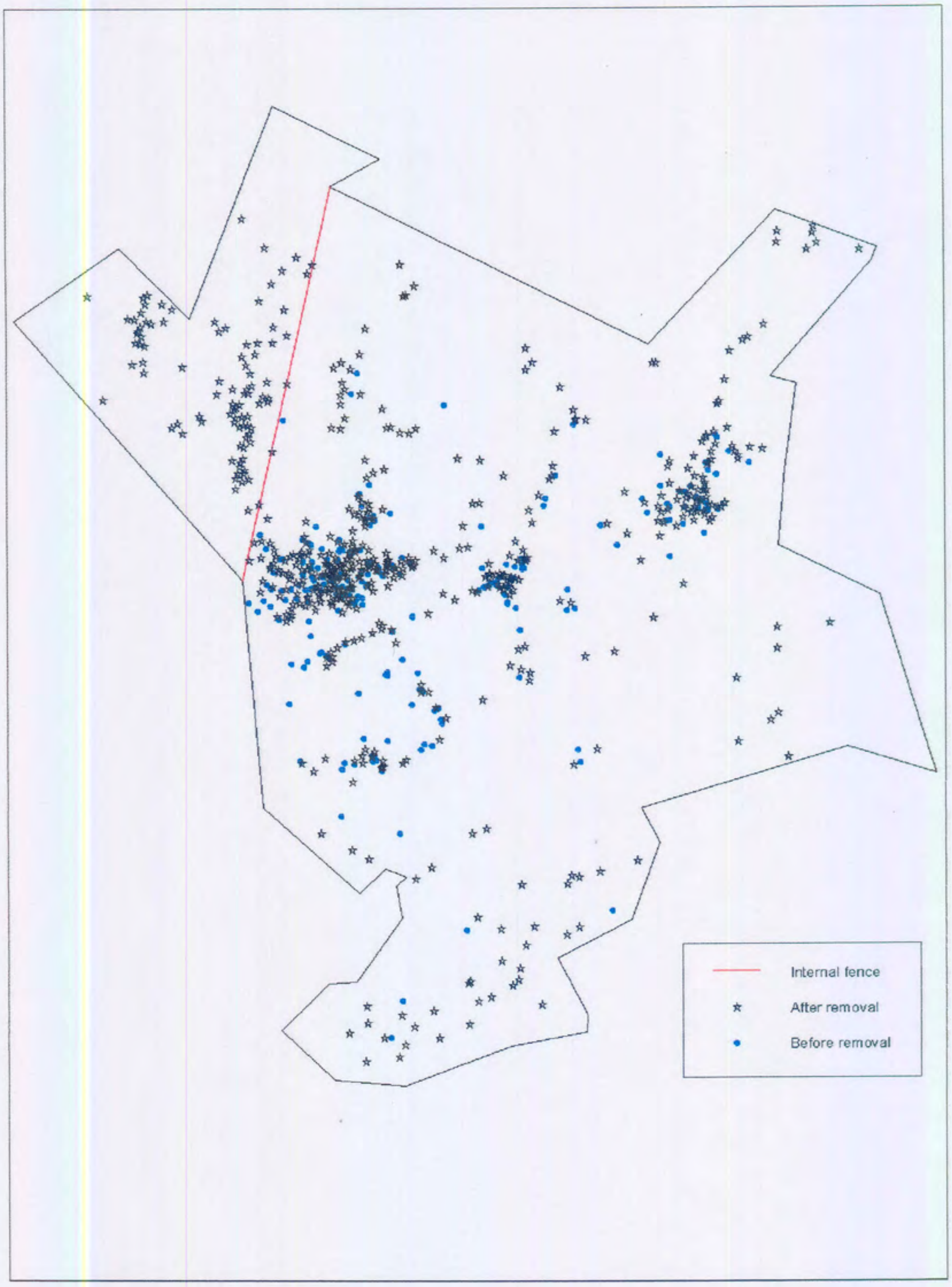

Figure 6.10. The distribution of lions 1 and 2 before and after an internal fence was removed, nine months after they were released on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

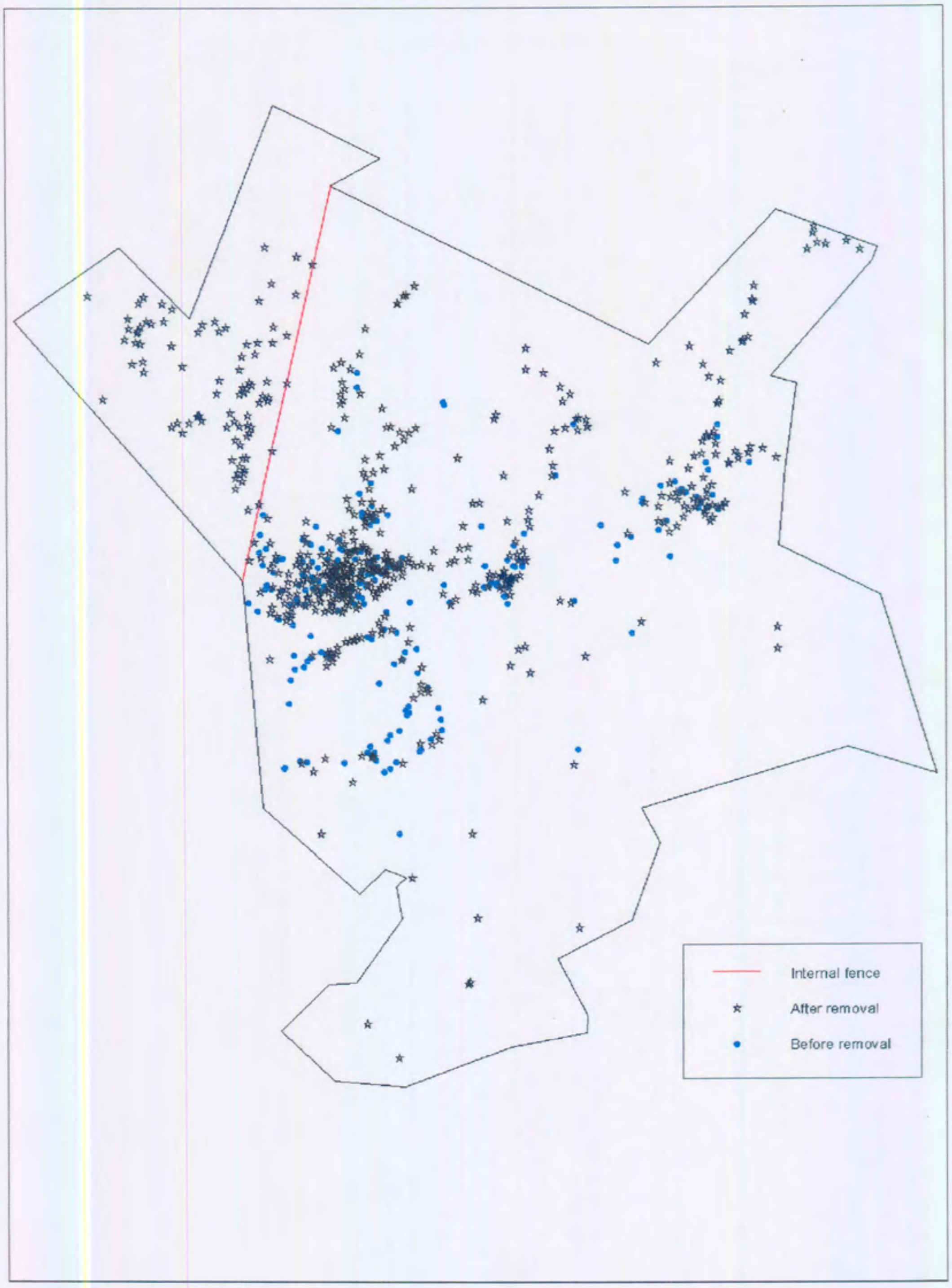

Figure 6.11. Distribution of lionesses 4 and 5 before and after an internal fence was removed, nine months after they were released on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

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Table 6.6. Habitat selection by lions on the Welgevonden Private Game Reserve in the Waterberg region of South Africa during the study period from January 1998 to May 2000. Chi-square analyses were used to test for selection of the different habitat types, based on the number of times that lions were observed in each habitat type. The expected number of observations was determined by using the percentage of each habitat type available to them. A negative O-E value indicate that the lions were observed less than expected in that particular habitat type.

HABITAT TYPE	PERCENTAGE OF HABITAT AVAILABLE	OBSERVED (O)	EXPECTED (E)	O - E	χ^2 VALUE	p-value	df
LIONS 1 AND 2							
Plateaux	17.95	328	119.91	208.09	361.09	<0.0001	3
Old lands	4.40	159	29.38	129.62	571.89	<0.0001	3
Hills	71.23	55	475.82	-420.82	372.78	<0.0001	3
Valley bottoms	6.42	126	42.89	83.11	161.05	<0.0001	3
LIONESSES 4 AND 5							
Plateaux	17.95	316	122.43	193.57	306.06	<0.0001	3
Old lands	4.40	152	29.99	122.00	496.27	<0.0001	3
Hills	71.23	80	485.79	-405.79	338.96	<0.0001	3
Valley bottoms	6.42	134	73.79	90.21	185.85	<0.0001	3

Habitat selection

All lions showed a definite selection for plateaux, old lands and valley bottoms, and a negative selection for hills (Table 6.6). Despite the hills forming 71.23% of the surface area of the reserve, only 8.2% and 11.7% of all sightings of lions 1 and 2, and lionesses 4 and 5 respectively were in the hills.

DISCUSSION

Range establishment and use

The range establishment of the lions on Welgevonden was similar to what was seen with other lion reintroductions elsewhere (Hunter 1998, Van Dyk *pers. comm.*). All the introduced lions settled down and established ranges within the boundaries of the reserve. The lionesses established small, exclusive territories in two parts of the reserve. One group of lionesses (lionesses 4 and 5) settled in the western and central parts of the reserve, while the single lioness (lioness 3) established her home range in the southern part of the reserve (Figures 6.2 and 6.3). The two-male coalition (lions 1 and 2) was associated with both these groups and had ranges covering those of both the lioness groups (Figure 6.1). Since the study period ended, the male coalition has split-up. The one male settled with the one lioness group in the central parts of the reserve, while the other settled with the single female and her female offspring in the southern parts of the reserve.

It is difficult to compare the range size of lions in Welgevonden with that of lions in other parts of Africa. Even within the same area, large variations in range size are observed (Table 6.2). Stander (1991a) observed that range size of lions ranged from 150 to 2075 km^2 in Etosha National Park, while Schaller (1972) noted a variation of

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40 to 400 km^2 in the Serengeti. However, from Table 6.2 it appears as if the range size of lions in dry areas like the Etosha National Park, Kaudom Game Reserve, Savuti Marsh and the central Kalahari, are larger than in the higher rainfall areas of East Africa, like Lake Manyara National Park and the Ngorongoro Crater. It seems that the range size of lions on Welgevonden (101 to 251 km^2) is comparable to that of the Serengeti because it falls within the observed range size of 40 to 400 km^2 for the Serengeti (Schaller 1972).

The available sample size is too small to make robust conclusions, but the range size of lions on Welgevonden appears to be amongst the four smallest range sizes known for lions in Africa. However, the conservation areas listed in Table 6.2 are all large, and the ranges of the lions there were not influenced by the presence of fences. The size of the ranges of lions on Welgevonden may well have been influenced by the presence of fences. The removal of an internal fence on Welgevonden during the study indicated that the lions did expand their ranges into the new area that became available. However, the core areas of the ranges did not change much (Figures 6.1, 6.2, 6.4 and 6.5). If the current fence between Welgevonden and Marakele National Park is removed as is being planned, some of the lions may expand their ranges further into Marakele. The fence between Welgevonden and Marakele forms a large part of the range boundary of the southern pride, and it appears from Figure 6.3 that their range size were limited in the southern parts of the reserve where the northern and southern fences were close to each other. They will therefore possibly expand their range once this man-made boundary has been removed.

Hunter (1998) used the kernel method to determine the ranges of the lions on Phinda Resource Reserve. The ranges [illegible] a single lioness to 130.20

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km^2 for a three male coalition. Hunter (1998) noted that the size of the ranges of females was amongst the smallest recorded for the species. The ranges of the reintroduced lions in Phinda were probably also limited by the presence of fences. The mean range size for female lions on Welgevonden was similar ($t = -0.84$, $p = 0.45$, $df = 4$) to that of female lions in Phinda (52.83 ± 35.69, $n = 3$). These results were to be expected given the fact that the prey density on Phinda (1996 kg/km^2) (Hunter 1998) and on Welgevonden (1860 kg/km^2) (Kilian 1999) is similar.

As was observed elsewhere, the reintroduced lions stayed close to their point of release for the first month after introduction, but then slowly increased and expanded their ranges before settling in a fixed range. However, a shift in an established range can occur, even if a single lion or a pride of lions used a range for a period. Hunter (1998) observed a case where a group of lionesses clashed with another group of lionesses, which caused the first group to move out of their old range and establish a new range elsewhere. On Welgevonden, lioness 3 initially established a small range with the other lions. Later, after lioness 5 joined the pride and clashed with the pride members, female 3 moved out of the old range and established a new range on her own (Chapter 4). It therefore appears as if some or other disruptive event, like the introduction of more lions, may cause the lions to adjust their ranges.

Although not enough data are available to prove the theory, it appears as if there is a trend for certain prey on Welgevonden, like eland, red hartebeest, and Burchell's zebra, to use the hills more extensively in the summer than in the winter. These small-scale movements are probably related to food, because the grazers are forced to concentrate on the old lands and plateaux with their somewhat sweeter grazing in order to fulfil their nutritional needs in the winter. However, despite this concentration of prey in the winter, only the male lions showed a significant decrease in the size of their ranges in the winter. This is in contrast to what Van Orsdol *et al.* (1985) observed in Rwenzori National Park where an increase in lean season biomass of prey resulted in a decrease in range size of lions. Because of the smaller size of Welgevonden compared to Rwenzori National Park, the scale of the movement of the prey animals and the resulting concentration of prey on Welgevonden is probably too small to cause significant changes in the seasonal range size of the lions.

Habitat selection

From Table 6.6 it is clear that the lions showed a definite preference for the old lands and plateaux, and a negative selection against hill slopes. The prey animals on Welgevonden also show a negative selection against hill slopes, and a positive selection for plateaux and old lands (Kilian 2001). Therefore, although the overall prey density over the whole reserve is relatively low, the density of prey on the old lands and plateaux is high. Predators will naturally seek high concentrations of available prey (Caro 1994) and this may explain the positive selection for these areas by the lions. Apart from the availability and density of prey, it appears that the availability of suitable habitat also plays a major role in range establishment and size of lions on Welgevonden. The old lands and plateaux areas also present suitable habitat in which to hunt because they are not densely vegetated, while still offering enough cover to lions when stalking prey. These areas are also relatively flat and have a low rock cover. It is therefore not surprising that the ranges of the lions centred in these areas. Although hill slopes cover 71.23% of the surface area of the reserve, they are largely excluded from the ranges of the lions. Suitable areas to establish ranges are therefore limited, and probably further explains the relatively small ranges of the lions in this study (Table 6.2).

The fact that the core areas of the ranges of the lions fall in areas with large concentrations of prey may lead to a considerable impact by lions on the prey populations of Welgevonden. The opportunity for prey to escape lion predation in small reserves is limited, and the problem might further be increased by the fact that prey are at times forced to concentrate in certain areas because of a lack of water and/or quality grazing. The lions on Welgevonden sought these high concentrations of prey, established the core areas of their ranges in these areas, and therefore killed significantly more prey in the old lands and plateaux than any of the other habitat types (Chapter 8).

The lion density on Welgevonden at present is one lion per 13.2 km^2. As the population is still growing, it is not feasible to compare the current lion density with those in other areas where the populations have reached equilibrium. The lion density will increase in the future, unless management actions are implemented to keep it low. It will be interesting to establish the long-term effect of increasing lion density on the range size and use of lions in small, enclosed reserves, as well as the density to which the lion population will increase before it regulates itself. However, predation on enclosed reserves can have a considerable impact on the prey populations (Hunter 1998) and therefore the density of lions on Welgevonden, like on most small reserves, can never be allowed to reach the high densities of lions in other areas like east Africa.

CONCLUSIONS

In the past, reintroduction attempts of felids have often failed because the animals failed to establish ranges in the new environment. The ease with which lions on Welgevonden established ranges indicates that they did not experience problems with adapting to their new environment.

It may be necessary to introduce more new lions from time to time in order to preserve the genetic integrity of the lion population. Such a second introduction may well force the new or established lions to move away in search of new ranges. The success of a second introduction will therefore largely depend on the presence of other lions in the immediate area of release. If possible, any new animals should be introduced into an area of the reserve where no immediate competition will exist with any lions already resident on the reserve. However, it will not always be possible to introduce lions into an area that falls outside the established ranges of a resident lion population. Managers must therefore bear in mind that a clash between different groups may cause some lions to leave a reserve in search of a new range.

Range establishment and use by lions on small reserves will obviously not be similar to that of lions in large areas. In small reserves, lions are restricted in their range use by the presence of fences. Both the predator and prey populations on these small reserves are usually managed extensively. Management actions will influence the distribution of the prey, which will have an obvious effect on the ranging patterns of the lions. Studies like the present one on Welgevonden cannot provide all the answers on how management practices on small reserves generally influence the ranging patterns of lions on small reserves. Further research should focus on this question, especially to quantify the factors that influence lion range-use patterns on small reserves.

POPULATION DYNAMICS

INTRODUCTION

Although previously considered controversial, reintroduction has become a viable method of establishing a new lion population. In the past, reintroduction attempts of felids had a mixed success (Mills 1991; Linnell *et al.* 1997; Hunter 1998) and this has led several authors to conclude that the reintroduction of felids is not understood well enough to justify relocation as a method of conserving large carnivores (Panwar & Rodgers 1986; Mills 1991). Although several successful reintroduction attempts have been done in Phinda Resource Reserve, Pilanesberg National Park, Madikwe Game Reserve, Makalali Game Reserve, Entabeni Game Reserve and others (Hunter 1998; Hofmeyr *pers. comm.*[1]; Van Dyk *pers. comm.*[2]), little data are currently available on the population dynamics of reintroduced lions. Reproduction and population growth are crucial factors in understanding the population dynamics of an animal population, while successful breeding is a good indicator of the success of a reintroduction programme (Linnell *et al.* 1997). Population dynamics should therefore be central to any study with the objective of determining the success of a reintroduction attempt.

Lion reproduction has been studied all over Africa (Schaller 1972; Eloff 1973a; Rudnai 1973; Caraco & Wolf 1975; Smuts, Hanks & Whyte 1978; Packer & Pusey 1983; Packer, Herbst, Pusey, Bygott, Hanby, Cairns & Mulder 1988; Packer, Scheel & Pusey

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1990; Stander 1991a; Bosman & Hall-Martin 1997; Funston & Mills 1997; Packer & Pusey 1997). Lions reproduce at rates that are in balance with the abundance of their resources (Rudnai 1973; Smuts *et al.* 1978). They do not have a distinct mating season, but in some areas, births may show a peak during certain times of the year (Rudnai 1973). The age at first conception varies in different areas, and ranges from 30 months in Nairobi National Park (Rudnai 1973), 40 to 54 months in the Serengeti (Schaller 1972), to 43 to 66 months in the Kruger National Park (Smuts *et al.* 1978). Males are sexually mature from an age of 30 months (Smuts *et al.* 1978), but seldom mate before 48 months of age. Social behaviour and competition by older males prevent young males from mating earlier. Gestation lasts about 110 days (Schaller 1972) and the inter-litter interval is usually two years (Rudnai 1973; Funston & Mills 1997). The mean litter size in the Kruger National Park is 3.08 cubs (Smuts *et al.* 1978; Bosman & Hall-Martin 1997), but it may be as high as six. Females can breed successfully to an age of 11 to 13 years (Smuts *et al.* 1978). However, the above studies were all done on established lion populations in large natural areas where little management intervention is present. It is not known whether the same patterns can be applied to small, reintroduced lion populations in small reserves that are heavily influenced by management practices.

Although some data on the reproduction of reintroduced bears *Ursus americanus* and *Ursus arctos* (Rogers 1986; Brannon 1987; Blanchard & Knight 1995) and wolves *Canis lupus* (Bangs & Fritts 1996) exist, such information on reintroduced felids is rare. Although studies on reintroduction of the Eurasian lynx *Lynx lynx* in Europe (Breitenmoser & Breitenmoser-Wursten 1990; Yalden 1993) and a female leopard

Panthera pardus in Kenya (Mills 1991) have been done, no details on the breeding of the reintroduced felids are given.

Hunter (1998) gives a detailed description of the population characteristics of a successful lion and cheetah introduction into Phinda Resource Reserve. The study by Hunter (1998) was the first concerted effort to establish population characteristics of reintroduced lions and cheetahs. Reintroduction of lions in Phinda Resource Reserve was largely successful because of low mortality and successful breeding causing a rapid growth in the population. Reintroduction in other areas was also attempted and was successful (Van Dyk *pers. comm.*), but no published data are available. The introduced lion population of Pilanesberg National Park and Madikwe Game Reserve are breeding exceptionally well, and several lions have been translocated from these areas to other areas, including Welgevonden. As the reintroduction of lions is becoming a more viable wildlife management option, more data on the population characteristics of reintroduced lions should become available in the future.

The current study is only the second known attempt to study the population characteristics of a reintroduced lion population. It should contribute to an increase in the knowledge on how reintroduction influences the population dynamics and breeding behaviour of reintroduced lion populations. In this chapter, it is furthermore attempted to use the population characteristics of the reintroduced lions on Welgevonden as an indication of a successful reintroduction. Patterns of reproduction are given, and the data were used in an attempt to model the population so as to be able to predict what will happen in the future. The effect of the population parameters on the viability of the population and future wildlife management actions are discussed.

METHODS

Oestrus patterns and matings

The data presented for this part of the study cover four years of study since the original reintroduction in January 1998 to January 2002. Daily observations during the early part of the study made it possible to observe and record all oestrus cycles and matings. For the latter part of the study, direct observations as well as reports from guides were used to determine the oestrus cycles. By using a gestation period of 110 days (Schaller 1972), dates of any births could therefore be calculated.

Birth of cubs

The sizes of most of the litters were recorded when the cubs first emerged from their dens, although some were counted while still in the den when this was possible. Therefore, the actual number of cubs born, and cub survival from birth to emergence from the den six to seven weeks after birth (Bothma & Walker 1999) is largely unknown. Packer *et al.* (1988) state that deaths of cubs before emergence is rare. For the purposes of this study, cub survival before emergence is therefore accepted as 100%. Deaths of cubs after emergence and the reasons for these deaths were recorded as they were observed or became known.

Population simulation using VORTEX

The lion population was modelled using VORTEX software. VORTEX is an individual-based Monte-Carlo simulation program for population viability analysis. It helps one to understand the effect of deterministic forces as well as demographic, environmental and genetic stochastic events on the dynamics of wildlife populations. VORTEX models population dynamics as discrete, sequential events that occur according to defined probabilities (Miller & Lacy 1999). It has been used successfully before to model lion and cheetah populations in Namibia (Berry *et al.* 1997). The input parameters for the viability analysis were as determined from the current study. Some factors were changed during the different simulations in order to model the influence of these factors on the population. Different possible wildlife management strategies were also modelled to determine what influence these strategies will have on the lion population.

VORTEX requires several input parameters in order to run the simulation. These parameters are inbreeding depression, catastrophes, age at first breeding, maximum age of breeding, percentage of females breeding per year, litter size, mortalities, starting population size and ecological capacity. Each of these input parameters is discussed separately. For each input parameter, the data used were those that were determined for Welgevonden, unless otherwise stated. When applicable data for Welgevonden were not available, published data were used.

Input parameters used in VORTEX

Inbreeding depression

In small populations like that of the lions on Welgevonden, inbreeding can potentially have a large effect on the population and its ability to survive. Inbreeding depression was run as a factor here because it may affect the ability of the population to survive or even reproduce. Inbreeding causes a loss in heterozygosity, which reduces the population's ability to adapt to environmental changes and increases the chance of losses due to diseases and catastrophes (Lacy 1987). No published data on inbreeding depression for lions could be found. Therefore, the mammalian mean of 3.14 lethal equivalents per individual was used, with 50% of the genetic load due to lethal alleles (Ralls *et al.* 1988).

