Best management protocols for lions (*Panthera leo*) in medium-sized reserves in South Africa.

by

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DECLARATION BY CANDIDATE

I hereby declare that the dissertation submitted for the degree M Tech: Nature Conservation, at Tshwane University of Technology is my own original work and has not previously been submitted to any other institution. This dissertation consists of a series of manuscripts that are to be submitted to various scientific journals. As a result, styles vary between chapters of the dissertation. I testify that the work in this dissertation is my own, although the papers benefited greatly from comments by my supervisor and referees.

Chantelle Gail Jolley

Pretoria, July 2006
DEDICATION

This is dedicated to my mom and dad (Jill and George) for their unending love and support. For nurturing and inspiring my dreams and for their constant support. I am truly blessed to have such wonderful, loving parents.
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ABSTRACT

The tourism industry in South Africa has increased substantially over the past few years. In order to capture this expanding tourism market, most large provincial and nature reserves (referred to as medium-sized; 100-1000 km²) have reintroduced most members of the guild of large carnivores, along with various ungulate species. The species of interest here, lions (*Panthera leo*) are generally specifically reintroduced into medium-sized reserves for tourism gain. However, with these reintroductions has come the need for responsible and cost effective management.

As each reserve is unique in terms of overall goals and objectives, as well as in demography and ecology, management of lions does vary. There are generic issues that affect every lion population and as such there is the need for a pragmatic management protocol. Issues such as population growth, genetic integrity, predator-prey relationships, monitoring approaches and financial implications greatly affect the management of lions in South Africa.

The success of a reintroduction depends on how these issues are managed. We established two management approaches, namely a metapopulation approach and a single population management approach. A quasi-metapopulation management approach has so far been very successful in the conservation of lions, but the approach is expensive and requires the participation of a number of reserves. The single population management approach is less conservation oriented, but may be more financially viable. Through a partnership with large national parks in South Africa, it is argued that the single
population management approach may, however, be as good or even better at achieving conservation objectives.

The genetic integrity of a lion population is dependent in part on the introduced founder population. We established a time relationship, indicating at which stages in the lifespan of a population, new genes should be introduced to minimize inbreeding. The time lags for this introduction depend on the number of prides and individuals in the population. We also found that reduced monitoring could still achieve goals and objectives, and used in conjunction with other management techniques, still achieve a lower financial expenditure. We forward a potential management tool that will enable managers to establish a minimum viable population, dependent on reserve size. Thereafter the genetic integrity of the population can be managed accordingly.

We therefore show that a healthy lion population can be maintained with a less intensive monitoring and management approach, where more natural aspects of the population are allowed to take place. These approaches, when undertaken responsibly, should still attain desired goals and objectives, satisfy the tourism demand, and be more cost effective.
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CHAPTER 1

GENERAL INTRODUCTION

Over the past few decades nature-based tourism in southern Africa, and in particular South Africa, has increased dramatically, with the establishment of many smaller protected areas. Most of these reserves primary goals and objectives focus on the use of natural resources for development and as a generator of income (Barnes, 2001). In certain instances this has resulted in good conservation ethics, and the conservation of biological diversity, being regarded as secondary or lesser goals. Management in these protected areas is greatly influenced by the huge interest the public holds in large carnivores, with lions (*Panthera leo*), being of particular interest.

Having being persecuted and widely exterminated in the past, lions are still very much in conflict with humans in many parts of Africa today (Baldus, 2004; Ogada *et al.*, 2003; Ogutu, Bhola & Reid, 2005; Packer *et al.*, 2005a). In South Africa, lions were extirpated from many areas by the turn of the 19th century, however, in contrast with many other areas in Africa, lions and other large carnivores have recently been successfully re-established in many smaller game reserves in South Africa (Hunter, 1999). By their own admittance this has mostly been to keep pace with an increasing tourism demand. However, with these introductions came the necessity and responsibility for pragmatic and acceptable lion management.
During the process of a lion reintroduction management invariably has to accept that each area and population will respond uniquely to an introduction, and adaptive management techniques and skills will be essential (van Dyk, 1997). Therefore, the establishment of generalized pragmatic management protocols is needed in South Africa.