Catastrophes

Catastrophes are a reality in the context of wildlife management (Miller & Lacy 1999), and VORTEX allows the user to include catastrophes as a factor in the population model. The probability of occurrence and the severity of the catastrophe can be changed. Berry *et al.* (1997) speculates that severe disease epidemics in felids can occur once in every 20 years, and that 20 to 35% of a population can die because of that. A 5% chance of a catastrophe every 100 years with a 25% reduction in survival, but with no effect on the reproduction following the catastrophe, was used for this model.

Age at first reproduction

For use in VORTEX, the age at first reproduction was defined as the age when the first offspring were born and not the onset of sexual maturity or the age at first conception (Miller & Lacy 1999). For this study, the mean age of the females with the birth of the first cubs was 44.3 months (SD = ±1.86, n = 3), and the mean age of the males was 41 months (SD = ±2.00, n = 2). VORTEX does not allow the use of a decimal or months in age of first reproduction, and therefore the age at first reproduction in this model was used as 4 years.

Maximum age of breeding

Female lions have a reproductive lifespan of 11 to 13 years (Smuts *et al.* 1978, Packer & Pusey 1997). Because of social pressure, reproducing males are usually not older than nine years (Bothma & Walker 1998), but they are physically able to reproduce for much longer. However, VORTEX does not differentiate between the maximum age at which males and females can reproduce. Therefore, the maximum age of reproduction for all lions used in the model was 11 years.

Sex ratio at birth

The sex ratio at birth is usually equal (Smuts 1978b), but it has often been seen that the ratio may favour males, especially just after a male take-over (Bothma & Walker 1998). Packer & Pusey (1987) also mention that the sex ratio might be more in favour of males in large litters. The actual observed sex ratio at birth for this study was three males per female, but it is expected for the sex ratio to become closer to parity over time. Therefore, a sex ratio of parity was used in the model. In order to test the influence of the different sex ratios on the model, the model was first run with both the actual observed and parity sex ratios, but it had little influence on the population over a period of 100 years.

Percentage of females breeding per year

For this study, the percentage of females breeding per year was 88.89% (SD = ±29.4%). This value was used in the model.

Litter size

The mean litter size for this study was 2.88 (SD = ±0.398, n = 8), and it was used in the model.

Mortalities

VORTEX requires data on the mortality rates of the different age classes when running the simulation. Unfortunately, it uses a fixed mortality rate for the whole simulation, which is not a good indication of what happens in establishing populations. There is evidence that cub survival in established populations is lower than in establishing populations (Hunter 1998). This may also be the case with adults. Keeping this in mind, different simulations were run for different levels of survival. A base scenario simulation was run with the actual observed survival rates for lions of various age classes on Welgevonden. To compensate for possible increases in mortality rates, further simulations were run with increased mortality rates for different age classes. Bosman & Hall-Martin (1997) state that cub mortality in lions can be as high as 80%. The mortality rates that were used for the various simulations appear in Table 7.1. VORTEX defines cubs as lions younger than a year, subadults as lions older than a year but younger than the age at first reproduction, and adults as older lions who had already mated.

Ecological capacity

The ecological capacity for animals as used in VORTEX, describes the upper limit for the size of the simulated animal population within a given habitat and is specified by the user. If the population grows above the ecological capacity at the end of a particular time cycle, additional mortality is imposed across all age and sex classes in order to bring the population back to the upper limit (Miller & Lacy 1999). Therefore, VORTEX does not allow the population to grow above the specified ecological capacity. In practice, natural populations often fluctuate above or below their ecological capacity, although it might be for short periods only before returning to equilibrium, usually when limited again by food resources. The degree of fluctuation depends on the ecological conditions that exist at a given time. Although it was determined that Welgevonden probably cannot carry more than 20 lions in the long term to remain in balance with their available prey (Chapter 9), ecological capacity was taken as 30 lions for use in the models. This was done to include the above mentioned fluctuations above the ecological capacity for short-term modelling, as VORTEX will not allow the population to grow larger than 20 lions, even for short periods of time. It was also done in order to exclude ecological capacity as a factor when modelling for various management actions that will keep the population as close as possible to 20 animals.

Modelling the effects of different management strategies

It was determined in Chapter 9 that based on the available prey at ecological capacity, Welgevonden can support a maximum of 20 lions in the long-term. To give an indication of possible management actions that might be required to keep the lion population as close as possible to 20 animals, while also minimizing the loss of heterozygosity and inbreeding, the lion population was simulated using different potential management strategies. These strategies are described in Table 7.2.

RESULTS

Age at first breeding

The mean age of the males at first successful mating was 38.0 ± 2.8 months (n=2), while the mean age of females at first conception was 41.3 ± 3.2 months (n=3). Table 7.1 gives details on the ages of each lion at first conception or successful mating.

Litter sizes

Twenty-three lion cubs were born in eight litters during the study period. The mean litter size for this period was 2.88 ± 0.398 (n=8) (Table 7.2). This mean represents all the lion cubs born on Welgevonden since introduction to January 2002.

Survival of cubs and subadults

Table 7.3 gives the details of the survival of each litter as well as the mean survival rate of all the cubs born on Welgevonden. Of the 23 lion cubs born on Welgevonden, 73.3 % reached the age of one year, and 100% of all cubs that reached the age of one year also reached independence. Cubs younger than one year or cubs that were still dependent at the time of writing, were not used in the analysis to determine survival. At the time of writing, all the cubs that had reached independence were also still alive.

Table 7.1. Ages of male and female lions at first successful mating and conception on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to January 2002.

LION	DATE OF BIRTH	DATE OF FIRST MATING	AGE AT FIRST MATING
MALES			
Lion 1	October 1995	October 1998	36 months
Lion 2	November 1995	March 1999	40 months
FEMALES			
Lioness 3	October 1995	February 1999	40 months
Lioness 4	December 1995	March 1999	39 months
Lioness 5	March 1995	October 1998	45 months

Table 7.2. Details of all lion cub litters born on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to January 2002.

LITTER	DATE OF BIRTH	LITTER SIZE
1	6 February 1999	2
2	15 June 1999	4
3	13 July 1999	3
4	5 September 2000	1
5	27 January 2001	3
6	2 April 2001	2
7	May 2001	4
8	29 August 2001	4
Mean ± SD		2.88 ± 0.398

Table 7.3. Details of survival of all lion cubs born on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to January 2002.

LITTER	LITTER SIZE	CUBS SURVIVING TO ONE YEAR	CUBS SURVIVING TO INDEPENDENCE	PERCENTAGE SURVIVAL TO ONE YEAR	PERCENTAGE SURVIVAL TO INDEPENDENCE
1	2	2	2	100.0	100.0
2	3	2	2	66. 7	66.7
3	4	4	4	100.0	100.0
4	1	0	0	0.0	0.0
5	3	3	d	100.0	d
6	2	x	d	x	d
7	4	x	d	x	d
8	4	x	d	x	d
Mean ± SD				73.3 ± 19.437	66.7 ± 23.570

x :cubs younger than 12 months old

d: cubs still dependent

The reasons for the deaths off the lion cubs

The first cub, age 11 months, had to be euthanased after it sustained a broken lower jaw. The manner in which it sustained the broken jaw is unknown, but closer inspection after death indicated that it was likely caused by a kick in the mouth by a large, hoofed animal. Apart from the broken lower jaw, all the front teeth and incisors were broken or kicked out. Unfortunately the incident was not observed and its circumstances cannot be verified.

The second cub that died was the only cub in the second litter of lioness 5. This cub was first observed in the lair a week after birth, and no signs of any other cubs could be found. The last time that it was seen was when the lioness moved it out of the lair to a giraffe kill when it was 2.5 weeks old. When the lioness was seen again two days later, the cub was not with her and the pride had moved out of the area. It can only be assumed that the lion cub was abandoned.

The third cub that died was part of the third litter of lioness 5. When the cubs were six weeks old, the lioness moved around with the pride as usual. The cubs had no choice but to follow. One cub was not as strong as its sibling, and was often seen trailing behind the pride. It was possibly left behind and died of exposure or starvation.

Patterns of reproduction

The patterns of reproduction of the lionesses appear in Figures 7.1 to 7.3. The mean inter-litter interval for all the lionesses was 466.8 ± 102.6 days (range: 210 to 737 days). The inter-litter interval for each lioness appears in Table 7.4. The inter-litter interval of 210 days for lioness 5 occurred when she lost her second litter, only to come into oestrus soon again (Figure 7.3). The inter-litter interval of 244 days of lioness 4 was not linked to a loss of her previous litter, which is low compared to the overall expected inter-litter interval of two years (Bothma & Walker 1999). In Phinda Resource Reserve, the shortest inter-litter interval for introduced lions was 504 days (Hunter 1998).

Population growth rate

The actual population growth for the lion population appears in Figure 7.4. This shows an increase of 400% in lion numbers since reintroduction in 1998 to 2002. The instantaneous growth rate (r) for the lion population was 0.72 (72%) per year.

VORTEX simulations

Modelling with different levels of survival

The results of the VORTEX simulations appear in Figures 7.5 and 7.6. Figure 7.5 represents the size of the population over a period of 100 years with an ecological capacity of 30 lions, and Figure 7.6 gives the probability of survival for the same data sets. The parameters used in the projections of the different scenarios were the same as for the base scenario, except for the higher mortality rates for the different age classes as listed in Table 7.5. Except for the high combined mortality scenario, the other populations reached their ecological capacities within the first 10 years, and then stayed stable just below the ecological capacity. The probabilities of survival for these scenarios were high, but there was only a 29% chance of survival for the lion population after 100 years, based on a combined high mortality rate.

Table 7.4. The mean inter-litter intervals, standard errors and ranges in days for the different lionesses on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to January 2002.

ITEM	LIONESS 3	LIONESS 4	LIONESS 5
Mean	737.0	404.5	394.0
Standard error	0.0	160.5	184.0
Range	737	244-565	210-578
Number of litters	2	3	3

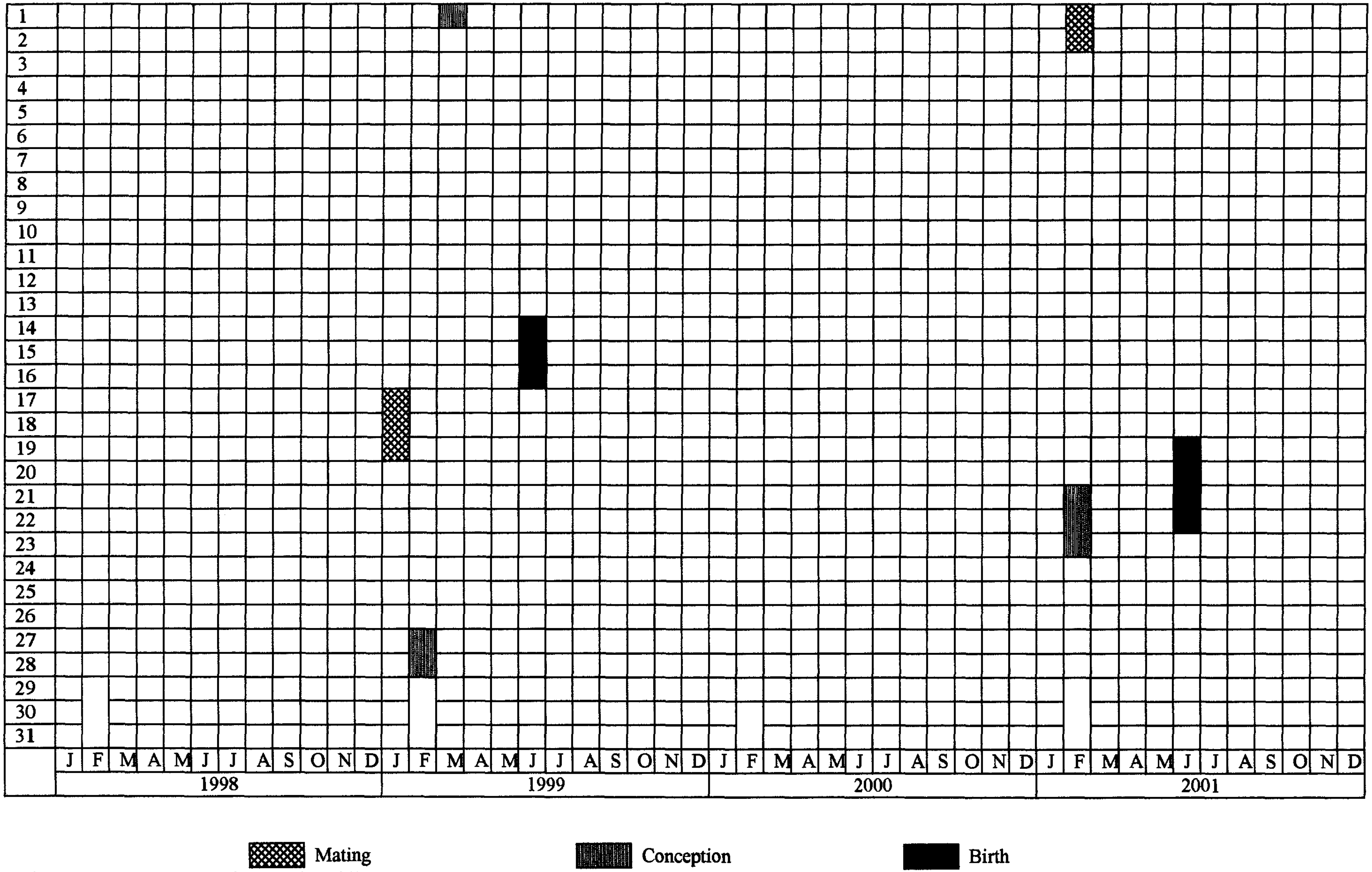

Figure 7.1. Reproductive cycle of lioness 3 on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to January 2002, showing the dates of matings, conceptions and births.

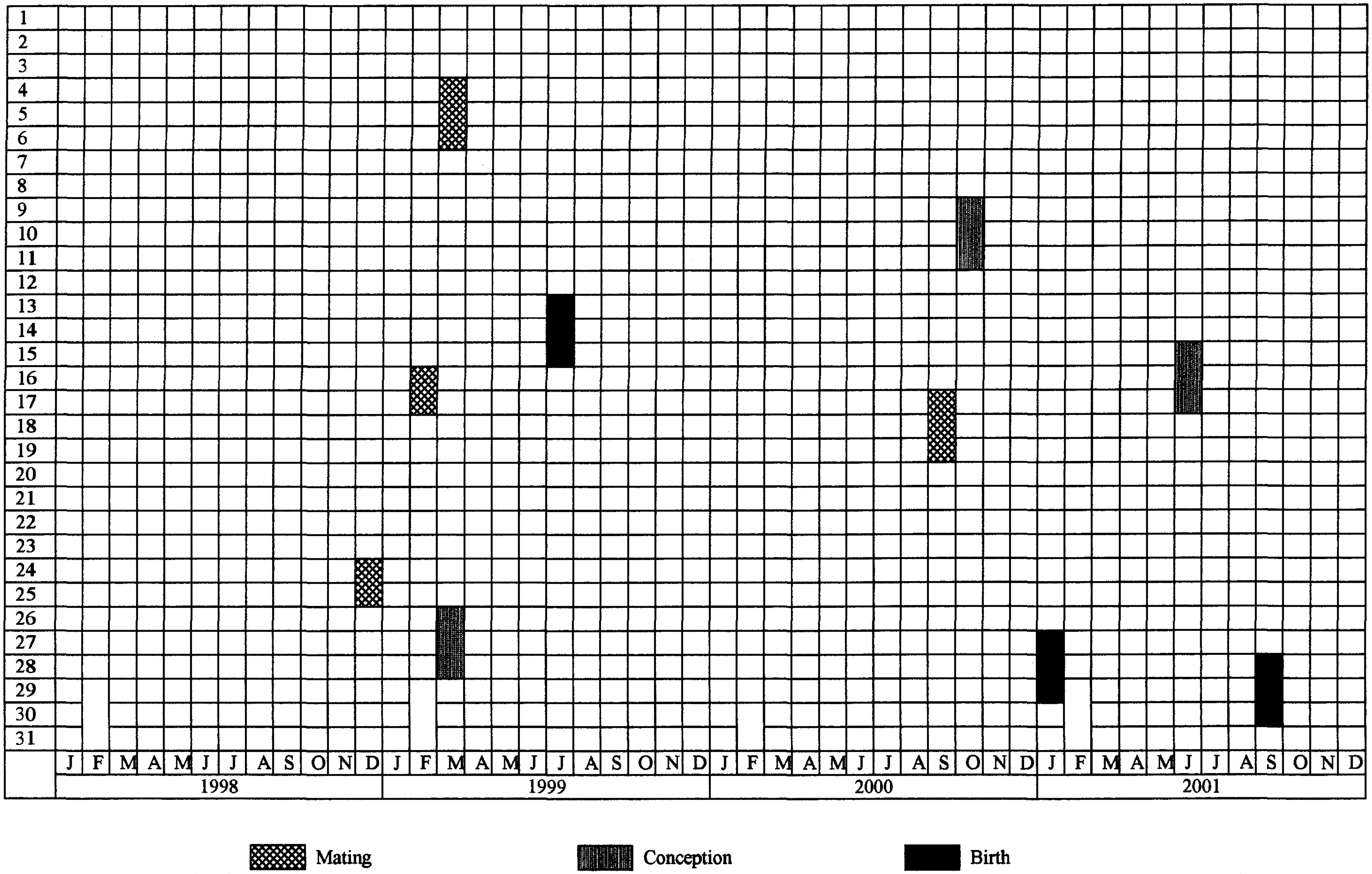

Figure 7.2. Reproductive cycle of lioness 4 on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to January 2002, showing the dates of matings, conceptions and births.

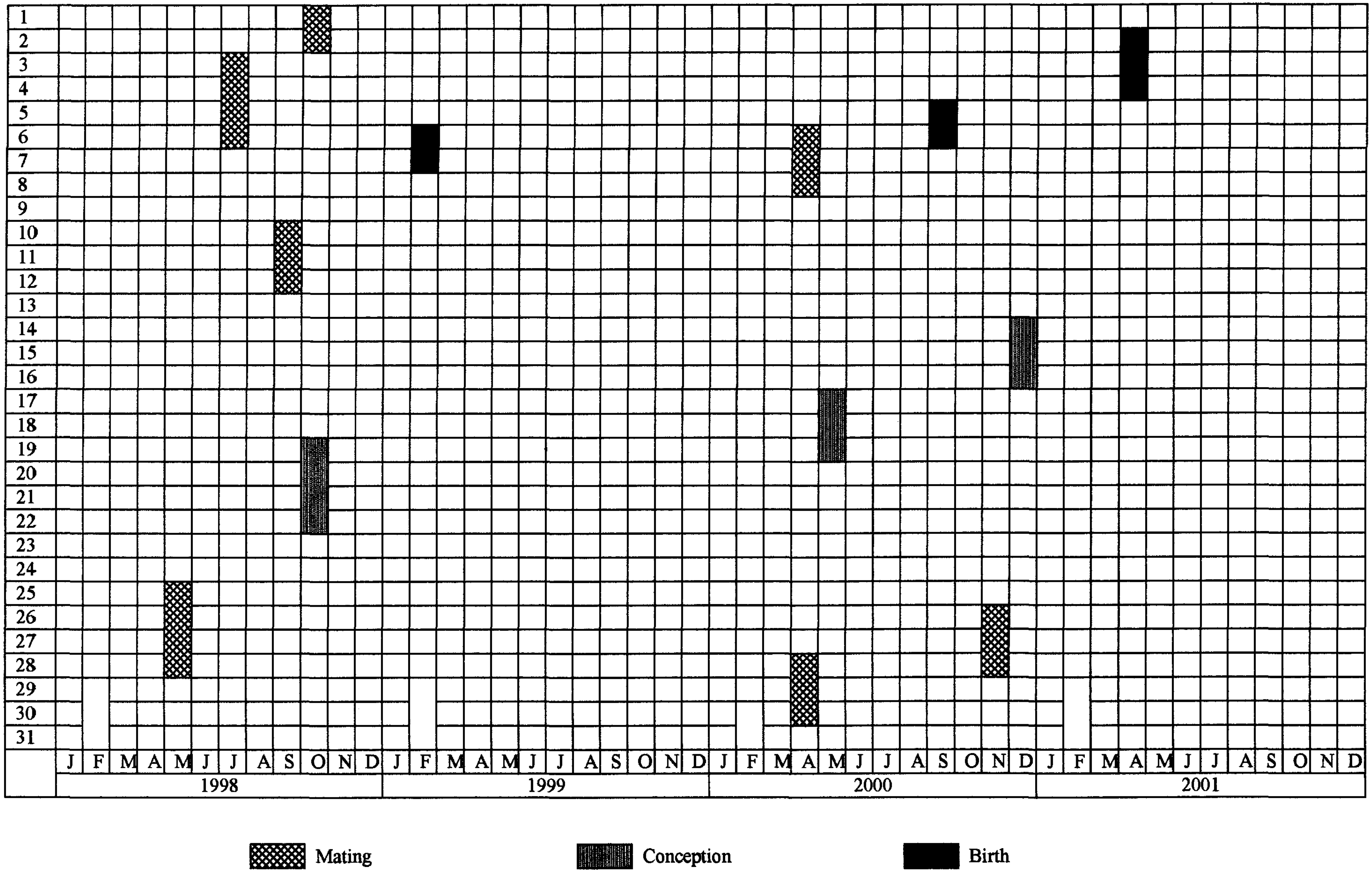

Figure 7.3. Reproductive cycle of lioness 5 on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to January 2002, showing the dates of matings, conceptions and births.

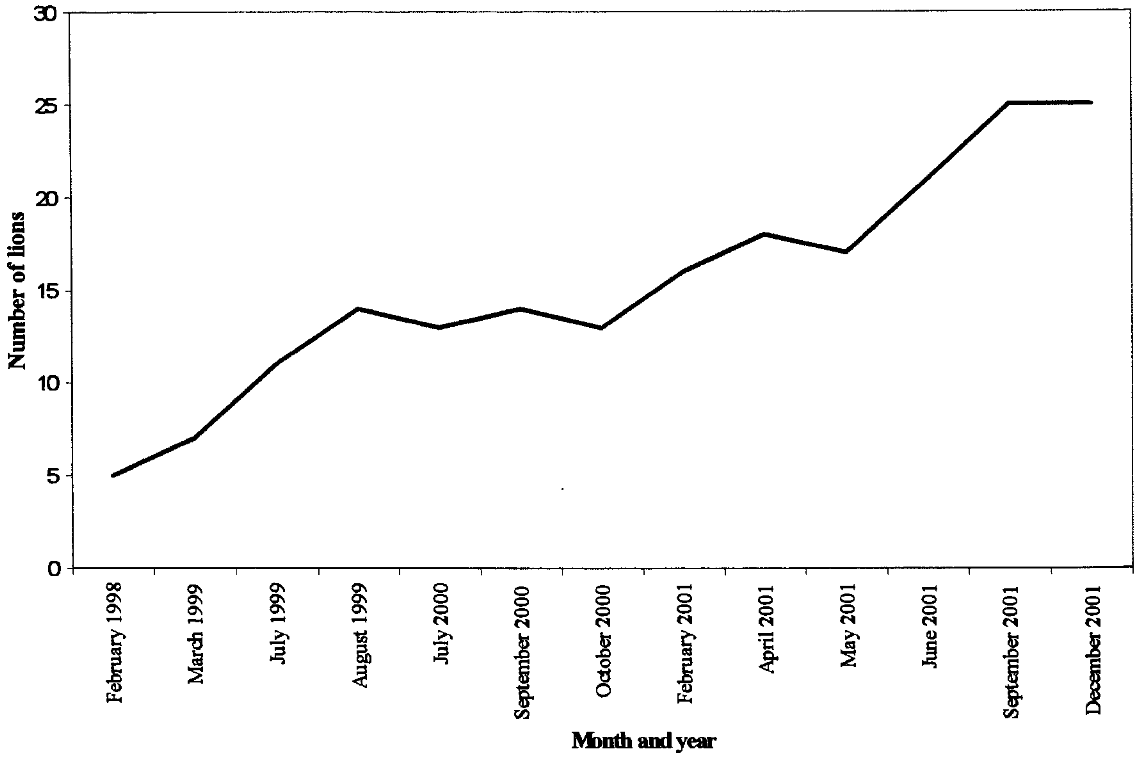

Figure 7.4. The actual growth of the reintroduced lion population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to January 2002.

Table 7.5. Details of mortality rates (percentages) as used in VORTEX for the different simulations of the lion population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

SIMULATION	CUBS	SUBADULTS		ADULTS	
		Males	**Females**	**Males**	**Females**
Base scenario	15	0	0	0	0
Simulation 1 (high cub mortality)	50	0	0	0	0
Simulation 2 (high sub-adult mortality)	15	10	10	0	0
Simulation 3 (high adult mortality)	15	0	0	10	10
Simulation 4 (high combined mortality)	50	10	10	10	10

Table 7.6. Details of the different management strategies that were used in the VORTEX simulations to give an indication of possible management actions that might be required to keep the lion population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa as close as possible to 20 animals.

STRATEGY	POTENTIAL MANAGEMENT ACTION
Base	Same data as was used in Base scenario in Table 7.2.
Strategy 1	Vasectomise young males at an age of four years, and keep females.
Strategy 2	Birth control of young females at an age of four years without vasectomising males.
Strategy 3	Combination of strategies 1 and 2.
Strategy 4	Removing young males and females from the population at an age of four years.
Strategy 5	Same as strategy 4, but additional vasectomising of two adult males every five years, plus introduction of two adult males every 5 years.
Strategy 6	Same as strategy 5, but removal of one less young female, but removal of an additional adult female.

Modelling the effects of different management strategies

The results of modelling the various management practices (Table 7.6) appear in Figure 7.7. The effect that these management practices will have on the genetic diversity and inbreeding coefficient of the lion population are shown in Figures 7.8 and 7.9. From Figure 7.7 it can be seen that all the proposed wildlife management actions will have little effect in regulating the lion population over a period of 100 years. Strategies 2 and 3 appear to be the only ones that will approximate a population of 20 lions in the long term. Figures 7.8 and 7.9 show that Strategies 5 and 6 are the only ones that will keep the inbreeding coefficient to a minimum, while also keeping the genetic diversity relatively stable.

DISCUSSION

The population dynamics of lions in large natural areas have been described in detail in various studies (Schaller 1972; Eloff 1973a; Rudnai 1973; Caraco & Wolf 1975; Smuts *et al.* 1978; Packer & Pusey 1983; Stander 1991a; Bosman & Hall-Martin 1997; Funston & Mills 1997; Packer & Pusey 1997). However, little is still known about how the introduction of lions into small reserves will affect the population dynamics of such predators. Hunter (1998) described the population dynamics of reintroduced lions in Phinda Resource Reserve, and showed that the population dynamics of the lions there differ markedly from those of lions in larger, self-contained systems. Introduced lions there showed a rapid population growth due to early breeding by both males and females because of a lack of socially limiting factors, as well as high survival rates of cubs and subadults.

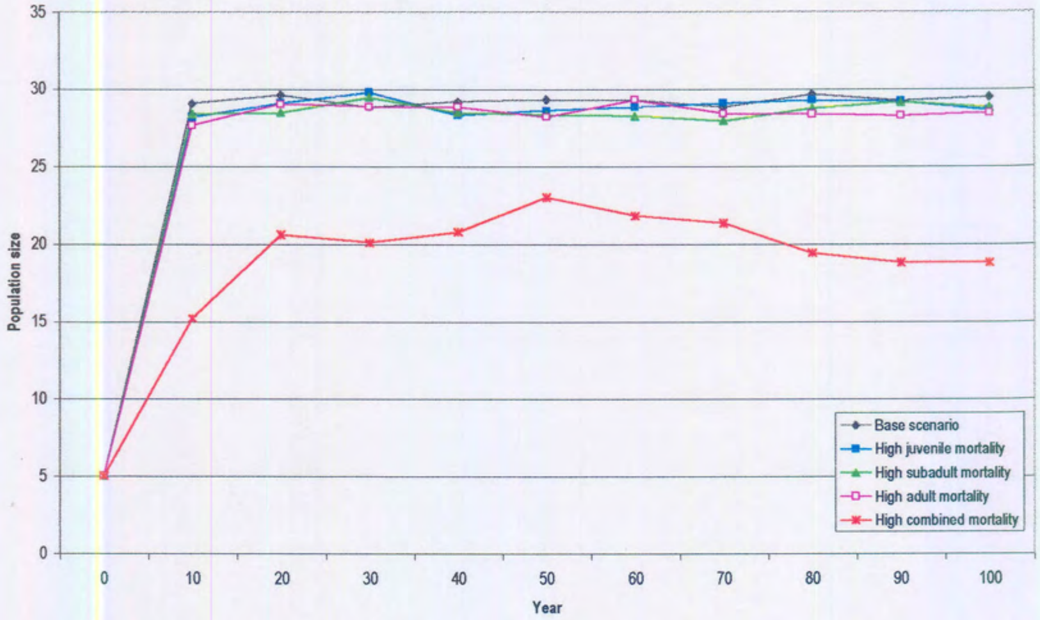

Figure 7.5. The size of the lion population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa for different levels of mortality, as projected by VORTEX at 10 year intervals for 100 years, starting from 1998 (Table 7.5).

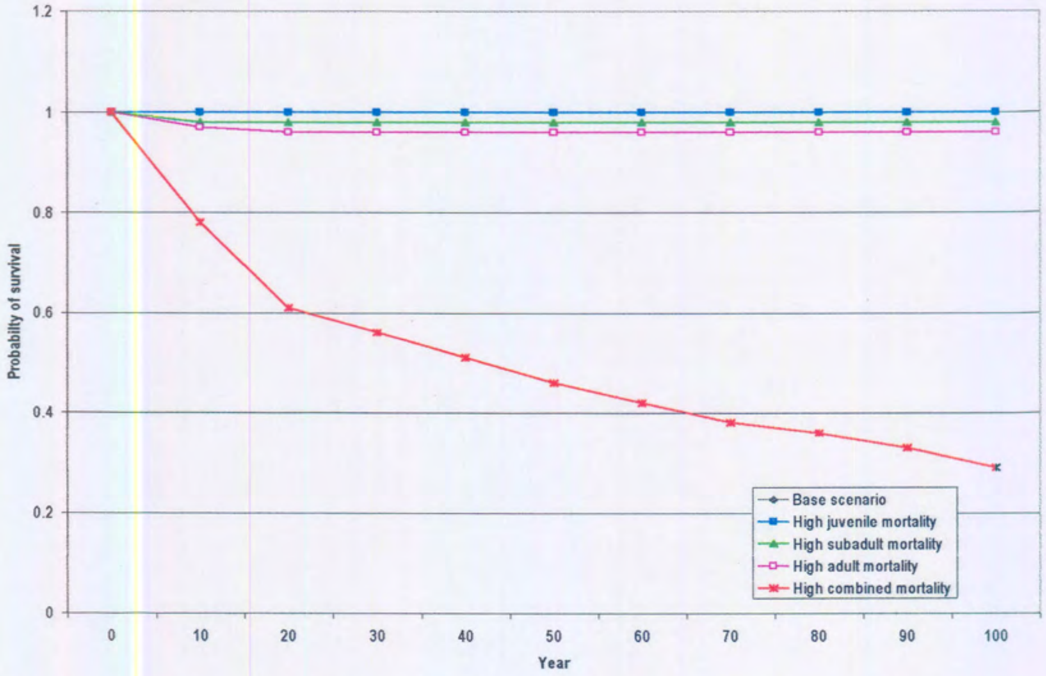

Figure 7.6. The probability of survival of the lion population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa for different levels of mortality, as projected by VORTEX at 10 year intervals for 100 years, starting from 1998 (Table 7.5).

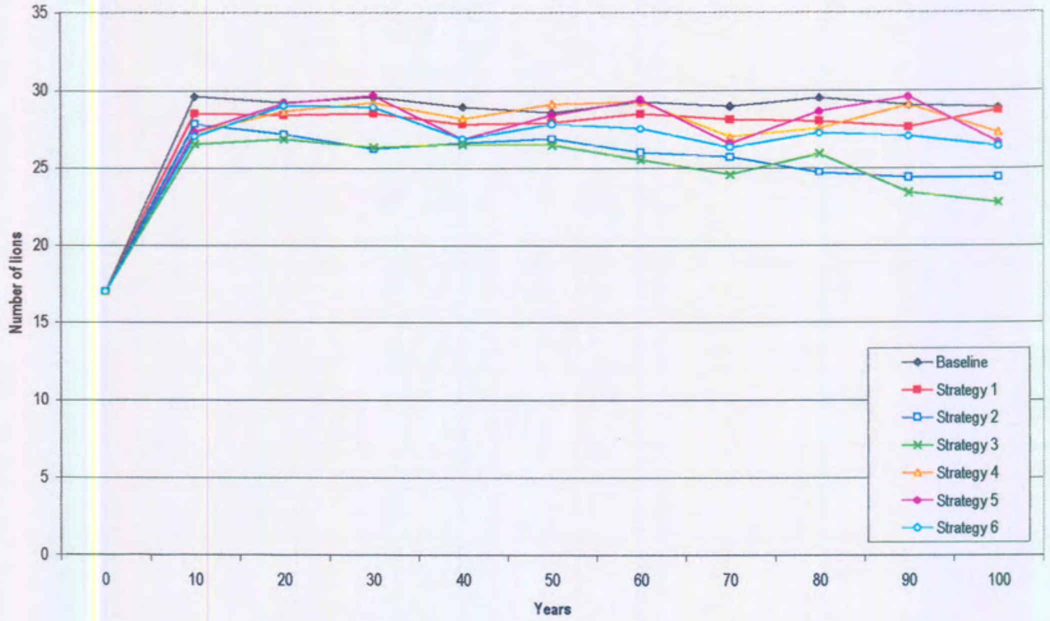

Figure 7.7. The influence of various management strategies on the size of the lion population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa, as modelled with VORTEX at intervals of 10 years over a period of 100 years starting from 2000 (Table 7.6).

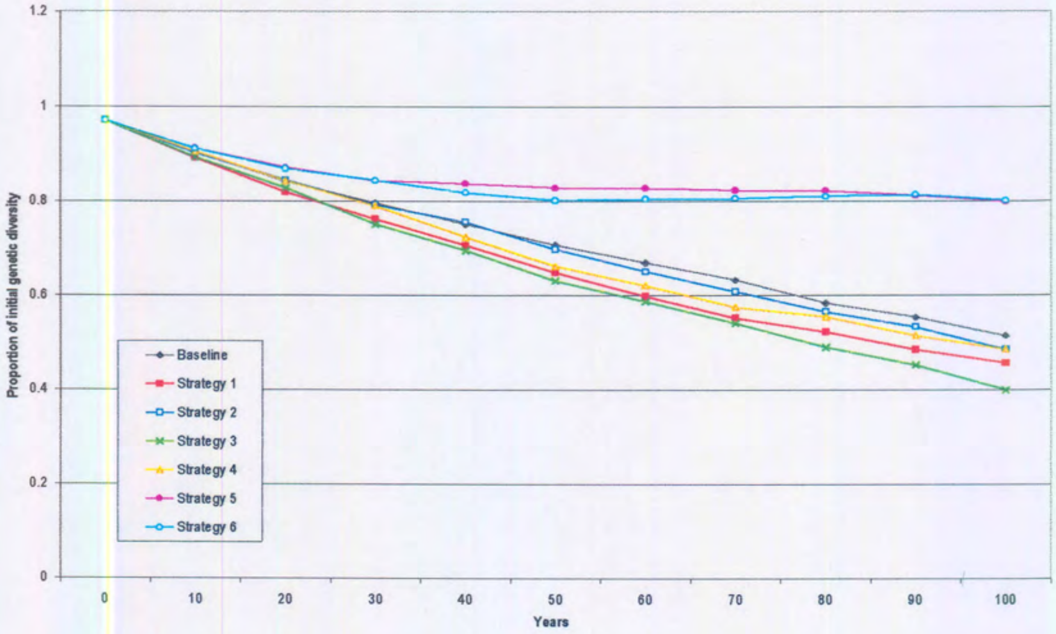

Figure 7.8. The influence of various management strategies on the genetic diversity of the lion population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa, as modelled with VORTEX at intervals of 10 years over a period of 100 years starting from 2000 (Table 7.6).

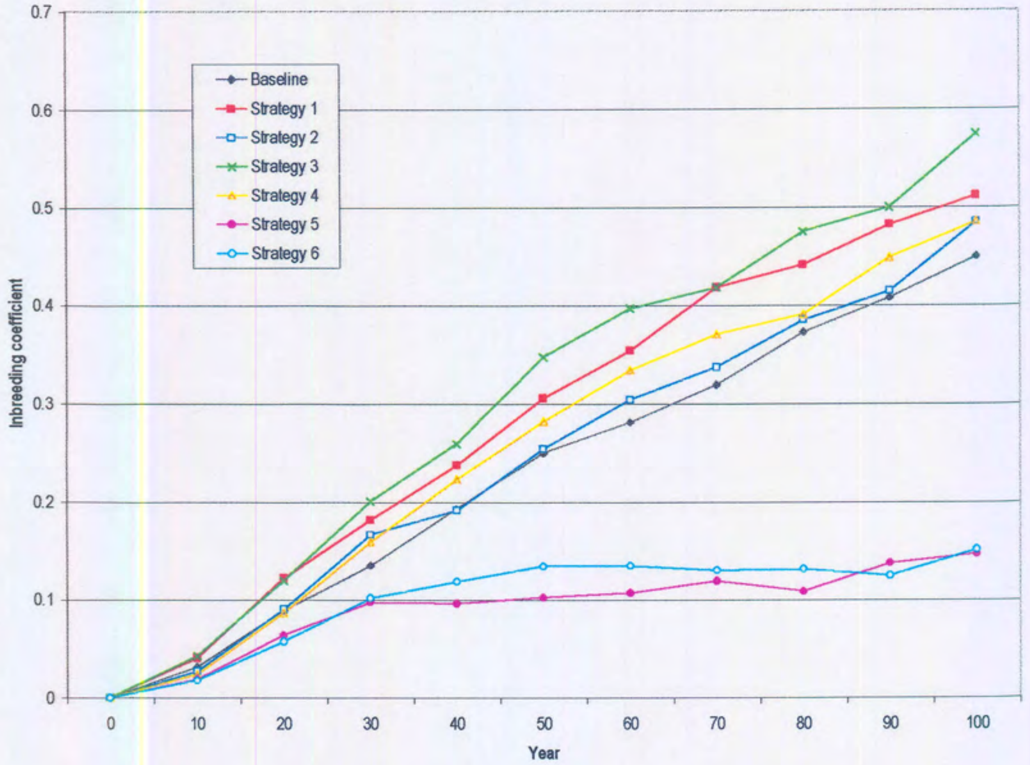

Figure 7.9. The influence of various management strategies on the inbreeding coefficient of the lion population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa, as modelled with VORTEX at intervals of 10 years over a period of 100 years starting from 2000 (Table 7.6).

The introduced lion population on Welgevonden displayed a similar rapid population growth during the study period as was observed in Phinda Resource Reserve. The Welgevonden population increased from a founder population of five lions to a population of 25 some four years after their reintroduction. This is an increase of 400% over 4 years. This indicates that lions are able to increase rapidly over a short period if introduced into areas where no lions exist at the time of introduction. Reserves that plan to introduce lion will have to keep this potential swift increase in mind when planning a lion introduction. They will have to ensure that their prey population will be able to sustain the swift increase in predation levels by the lions.

Age at first breeding

The rapid increase in the lion population may be caused by several factors. Hunter (1998) showed that introduced lionesses in Phinda Resource Reserve conceived at a much younger age than the normal mean age of 42 to 43 months for lionesses in the Serengeti (Schaller 1972). On Welgevonden, two of the three introduced females were younger than the mean age at which lions usually conceive. The introduced males on Welgevonden also mated successfully at a younger age than would normally happen in established lion populations.

Although Smuts *et al.* (1978) showed that the onset of spermatogenesis in male lions starts at 26 months, the normal social structure of lions usually prevents males from breeding until they are much older. In established lion populations, males will seldom breed when younger than four years of age. The phenomenon of introduced lions that start to breed early was also observed in Pilanesberg National Park and Madikwe

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Game Reserve (Van Dyk, *pers. comm*[3]). The most likely cause was low lion density and a lack of a stable social structure. It is known that social factors, such as the absence of a dominant female, can regulate reproduction in carnivores, and that subordinate females can then reproduce at a younger age than normal. Lions that are introduced are more often than not young animals that are introduced into a vacant area. There are therefore no dominant or older lions present to suppress the reproduction of the young, introduced lions socially. This is especially the case with males, in which the older males normally will prevent the young males from participating in breeding. It is doubtful whether the same situation will apply if young lions are introduced into areas where there are already lions with a stable social structure. A test of this hypothesis in the future should such an opportunity arise, should be valuable.

Survival of cubs and subadults

Further factors that assisted in attaining a rapid population growth are high survival rates for the cubs and subadults, and the absence of any mortality of the initial adults that were introduced. In the Serengeti, up to 66% of all the lion cubs that are born do not reach the age of one year (Packer *et al.* 1988). This high mortality rate is caused by male infanticide after take-overs, and by low prey availability. These factors did not play a role on Welgevonden, possibly explaining the high cub survival rate of 84.6%. There were no male take-overs on Welgevonden during the study period, with the result that the males killed no cubs during that time. The only mortalities of cubs were caused by injury while hunting, or by abandonment. The high cub survival rate

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[3] Van Dyk, G.: Field Ecologist. North , Rustenburg, 0030.

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is unlikely to occur indefinitely, and possible male take-overs and/or the introduction of adult males in the future should lead to a higher cub mortality rate.

Furthermore, den sites of cubs on Welgevonden were close to areas with high concentrations of prey. This meant that the lionesses did not have to leave the young cubs alone in the den for extended periods while searching for food. The cubs also did not have to travel for long distances to kills once they started to eat solid food. Eloff (1980) mentioned that the long distances that the cubs had to travel to food (prey) were one of the major causes of cub mortality in the southern Kalahari.

There also was a low density of other large predators on Welgevonden, which could have threatened the lion cubs. There are no spotted hyaenas present on Welgevonden, which means that only leopards, baboons *Papio hamadrya* and possibly brown hyaenas *Parahyaena brunnea* posed any threat to lion cubs when they were left alone at the den site. Low density of conspecifics and competing predator species would also explain the 100% survival rate of the subadult lions. Although the survival rate of the cubs and subadults was high, VORTEX analysis indicated that even a 50% mortality rate for the cubs would not have reduced the probability of survival of the lions on Welgevonden. Only an increase in the mortality rate of adults will cause an expected slight reduction in the possibility of survival of the lion population. From VORTEX analysis it appears that, although cub and subadult survival was important, the 100% survival rate of the adults was the most important factor in the rapid growth of the population. The fact that all the introduced lions survived the initial introduction phase is indicative that there was little or no pressure on them from other predators, and that food was readily available.

Inter-litter intervals

Except for the fact that the lions bred earlier than would normally happen, the inter-litter interval was much shorter than what would be expected in established populations under natural conditions. The inter-litter interval for lioness 3 was the same (730 days) as the normal inter-litter interval of two years for lions elsewhere (Bothma & Walker 1999), but it was much shorter for the other two lionesses. The reason for the low inter-litter intervals of the other two lionesses is unknown. A possible cause could be the little pressure that was exerted on the introduced lions. Food was abundant and there were no major competitors. The vacuum that existed when the lions were introduced could also have caused the lions to accelerate their breeding by reducing their inter-litter intervals. It is doubtful that the short inter-litter intervals will continue as the lion density increases.

Genetic diversity

The rapid growth of the population and the short inter-litter intervals mean that Welgevonden may face inbreeding problems much earlier than what has been expected, or than what would have been the case in large natural areas. Despite the fact that the adult males are only seven years old, they have already sired three litters with the same females. This implies that they can mate with their own daughters from the age of seven years onwards. This situation is probably not unique to Welgevonden and will be a problem on all small reserves that introduce lions. The fact that these small reserves cannot sustain a large number of lions create a situation where few or no new adult males can potentially take over the prides and increase the genetic diversity. Should the adult males stay in control of the prides for long periods of time, mating with their daughters and granddaughters will occur. Managers on small

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reserves will have to keep this potential problem in mind, and will have to intervene to prevent this from happening. If not, they may face the same problem as the Hluhluwe-Umfolozi Park (Grubbich 2001), where the lion population also originated from a maximum of five lions and showed a rapid population increase. Inbreeding there soon caused the population to suffer from an immuno-deficiency syndrome, and the population started to decline.

It was furthermore shown with VORTEX analysis how the genetic diversity declines and the inbreeding coefficient increases if the population is left unmanaged. Managers will have to find ways to keep the genetic diversity at a maximum, and still keep the population within the limits of what the prey in the reserve can sustain. The use of contraceptives in female lions could reduce the overall breeding in the lion population on the reserve. Different management strategies have various influences on the genetic diversity and inbreeding of the population in the VORTEX model. Vasectomising males is becoming an increasingly popular strategy to decrease the breeding rate and to prevent inbreeding. However, there are also disadvantages to this method that should be considered. The female lions will come into oestrus every three weeks if they do not mate successfully. This can be expected to occur if all the males in the population are vasectomised. Also, it does not increase the genetic diversity in the lion population. This can only be done by bringing in new genetic material from other, unrelated populations. The introduction of new genetic material by bringing in new males caused an immediate increase in the genetic diversity in the VORTEX simulation. In order for this to work effectively, managers will have to ensure that inbreeding in the lion population in the reserve is kept to a minimum and that any animals that are exchanged or introduced do not already suffer from a lower genetic heterosygosity. Few reserves are large enough to naturally sustain the number of lions that are required to maintain the genetic diversity of the population in the long term. Small reserves will have to work together to manage the lions as a meta-population. This should involve regular interaction between the management staff of the various reserves to discuss matters, and to properly plan the exchange of genetic material between reserves.

CONCLUSIONS

Reintroduction is a viable method of establishing a new lion population in areas where they have become extinct. The rapid increase in the reintroduced lion population on Welgevonden indicates the success of the reintroduction attempt. The rapid growth rate of the reintroduced population was caused by several factors. The lions on Welgevonden started breeding at a younger age and had shorter inter-litter intervals than lions in established populations. This was largely due to a lack of social pressure, as the lions were introduced into an area where there were no other lions present. A low density of conspecifics and competing predators also ensured a high survival rate of cubs and subadult lions.

Small founder populations and the rapid growth of reintroduced lion populations in small game reserves mean that these lion populations will face problems with inbreeding and low genetic heterosygosity. Managers will have to find ways to keep the genetic diversity at a maximum, and still keep the lion population within the limits of what the prey on the reserve can sustain. Males could be vasectomised to prevent them from breeding with their own offspring. However, it will also be necessary to

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bring in new genetic material in the way of new males to increase the genetic diversity of the lion population. The use of contraceptives in females can also be a valuable tool in reducing the overall breeding of the lions on a reserve. Small reserves will therefore have to cooperate to manage their small, individual lion populations as one meta-population in order to preserve the genetic vigour of the lion population as a whole.

There still is much to be learned about the population dynamics of introduced lion populations in small reserves. Introductions like those on Welgevonden and other small reserves will serve as continual experiments on how wildlife management techniques and actions influence the genetic viability and persistence of lion populations, not only on the individual reserve, but as part of a larger population of all the various reserves combined.

CHAPTER 8

FEEDING ECOLOGY

INTRODUCTION

Predation is an important component of the biotic environment of wild ungulates, and has probably exerted considerable influence on ungulate populations throughout their evolutionary history. Agricultural and industrial advancement has led to the extermination of large predators from most of their original ranges in southern Africa. However, they still occur in national parks, game reserves and other wilderness areas. Although such areas are often quite small, people still want these areas to maintain a wide diversity of mammals, including large predators. Therefore, a thorough understanding and knowledge of predator-prey relationships is important for the scientific management of these areas (Van Dyk 1997).