The main aspects that need to be addressed by management include population growth, genetic integrity and predator-prey relationships. Lion populations can increase rapidly under conditions of plenty (Druce et al., 2004a; Kilian & Bothma, 2003), and thus need to be managed to regulate population growth (Peel & Montagu, 1999). Population regulation, and to a lesser extent maintaining genetic integrity of lion populations, appears to govern most current management strategies for reintroduced lion populations (van Dyk, 1997; Kilian & Bothma, 2003).

This study aimed to outline some management options for re-established lion populations in terms of lion population dynamics, genetics and monitoring. In so doing, a decision support system was developed for reserve managers that can be applied as a management tool. The monitoring regime used in Pilanesberg National Park was investigated specifically, as this reserve in many respects pioneered now widely used methods of lion management and monitoring (van Dyk, 1997).

This study incorporates lions that can be considered “free ranging” and does not in anyway consider lions held in captivity or for the purpose of hunting in artificial circumstances. “Free ranging” represents lions which roam freely, interact socially,
occupy an area similar to a natural home range of a pride of lions, hunt their own prey and are not fed.

Throughout this dissertation the term “reserve” is used to refer to protected areas, national and provincial parks, game reserves and private game ranches in which free-ranging lion populations have or will be introduced. We classified reserves according to three size scales, and for the purposes of this study, aimed the analysis specifically at the management of lions in medium-sized reserves (100 – 1000 km²), in which semi-intensive management practices tend to be applied. The large size reserves (> 1000 km²) tend to opt for extensive management, e.g. Kruger National Park, where management have accepted a “hands off” approach. Population regulation, avoidance of inbreeding, and predator-prey dynamics (Mills & Shenk, 1992) are all self regulatory. Management of lions is thus concentrated mainly on problem animals and situations of conflict, where for example, lions exit the park and come into contact with humans.

Many recently established reserves in South Africa represent the following class – medium-sized reserves. Reserves such as the Madikwe Game Reserve and Pilanesberg National Park are size representatives of the third class. In medium-sized reserves some natural functions are allowed to take their natural course, while other aspects tend to require some form of management (semi-intensive) (Bothma, 2002). It was decided to case study Pilanesberg National Park as it represents many of the current management practices as used within other reserves in South Africa. Small reserves (<100 km²), on the other hand, seem to be inexorably linked to intensive management, and in most the possibility for natural ecological dynamics of both
predator and prey populations is questionable (Power, 2003). It should be noted that most of the reserves found within South Africa fall within the third and fourth classes in terms of reserve size.

Most reserves in South Africa are initially established in order to maintain biodiversity in its natural facet and to preserve and conserve wilderness qualities within an area. However, in larger reserves such as the Kruger National Park the ecosystem functions naturally without the need of human interference while in small- to medium-sized reserves human intervention is necessary. The need for management intervention is especially required when a suite of predators are involved. Small- to medium-sized reserves, in attempting to conserve aspects such as biodiversity, require funding to maintain themselves and often predators are introduced to serve this purpose. Tourism is the major reason for lion reintroductions. Throughout the study we will attempt to provide a pragmatic management approach that best suits the attainment of the tourism as well as conservation objective.

1. BACKGROUND & LITRATURE REVIEW

By 1999 at least ten projects had been attempted to re-establish free-ranging lion populations into areas from which they had been previously eradicated in South Africa (Hunter, 1999). This number has escalated rapidly over the last few years to at least twenty projects by 2004 (Druce et al., 2004a). Despite the numerous reintroduction projects relatively little literature is available on how to manage lions and other large carnivores in these reserves (Hunter, 1999).
The most important aspect to consider when reintroducing lions is the reason for doing so (van Dyk, 1997). Some reserves’ primary goals and objectives may, however, not be compatible with sound lion conservation, with many reserves seemingly introducing lions purely for tourism and financial gain, and not for their ecological role or conservation value.

Reintroduced lion populations in South Africa have the potential to expand until they reach the local carrying capacity (Druce et al., 2004a; Hunter, 1999). Population densities in reserves will vary to a considerable degree depending in part on prey biomass (Van Orsdol, Hanby & Bygott, 1985), and the detailed geography of each reserve (Hunter, 1999).

Due to the closed (fenced) nature of most reserves in South Africa, and the emphasis placed on fencing standards to hold species such as lions, changes in prey community composition should be expected (Peel & Montagu, 1999). Some species seem to decline in the presence of lions, whilst others do not (Power, 2003; Hayward & Kerley, 2005). Hunter and Skinner (1998) recorded modified vigilance behaviour by herbivores following lion reintroductions. However, Druce et al. (2004b) suggested that manipulation of pride size for the purpose of controlling predation on large ungulates may not be as effective as originally assumed, as this did not reduce predation on medium-sized ungulates in Makalali Game Reserve.

It is imperative that management recognizes that reproduction rates of reintroduced lion populations are usually substantially higher than under normal conditions because
of the easy access to naïve prey and the lions being below carrying capacity (Druce et al., 2004a; Kilian & Bothma, 2003).

Lions do not breed seasonally and females living in the same pride often come into oestrus synchronously (Schaller, 1972; Bertram, 1975). Lions have naturally low adult mortality and high birth rates (Packer et al., 1988). Cub mortality is considerably influenced by food supply and infanticide following pride takeovers (Bertram, 1975; Packer & Pusey, 1983a, b). The takeover of a pride by a new coalition of adult males synchronizes the reproductive status of the females. This is due to infanticide often associated with takeovers. The new pride males either kill dependant cubs from the prior male coalition or evict subadult cubs (Packer & Pusey, 1983a), causing the remaining females to cycle back into oestrus. Management approaches that influence reproduction in lions need to consider that females losing cubs due to infanticide, hunting or removals, may fall pregnant sooner.

Currently lion management in medium-sized tends to rely on manipulating certain population parameters. For example pride size is typically held at moderate sizes (three adult lionesses per pride). Although this may minimise the chance of large prey being killed (van Dyk, 1997), Packer et al. (1988) found that prides of this size have the highest reproductive rates. Cropping also increases the proportion of subadults or cubs, which in relation to body weight, eat more than older lions (Smuts, 1978a).

The acquisition of lions and the release process is only the beginning of a series of seemingly complex management issues. However, the current levels of manipulation
of lion populations by management may need to be reviewed in the future, as their financial sustainability and public approval (Cotterill, 1997) may come into question.

1.1 Genetics and Inbreeding

One of the fundamental problems in conservation biology is the risk of inbreeding, especially in small, isolated populations (Bjorklund, 2003; Soule, 1987). Inbreeding influences important fitness determinants such as fecundity, survival, growth and susceptibility to environmental stress (Bjorklund, 2003; Frankham, Ballou & Briscoe, 2002). There is evidence, however, that ecological isolation of reserves may allow for local adaptation and co-adaptation to take place (Franklin, 1980). This may increase overall genetic variation by increasing variation between populations (Boecklen, 1987). This would ultimately, if applied as metapopulation management, allow for the introduction of genes from other source populations.

Facilitating artificial dispersal within sub-populations could increase the effective founder populations, and thus stem inbreeding depression (Grubbich, 2001; Maguir & Servheen, 1992). In the case of small populations of free-ranging lions in South Africa, it can be argued that the human-fragmented reserves represent a transient, non-equilibrium situation, in which the previously more continuous population has become divided into smaller units, representing a “sample effect” (Wilcox, 1980). Beier (1993) found that immigration levels as low as between one and four animals per decade could decrease the risk of inbreeding depression in cougars in areas below 2200 km². As such, management facilitated migration between different lion populations, could reduce the probability of inbreeding depression.
The threat of extinction due to long-term inbreeding in small populations is real. Kissui and Packer (2004) clearly showed that endangered populations can remain at serious risk, even with a stable food supply, and no real threats from competing species when genetically compromised. Currently, intensively managed lion populations are manipulated genetically, in terms of paternity and maternity through vasectomization and contraception. This adds substantially to the level and cost of intervention required. A study conducted in Zimbabwe showed how popular lions are with tourists, but also highlighted that most tourists would be strongly opposed to the manipulation of lion prides, as is typically done (Cotterill, 1997).