Many studies have been done in the past to determine different aspects of lion predation. The majority of these studies focussed on diet, feeding behaviour and feeding patterns (Mitchell, Shenton & Uys 1965; Pienaar 1969; Schaller 1972; Eloff 1973b, 1984; Rodgers 1974; Rudnai 1974, 1979; Saba 1979; Smuts 1979, 1982; Mills 1984; Van Orsdol 1984; Ruggiero 1991; Stander 1991b; Van Valkenburgh 1996; Viljoen 1997). The current emphasis of predation studies is changing, becoming more focussed on the effects of sociality (Cooper 1991; Scheel & Packer 1991; Stander 1992; Funston & Mills 1997; Funston 1998) and ecological factors (Mills & Biggs 1993; Mills, Biggs & Whyte 1995) on predation. The impact of mammalian predators on their prey is a complex and controversial aspect of predator ecology (Mills & Shenk 1992) and is currently receiving considerable attention (Mills & Shenk 1992; Hunter 1998; Peel & Montagu 1999). However, the majority of the studies mentioned above were done in large, self-sustaining reserves and ecosystems. Yet, there is an increasing trend towards keeping lions on small, highly managed reserves. Although some work on lion predation on small areas has been done (Hunter 1998; Peel & Montagu 1999), the feeding ecology and dynamics of lions on small reserves are still largely unknown. Ecosystems are dynamic, and therefore data cannot be extrapolated from one area to another, or even from one period to another in the same area (Mills & Shenk 1992). This was a primary motivation for doing the current study on Welgevonden.

Lions eat a wide spectrum of food, depending on the type and abundance of prey available. In the Kruger National Park, lions utilise 38 different types of prey, with the blue wildebeest the major prey choice (Pienaar 1969). In the Kafue National Park, lions utilise 19 types of prey, with the buffalo the major prey of choice (Mitchell *et al.* 1965). In the southern Kalahari, lions utilise 18 different types of prey (Eloff 1984), as is done in the Serengeti National Park with its numerically rich prey base (Schaller 1972). In Etosha National Park, 17 types of prey are utilised (Stander 1991b), while 15 types of prey are utilised in the Savuti (Viljoen 1997). Lions are opportunistic feeders and will utilise almost any prey that is encountered (Scheel and Packer 1995). This accounts for the wide range of prey killed by lions in the different regions.

Lions normally kill prey that are between 20 and 800 kg in weight, although they are quite capable of killing larger prey, and also do use smaller prey. It has often been reported that lions kill larger prey like the white rhinoceros, the black rhinoceros *Diceros bicornis*, the hippopotamus *Hippopotamus amphibius* and the elephant (Pienaar 1969; Rodgers 1974;

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Van Orsdol 1984; Ruggiero 1991; Scheel & Packer 1995). Ruggiero (1991) found an unusually high proportion of young elephants in the diet of the lions in Manovo-Gounda-St. Floris National Park in the Central African Republic. One possible reason for this was the high rate of poaching on adult elephants, leaving orphaned and vulnerable elephant calves. The abundance of smaller prey in the lion's diet depends on the area and prevailing conditions at specific times of the year. Eloff (1973b, 1984) found that small animals like the porcupine *Hystrix africaeaustralis* make up a large proportion of the diet of lions in the southern Kalahari. Under normal circumstances, the number of small animals that lions will utilise is small. Moreover, they are usually only utilised during drought or migration when large prey is scarce (Scheel and Packer 1995). Kruuk & Turner (1967) found that the size of the prey increases as the size of the lion pride increases. This happens because small prey killed by a large pride leads to intense competition between pride members at the kill, which is detrimental to the pride as a whole. It is also energetically inefficient for a large pride to hunt small animals, as the energy used to kill small animals cannot be gained by the small volume of food acquired from such a kill (Griffiths 1975).

The results of several studies (Mitchell *et al.* 1965; Hirst 1969; Makacha & Schaller 1969; Pienaar 1969; Schaller 1972; Van Orsdol 1982, 1984) also indicate that lions kill a greater proportion of males and young animals of several types of prey than would be expected from the relative abundance of such food categories in the prey population. However, this is not a fixed rule and other studies indicate no such disproportionate selection (Mills & Schenk 1992). The proportion of certain sex or age groups in lion kills also seems to differ from region to region, and again emphasises that lions are opportunistic hunters.

The estimated number of annual lion kills ranges from about 11 to 50 prey animals per year in various studies, but most are fewer than 35 animals (Whright 1960; Kruuk & Turner 1967; Makacha & Schaller 1969; Pienaar 1969; Schaller 1972; Eloff 1984; Stander 1991b; Viljoen 1997). The southern Kalahari lions kill 50 animals per year, which is considerably higher than anywhere else (Eloff 1984). However, these lions kill many more small animals than lions in other areas. The food that is required daily by a large carnivore varies from 4% to 6% of its body weight (Schaller 1972; Berry 1981), although a lion can eat up to 25% of its body weight within a few hours (Bertram 1975). The quantity of meat required by lions ranges from 5 to 7 kg per lion per day (Schaller 1972, Viljoen 1997). Lions consume large prey as completely as possible, but some uneaten portions can remain (Schaller 1972). Small animals are often consumed completely, leaving only the hooves and some hair in most cases (Eloff 1984). During the rainy season, the food intake of lions can be up to 1.6 times higher than during the dry season (Viljoen 1997).

METHODS

Many studies on the feeding habits of lions have been done in the past. A variety of techniques were used for these studies, including stomach and faecal analyses (Smuts 1979), opportunistic observations (Wright 1960; Kruuk & Turner 1967; Pienaar 1969; Schaller 1972; Mills 1984), tracking by spoor (Eloff 1973b, 1984), radio-tracking (Bertram 1982; Stander 1992; Viljoen 1997) and direct observations (Schaller 1972; Van Orsdol 1984; Stander 1992; Viljoen 1997). Mills (1992) made a comparison of all these methods and came to the conclusion that direct observations done by following the animals in a vehicle for extended periods is the least biased method to study the feeding habits of large carnivores, particularly in assessing predator-prey relationships.

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For this part of the current study, the study period was from 16 January 1998 to 3 October 1999. Logistical reasons made it difficult to spend more time with the lions to collect more long-term continuous observation data. Therefore, for the purposes of this study, a combination of several methods was used to determine the feeding ecology of the lions on Welgevonden.

Observations of type, sex and age of prey

Radio-telemetry was used to locate the lions, whereafter they were followed in a vehicle wherever possible, and direct observations of kills were made. The lions were followed at a distance where neither predator nor prey were disturbed (Mills 1992), but close enough to maintain visual contact. When the lions were followed at night, a spotlight was used to maintain visual contact, but the light was switched off when possible prey animals were encountered. During the early part of the study, a spotlight with a red filter was used. However, it soon appeared that the normal light did not disturb the lions more than one fitted with a red filter. Consequently, a normal spotlight was used later during the study. By listening to the sounds and noises made by prey animals and the lions, it was possible to tell whether a kill had been made. Where possible, the kill site was then approached to determine the type of prey, as well as the sex and age of the prey animal. Where it was impossible to do, the kill site was approached on foot after the lions had left. Where it was impossible to determine the type of prey, the kill was recorded as an unknown kill. It often happened that lions were already on a kill when they were located. In these cases, it was attempted to determine whether the kill was actually made by the lions or whether it was scavenged. Signs in the area of the kill often gave clues as to whether the animal had been killed or scavenged. For example, obvious signs of a struggle indicated a kill. The freshness of the kill also gave a good indication of whether the prey had been killed or scavenged.

In the latter part of the study, guides doing game drives provided many observations of kills or carcasses. The guides were proficient in identifying the type of prey, as well as the sexes and ages of the prey. All reports of kills by the guides were followed up by visiting the kill site to determine its location by GPS, and to determine or confirm the type of prey, and its sex and age where possible.

For all the kills, the type of prey, and its age and sex where possible were determined. The time of the kill, the individual lions present at the kill, and the habitat type in which the kill was made were also recorded. In order to get some indication of the prey size of unknown kills, a method used in Phinda by Hunter (*pers. comm.*[1]) was also used. This method makes use of a score of the belly size of the lions as an indication of the size of prey that was killed. The belly size was scored on a five-point scale. A score of 1 indicated that it could just be seen that the lion had fed, with a score of 5 when the lion was fully gorged. A reference list was drawn up to determine the size of the prey animal according to the belly size. The prey was recorded only as small, medium or large. This method is subjective and biased towards larger prey, and only gives a crude indication of the size of the prey, and not prey type. The fact that lions were seen almost every day made it easy to see whether an animal had fed since the previous observation and helped to limit this source of bias.

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Kill rate

Killing frequencies by lions have often been calculated, but are of limited practical value due to the large variation in the body weight of prey. The estimated amount of food consumed allows a better basis for comparison between different areas (Viljoen 1997). For the present study, both the annual killing rate, for use in the model in Chapter 8, as well as the amount of food consumed were determined. The annual killing rate was calculated by using the following equation (Mills & Schenk 1992):

Kill rate per lion per year = (number of prey killed x number of hours in a year) ÷ (number of hours spent observing the lions)

Food consumption

The amount of food consumed was determined by using the tables of Meissner (1982) as well as Bothma, Van Rooyen & Du Toit (1995) as a guide in determining the weights of the different types of prey for different age classes. The edible biomass for the different weight classes was estimated as follows (Viljoen 1997):

< 50 kg	: 80% of live weight
50 - 150 kg	: 75% of live weight
151 - 250 kg	: 70% of live weight
251 - 500 kg	: 65% of live weight
> 500 kg	: 60% of live weight

For each kill, an estimate of the percentage of edible meat left on the carcass was made.

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Prey preference

If a preference by lions for a certain type of prey is to be determined, it is important to relate it to the number of that prey that is available. For this, a preference rating for the different types of prey killed was determined, using the following equation (Pienaar 1969; Mills & Biggs 1993):

Predation rating = number of prey killed ÷ relative abundance of that prey in the region

The numerical abundance of different types of prey present on the reserve and their relative abundance were based on the annual aerial animal count data, as well as monthly vehicle drive counts to determine the wildlife numbers in the different areas of the reserve (Kilian 2001).

Chi-squared analysis was used to determine whether the lions were selecting for a certain type of prey or not. This was done by comparing the number of each type of prey killed with the relative availability of that prey on the reserve. The same method was used to determine whether there was any selection for specific sex or age classes of prey.

Number of lions versus prey size

Smuts, Robinson & Whyte (1980) state that a lioness weighs a mean of 124.2 kg, and that adult males are 50% heavier than females. A weight of 124.2 kg for a female was consequently used as a female equivalent of 1, while an adult male had a female equivalent of 1.5. In order to determine whether there was a change in prey selection when the group size increased, it was necessary to determine the number of lions on each kill in terms of female equivalents. Equations developed by Smuts *et al.* (1980) to determine the weight of a lion by its age, were used to determine the female equivalents at each kill. These equations were derived separately for males and females and are as follows:

Males: $y = 4.21x + 5.29$

Females: $y = 3.31x + 6.64$.

where y = body weight

x = age in months

Single linear regression analysis was used to determine whether there was an increase in prey weight when the group size increased. For this analysis, only observed kill data were used. This was done to exclude the possible bias towards larger prey at unobserved kills, as was explained earlier.

RESULTS

Prey types

During the study period, lions killed 21 types of prey on Welgevonden (Table 8.1) of which 99.5% were mammals. Only one known non-mammalian kill was made, consisting of an adult female ostrich *Struthio camelus*. One carnivore, an adult male brown hyaena was killed, but it was not eaten and can therefore not be regarded as prey. Since the end of the study period, two more brown hyaenas were killed (*pers. obv*). During the study, five bushpigs *Potamochoerus porcus* were killed, but four were abandoned without being fed on. The reason for abandoning the carcasses is unknown, but has also been noted in Phinda Resource Reserve for the bushpig (Hunter 1998). A young bushpig was once partially consumed by the single lioness after she was injured just after release. Since the end of the study, two more bushpig kills were made by subadult lions. In both cases, the carcasses were completely consumed. In one of these cases, an adult male took the kill from the subadults and consumed most of it. The same male was previously seen to abandon a bushpig that he had killed himself, without feeding from it.

Number and biomass of prey killed

The most abundant prey animals killed in terms of numbers and biomass appear in Figures 8.1 and 8.2 respectively. In terms of numbers, the blue wildebeest was killed most, followed by the warthog *Phacochoerus africanus*, eland and red hartebeest. In terms of biomass, the eland was the killed the most, followed by the blue wildebeest, red hartebeest and greater kudu *Tragelaphus strepsiceros*. Although warthog were killed the second most often in terms of numbers, it only forms the fifth ranked prey in terms of biomass killed. The five most abundant animals killed, the blue wildebeest, warthog, eland, red hartebeest and kudu formed 78.3% and 82.4% of the total number of animals and total biomass killed respectively.

Table 8.1. Complete list of animals killed by lions on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to October 1999, based on observed kills and carcasses found.

PREY	NUMBER KILLED	PERCENTAGE OF TOTAL	BIOMASS IN KG	PERCENTAGE OF BIOMASS
Aardvark	1	0.5	36.0	0.2
Baboon	1	0.5	16.0	0.1
Blue wildebeest	49	23.1	5476.6	24.8
Brown hyaena	1	0.5	36.0	0.1
Burchell's zebra	11	5.2	1627.8	7.4
Bushpig	5	2.4	201.6	0.9
Eland	26	12.3	6810.0	30.8
Gemsbok	2	0.9	287.0	1.3
Giraffe	1	0.5	462.0	2.1
Impala	11	5.2	382.0	1.7
Kudu	19	9.0	2002.1	9.1
Ostrich	1	0.5	90.0	0.4
Porcupine	2	0.9	24.0	0.1
Red hartebeest	24	11.3	2171.5	9.8
Reedbuck	2	0.9	112.5	0.5
Sable antelope	1	0.5	147.0	0.7
Scrub hare	1	0.5	1.6	0.0
Steenbok	2	0.9	48.0	0.2
Tsessebe	2	0.9	182.25	0.8
Warthog	48	22.6	1764.5	8.0
Waterbuck	2	0.9	255.0	1.2
Total	212	100.0	22097.5	100.0

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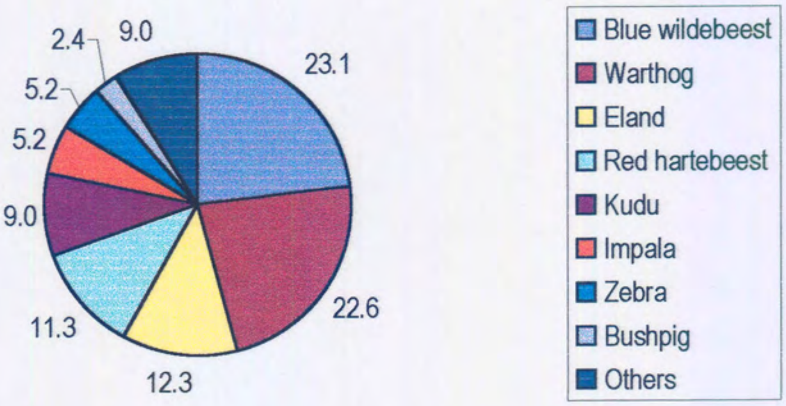

Figure 8.1. The animals killed by lions on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to October 1999, expressed as the percentage of the total number of animals killed. Others include the aardvark, baboon, brown hyaena, gemsbok, giraffe, ostrich, porcupine, reedbuck, sable antelope, scrub hare, steenbok, tsessebe and waterbuck.

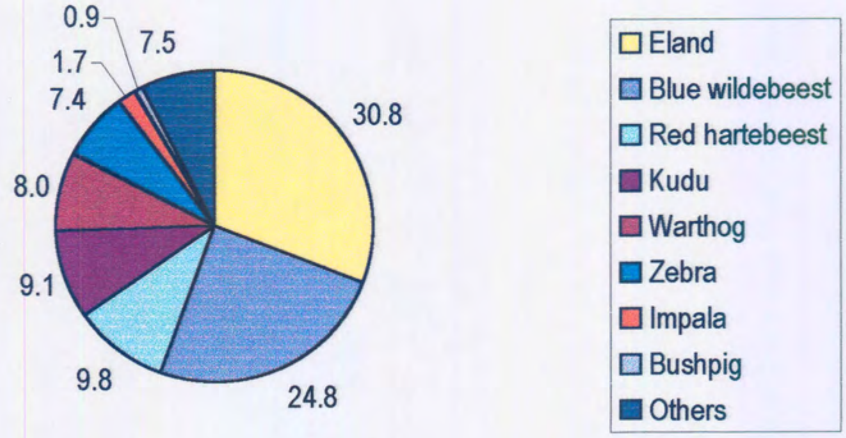

Figure 8.2. The animals killed by lions on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to October 1999, expressed as the percentage of the total biomass of animals killed. Others include the aardvark, baboon, brown hyaena, gemsbok, giraffe, ostrich, porcupine, reedbuck, sable antelope, scrub hare, steenbok, tsessebe and waterbuck.

Frequency of predation

Table 8.2 gives an indication of the frequency of predation by lions on 11 types of ungulates, and the frequency with which these ungulates occurred on the reserve during the study. The blue wildebeest, warthog, eland and red hartebeest were killed in greater frequencies than expected by their occurrence, while the impala *Aepyceros melampus*, Burchell's zebra *Equus burchellii* and waterbuck *Kobus ellipsiprymnus* were killed less frequently than expected based on their occurrence. The warthog and red hartebeest were preyed upon twice as often as what their availability would have suggested. Predation on kudu, gemsbok *Oryx gazella*, tsessebe *Damaliscus lunatus lunatus* and giraffe *Giraffa camelopardalis* reflected their degree of availability.

Prey preference

Pienaar (1969) used an equation to determine a prey preference rating by dividing the kill frequency of a particular type of prey by its relative abundance in an area. This equation has since been used in several other studies (Rudnai 1974, Berry 1981, Ruggiero 1991). However, it has been suggested that this method of prey preference rating gives an indication of prey vulnerability rather than prey selection (Sunquist & Sunquist 1989). Keeping this in mind, the preference rating of Pienaar (1969) was applied for different prey on Welgevonden. Warthog and red hartebeest had the highest preference ratings, followed by eland and blue wildebeest. Four of the five most often killed types of prey were blue wildebeest, warthog, eland and red hartebeest. They were killed in greater frequencies than expected based on their relative abundance on the reserve. Warthog and red hartebeest, which had the highest preference rating, were preyed upon twice as often as what would have been expected by their availability.

Table 8.2. Kill ratios and predation ratings of the 11 animals most often killed by lions on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to October 1999. The chi-square value for the data is $\chi^2 = 103.49$ ($p<0.001$, df = 10).

PREY	**PERCENTAGE RELATIVE ABUNDANCE**	**LION KILLS**		**PREDATION RATING**
		Number	**Percentage**	
Blue wildebeest	17.33	49	25.26	1.5
Warthog	11.86	48	24.74	2.1
Eland	8.59	26	13.40	1.6
Red hartebeest	5.90	24	12.37	2.1
Kudu	7.43	19	9.79	1.3
Impala	19.64	11	5.67	0.3
Zebra	22.14	11	5.67	0.3
Gemsbok	1.12	2	1.03	0.9
Tsessebe	1.31	2	1.03	0.8
Waterbuck	4.68	2	1.03	0.2
Giraffe	0.78	1	0.52	0.7

*: (Pienaar 1969; Biggs 1993)

Scavenging

Lions were only observed to scavenge twice during the study period. The two adult males once fed on an eland carcass that had been killed by the females four days earlier. Although they had not eaten for six days, they only fed for 30 minutes before leaving the carcass, which still had untouched meat on it. One male lion was also observed to scavenge a zebra carcass. The cause of death of the zebra was unknown. Lions were observed locating four other carcasses without feeding from them. Three of these carcasses, two of a warthog and one a zebra foal, had died from unknown causes, while the fourth was an adult blue wildebeest that had possibly died from gifblaar *Dichapetalum cymosum* poisoning.

Figure 8.3 shows the percentage of different animals that were killed by different social groups of lion during the study period. Not enough data were available to calculate a reliable percentage for the single lioness. Lionesses with cubs only killed five types of prey compared to 10 by lionesses without cubs, but the sample size for lionesses with cubs was only eight kills. The number of prey types killed might well increase if the data set were to increase. The prey animals that were killed by lionesses with cubs reflect the animals that were available in close vicinity of the dens. In general, no real pattern of kills by different social groups was found, because the data sets for the different groups of lions are too small, and they might not give a true reflection of possible social group bias in prey choice.

Selection for age and sex classes of prey

Table 8.3 shows that, except for Burchell's zebra, there was no selection for any age class and that the lions preyed mostly on the different age classes in the frequency in which they occurred in the p s zebra, the lions preyed

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significantly less on adults and more on subadults than the frequencies in which they actually occurred. Table 8.4 shows the lion predation by sex classes. There was no selection for any sex class of prey, and the lions preyed upon the different sexes in the frequencies in which they actually occurred during the study.

Number of lions versus prey size

There was no significant relationship between the body weight of the prey killed and the number of lions in terms of female equivalents present at the kill ($F = 0.389$, $p = 0.53$, $r^2 = 0.0019$, $df = 209$) (Figure 6.4).

Meat consumed

The lions killed a mean of 30.6 prey animals per lion per year. In terms of female equivalents, this amounted to 27.2 kills per female equivalent per year. A mean meat intake of 6.8 kg per lion per day, and 6.1 kg per female equivalent per day was calculated. This amounts to 2478.4 kg of meat per lion per year, or 2219.2 kg of meat per female equivalent per year. Blue wildebeest formed 26.1% of all the meat eaten by the lions, followed by the eland (25.1%), red hartebeest (12.1%) and kudu (10.8%).

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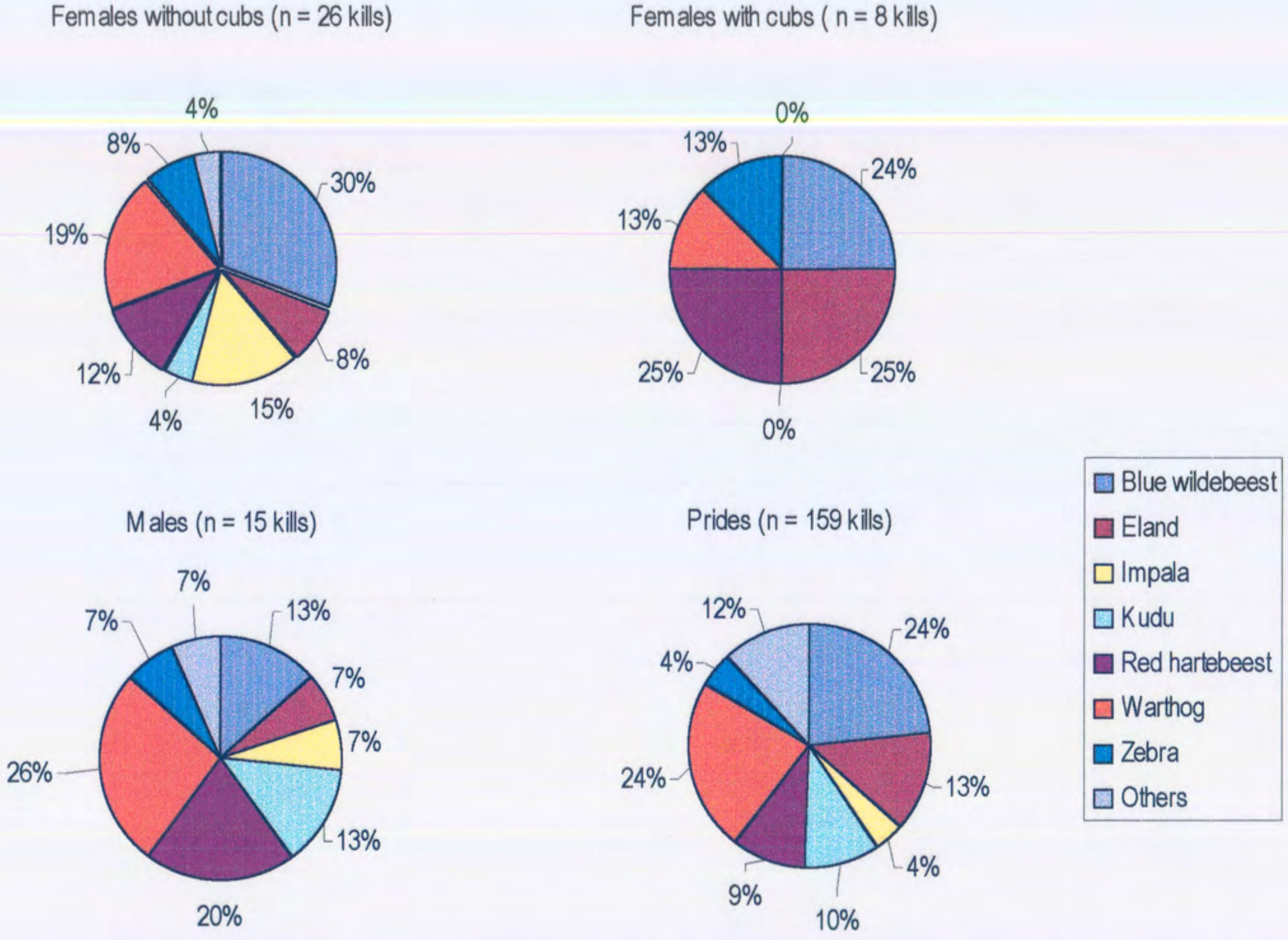

Figure 8.3. Percentage of different types of prey killed by different social groups of lions on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to October 1999.