1.2 Population regulation

Lions have few mammalian enemies, except their own kind, and it has been found that their numbers are regulated both by food and social behaviour (Bertram, 1973, Packer et al., 2005b). Sex ratios may even be influenced by physical features of the habitat. Prides occupying small, isolated habitats may have higher female: male ratios because of increased mortality of emigrating males, decreased immigration of potential male rivals, and multiple pride tenure by male coalitions (Van Orsdol, 1984).

The primary lion population regulation measures used in medium-sized reserves is the capture and removal of subadult lions (usually two years old) from the population, with older individuals occasionally being hunted (Vartan, 2001). The former, however, results in almost immediate compensatory reproduction, thus effectively increasing the reproductive rate and reducing the birth interval of the population. It has been found that the interbirth intervals are substantially longer in the Kruger National Park (Funston et al., 2003), than in most medium-sized reserves with
reintroduced lions (Kilian & Bothma, 2003). Also in Kruger, subadults tend to stay close to their natal home ranges until they are about five years of age before either dispersing or gaining a territory (Funston et al., 2003). It may, therefore, be possible to allow subadults to reside in a population for longer, before they are removed, and thus ultimately slowing the reproductive rate.

However, this approach may also increase the probability of subadults dispersing out of reserves and causing conflict (Anderson, 1981; Stander, 1990), which is probably an overriding concern for reserve managers (van Dyk, 1997).

In large natural systems carnivores regulate ungulate populations, with the only exception being in ecosystems with very large resident or large migratory game populations (Caughley & Sinclair, 1994; Fryxell, Greever & Sinclair, 1988; Mills & Shenk, 1992). Ungulate populations in medium-sized reserves are always sedentary, due to being fenced, and are never large enough to escape the regulatory effect of predation. Large carnivores are thus likely to strongly regulate theses populations.

Van Orsdol et al. (1985) found that pride size (measured in terms of average number of animals per pride and average number of adult females), and cub survival, correlated strongly with lean season food abundance. However, no relationship was found between group or litter size and any of the other measure of food supply. This indicates that females exhibit self-regulatory patterns only in times of decreased food supply. In small reserves they may thus ultimately regulate their own numbers, if allowed to establish without management interference. This situation has, however, to
date not been permitted to establish itself on any medium-sized reserve in South Africa.

Another important function of predation is that as the intensity of predation increases, so the incidence of diseases decreases (Schaller, 1972), thus it can be concluded that when predation holds species below their ecological carrying capacity, it keeps them at a level at which disease, starvation and other regulatory forces, associated with poor nutrition, can not take effect. Schaller (1972) adds that predators constitute an important check on ungulate populations, dampening the tendency of populations to increase beyond the carrying capacity. Predators may thus act as excellent “pasture managers” by keeping herbivore numbers below veld carrying capacity to ensure optimal grazing potential.

Some of the current management practices rely on limiting both population and pride size in an effort to reduce impact on the prey base (van Dyk, 1997). The latter practice is said to reduce the ability of lions to hunt larger more expensive game species such as buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), and black and white rhino (*Diceros bicornis*; *Ceratotherium simum*).

Contraception was investigated as a means of controlling population growth in Etosha National Park, Namibia (Orford, Perrin & Berry, 1988). Comparisons of the effect of contraceptive treatment in a group of wild free-ranging lionesses with a like group of controls were made. The major objective was to show that if the method was practical for free-ranging lions, it would provide for an effective alternative to culling lions in national parks. The methods resulted in similar values of quantified behaviour in both
control and experimental groups. Contraception is thus possibly more morally acceptable than culling, and should be practical in a small lion population. Furthermore it seems to cause less disruption of biological processes, is reversible, and prevents the loss of genetic reserves in a species (Orford et al., 1988).

It would seem that it is important for managers to establish clear goals and objectives prior to a lion reintroduction, and follow sound management principles in an effort to alleviate problems after their release. Furthermore managers need to accept that ecosystems are dynamic, and as far as possible should show a willingness to allow natural processes to occur.

1.3 Economics of monitoring and management

It is a well-known fact that the feasibility of maintaining a healthy population of a species in a wildlife area is dependant on the availability of the basic resources required by that species (Killian & Bothma, 2003; van Dyk, 1997). However, as utilization of wildlife on private land is an industry, it is often economic factors rather than ecological factors that determine the conservation effort allocated by owners to a particular species. The future of many species in these areas thus depends on a delicate balance between ecology and economics (Cotterill, 1997).

Financially beneficial activities such as hunting can be combined with certain management techniques, such as removing males every three to four years. Van Dyk (2001) suggested that hunting to achieve a population manipulation objective remains a viable income generating option. Lionesses can also potentially be removed without influencing the habituated nature of the pride (van Dyk, 2001).
Ultimately the population viability, genetic integrity and financial implications of lion management are vital in the establishment of management practices and a more comprehensive understanding of lion management needs to be established.

2. RATIONALE FOR THE STUDY

2.1 Rationale for the study
Lions remain one of the most studied carnivore species throughout the world, yet little research has been published on the management of reintroduced populations. Many unanswered questions remain on the best management approach for reintroduced lions in these reserves. This study investigated management methods currently used in South Africa, and then established some pragmatic management approaches that could be applied in medium-sized reserves. The management approaches essentially investigated issues of genetic integrity, economic viability, monitoring, and degree of manipulation required in managing a viable lion population.

2.2 Research Aim
The aim of this study was to ascertain which management aspects are important in medium-sized reserves in South Africa where lions have been reintroduced. Management intensities according to reserve size, manipulation, and genetic policies were investigated. With the establishment of these key issues, the final aim was to propose some pragmatic management approaches which could be incorporated and augment these aspects. The study attempts to define alternative measures in terms of genetic management, monitoring strategies, and financial expenditure. Further to this, the aim was to provide management approaches that can be utilized under varying
circumstance and situations, as well as in combination with varying intensities of monitoring.

2.3 **Key Questions**

- What management aspects are classified as vital in the management of reintroduced lion populations?

- What extent of management is needed to achieve the overall goals and objectives with a minimum financial output?

- Would alternative management approaches, than those currently employed in most reserves in South Africa, yield better or similar results in terms of lion conservation and economics?

- Can a lower budget still achieve the stated goals and objectives of a lion reintroduction whilst still maintaining adequate levels of monitoring and a healthy gene pool?

- Would a metapopulation management approach or a single population management approach best satisfy a broad spectrum of reserve goals and objectives, especially where tourism is a key aspect?
2.4 Hypothesis

The varied goals and objectives of medium-sized reserves, and their established objectives for introducing lion populations, lead to a diversity of management options. Financial implications have become increasingly important to reserve management.

Lion reintroduction programmes into medium-sized reserves in South Africa are undertaken in order to enhance the tourism potential, however, other management issues seem to influence management to a greater degree. We hypothesize that alternate management approaches, than those currently utilized, can be as effective in attaining reserve goals and objectives. Current management methods regarding genetic management and monitoring techniques are costly and may not yield the desired or best results. Management approaches that strive to attain these goals and objectives and incorporate alternate genetic maintenance programmes, as well as a more cost effective monitoring programme, are possible in medium-sized reserves in South Africa.

3. OUTLINE OF THE DISSERTATION

In answering the key questions of this dissertation various chapters were drafted. These draft documents will be combined in a final form for publication in scientific journals. Each chapter covers an important management aspect the management of lions in South Africa. In this outline the structure of the dissertation is presented, and the associations within each chapter.
In order to forward various management protocols, we investigated, through the use of a questionnaire, current management and manipulation techniques in use in medium-sized reserves in South Africa. The results of the questionnaire are presented in Chapter 2. I also established a relationship between reserve size and carrying capacity to determine what size reserve would be required to support a viable lion population.

With the establishment of many private reserves in South Africa and the increase of tourism to the sub-continent, the financial expenditure by reserves on lion populations has become very important. Most funds are spent on the monitoring of populations as this forms the database for management decisions. Chapter 3 thus investigates a generic monitoring and management technique and the financial implications of these techniques. Thereafter an alternative monitoring technique of lower financial cost, and differing degrees of manipulation and monitoring, is presented.