Table 8.3. Chi-square analysis of lion predation on sex classes of prey on Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to October 1999, using the percentage of occurrence of the sex classes in the population as expected values.

PREY	**KILLS**				**PERCENTAGE OCCURRENCE IN POPULATION**		**CHI-SQUARE TEST**		
	Males		**Females**		**Males**	**Females**	χ^2	**P**	**df**
	Number	**Percentage**	**Number**	**Percentage**					
Blue wildebeest	13	37	22	63	27	73	1.83	>0.05	1
Warthog	11	42	15	58	41	59	0.02	>0.05	1
Eland	6	30	14	70	29	71	0.01	>0.05	1
Red hartebeest	8	38	13	62	45	55	0.41	>0.05	1
Kudu	7	44	9	56	25	75	3.00	>0.05	1
Impala	4	40	6	60	40	60	0.00	>0.05	1
Burchell's zebra	1	14	6	86	39	61	1.80	>0.05	1
Gemsbok	1	50	1	50	57	43	0.04	>0.05	1
Tsessebe	1	50	1	50	36	64	0.16	>0.05	1
Waterbuck	1	50	1	50	41	59	0.07	>0.05	1
Giraffe	1	100	0	0	52	48			

Table 8.4. Chi-square analysis of lion predation on age classes of prey on Welgevonden during the study period, using the percentage of occurrence of age classes in the population as expected values.

PREY	KILLS						PERCENTAGE OF OCCURRENCE IN THE POPULATION			CHI-SQUARE TEST		
	Adults		Subadults		Juveniles		Adults	Subadults	Juveniles	χ^2	P	df
	No.	Percent.	No.	Percent.	No.	Percent.						
Blue wildebeest	31	63	8	16	10	20	62	21	16	1.12	>0.05	2
Warthog	27	57	8	17	12	26	57	16	27	0.07	>0.05	2
Eland	14	54	7	27	5	19	62	21	16	0.88	>0.05	2
Red hartebeest	19	79	3	13	2	8	87	8	5	1.31	>0.05	2
Kudu	12	63	3	16	4	21	69	20	11	2.01	>0.05	2
Impala	7	64	2	18	2	18	60	17	23	0.14	>0.05	2
Burchell's zebra	4	36	3	27	4	36	75	13	12	9.35	<0.01	2
Gemsbok	2	100	0	0	0	0	100	0	0			
Tsessebe	2	100	0	0	0	0	79	7	14	0.53	>0.05	2
Waterbuck	2	100	0	0	0	0	77	15	13	0.70	>0.05	2
Giraffe	0	0	1	100	0	0	62	33	5	2.03	>0.05	2

Table 8.5. Chi-square analysis of lion predation in different habitat types on the Welgevonden Private Game Reserve in the Waterberg region of South Africa from January 1998 to October 1999. The expected number of kills in each habitat type was based on the percentage occurrence of prey in each habitat type.

PREY	OBSERVED NUMBER OF KILLS				EXPECTED NUMBER OF KILLS BASED ON PERCENTAGE OCCURRENCE OF PREY				CHI-SQUARE		
	Old lands	**Plateaux**	**Hills**	**Valleys**	**Old lands**	**Plateaux**	**Hills**	**Valleys**	χ^2	**P**	**d**
Blue wildebeest	21	25	0	3	21.1	22.3	2.6	3.1	2.90	>0.05	
Warthog	24	12	0	12	27.5	11.8	1.1	7.7	3.96	>0.05	
Eland	8	14	1	3	6.3	5.7	12.8	1.3	25.92	<0.001	
Red hartebeest	12	12	0	0	12.8	9.9	1.2	0.2	1.83	>0.05	
Kudu	2	10	1	6	1.7	5.0	5.5	6.8	8.75	<0.05	
Impala	3	5	0	3	3.0	4.5	0.7	2.9	0.79	>0.05	
Zebra	6	4	1	0	2.6	4.1	3.7	0.7	7.13	>0.05	
Tsessebe	1	1	0	0	0.7	1.0	0.1	0.2	0.41	>0.05	
Waterbuck	2	1	0	1	0.7	0.3	0.2	0.7	2.38	>0.05	
Giraffe	1	0	0	0	0.3	0.7	0.0	0.0	2.99	>0.05	
Other	6	7	0	4							
TOTAL	84	91	3	32	9.2	37.7	145.6	13.5	810.78	<0.001	

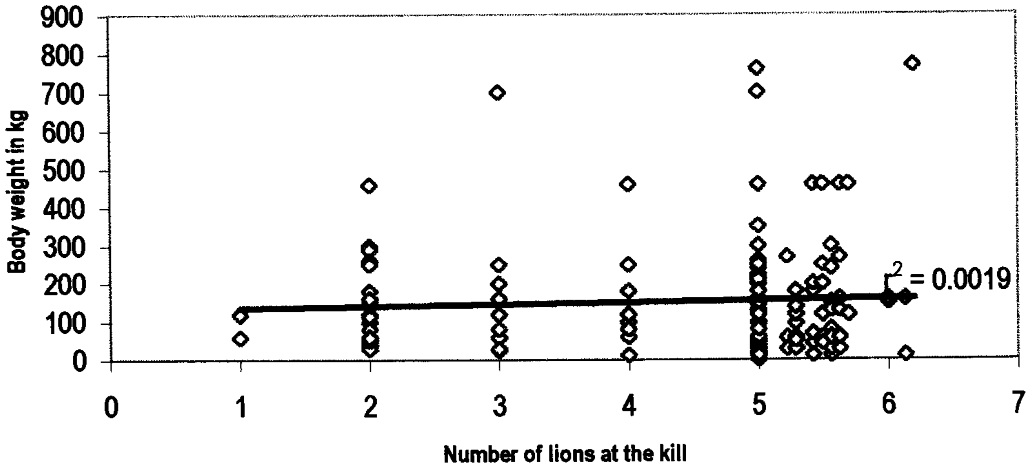

Figure 8.4. The relationship between the body weight of the prey killed and the number of lions present on the kill, expressed as female equivalents, on the Welgevonden Private Game Reserve from January 1998 to October 1999. The linear regression line and the r^2 – value of the data set are also indicated.

Habitat types

Table 8.5 shows the actual kills that were made in each habitat type, in comparison with the expected number of kills in each habitat type. The expected number of kills in each habitat type was determined from the percentage occurrence of each prey type in the specific habitat type. Both the eland ($p<0.001$) and kudu ($p<0.05$) were killed significantly more than expected on the plateaux and less so in the hills. Of all the kills, 83.3% were made on the old lands and plateaux. Although the hills cover 71.2% of the surface area of the reserve, only 1.4% of kills were made in hills. There were significantly more kills made in old lands, plateaux and valleys, and fewer in the hills than was expected based on their occurrence in the reserve ($p<0.001$). This reflects the known habitat selection of the lions (Chapter 5) that showed a positive selection for old lands and plateaux, and a negative selection for the hills.

DISCUSSION

Prey types

The general pattern of lion predation that was found during this study is similar to that observed for lions elsewhere. Schaller (1972) noted that although lions kill a wide variety of prey, fewer than five medium to large types of prey generally form 75% of the diet. Other authors such as Smuts (1979), Stander (1991b) and Hunter (1998) also noted the same pattern in other areas. The lions on Welgevonden were no different from lions elsewhere, and 21 different types of prey were killed. Of these, only five formed the bulk of the numbers and biomass of prey killed. These five formed 78.29% of the number and 82.43% of biomass of prey killed respectively.

Prey size, availability and abundance clearly influence the choice of prey (Schaller 1972, Stander 1991b, Hanby *et al.* 1995) and lions in different areas kill a different variety of prey types. It appears as if the variety of prey that is available in the area is reflected in the variety of prey that is killed by lions. The wide range of prey killed on Welgevonden reflects the wide diversity of ungulates that could serve as potential prey for the lions there. It is also a further indication that lions kill almost any prey that they may encounter (Schaller 1972; Smuts 1982; Stander 1991b).

Prey selection

Prey selection by lions has often been studied in the past. It is difficult to determine an actual selection for a certain type of prey, unless direct observations can be made of the lions selecting a particular prey, when several other types of prey are available in the same locality. Two such cases were observed on Welgevonden. In the first, a herd of Burchell's zebra and one of blue wildebeest were grazing on the same plain, with the zebra herd between the lions and the blue wildebeest. The blue wildebeest herd was some 100 m beyond the zebras. Two adult female lions stalked around and past the zebras and attempted to kill a blue wildebeest. Although the kill was unsuccessful, this incident does indicate that lions might actively select for a given type of prey when given the choice. The second case was similar, but this time the lions stalked past some impala and killed a red hartebeest further away. This behaviour may also have been incidental, and more data are needed for a clear conclusion of active prey choice. However, Hunter (1998) also observed similar cases of prey selection in Phinda, where it was noted that the lions selected for larger rather than smaller prey when they had a choice in one locality.

Blue wildebeest

The abundance of the blue wildebeest as lion prey on Welgevonden is illustrated in Figures 8.5 and 8.6. It was the most numerous prey killed, and second most abundant prey of lions in terms of biomass killed. However, it was also the most abundant prey in terms of the percentage of total meat consumed by the lions, although the eland was the most abundant prey in terms of biomass killed. This is due to the lion prides on Welgevonden being small. One pride cannot completely consume a carcass of an adult eland, leaving a large portion of the carcass unutilised. Hunter (1998) noted that lions rarely abandoned large kills before they were entirely consumed, and would stay at a kill for three to four days until the carcass was fully consumed. This was not the case on Welgevonden where the lions rarely stayed at a kill for more than two days. Therefore, large carcasses were often abandoned before they were completely consumed.

It is interesting to speculate on why the lions only stayed at their kills for a limited time, before abandoning the carcasses while there was still some meat left. There are no spotted hyaenas on Welgevonden to create competition pressure for the lions. Similarly, competition from other predators at the kills was non-existent and could not cause the lions to abandon their kills. This behaviour could possibly be an indication of the ease with which the lions could locate and kill prey. The lions killed at a mean interval of once every 2.96 days (SD = 1.71 days, range: 0-10). It was therefore not necessary for them to completely consume their kills because it was unlikely that they would stay without food for long enough to go hungry.

Warthog

The warthog was an abundant prey item of the lions on Welgevonden, especially during the earlier part of the study. Following the first three months after the release of the lions, the number of warthog killed was double that of blue wildebeest, the second most killed prey at that time. The lions were only two years old when they were captured, and could not have had much time to gain hunting experience before they were captured. Therefore, warthog was probably the easiest prey to hunt and kill for the inexperienced lions. Moreover, because the warthog on Welgevonden were unfamiliar with lions at that stage, they often foraged after dark. This made them relatively easy prey for the lions. Warthog were also dug out of their burrows by lions when they did not manage to kill any prey for several days early in the study. This behaviour decreased during the latter part of the study, probably indicating that a lack of hunting experience and not hunger was the main motivation for this behaviour earlier on. Hofmeyr (*pers. comm.*[2]) also observed that young lions in Madikwe Game Reserve dug out warthog.

Although the warthog was only the fifth most abundant types of prey in terms of both biomass of prey killed and consumed, it probably served an import role as a prey buffer for the blue wildebeest and red hartebeest, especially on the old lands. Warthog were the most available prey and the most frequently killed prey on the old lands. The number of blue wildebeest and red hartebeest killed there would probably have been higher if warthog had not been present.

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It also appears as if the warthog serves as a valuable prey for subadult lions just after they leave their prides and when they are still relatively inexperienced in hunting. Although the lions often sustained minor injuries when hunting a warthog, warthog were relatively easy to stalk and catch in the medium to tall grasslands of Welgevonden.

Eland

Despite its large size, the eland also appear to be easy prey for lions. Eland are slow and it is easy for lions to catch up with them. They also seldom put up a fight when caught (*pers. obs.)*. During the early part of the study, the larger prey animals were not accustomed to large predators and were possibly not as vigilant as prey in areas where large predators have occurred for a long time. Eland seemed to be particularly susceptible to lion kills during the early part of the study, and was the prey involved in the only observed case of surplus killing on Welgevonden when a single lioness managed to kill three eland in a space of 15 minutes in the southern parts of the reserve, after being the first lion to move into these parts of the reserve. It was therefore the first lion encountered by prey in this part of Welgevonden.

Surplus killing by carnivores has been described previously (Kruuk 1972), and is regarded as the instinctive response to superabundant, vulnerable prey. It is often an adaptive behaviour, and is undertaken by a predator after the evaluation of a chance to acquire much food at low expense (Kossak 1989). That eland are easy prey for lions is evident from the fact that eland were killed more often than expected in all the habitat types, except the hills (Table 8.5). The low kill frequency in the hills is probably caused by the limitations placed by this habitat on lion mobility and not by the eland themselves. The number of eland killed decreased towards the end of the study. Where they have concentrated in large numbers on the old lands early in the study period, lion pressure had caused them to disperse into other areas later.

Red hartebeest

The red hartebeest population underwent a considerable decline since the introduction of the lions (Chapter 9). For unknown reasons, the red hartebeest had the highest preference rating of all prey for lions during the study period. Red hartebeest are fleet-footed animals and can easily outrun any lion. Yet, they were still killed frequently. No data are available on their vigilance, but low vigilance could be a possible reason for red hartebeest being killed often by the lions. A high encounter rate with lions could also have caused this high kill frequency. Like lions, the red hartebeest selected the old lands and plateaux as preferred habitat (Kilian 2001). The lions therefore encountered them regularly. Also, a red hartebeest is a medium-sized animal, and it has almost no chance of escaping once a lion has caught it.

Impala

The fact that the kill frequency of prey by lions depends on more than the relative abundance of the prey only is demonstrated by the different kill frequencies of impala and blue wildebeest. Although both these types of prey occur at almost the same relative abundance (19.6% for impala to 17.3% for blue wildebeest), the number of blue wildebeest killed is 4.5 times higher than the number of impala killed. In Phinda Resource Reserve, the blue wildebeest was also killed at a higher frequency than the impala, although the impala was more abundant there than the blue wildebeest (Hunter 1998).

There are several possible reasons for the low kill frequency of impala by the lions on Welgevonden. Hunter & Skinner (1998) found that the impala was more vigilant than the blue wildebeest, therefore decreasing its chances of being killed by predators. Impala on Welgevonden have always been subjected to leopard predation and are possibly more vigilant for predators than most of the other lion prey. Hunter & Skinner (1998) also found that an increase in herd size created an increase in vigilance behaviour. The mean impala herd size on Welgevonden was 12.5 ± 0.98 at the time of the study, compared with a mean herd size of 8.2 ± 0.71 for blue wildebeest ($t = 3.49$, $p = 0.0005$, $df = 294$). It is therefore possible that the larger herd size of impala increased their vigilance and that they therefore were killed at a lower kill frequency by lions than most of the other prey animals on Welgevonden.

Burchell's zebra

In the Kruger National Park, both the impala and Burchell's zebra were part of the three most frequent prey of lions (Smuts 1979; Mills & Biggs 1993). Burchell's zebra was also one of the three most frequent prey of lions in several other areas (Schaller 1972; Rudnai 1979; Stander 1991b). The low frequency at which Burchell's zebra were killed by lions on Welgevonden can possibly be explained by the fact that the zebra on Welgevonden utilised the hills, a habitat that was generally avoided by the lions. It appeared as if the zebra move into the hills in the summer, but sufficient data are not available to support this. There are certainly fewer zebras on the plains and plateaux in the summer than in the winter. Smuts (1982) characterised lion predation as favouring easier prey. Burchell's zebras are difficult to hunt because they can run fast, are strong, and can deliver a lethal kick to an attacking lion. Because of this, they often escape after being caught by lions. The number of zebras with wounds and scratches on their rumps are an indication of the difficulties that the lions experience in pulling down an adult zebra. If lions have the choice, they would therefore probably rather attempt to kill easier prey such as a blue wildebeest or an eland.

Prey size and meat intake

Previous studies have suggested that that the size of the prey of lions appears to increase with an increase in the number of lions in the pride (Kruuk & Turner 1967; Caraco & Wolf 1975), and that the pride size in a given area is determined by the optimal size of those prey that can meet the energetic requirements of individual pride members. Therefore, there is an optimum pride size for the available food resources. However, no such relationship between the size of the prey and the number of lions in the pride could be found on Welgevonden. Hunter (1998) also noted this on Phinda Resource Reserve.

It has also been suggested that by limiting the size of the prides, the predation on larger prey animals can be reduced (Van Dyk 1997), and that keeping the prides small can prevent large and valuable animals like the giraffe and buffalo from being killed by lions. Evidence from the current study suggests differently, and there was no relationship between the size of the prey and the size of the pride. Small lion prides will therefore not necessarily prevent large animals like the buffalo, eland or giraffe from being killed. A single lioness was observed to kill a full-grown eland bull weighing close to 800 kg, during the study period. Although such predation can therefore not be prevented, the risk of these animals being killed will nevertheless be reduced if the prides are kept relatively small. Although several attempts to kill buffalo were made by the lions on Welgevonden during the study period, these attempts were largely unsuccessful. If larger prides had been present at the time of these attempts, more buffalo could well have been killed. After the end of the present study, when the prides were larger and the lions more experienced, the lions killed a subadult female, an adult female and an adult male buffalo on Welgevonden.

Small and large prey were killed in almost equal proportions on Welgevonden. The southern Kalahari is the only known place where lions consistently feed on a large proportion of small mammals. Stander (1992) showed that lions hunting in pairs can meet their minimum daily requirements of energy by hunting the springbok *Antidorcas marsupialis* that weighs less than 50 kg. On Welgevonden, the mean meat intake per day per lion was 6.8 kg, or 6.1 kg per female equivalent. This is well within the minimum daily requirement range of 5.0 to 8.5 kg per day per lion as determined by Green, Anderson and Whateley (1990). The pride sizes of the lions on Welgevonden during the study period were small (mean: 4.1, SD: 1.5) and the large proportion of small to medium prey killed was probably sufficient to meet the food and energy requirements of all the individuals in the pride.

Age of prey

The selection of different age prey indicates the difficulty with which lions kill adult Burchell's zebra. For all types of prey only adult zebras were significantly selected against, with a clear selection for subadults. The ages of all other prey killed during the study period were in the same frequencies with which they occurred on Welgevonden.

Habitat types

The relative use of the habitat types in which kills were made by the lions reflect the habitat preference of the lions as described in Chapter 6. The habitat preference of the main prey was similar to that of the lions. Significantly more kills were made on the old lands, plateaux and valley bottoms than were expected, based on their relative occurrence in the reserve, and significantly fewer in the hills. The frequency with which kills was made in the different habitat types indicates that prey availability may be a major factor in determining habitat selection by lions. However, the suitability of the habitat for hunting is important in determining the success with which kills can be made in the different habitats. For example, eland, kudu and zebra show a degree of selection for the hills, but the kill rate of lions for kudu in the hills was much lower than expected. The hills are steep and extremely rocky and it is almost impossible for lions to hunt successfully there. All three known kills that were made by lions in the hills, an eland, a kudu and a Burchell's zebra, were on terraces where the terrain was more suitable to hunting. These terraces are flat and relatively open areas, and kudu, eland and Burchell's zebra are often associated with them.

The fact that the hills cover the largest surface area of the reserve severely limits the hunting area available to the lions. Therefore, it has an indirect effect on lion prey selection. The hills force wildlife, but especially grazers such as the blue wildebeest, red hartebeest and warthog to concentrate in large numbers on the old lands and plateaux. These animals were three of the four most frequent prey of lions on the entire reserve. A habitat more suitable to ungulates would probably have caused a more even distribution of prey throughout the reserve, and the frequency of animals like the impala and Burchell's zebra in the kills of the lions could possibly have increased.

CONCLUSIONS

Bothma (1997) states that the interrelationships between the larger carnivores and their prey are so complex that no human interference should happen in larger conservation areas. However, small game reserves cannot afford this approach and are often forced to intervene to save types of prey that might occur in limited numbers on the reserves. Not one of the small reserves in southern Africa is large enough to stock a sufficient prey base allow a hands-off approach to lion management. It was shown earlier that lions will kill almost anything which they encounter. Prey occurring in small numbers on small reserves will therefore be under constant pressure to survive.

It is difficult to implement management techniques that aim to change the selection of prey by lion or that will prevent kills of rare or expensive species. By increasing the population size of buffer prey, the impact that predation will have on the rarer species could be reduced. Although it has been shown that lions do actively search for larger prey (Van Orsdol 1984, Hunter 1998), an increase in the number of the more common small prey might go a long way towards reducing the risk of rare or larger species being killed. However, this should be done with care and the possible impacts that this might have on the available habitat should always be kept in mind and monitored.

It also possible that by limiting the size of the prides, the risk to large animals like the buffalo and giraffe of being killed can be reduced, although the current study indicated differently. However, the above practices will not prevent all kills of rare prey, and the effect of predation on these prey animals should be monitored closely. Managers will therefore have to decide whether the risk of these animals being killed is acceptable or not. Ultimately, the only way to prevent small populations and rare or expensive animals from being killed is to protect these animals in separate lion-proof enclosures.

CHAPTER 9

MODELLING THE IMPACT OF THE LIONS ON THE PREY POPULATIONS

INTRODUCTION

Predation is now generally believed to have little impact on prey populations in large, self-contained ecosystems. However, published work on predator-prey interactions show such variable results that such generalisations cannot be made without qualifying the exceptions. For example, there is evidence that resident populations of prey in the Serengeti may be more heavily influenced by predation than migrating ones (Sinclair 1995). Moreover, Schaller (1972) showed that predation alone had little impact on the migrating brindled wildebeest population in the Serengeti, but in the Ngorongoro Crater predation had a marked impact on the resident brindled wildebeest population (Kruuk 1972). Eloff (1973b) also found that predation may regulate the population of sedentary gemsbok in the southern Kalahari. In the Nairobi National Park, lions were apparently responsible for a marked decline in wildebeest numbers between 1961 and 1966 (Foster & Kearney 1967).

It appears therefore that predation may limit the growth of a particular prey population in one area, whereas its effect may be almost negligible in another. Predation evidently needs to be analysed individually for each particular situation because its influence on the prey may vary spatially and temporally within a certain area. In situations where the area is small and the system not self-contained because of management actions and human interference, predation can have a major impact on the resident prey population. Mills & Shenk (1992) state that predators can regulate resident herbivores at low population densities, whereas such regulation is rare for large migratory herds. Despite its size, the Kruger National Park is not a self-contained ecosystem. It is at least partially fenced and therefore several management actions are necessary to keep the ecosystem healthy. It has previously been shown that lions can have an impact on resident blue wildebeest and semi-migratory Burchell's zebra populations in the Kruger National Park (Smuts 1978a; Mills & Shenk 1992). The impact of lions on the prey populations of small reserves can be even more severe. Prey usually occurs in low densities on small reserves, and cannot migrate because of the presence of fences. The space to escape predation is limited and prey animals there are usually subject to predation all year round. It was shown in Chapter 5 that the ranges of the lions on Welgevonden covered most of the reserve, leaving few areas where prey animals could escape predation for extended periods.

Welgevonden is a small reserve with a small prey population. The impact of predation on the available prey population can be severe if careful management is not undertaken. In this chapter, it is attempted to determine the impact of lion predation on the prey population of Welgevonden. It is also attempted to predict the future impact of lion predation on the prey population with the help of a model. The model was created as a management tool to help Welgevonden Management to make informed decisions about their lion and prey populations.