As the genetic integrity of lion populations in medium-sized reserves is an important management consideration Chapter 4 investigated aspects of the genetic management of lions in a range of reserve sizes (determined by the number of prides each could support). Here the various manipulation techniques typically used in South Africa for the maintenance of lion populations were considered, before alternative methods of maintaining genetic integrity were forwarded. In this chapter a computer model was used to simulate a number of scenarios regarding population size in relation to events of close breeding. From these simulations the time relationship in which managers would need to introduce new individuals in order to curb inbreeding within the population was established.
In Chapter 5 two different management approaches are discussed that could form the basis of best management protocols, these are a metapopulation approach or a single population management approach. Potential costs of each approach are presented and compared. This chapter also summarizes the various results and best management protocols that can be applied in conjunction with the differing genetic and monitoring techniques.
CHAPTER 2

LION MANAGEMENT STRATEGIES IN SOUTH AFRICA

2.1 INTRODUCTION

In South Africa lions are conserved and managed at multiple scales, and it is generally accepted that management intensity is dependant on reserve size (Bothma, 2002), with the extent of management increasing dramatically in the smaller reserves. In large parks like Kruger National Park and Kgalagadi Transfrontier Park, the lion populations are self-regulating and large, and are thus managed extensively in the sense that only lions that become problem animals are either destroyed or translocated. Little management and no manipulation is applied, although in the past semi-intensive management was applied locally (Smuts, 1976). In Kruger the routine culling of lions and hyenas from 1903 to 1960, and the specific culling of lions in the 1970’s to try curb the declining wildebeest and zebra numbers and to protect locally rare populations of sable and tsessebe, typifies this past management approach (Smuts, 1978b). These policies were conducted according to specific ecological hypotheses that predators limit or reduce prey populations, even decreasing local diversity of herbivore species. The programme was halted in 1980 as no evidence was found to prove such hypotheses. Today managers in the Kruger National Park manage only conflict situations, where lions break out of the reserve and come into contact with people. Lions are managed in a similar way in the very large Kgalagadi Transfrontier Park (Funston, 2001).
The Hluhluwe-Umfolozi Park being much smaller than the Kruger National Park, applied a slightly more intensive management to their reintroduced lion population. After initial lion break outs and financial compensations, the reserve managers introduced a culling policy aimed at reducing conflict (Anderson, 1981). Recently, perhaps as a consequence of the population not being managed genetically, it was found that the Hluhluwe-Umfolozi Park lion population was suffering from inbreeding effects (Stein, 1998). Management thus introduced lions from the Pilanesberg National Park in order to increase the genetic diversity of the population (Reid, 2002), the success of which is part of an ongoing research programme.

Present day management techniques that are applied in most medium-sized reserves were mainly developed by the North West Parks & Tourism Board, specifically within the Pilanesberg National Park, and at Phinda Resource Reserve. Management is applied by manipulating population dynamics, pride and coalition composition, controlling of numbers through removals, hunting, contraception and vasectomization, and by applying intensive monitoring (van Dyk, 1997).

In very small reserves, such as the Madjuma Lion Reserve (smallest reserve in South Africa holding free-range lions), almost every aspect of ecosystem dynamics is managed (Power, 2003). Here predator-prey interactions are managed through the introduction of live prey, specifically to satisfy the appetites of the lions. A single pride is maintained, again through manipulation of dynamics and contraception.

The extent of management that lions are exposed to in South Africa is unprecedented in any other country in which the species occurs. In order to ascertain the
management philosophies currently used in South Africa, data was gathered from a sample of medium-sized reserves with reintroduced lion populations via a questionnaire survey.

The objective behind this analysis was to contextualize the various approaches taken to managing lions in South Africa, specifically within medium-sized reserves. I further aimed to investigate the rationale behind lion reintroductions in medium-sized reserves, the scales of management in different reserves, and the feasibility thereof. Reserve size was deemed important to the reintroduction process and I aimed to establish a means of calculating how many lions could be held within various reserve sizes, such that an effective population size could be obtained. For the purposes of this dissertation the term effective population size (Ne) means the number of breeding adults that contribute to the gene pool of the next generation (Freeman & Herron, 1998).