METHODS

Developing the model

The predator-prey relationship model that was originally developed by Mills & Shenk (1992) for blue wildebeest and Burchell's zebra in the Kruger National Park was adopted for use in this part of the present study. This model was also used with good results by Funston (1999) to model the effects of lions on prey populations in the Kruger National Park. The model of Mills & Shenk (1992) is simple, but it gives accurate estimates of the predator-prey relationships between lions, blue wildebeest and Burchell's zebra. The parameters and approach used in the models are also similar to those of Peel & Montagu (1999) who successfully modelled the effect of lions on blue wildebeest on a small wildlife ranch in Limpopo.

Input data

The annual aerial count data for Welgevonden were used as estimates of the total population sizes of the different prey populations and were not changed for use in the models. Data from monthly vehicle counts were used to determine the different population parameters necessary in the model (Kilian 2001).

The methods of collecting the kill data were described in Chapter 8. The type of prey killed, the kill rate, and the sex and age classes killed were the same data as used in Chapter 8. It was found in other studies that females do most of the killing (Schaller 1972; Van Orsdol 1986; Stander 1992). On Welgevonden, female lions made 94.1% of all the observed kills. Funston (1999) found that subadult and non-territorial males obtain most of their food by killing for themselves and that territorial males kill 50.0%

of their prey themselves, being in attendance with pride females for 25.0% of their time. For use in the models, killing lions were therefore regarded as females and non-territorial males older than two years, while a territorial male was regarded as being equivalent to 0.5 killing lions.

The kill data were collected for a period longer than a year. Therefore, it was necessary to relate all the kills to a standard of one killing year per lion. The following equation of Mills & Shenk (1992) was used to determine the annual kill rate:

Kill rate per lion per year = (number of prey killed x number of hours in a year) ÷ (number of lion hours)

where

(the number of lion hours) = (number of observation hours) x C

and

C = a consumption factor

It was necessary to include the number of lion hours in the above equation in order to take the different food requirements and consumption rates of different ages and sexes of lions into account. Van Orsdol (1986) calculated consumption factors (C) per female equivalent for the different sex and age classes of lions when they occurred together and separately at kills. The total food consumption depends on the individuals feeding on the carcass, and was determined for each kill during the study period before a consumption factor for the total study period could be determined for all the lions on Welgevonden.

Some of the parameters, such as the population size, age structure and sex ratio of the prey were used in the first year of the model only, and these parameters were called initialising parameters by Mills & Shenk (1992). The population and kill parameters that were used in the model as initialising parameters are presented in Table 9.1 (Kilian 2001). From the second year on these parameters were determined by the model. The kill parameters, calving percentages and juvenile survival of each prey type were kept identical for each year that the model was run.

Survival of the prey population in the model

Each model represents the particular prey population immediately after the birth season. For the following year, it is required to determine the population at time t+1. The calculation of yearlings at time t+1 is complex because there are a number of factors that may affect the number of juveniles in the population. In order to determine the population at time t+1, the fecundity and survival rates for the different age classes are important. Mills & Shenk (1992) used fecundity rates for adults and yearlings to determine the number of calves at time t+1. In the present study, no such detailed data of fecundity rates for adult and subadult (yearling) females were available. Consequently, calving percentages were used in these models, but in order to do so, some assumptions had to be made. It was assumed that the number of yearlings (subadults) that gave birth was negligible and that the number of calves for the next season was determined by calving percentages of adult females only. This probably gave an underestimate of the number of juveniles at time t+1, but for the purposes of this model, an underestimate of the number of juveniles is more acceptable than an overestimate. An overestimate of the number of juveniles would show that the effect of the lions on the population is smaller than what is the case in practice (*pers obs.).* When managing small reserves like Welgevonden, one cannot afford to underestimate the effects of predators on the prey populations. It was therefore accepted that the calving percentages were sufficient for the purpose of this model. Moreover, test runs of the model gave acceptable results.

The survival rates for the different age classes of prey were determined by using the observed age structures of killed prey, except for the survival rate of the juveniles (jsurv) that was determined with the monthly prey population surveys. The equations used to calculate the various survival rates of prey were:

$\text{sasurv}_{t+1} = 1-[(\text{kill rate} \times \text{number of killing lions} \times \text{sakill}) \div \text{sa}_t]$

$\text{afsurv}_{t+1} = 1-[(\text{kill rate} \times \text{number of killing lions} \times \text{afkill}) \div \text{af}_t]$

$\text{amsurv}_{t+1} = 1-[(\text{kill rate} \times \text{number of killing lions} \times \text{amkill}) \div \text{am}_t]$

where:

sasurv_{t+1} = survival of subadult prey at time t+1
afsurv_{t+1} = survival of adult female prey at time t+1
amsurv_{t+1} = survival of adult male prey at time t+1
sakill = percentage of subadult prey killed
afkill = percentage of adult female prey killed
amkill = percentage of adult male prey killed
sa_t = number of subadult prey
af_t = number of adult female prey
am_t = number of adult male prey

Table 7.1. The population and kill parameters for each type of prey that were used to model the number of killing lions that can be supported by the prey populations on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

ITEM	TYPES OF PREY						
	Blue wildebeest	**Eland**	**Red hartebeest**	**Warthog**	**Impala**	**Kudu**	**Burchell's zebra**
Population parameters:							
Population size	576	281	208	291	738	253	740
Percentage juveniles	21	16	5	27	23	11	12
Percentage subadults	16	21	8	16	17	20	13
Percentage adult females	45	44	48	34	36	52	46
Percentage adult males	18	18	39	23	24	17	29
Calving percentage	46	35	26	128	75	40	26
Percentage survival of juveniles	65	46	51	67	65	37	39
Kill parameters:							
Percentage juveniles killed	20	19	8	27	18	21	27
Percentage subadults killed	16	27	13	18	18	16	18
Percentage adult females killed	43	38	50	29	36	42	36
Percentage adult males killed	18	15	29	20	15	21	9
Kill rate per lion per year*	9.4	6.2	6.9	7.5	2.5	4.4	2.5

* Kill rate per lion per year = (number of prey killed x number of hours in a year) ÷ (number of lion hours) (Mills & Shenk 1992)

Size of the prey population in the model

The size of the prey population at time t+1 was determined as follows:

j_{t+1} $= af_{t+1} \times \%c$

sa_{t+1} $= j_t \times jsurv$

af_{t+1} $= (sa_t \times sasurv_t \times \%af) + (af_t \times afsurv_t)$

am_{t+1} $= (sa_t \times sasurv_t \times \%am) + (am_t \times amsurv_t)$

where:

j_{t+1} = number of juveniles at time t+1

sa_{t+1} = number of subadults at time t+1

af_{t+1} = number of adult females at time t+1

am_{t+1} = number of adult males at time t+1

%c = calving percentage

%af = percentage of adult females in the prey population

%am = percentage of adult males in the prey population.

Stability index of the prey population

In order to determine the number of killing lions that could be supported by the prey population, a stability index (SI) was determined in the same way as was done by Mills & Shenk (1992). The stability index shows the smallest change in the size of the prey population in the number of years (n) that the model is run, for a specific number of killing lions. It was determined by using the following equation:

$$SI = (totalpop_{1+n} \div totalpop_1) - 1$$

where:

totalpop_1 = total prey population in year 1

totalpop_{1+n} = total prey population in year 1+n

Running the model

Model 1

The model was first run in an attempt to establish the number of killing lions that will keep the population size of each prey type constant over a period of 10 years. Unfortunately this model uses only lion kills as a mortality factor in the prey population and does not include predation by other predators to determine the survival rate for each age and sex class. However, this can be included in the future if suitable data on the predation of other predators can be collected.

The number of killing lions was used to control the model, and it altered the outcome of each model. Each model assumed a constant number of killing lions throughout the modelling period, and does not allow for an increase in lion numbers over time.

In running the model, some population parameters for each type of prey were changed to test the sensitivity of the model for the various population parameters. By changing these parameters, the model gave an indication of the factors that limit the size of each prey population.

Model 2

For the second model, the initial model was adapted and ran for the period 1998 to 2002 to give an expected size of the prey population in 2002, with only lion kills as a

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cause of death. Contrary to model 1, the actual number of killing lions present on the reserve for each year that the model was run, was used in model 2 to determine the sizes of each prey population. The modelled values were then compared with the actual prey count data of 2002 to give an indication of the influence of the lions on the different prey populations.

RESULTS

The lions were observed for a total of 3 264 hours. By applying Van Orsdol's (1986) weighting factor, this relates to 14 035 lion hours. The kill rate for each type of prey was then determined as described in the methods.

Model 1

Figures 7.1 to 7.7 show the number of killing lions that can be supported by the different prey populations. The effects of the changes of parameters like kill and birth rates on the prey populations are also indicated. The sensitivity of the populations for the parameter changes varied from prey type to prey type.

For red hartebeest, kudu, eland and Burchell's zebra, changes in the birth rate had the same effect as changes in the kill rate. This indicates that the kill rate is not the only limiting factor in these populations, but that low birth rates also influence these populations. All four these populations had low birth rates and will therefore be more sensitive to changes in the kill rates.

For the blue wildebeest, impala and warthog, changes in birth rate had a smaller effect on the population than changes in the kill rate. Therefore, kill rate was more important as a limiting factor than the birth rate in these three prey types.

Model 2

Figures 9.8 to 9.14 show the results of running model 2, where the actual number of killing lions for each year of the modelling period was used to model the prey populations of Welgevonden. The modelled populations were then compared with the actual aerial count data of prey on Welgevonden to give an indication of the actual effect of the current lion population on the prey populations on the reserve.

It can be seen in Figures 9.8 to 9.14 that, except for red hartebeest, the modelled totals for all the prey populations were higher than the actual count totals. This was probably caused by predation by other predators that were not taken into consideration by the model due to a lack of sufficient data. If this predation can be included, the modelled and actual totals could possibly be closer to parity.

Both the modelled and actual count totals of red hartebeest and eland are showing a downward trend. It was shown earlier with model 1 that these two prey types cannot sustain predation of the current lion population. However, this is not only due to lion predation, but low breeding and predation by other predators also played a role here. Even if the lion population was reduced by half, the red hartebeest population would still have shown a downward trend.

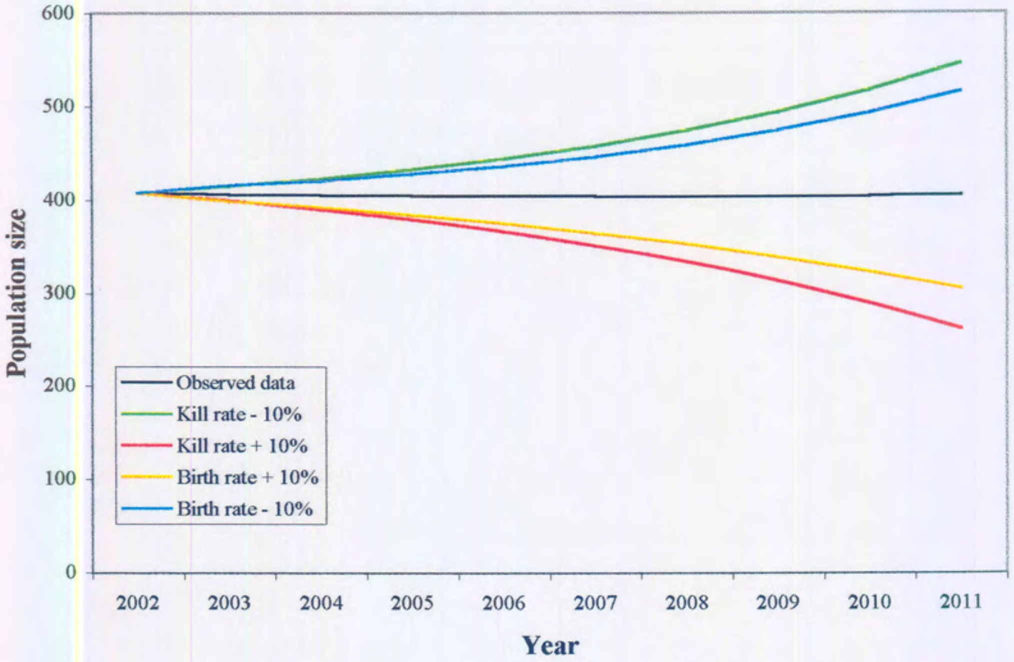

Figure 9.1. The results of model 1, showing the effect that 11.2 killing lions and certain parameter changes will have on the blue wildebeest population of the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

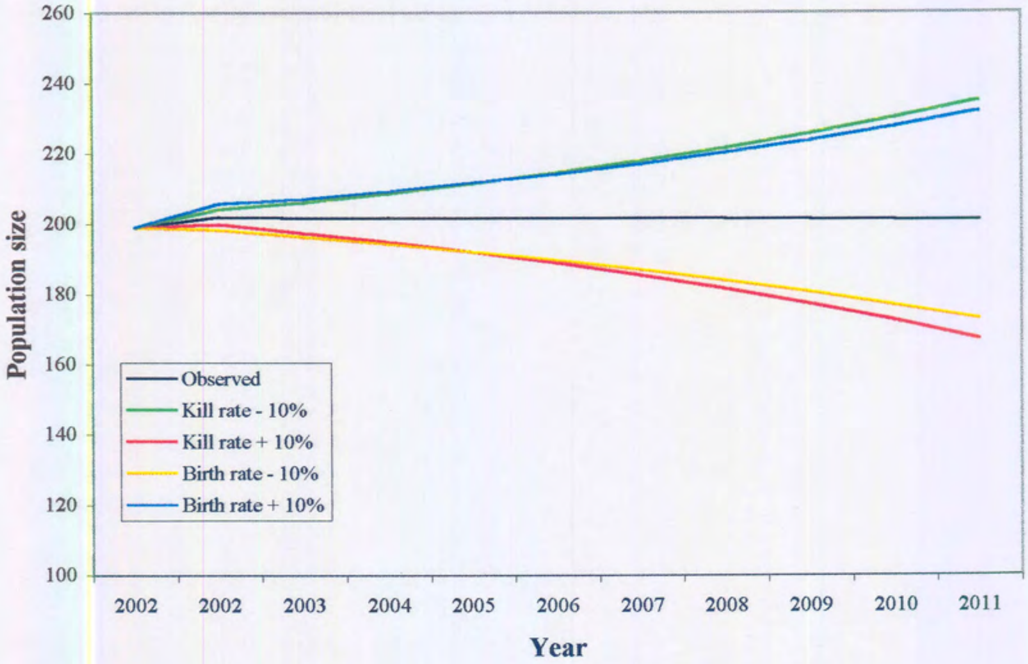

Figure 9.2. The results of model 1, showing the effect that 4.75 killing lions and certain parameter changes will have on the eland population of the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

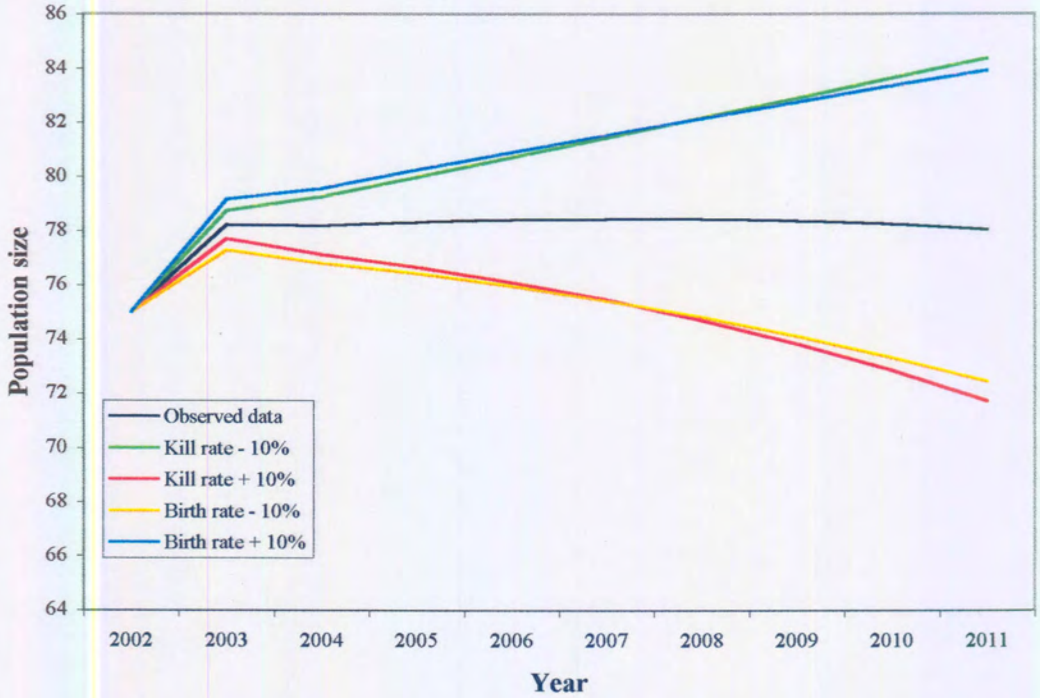

Figure 9.3. The results of model 1, showing the effect that 1.95 killing lions and certain parameter changes will have on the red hartebeest population of the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

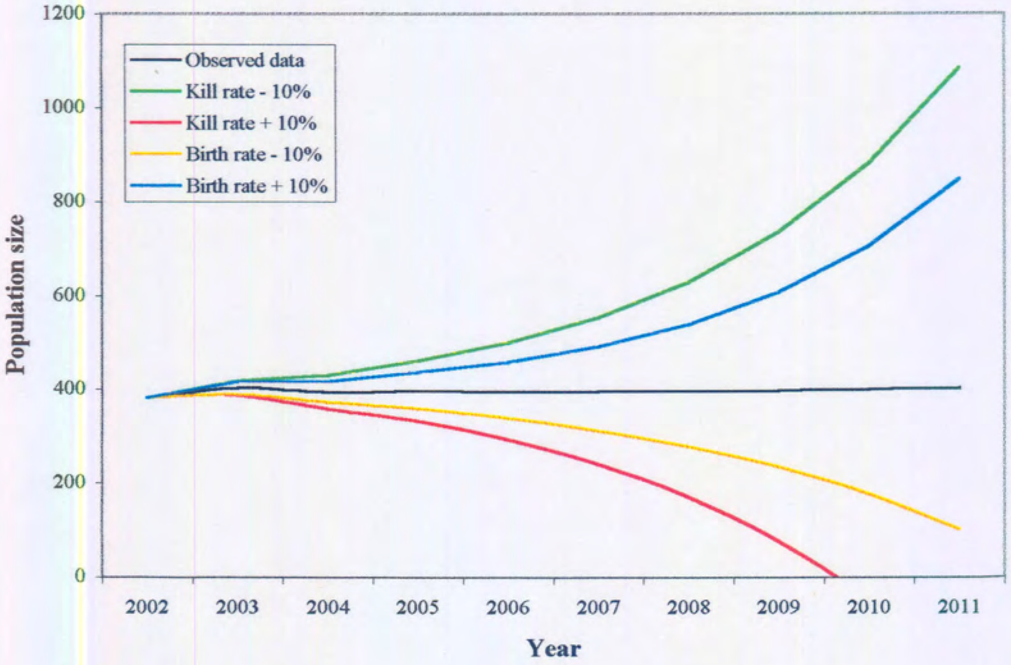

Figure 9.4. The results of model 1, showing the effect that 13.65 killing lions and certain parameter changes will have on the warthog population of the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

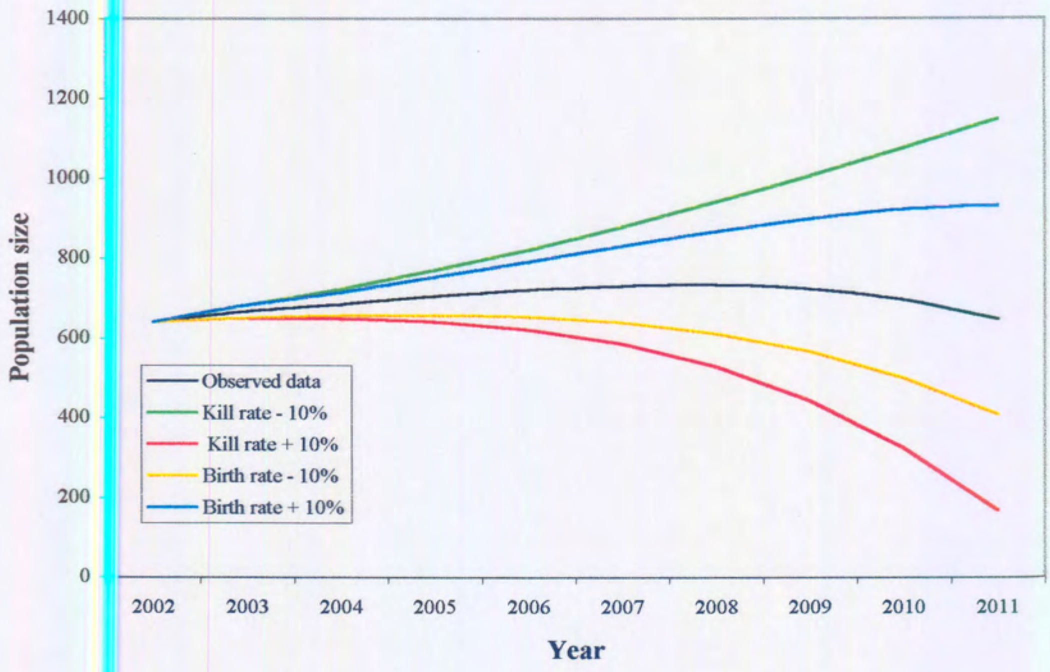

Figure 9.5 The results of model 1, showing the effect that 61.0 killing lions and certain parameter changes will have on the impala population of the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

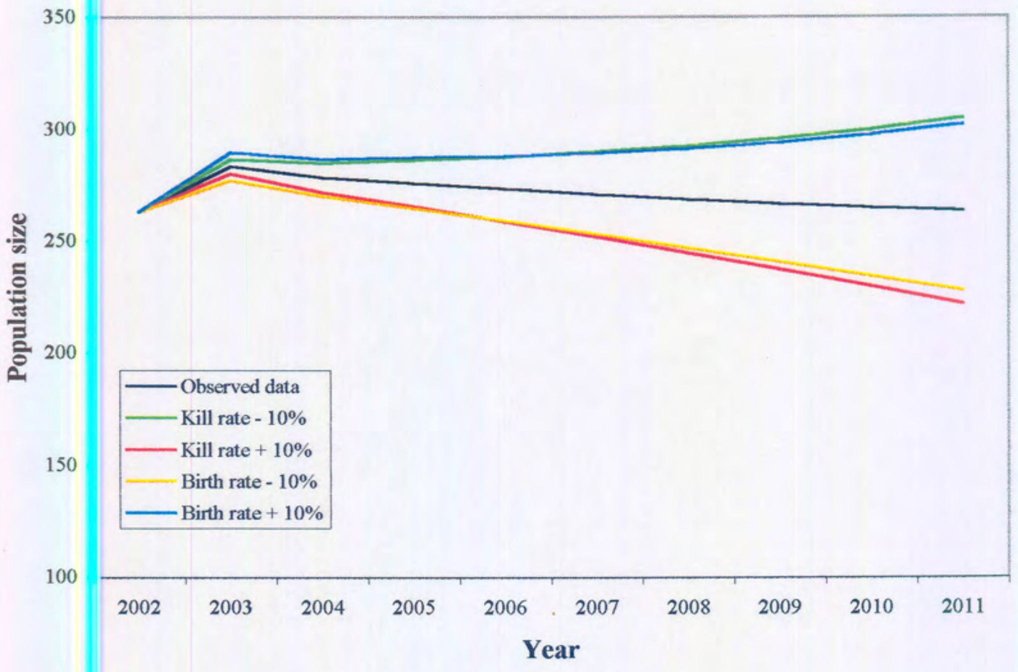

Figure 9.[illegible]. The results of model 1, showing the effect that 6.9 killing lions and certain parameter changes will have on the kudu population of Welgevonden Private Game Reserve in the Waterberg region of South Africa.