2.2 METHODS

A questionnaire (Appendix 1) was distributed to several medium-sized reserves throughout South Africa. For the purpose of this both open-ended and closed questions were used. It was felt that the use of both question types would enhance the questionnaire, and provide more data from the reserve managers. There is little evidence to show that one technique is better than the other (Clayton & Mendelsohn, 1993), with dichotomous choice and open-ended questions yielding similar average estimates (Kealy, Dovidio & Rockal, 1988).
There was an average response to the questionnaire, with a final total of ten successful respondents out of 20 requests. All questionnaires were addressed to, and completed by, the relevant reserve managers (Appendix 2). Of the respondents the largest reserve was Marakele National and Contractual National Park, which combined is 900 km² in extent. The smallest reserve in the survey was Karongwe Game Reserve, which is only 85 km². Forty percent of the respondents had already been managing an introduced lion population for more than 10 years.

The questionnaire initially aimed at establishing rationale for lion reintroductions. We sought to confirm that the purpose for lion reintroductions was that of tourism, as had been previously found by Vartan (2001). Thereafter, details of the reintroduction process and the results thereof were investigated, in terms of the lion population dynamics (birth and death rates, population increase). We examined the management practices and techniques that were used, such as vasectomization, contraception, culling practices, sales and monitoring programmes. We also sought to establish the extent of financial expenditures throughout the reintroduction programmes.

In summarizing the various management intensities applied in the management of lion populations, it is important to grasp the differences between reserves. With varying habitat types, topographies, prey species compositions and densities, and ultimately size, managers are forced to apply differing management techniques to their lion populations.

At the onset of a reintroduction programme, management establish the number of lions they wish to introduce. The establishment of this number would seem to be
dependant on the extent of genetic variation that can be achieved. It is recommended that the establishment of size of the founder population be based not only on achievement of genetic variation but also on reserve size.

2.3 RESULTS

2.3.1  Questionnaire survey results

Of the responding reserves, 80% had undertaken lion reintroduction programmes, with only Venetia-Limpopo Nature Reserve and Hluhluwe-Umfolozi Park reporting that natural immigration of lions had occurred into the reserves (although in Hluhluwe-Umfolozi Park some lions were reportedly introduced). The majority of the reserves within the study (80%) stated that tourism, and the attainment of ‘Big 5’ status, was the primary objective for the reintroduction of lions. Specific goals and objectives for the reintroduction of lions were poorly defined, with only 30% of respondents acknowledging the establishment of any such objectives (Figure 2.1).

Figure 2.1  Primary and specific objectives/rationale for the reintroduction of lions into medium-sized reserves in South Africa
Very few of the reserves (30%) confirmed that specific initial studies were undertaken prior to the lion reintroduction, with only the Pilanesberg National Park completing a comprehensive economic assessment specifically regarding lions. In most cases (70%), general management plans, game stocking rates and ecological monitoring were used as guidelines for the reintroduction of lions, but without a species specific management plan being developed.

Etosha National Park, Namibia, was the primary source of lions for reintroduction programmes stocking 60% of the responding reserves either directly or indirectly via excess animals from Pilanesberg National Park and Madikwe Game Reserve. The main motivations for the chosen origin was that Etosha National Park lions were believed to be disease free (not infected with Feline Immunodeficiency Virus), were a genetically healthy population, and were readily available (Table 2.1).

All reserves questioned, established lion populations with less than twenty founder individuals, the average being $8.3 \pm 2.0$ (Table 2.1). Pilanesberg National Park introduced the maximum number with 19 individuals, whilst the smallest reintroduced population was established in the Marakele National Park, only three male individuals. However here the plan was to remove the Welgevonden Game Reserve boundary fence, and in this way link these lions to an already established lion population. As such, the introduction of the three males can be seen as an introduction of new genes, as opposed to a true population reestablishment. Although debated, the Hluhluwe-Umfolozi Park re-colonization seems to have comprised 6 individuals (Anderson, 1981), while the number of lions that entered Venetia-Limpopo Nature Reserve would seem to have been about eight individuals (Cotterill, 1996).
Table 2.1 Results of questionnaire survey including demographic data of the reintroduced lion populations