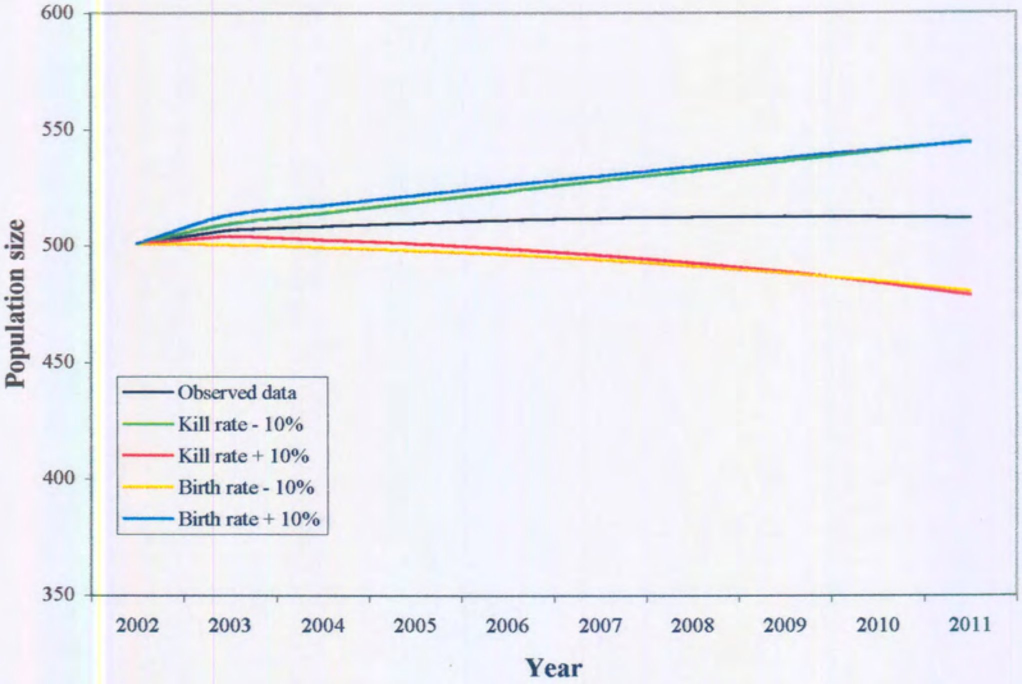

Figure 9.7. The results of model 1, showing the effect that 22.0 killing lions and certain parameter changes will have on the Burchell's zebra population of the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

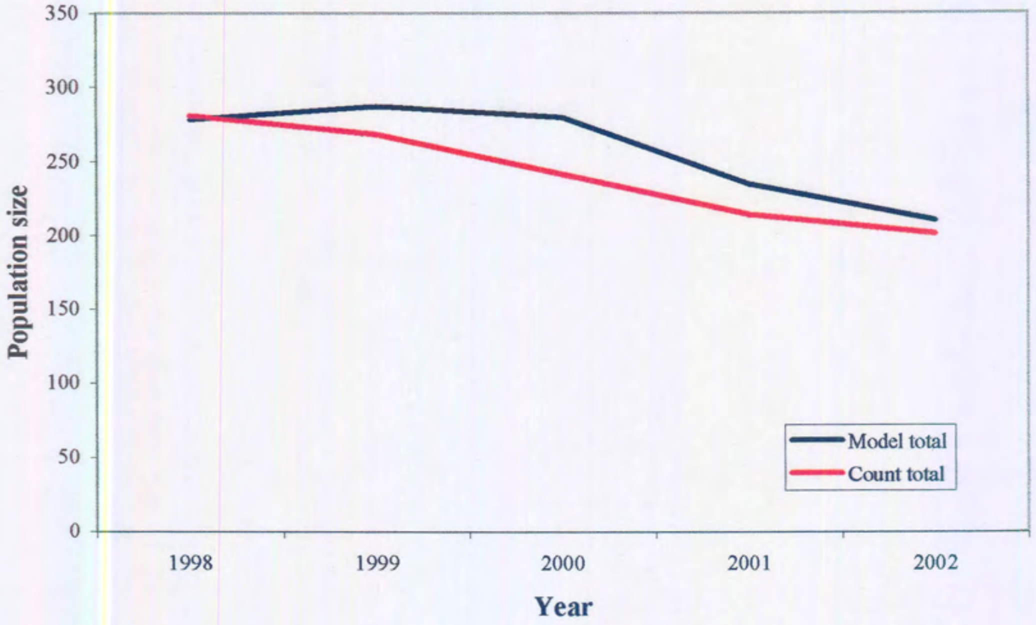

Figure 9.8. The results of model 2, showing the predicted versus the actual count totals for the eland population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

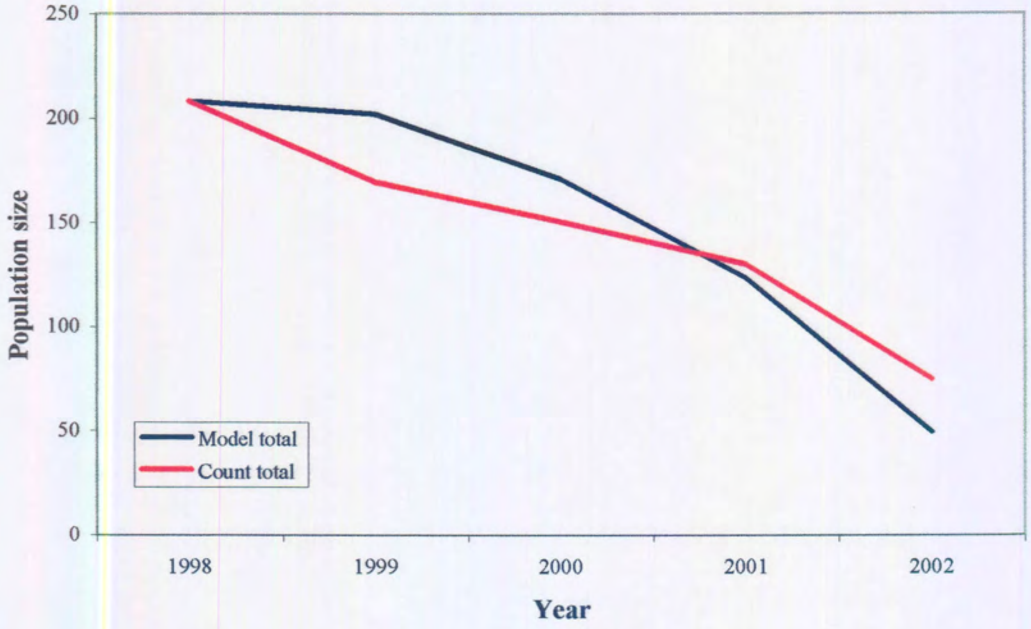

Figure 9.9. The results of model 2, showing the predicted versus the actual count totals for the red hartebeest population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

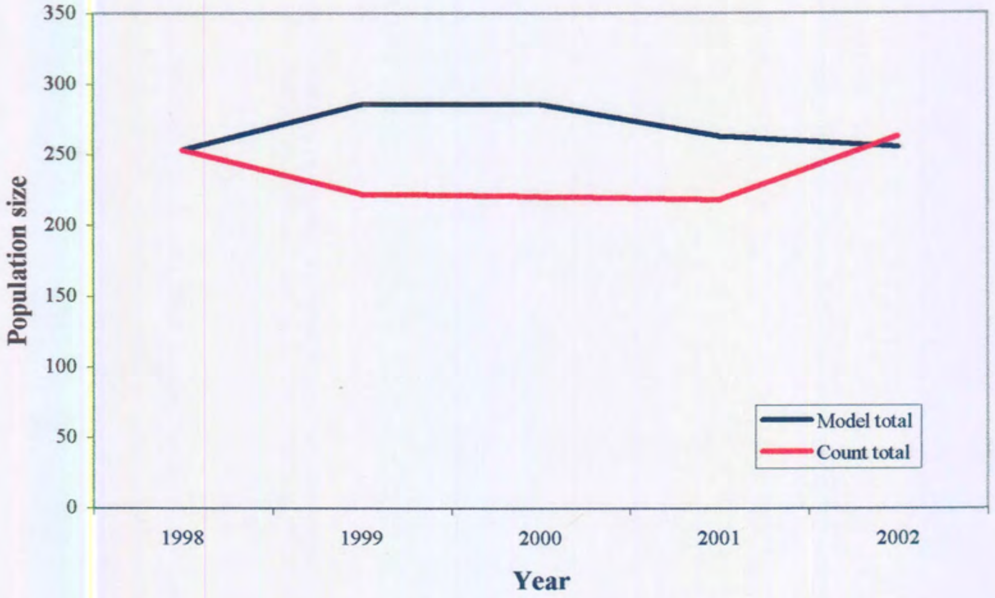

Figure 9.10. The results of model 2, showing the predicted versus the actual count totals for the kudu population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

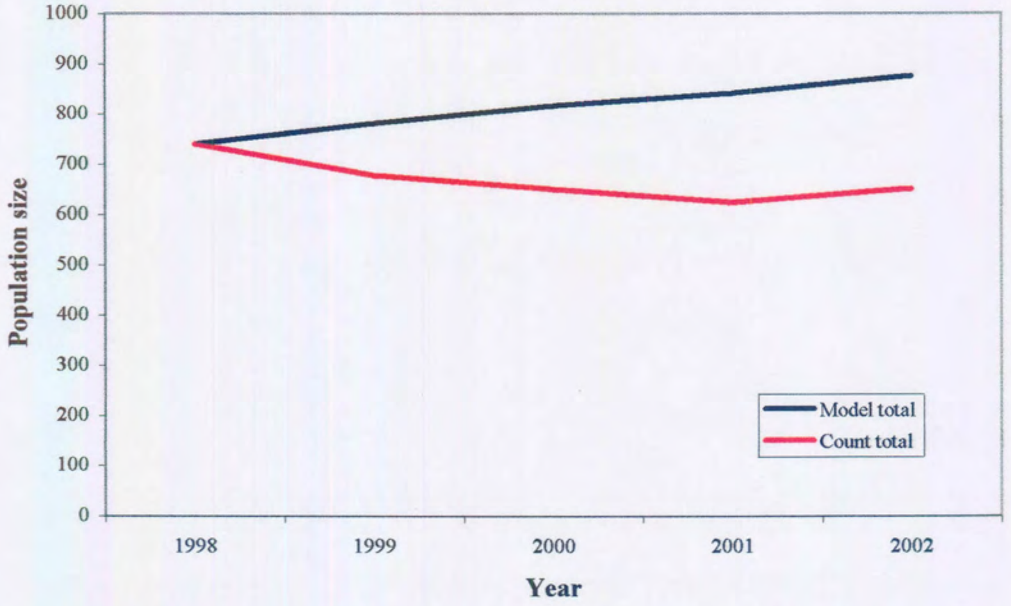

Figure 9.11. The results of model 2, showing the predicted versus the actual count totals for the Burchell's zebra population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

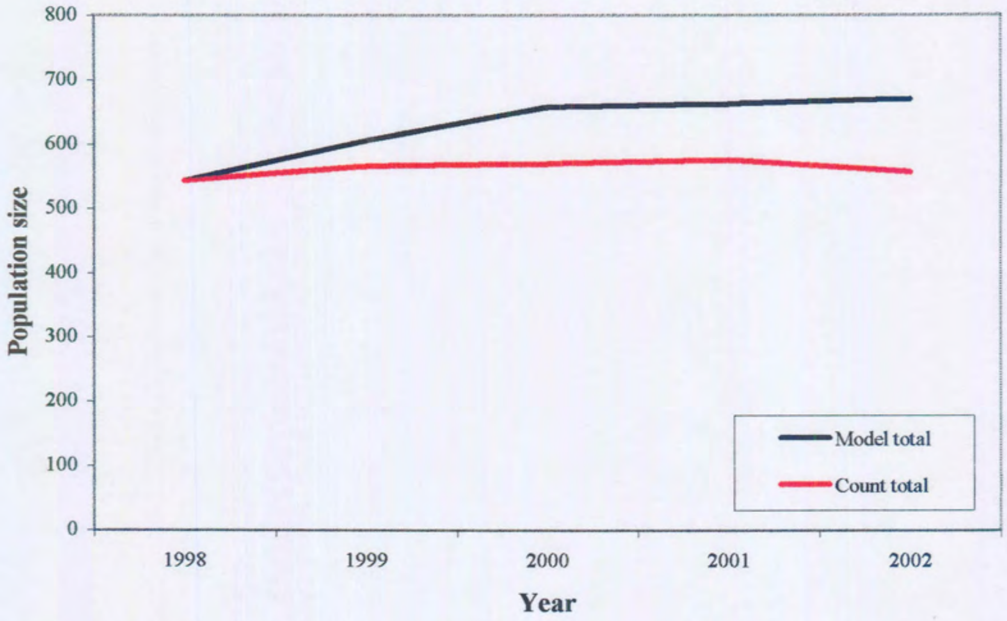

Figure 9.12. The results of model 2, showing the predicted versus the actual count totals for the blue wildebeest population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

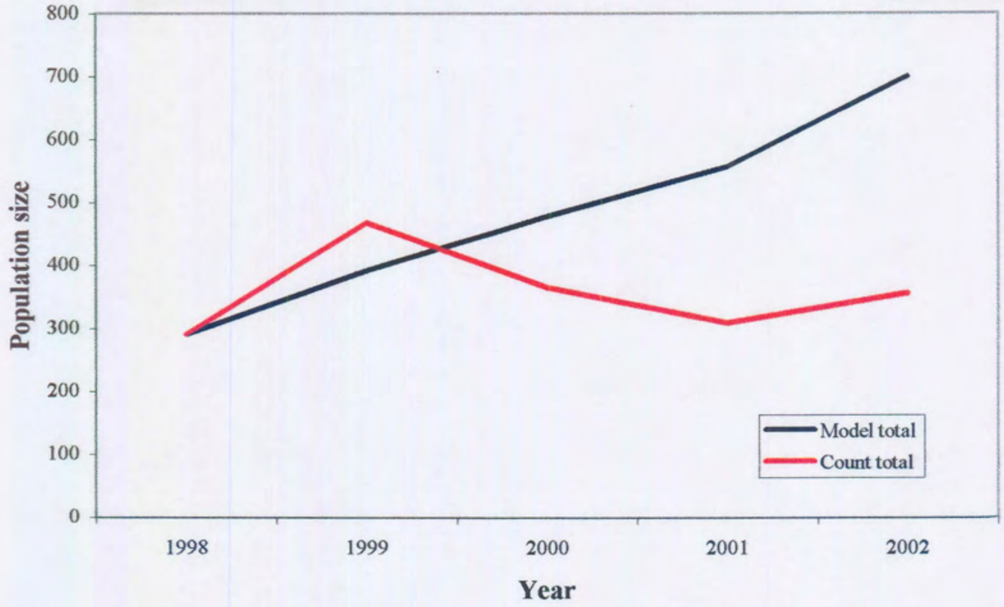

Figure 9.13. The results of model 2, showing the predicted versus the actual count totals for the warthog population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

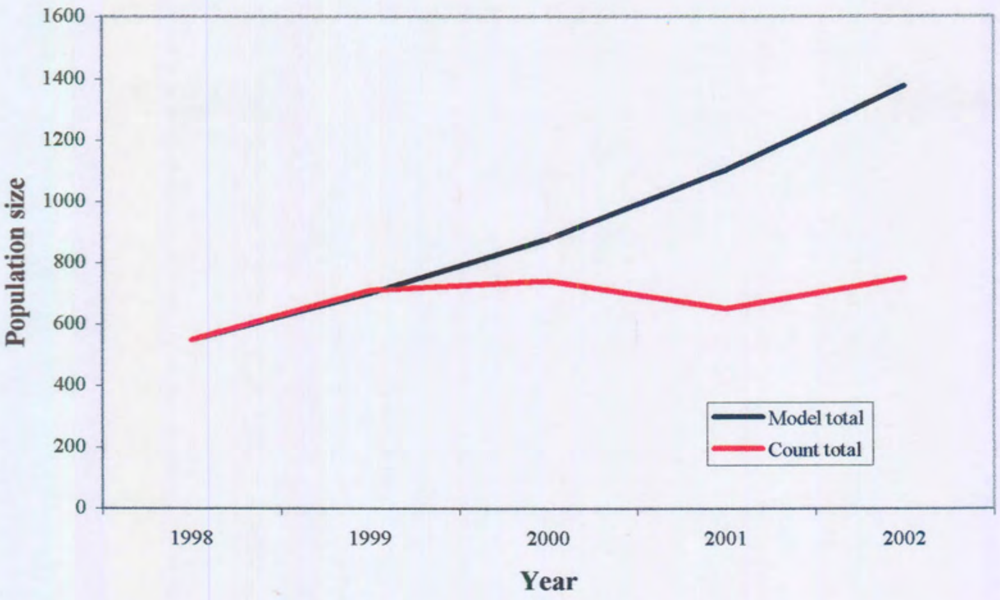

Figure 9.14. The results of model 2, showing the predicted versus the actual count totals for the impala population on the Welgevonden Private Game Reserve in the Waterberg region of South Africa.

DISCUSSION

The influence of lions on prey populations has previously been tested by culling predators in one area and comparing the prey numbers with that of a similar, neighbouring area where no culling took place (Smuts 1978a, Whyte 1985). It is difficult to use similar studies in the modern conservation situation with its abundance of small game reserves. Most of these reserves have low concentrations of predators and prey, and their owners cannot afford to sacrifice any animals to studies involving culling. A more pragmatic approach is to use models to test the influence of predators on the prey populations. These models are not intended to mimic the real-life situation, but rather attempt to give an indication of what is or could be happening in the population under given circumstances. Several other studies have used predator-prey models for this purpose with good results (Mills & Shenk 1992, Mills & Biggs 1993, Mills, Biggs & Whyte 1995, Funston 1999, Peel & Montagu 1999). The same approach was also used for this study, with seemingly good results. However, it also revealed questions about the prey populations on Welgevonden that could not be answered with this study and which will need more focussed studies.

Model 1

In the first model, it is clear how lion predation will affect the different prey populations on Welgevonden. An indication of why certain prey is affected more heavily than others was found when some prey population parameters were changed. The blue wildebeest population, the most heavily utilised prey of the lions on Welgevonden can support 11.2 killing lions, while the red hartebeest population can only support 1.95 killing lions. By comparing the model results (Figures 9.1 to 9.7) of the red hartebeest, eland and kudu that can support the least number of lions, with prey such as the blue wildebeest, warthog and impala that can support more killing lions, clear differences are evident. Changes in the kill rate had a more drastic influence on the prey populations that could support more killing lions, compared to prey populations that could support fewer killing lions. In the populations of red hartebeest, eland and kudu, changes in the birth rate had the same effect on the population as did changes in the kill rate. Therefore, lion predation is not the only limiting factor in these prey populations because a low birth rate also appears to limit these populations. Although the Burchell's zebra population can sustain more killing lions than that of the eland, red hartebeest and kudu because of a larger initial population, they are all limited in terms of growth by a low birth rate. Changing the birth rate in the zebra model had the same effect on the zebra population as changes in the kill rate.

The above results may have far reaching consequences for the prey population on Welgevonden. Welgevonden currently has 19 lions in total, which relates to eight killing lions, with a mean of five killing lions over the last four years. The current eland and red hartebeest populations have been unable to support this mean number of killing lions for the last four years. Therefore, the possibility of future extinction of these prey animals on Welgevonden cannot be excluded. The declining trend of these populations over the last four years already indicates that this possibility is becoming real (Figures 9.9 and 9.10).

Model 2

In model 2, the influence of the actual number of killing lions on the prey population of Welgevonden was modelled, and the results were compared with the actual count data for the last four years. It appears that predation by lions may already have resulted in the decline of the eland, red hartebeest and kudu populations on Welgevonden.

Eland

It is clear from Figure 9.8 that the modelled and actual counts for the eland are similar, indicating that lion predation was largely responsible for the observed decline in eland numbers on Welgevonden, and that predation on eland by other predators was probably limited. Leopards kill young eland calves occasionally elsewhere (Bothma 1998), but on Welgevonden with its varied prey resource, it would probably be the exception rather than the rule.

A low calving rate of 35% and a survival rate of 46% of the juvenile eland cohort means that in the current eland population of 214 animals, a mean of only 15.2 animals are added to the eland population each year. Eland on Welgevonden suffer from high tick infestations during the summer months, and some eland die every year as result of this. If these and other natural mortalities, such as old age are added to those that are killed by lions each year, it becomes clear why the current eland population on Welgevonden is declining (Figure 9.8).

Red hartebeest

Figure 9.9 indicates an actual sharp decline in the red hartebeest population. However, although the model also predicted this decline, it indicated a sharper decline than what was actually observed. It was shown in Chapter 8 that lions selected for red hartebeest in the same frequency with which they occurred on the reserve. As the red hartebeest population declined, so would have the expected frequency of red hartebeest in the kills. Unfortunately the model used does not take such changes into account. Therefore it indicates a lower expected total than the actual number of red hartebeest present on the reserve.

However, the lions are not solely responsible for the decline of the red hartebeest population. For example, it has been shown that a 10% increase in birth rate in the red hartebeest would have a similar effect as a 10% decrease in the kill rate. With an actual birth rate of only 26%, and a survival rate of 51% for juveniles, it is impossible for the red hartebeest population to sustain any predation pressure. Even if the lion population were to be reduced to only two lions, the red hartebeest population would still have declined (Figure 9.3). If the above figures for the known birth and survival rates are substituted into the 2001 red hartebeest population of 130 animals, only 8.3 juveniles will be added to the population every year. This is may not even be enough to counter deaths from reasons other than predation, such as old age, injury and diseases, let alone predation by lion. If further predation by leopards and other predators is added, the sharp decline in the red hartebeest population is obvious, and probably irreversible.

Kudu

The effect of the lions on the kudu population of Welgevonden appears in Figure 9.10. Although the modelled population showed an initial population increase, a sudden increase in killing lions in 2001 caused a considerable decrease in the modelled population. A slight decline was also observed in the actual kudu counts for 1999 compared with 2001, but increased again from 2001 to 2002. Although no data on calving and survival rates for 2002 are available yet, initial estimates indicate an increase in the calving and survival rates for kudu in 2002. The model should also indicate an increase in the kudu population for this period once the new data on calving and survival rates are available and have been imported into the model.

No data on the predation of leopards on kudu on Welgevonden are available, but kudu carcasses from leopard kills are found regularly on the reserve. This indicates that leopards must affect the kudu population to some degree. Adding to the number of kudu killed each year is a low calving rate and a low calf survival rate before 2001. With previous calving and survival rates of 40% each, only 15.7 animals were added to the adult kudu population each year before 2001. This is probably less than the number of kudu that will be lost to predation and other natural causes each year. However, kudu are difficult to count with aerial counts, and as the count data were taken as a total count for use in the model, it is likely an underestimate of the actual data. The kudu population is probably larger than what the counts revealed. Therefore, the effect of the lions on the Welgevonden kudu population could be somewhat overestimated by the model.

Burchell's zebra

Figure 9.11 indicates that the observed decline in Burchell's zebra numbers was not due to lion predation. The modelled total indicates that the Burchell's zebra population was expected to increase with the current lion predation, even though the zebras had a low birth rate of 26% and low survival rate of 39% for the juveniles. This means that 29.1 animals are expected to be added to the current zebra population of 624 every year. The lions only killed a mean of 5.8 zebras per year during the study period. With lions probably being the only major predator of the Burchell's zebra on Welgevonden, it would have been expected that the population should have increased, as indicated by the model. The reason for the actual decline in Burchell's zebra numbers cannot be explained from the data collected with this study. Detailed research specifically on this topic will be needed to find the reasons for the declining population. It may well be a factor of food quality and quantity rather than predation. However, it has been described in Chapter 8 that the lions were still young and inexperienced during the study period and that they possibly found it difficult to hunt Burchell's zebra initially. It could therefore be that the lions are now older and more adept at killing Burchell's zebras than initially.

Blue wildebeest

The blue wildebeest population stayed relatively stable, despite the fact that it is the major prey of lions on Welgevonden (Figure 9.12). This can largely be attributed to a calving rate of 46% and a survival rate of 65% for the juveniles. However, the model expected the blue wildebeest population to have increased even more. The levels of predation by leopards and other predators such as jackal, on the blue wildebeest are largely unknown, but could possibly have contributed to the reduced growth in the blue wildebeest population.

Warthog

The actual warthog numbers on Welgevonden showed an overall decline over the last four years, although there was a slight increase in their numbers during 2002 (Figure 9.13). The lions initially killed a large number of warthog after they were first released from the boma in 1998, but the number of warthog killed decreased as the lions became more experienced in hunting other prey (Chapter 8). Subadult lions generally kill a large number of warthog soon after they leave their prides when they are still relatively inexperienced (*pers. obs.*). So did the current adult lions after they were first released from the boma in 1998. There were eight subadult lions on Welgevonden during 2000 and 2001, and they mostly killed warthog during that time. This could explain the decline in the warthog population at that time. These subadult lions were sold and removed from Welgevonden early in 2002, and there were no subadult lions in the Welgevonden lion population during the rest of that year. This could possibly have resulted in the actual increase in warthog numbers during 2002.

Impala

Figure 9.14 indicates that the model expected the impala population to grow more than what is shown by the aerial count data. However, it must be kept in mind that lion predation is the only form of predation used in the model. It has been shown that the effect of lion predation (Figure 9.5) on the impala population is small, and that lions kill only a small number of impala annually. However, impala carcasses are often found on the reserve, and impala probably forms an important part of the diet of leopards on Welgevonden. Impala are probably also killed by other predators such as the caracal *Caracal caracal*. Predation by leopard, caracal and other predators such as jackal probably caused the difference between the modelled and observed values for the impala population.

Stocking rate of the lions

The overall objective of the reserve as set by the owners of Welgevonden, as well as the objectives of the lion introduction, will determine the number of lions that the reserve will eventually carry. If the objective is to maintain the ungulate population at the levels in which the animals currently occur, the lion population should be adjusted to levels where they will have the least impact on the prey population. The model clearly indicated that the red hartebeest population can only sustain 1.95 killing lions, and that the eland population can only sustain 4.75 killing lions. However, it is not realistic to keep such low lion numbers on Welgevonden, both in terms of viability of such a small lion population, as well as the main objective of the lion introduction, which was to enhance the game viewing experience on Welgevonden by creating a Big Five reserve. Therefore, the lion numbers should be high enough to meet this objective.

This means that the prey population will have to be supplemented continuously, or alternative ways of increasing the low birth rates of the declining ungulate populations, the like red hartebeest, eland and tsessebe will have to be found. If not, the possibility of extinction of these populations on Welgevonden cannot be excluded. It is known in wildlife management that by increasing the initial population of ungulates that are decreasing, the threshold value that limits growth in the populations might be exceeded and the birth rates could possibly increase. However, although it was not investigated in this study, it appears as if the current ungulate population on Welgevonden already exceeds the ecological capacity of the reserve. It has also been shown previously that ungulate numbers can decline in response to an adjusted ecological capacity for herbivores (Ben-Shahar 1993). The same situation could exist on Welgevonden where the ungulate population may still be adjusting to the ecological capacity of the reserve for herbivores, explaining the decline in most herbivore populations. Hence, a further increase in ungulate numbers would not stop the animal population from deteriorating further.

Although no large-scale starvation and loss of condition were found in the ungulate population of Welgevonden, the quality of the food resources possibly caused the ungulates to struggle to meet their optimal nutritional requirements on Welgevonden's sourveld grazing. Such a nutritional deficiency will affect the herbivore populations secondarily, resulting in a reduced birth and a decreased survival rate in the juvenile animals. It has been shown elsewhere that limits in certain nutrients will cause a lower fertility rate in female ungulates (Snyman 1995). It can also reduce lactation in ungulate females, resulting in lower calf survival rates. Supplementary feeding could possibly initiate an increase in the birth rates of the ungulate population on Welgevonden.

If the objectives of the owners are to maintain the current diversity of ungulates, as well as lion numbers at the levels in which they currently occur, the decreasing ungulate populations will have to be supplemented continually with new animals from other sources. Although this will temporarily increase the sizes of these populations, the situation will soon repeat itself, and might not be viable in the long term. However, it should also be considered whether it is ethically acceptable to introduce animals into areas where they did not previously occur and where it is known that their populations will not survive in the long term without being supplemented with food and new members.

Alternatively, the best option would possibly be to let nature take its course. It should then be accepted that animals like the red hartebeest or tsessebe possibly never occurred permanently in large numbers in the area currently covered by Welgevonden, and that the available habitat is not suitable for them. The red hartebeest and tsessebe populations can therefore be expected to struggle to survive in the long term, even in the absence of large predators. Consequently, the extinction of these animals on Welgevonden, as has happened to the previously abundant blesbok *Damaliscus pygargus phillipsi*, will be ecologically acceptable. The lion numbers should then be adapted to levels where they are in balance with the remaining ungulate populations.

CONCLUSIONS

The above discussion emphasises the care with which predator management actions should be introduced on small game reserves. Most of the small game reserves are entirely fenced, and herbivores are limited in their ability to move away from areas of high predation pressure. Predation can therefore have a considerable influence on the ungulate populations of small game reserves. Prey that occur at low densities may undergo a population decline because of their inability to sustain predation pressure.

This might reduce their numbers to a level from which the population is unable to recover. The effect of lions on their prey on small game reserves is still a relatively new field, and little knowledge exists on how to regulate the predator-prey relationship properly.

In order to manage the reintroduced lion populations successfully, experiments of various management actions will have to be made and adapted to suit the needs and ecological circumstances of each small reserve. The predator and prey populations should then be monitored closely to establish the results of these experimental management actions. However, considerably more research on a whole range of predator-prey issues and relationships is necessary before the manner in which it operates on small reserves, will be understood.

CHAPTER 10

MANAGEMENT IMPLICATIONS

Carnivores have received considerable attention from wildlife scientists and researchers over the past 30 years. Despite all the research and studies, our knowledge of the exact role of carnivores in the ecosystem is limited. This is particularly true for the role of carnivores on small game reserves. The lack of adequate knowledge often causes controversy when it comes to making management decisions. Although several successful lion translocations and introductions have been done during the last decade, this practice is still in its infancy. Limited knowledge is available on the factors that control the way in which lions react to an introduction. Studies like the current one, and others like Hunter (1998) are invaluable to increase the knowledge of the ecology of reintroduced lions, as well as measuring the success of lion introductions. These studies should assist in providing guidelines for future introductions, as well as in measuring the success of management techniques that should be applied during the introduction process.

Reintroduction and translocation have previously been questioned as a management practice to conserve or establish large carnivore populations (Mills 1991). This was likely caused by a lack of knowledge of the factors that control the success of an introduction. Since then, several successful reintroduction attempts have been made in various reserves. The reintroduction of lions to Welgevonden was a definite success, and the new population soon established ranges, produced and raised offspring, and hunted successfully.

MANAGEMENT CONSIDERATIONS

Several management aspects that contributed to the success of the lion introduction in Welgevonden are clear. They are:

Age of introduction

The age at which the lions were introduced was probably one of the most important factors that contributed to the success of the project. The lions were captured at the age of 24 to 30 months, which is when lions would normally start dispersing from their natal prides under natural conditions (Smuts, Hanks & Whyte 1978; Funston & Mills 1997). This meant that they had not yet established themselves in a specific pride or territory when they were captured. The fact that they had not established themselves in prides would have contributed to the success of the bonding of unrelated animals when introduced into the boma.

An attempt to introduce two male cheetahs to Welgevonden failed probably because of their ages of five to seven years when they were captured. By then they had already established themselves in a territory. Although they were kept in a boma for two months before they were released onto the reserve, they returned to their capture site a week after their release on Welgevonden. Younger animals that have not yet had established territories would possibly have had a better chance of staying on the reserve. This is probably even more important with males than with females. The fact that the lions were young when they were released on Welgevonden would have contributed further to the success of the introduction by providing them with a chance to settle down before they started breeding.

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Time spent in the boma

The lions were first kept in a boma for almost three months, during which time they had enough opportunity to settle in their new environment. The lions were mostly unrelated (Table 2.1), and the long period together in the boma provided them with ample time to establish bonds between previously unrelated animals. It also provided the animals with an opportunity to get accustomed to the fence, which would have contributed to them staying inside the reserve after their release. During their time in the boma, they had little contact with humans and did not learn to associate humans with food. They were also not overfed while in the boma, which meant that they did not grow fat and lazy because of the lack of exercise in the boma. They were therefore in a prime condition when they were released on the reserve. The time spent in the boma was instrumental in increasing the chances of project success, and should be seen as essential when large carnivores are to be introduced into any area.

Place of release

The lions were released into an area of suitable habitat with large numbers of potential prey. It was shown how the lions remained close to the release site for the first two months after release, before dispersing into the reserve (Chapter 5). Release into a suitable area with an abundance of prey will give the lions a chance to get used to their new environment, and increase their hunting experience before dispersal into the reserve. This should significantly increase the chances of the lions staying in the reserve after their release, which should also considerably increase the chances of project success. The placement of the boma is therefore crucial and should be kept in mind in planning any lion introduction.

Post-release monitoring

The majority of lion reintroductions today are being done in small game reserves. This creates the potential of considerable impact on the prey population of these small reserves. Predator-prey relationships are, and always will be, controversial. The success of such a programme is difficult to measure, and it is even more difficult to manage. Managers of small reserves will have to be conscious of this fact and should put in place proper monitoring projects to measure the effect of the lions on the prey population. These monitoring projects should be continual, long-term projects, which should stretch beyond the post-release period. This will require considerable resources, both financially and in manpower, but are essential for the long-term success of an introduction. Monitoring of range use and population dynamics will be important indicators of whether the introduction was successful or not, and whether the lion population is healthy. Monitoring projects should provide sufficient data to allow the management staff of the reserve to make informed decisions.

Genetic health

Management should also be aware of the factors that could influence the long-term success of a reintroduction. Not only are the long-term effects of the lions on the prey populations important, but the genetic health of the lion population should also be monitored closely. Introduced populations usually start with a small number of founder animals, and inbreeding can potentially occur within a few years after introduction. The loss of genetic diversity could lead to the eventual extinction of the population. However, it can also cause other immediate problems like an immuno-deficiency syndrome (Hunter 1998), poor spermatozoa quality, and high cub mortalities. Individual recognition of animals is therefore important, and all births should be recorded carefully. A complete studbook listing all the births, including the parents of each cub, should be kept to detect and prevent any possible inbreeding that might occur.

None of the small reserves is large enough to sustain a sufficient population of lions to prevent inbreeding in the population. This will have to be managed, and managers will have to ensure that enough new genetic material from other sources is brought into the population from time to time to keep inbreeding to a minimum. The lions in all the small reserves in a specific region should be managed as one meta-population, and the exchange of genes between reserves should be monitored carefully, and managed properly. Managers of these small reserves therefore have to work closely together to ensure adequate gene flow beyond the reserve level and in the lion meta-population as a whole.

Future management

The managers of small lion populations have to be aware of potential future difficulties in lion management. The number of small reserves that have introduced lions has increased markedly over the last few years. This will lead to a question that will increasingly have to be faced in the future on what to do with the excess lions. The small reserves are limited in the number of lions that they can support and will be forced to remove lions from the reserve from time to time. Reserves will be faced with a situation in which they will have nowhere to go with their excess lions. Because of the limited number of lions that small reserves can support, the market for lions for conservation purposes is declining. However, there is an increase in the demand for lions in the trophy hunting market. Unless alternative methods can be found to control the population, reserves will increasingly be forced to use the hunting market to remove excess lions from the reserves. This is a highly controversial and sensitive subject and will continue to be so in the future. The various role players will have to work together to find solutions to the problems that might arise. More research in the field of birth control in felids might provide some of the answers in the future.

The management actions that could influence the success or not of an introduction of lions can be summarised as follows:

1. Young lions that were captured before they could establish territories at the capture site will be more suited for reintroduction.
2. Lions that came from different prides or reserves should be kept in the boma long enough for them to form a social bond, to settle in their new environment, and to get accustomed to the fences.
3. The lions should be released in an area with suitable habitat, an abundance of prey and, if possible, away from direct competitors.
4. The lions should be monitored extensively after their release to determine the success of the introduction, their population dynamics and the predator-prey relationships.
5. The genetic health of the population should be monitored carefully, and new genetic material should be introduced into the population from time to time.

The reintroduction of large carnivores in small reserves has changed from a situation where it was not sufficiently successful to justify its continuation as a rational conservation and management policy (Mills 1991), to one that faces problems with what to do with the excess lions from the successful reintroductions. Ongoing research will increase the knowledge on reintroductions, and will hopefully provide answers on how to successfully manage these populations in the future. Continued research and management will be necessary to ensure the long-term survival of any reintroduced lion populations.

SUMMARY

The development of the eco-tourism industry in southern Africa, and the creation of new wildlife reserves have led to a demand for the introduction of large predators. However, most of these areas are too small to be self-sustaining and have viable populations of lions. Therefore, intensive management is necessary to keep these populations viable. Little information on the ecology of reintroduced lions on small game reserves exists. The current study was initiated in an attempt to overcome this lack of information, and to provide data on which sound management decisions can be based.

Five lions were introduced into a boma on Welgevonden in October 1997, where they were first kept for three months. They were then released into the reserve in the hope that they would stay together. However, one lioness soon broke away from the group and moved away on her own. She was later captured again after sustaining an injury when killing a bushpig, and was returned to the boma for another month to recover. The other lions initially stayed close to the boma and rarely moved more than 4 km away from it during the first three months. The lions increasingly increased their distance away from the boma over the first three months after their release. The daily distance moved also increased significantly over this period. The daily direction of travel was random, and the lions did not show any consistent homing movement in the direction of the original capture sites at Pilanesberg National Park and Madikwe Game Reserve.

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All the lions established ranges within the boundaries of the reserve. There was a significant increase in range size over the first three months, until it reached a mean range size of 103.3 km^2 for the two males, and 80.0 km^2 and 60.0 km^2 respectively for the two lioness groups. The ranges on Welgevonden were largely centred around the old lands and plateaux, which were the habitat types for which the lions showed a positive selection. The ranges of the male lions reduced from 183.8 km^2 in the summer to 83.5 km^2 in the winter, but there was no significant difference in the seasonal ranges of the females. The removal of an internal fence caused the lions to shift their range boundaries and to increase the size of their ranges as they moved into the new area.

Both males and females bred at an earlier age than normal in natural areas. This was probably caused by the absence of older animals who would normally have suppressed the young lions from breeding at such an early age. The mean litter size was 2.9, and 84.6% of all the cubs born survived to the age of a year. All the cubs that reached an age of a year also survived to independence. Two of the original three lionesses had smaller mean inter-litter intervals than the published data in large, natural areas. The early breeding, high survival rates of the adults and subadults, and low inter-litter intervals all contributed to the rapid population growth of 400% over the first four years after introduction. Modelling the lion population by using VORTEX analysis indicated that the population will reach its ecological capacity for Welgevonden within the first 10 years after introduction, and that the genetic diversity will decline and the inbreeding coefficient increase if the population is left unmanaged. New genetic material will therefore have to be brought in by introducing more lions from unrelated gene pools, or by exchanging breeding age males with other reserves.

The lions killed 21 different types of prey during the study period. Blue wildebeest, eland and red hartebeest were three of the four most often killed prey in terms of both numbers and biomass killed. Warthog was killed fourth most frequently, while kudu ranked fourth in terms of biomass killed. Blue wildebeest, warthog, eland and red hartebeest were killed in greater frequencies that what would have been expected by their availability. However, impala, Burchell's zebra and waterbuck were killed less often than what would have been expected. There was generally no selection for any age or sex class of prey killed. Only adult Burchell's zebra were killed less often than expected. Of all the kills, there were significantly more kills made on the old lands, plateaux and valley bottoms, and fewer in the hills than would have been predicted by its occurrence in surface area in the reserve. No relationship was found between the number of lions on a kill and the weight and size of the prey involved.

The predator-prey relationships of lions on Welgevonden were modelled. From these models it appeared that the red hartebeest population can only sustain 1.95 killing lions, and could possibly disappear from the reserve soon. The eland population can only sustain 4.75 killing lions and can also potentially face extinction on Welgevonden soon. With the exception of the blue wildebeest, warthog and impala, it appears that low calving and calf survival rates negatively affected the ungulate populations as much as lion predation did. Most of the ungulate populations on Welgevonden are currently under pressure, and ways should be found to increase the low calving and survival rates for most of them.

This study has shown that the reintroduction of lions can be used to successfully establish populations on small game reserves, but that specific management actions will increase the chances of success. However, continual monitoring and management will be necessary to ensure the long-term viability of both the lions and their prey populations.

OPSOMMING

Die vinnige vooruitgang van eko-toerisme in suidelike Afrika, en die gepaardgaande ontstaan van nuwe natuurreservate het 'n vraag na leeu hervestigings laat ontstaan. Die meeste van hierdie reservate is egter te klein om 'n selfversorgende, lewensvatbare leeubevolking op 'n natuurlike wyse te kan onderhou, en intensiewe bestuur is nodig om hierdie leeubevolkings se voortbestaan te verseker. Daar bestaan egter min inligting oor die ekologie van hervestigde leeus op klein natuurreservate waarop bestuursbesluite gegrond kan word. Die doel van die huidige studie was om data te veskaf waarop bestuursbesluite op Welgevonden Privaat Natuurreservaat geneem kan word. Dit was terselfdertyd 'n poging om die beskikbare inligting oor leeus in klein reservate aan te vul.

Vyf leeus is in Oktober 1997 in 'n aanhoudingskamp op Welgevonden geplaas waar hulle vir drie maande aangehou is voordat hulle in die reservaat vrygelaat is. Met die vrylating was daar gehoop dat die leeus bymekaar sou bly, maar een wyfie het dadelik van die trop weggebreek. Sy is weer later gevang en terug geplaas in die aanhoudingskamp nadat sy 'n besering opgedoen het in 'n poging om 'n bosvark te vang. Die ander vier leeus het geleidelik verder en verder van die aanhoudingskamp begin wegbeweeg gedurende die eerste drie maande na vrylating. Hulle het egter selde verder as 4 km van die aanhoudingskamp af wegbeweeg. Gedurende hierdie tyd was hulle daaglikse bewegingsrigting ewekansig, en daar was geen aanduiding dat hulle wou terug beweeg na waar hulle oorspronklik in die Pilanesberg Nasionale Park en Madikwe Natuurreservaat gevang is nie.

Daar was 'n betekenisvolle toename in the grootte van hulle loopgebiede gedurende die eerste drie maande. Al die leeus het loopgebiede binne die reservaat gevestig. Die uiteindelike gemiddelde grootte van die loopgebiede van die twee mannetjies was 103.3 km^2, en 80.0 km^2 en 60.0 km^2 onderskeidelik vir die twee groepe leeuwyfies. Die loopgebiede van die leeus op Welgevonden was gesentreer rondom die ou lande en platos, en hulle het 'n positiewe seleksie vir hierdie habitattipes getoon. Die loopgebiede van die leeumannetjies het van 183.8 km^2 in die somer na 83.5 km^2 in die winter verklein, terwyl daar nie 'n betekenisvolle seisonale verandering in die loopgebiede van die wyfies was nie. Die verwydering van 'n interne heining het 'n verplasing van die loopgebied veroorsaak, en die loopgebiede van die leeus het vergroot soos wat hulle in die nuwe gebied inbeweeg het.

Beide mannetjies en wyfies het vroeër geteel as wat in natuulike gebiede verwag kan word. Dit kan heelwaarskynlik toegeskryf word aan die afwesigheid van ouer leeus wat die jong leeus normaalweg sou verhoed het om so vroeg te teel. Die gemiddelde werpselgrootte was 2.9 kleintjies per werpsel, en 84.6% van alle welpies wat gebore is, het 'n ouderdom van 'n jaar bereik. Verder het alle leeus wat 'n ouderdom van 'n jaar bereik het, ook oorleef tot onafhanklikheid. Twee van die drie wyfies het kleiner tussen-werpsel intervalle as die gepubliseerde data in groot natuurlike gebied gehad. Vroeë teling, hoë oorlewingsyfers en kort tussen-werpsel intervalle het bygedra tot 'n bevolkingsgroei van 400% gedurende die eerste vier jaar na vrylating. VORTEX-analise is gebruik om die Welgevonden leeubevolking te modelleer, en die model het aangedui dat die leeubevolking reeds sy ekologiese kapasiteit binne die eerste 10 jaar na vrylating op Welgevonden sal bereik. Dit het ook aangedui dat die genetiese diversiteit sal afneem, en dat die intelingskoëffisiënt sal toeneem indien die leeubevolking nie aktief bestuur word nie. Dit sal nodig wees om nuwe genetiese materiaal van ander gene-poele af in te bring deur nuwe leeus te hervestig, of deur teelmannetjies met ander reservate uit te ruil.

Die leeus het 21 verskillende prooisoorte gedurende die studietyd gehad. Blouwildebeeste, elande en rooihartbeeste was die prooisoorte wat die meeste in terme van getalle en biomassa deur die leeus gevang is. Vlakvarke was die vierde meeste gevang in terme van getalle, terwyl koedoes die vierdie meeste in terme van biomassa gevang is. Blouwildebeeste, vlakvarke, elande en rooihartbeeste was in groter getalle gevang as wat verwag kon word uit hulle beskikbaarheid op die reservaat, terwyl rooibokke, bontkwaggas en waterbokke minder as wat verwag sou word, gevang is. Behalwe vir bontkwaggas, waar minder volwassenes as wat verwag was gevang is, was daar geen seleksie vir of teen 'n spesifieke ouderdomsgroep van enige prooisoort nie. Meer prooi is op die ou lande, platos en valleie gevang as wat verwag kon word uit die oppervlaktes wat hulle beslaan op die reservaat, en minder prooi is in die heuwels gevang as wat verwag was. Daar was ook geen verhouding tussen die grootte van die prooi en die aantal leeus by 'n vangs nie.

'n Model is gebruik om die roofdier-prooi interaksies op Welgevonden te simuleer. Die model het aangedui dat die huidige bevolking rooihartbeeste net 1.95 volwasse leeus kan onderhou en dat rooihartbeeste van die reservaat af kan verdwyn. Die huidige bevolking elande kan net 4.75 volwasse leeus onderhou, en kan ook moontlik van die reservaat af verdwyn. Met die uitsondering van blouwildebeeste, vlakvarke en rooibokke, blyk dit dat lae kalfpersentasies en kalfoorlewing dieselfde invloed op die prooibevolkings het as die invloed van predasie deur leeus.

Hierdie studie het getoon dat leeus wel suksesvol in klein reservate hervestig kan word, maar dat sekere bestuursaksies die kanse van sukses sal verbeter. Aanhoudende monitering en bestuur is egter nodig om die langtermyn oorlewing van die bevolkings roofdiere en prooi op die klein reservate te verseker.

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APPENDIX I

COMMON AND SCIENTIFIC NAMES OF ALL THE ANIMALS MENTIONED IN THE TEXT

COMMON NAME	SCIENTIFIC NAME
Herbivores	
Aardvark	*Orycteropus afer*
Baboon	*Papio hamadrya*
Black rhinoceros	*Diceros bicornis*
Blesbok	*Damaliscus pygargus phillipsi*
Blue wildebeest	*Connochaetes taurinus*
Buffalo	*Syncerus caffer*
Burchell's zebra	*Equus burchellii*
Bushpig	*Potamochoerus porcus*
Common reedbuck	*Redunca arundinum*
Eland	*Taurotragus oryx*
Elephant	*Loxodonta africana*
Gemsbok	*Oryx gazella*
Giraffe	*Giraffa camelopardalis*
Hippopotamus	*Hippopotamus amphibius*
Impala	*Aepyceros melampus*
Kudu	*Tragelaphus strepsiceros*
Porcupine	*Hystrix africaeaustralis*
Red hartebeest	*Alcelaphus buselaphus*
Sable antelope	*Hippotragus niger*
Scrub hare	*Lepus saxatalis*
Springbok	*Antidorcas marsupialis*
Steenbok	*Raphicerus campestris*
Tsessebe	*Damaliscus lunatus lunatus*
Warthog	*Phacochoerus africanus*
Waterbuck	*Kobus ellipsiprymnus*

(cont.)

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COMMON NAME	SCIENTIFIC NAME
White rhinoceros	*Ceratotherium simum*
Carnivores	
Black bear	*Ursus americanus*
Brown hyaena	*Parahyaena brunnea*
Cheetah	*Acinonyx jubatus*
Eurasian lynx	*Lynx lynx*
Grizzly bear	*Ursus arctos*
Leopard	*Panthera pardus*
Lion	*Panthera leo*
Mountain lion	*Puma concolor*
Spotted hyaena	*Crocuta crocuta*
Birds	
Ostrich	*Struthio camelus*