<table>
<thead>
<tr>
<th>Reserve</th>
<th>Size (km²)</th>
<th>Number of introduced lions</th>
<th>Origin</th>
<th>Introduction motivation *</th>
<th>Current population size</th>
<th>Further reintroductions</th>
<th>Number of males</th>
<th>Number of females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Venetia</td>
<td>340</td>
<td>Unknown Unknown Unknown</td>
<td>Botswana Reserve (Tuli Game Reserve)</td>
<td>Natural dispersion</td>
<td>13</td>
<td>No</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Madikwe</td>
<td>620</td>
<td>12 7 5</td>
<td>Etosha</td>
<td>Disease free</td>
<td>46</td>
<td>Yes</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Phinda</td>
<td>185</td>
<td>13 5 8</td>
<td>Mpumalanga/Pilanesberg</td>
<td>Availability genetics</td>
<td>18</td>
<td>Yes</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Marakele</td>
<td>900</td>
<td>3 3 0</td>
<td>Kalahari</td>
<td>Genetics / Fence trained</td>
<td>3</td>
<td>No</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tembe</td>
<td>300</td>
<td>4 2 2</td>
<td>Madikwe/Pilanesberg</td>
<td>Disease free</td>
<td>10 – 12</td>
<td>No</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Welgevonden</td>
<td>330</td>
<td>5 2 3</td>
<td>Madikwe/Pilanesberg</td>
<td>Availability genetics</td>
<td>25</td>
<td>No</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Karongwe</td>
<td>85</td>
<td>4 2 2</td>
<td>Kapama/Makalali</td>
<td>Availability genetics</td>
<td>8</td>
<td>No</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pilanesberg</td>
<td>500</td>
<td>19 6 13</td>
<td>Etosha</td>
<td>Disease free</td>
<td>31</td>
<td>Yes</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Hluhluwe-Umfolozi Park</td>
<td>890</td>
<td>Unknown 1 3</td>
<td>Mozambique/Kruger</td>
<td>Availability</td>
<td>70</td>
<td>Yes</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>Shamwari</td>
<td>160</td>
<td>6 2 4</td>
<td>Madikwe/Pilanesberg</td>
<td>Disease free</td>
<td>15</td>
<td>No</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

* Implies the specific reason why reserve management chose to introduce lions from the specified origin (original location).
2.3.2 Monitoring and management techniques

Lion reintroduction programmes have been poorly documented in the past (Linnell et al., 1997; Hunter, 1999) but it would appear that many reserves (80%) now actively monitor and manage their lion populations, and from this several studies have been undertaken (Druce et al., 2004a, b; Kilian & Bothma, 2003; Peel & Montagu, 1999), with many still currently ongoing.

Results revealed that 80% of the reserves fitted their lion population with radio collars and monitored the population on a daily basis. Collars are usually fitted at a minimum of one collar per pride and one collar per male coalition. Radio telemetry was used everyday to track and record movements, impacts and population dynamics of the reintroduced populations. Many reserves opted for intense monitoring of their small populations and branded all individuals so as to promote individual recognition.

In the Venetia-Limpopo Nature Reserve monitoring was not conducted by the reserve management, but the population did form part of a Tshwane University of Technology study (Funston & Janse van Rensburg, 2003; Funston, 2004a). In Marakele National Park no monitoring with the exception of fence patrol sightings was conducted.

Most of the respondents (70%) stated that their management was only moderate in intensity (Figure 2.2), with pride and coalition size and population growth being manipulated. Management intensity categories where defined as:

Extensive (Low) – No veterinary assistance, population monitoring or manipulation applied.
Moderate (Medium) – Daily monitoring and some population dynamics manipulation
High – Veterinary assistance, daily monitoring, manipulation of all or most population processes.

Most reserves indicated that manipulation and management techniques such as sale of individuals (usually subadults), translocation, vasectomies, contraception and hunting were in use. Tembe Elephant Park and Marakele National Park indicated that to date no population manipulation techniques had been imposed. Hluhluwe-Umfolozi Park indicated that management manipulated the population only in cases of breakouts, and in the euthanasia of sick individuals, although an extensive supplementation programme was currently being undertaken.

Coalition size was maintained at two males per coalition in 80% of the reserves studied, with the Venetia-Limpopo Nature Reserve and Marakele National Park not manipulating coalition size. Pride size was highly variable, from two females per pride in Madikwe to 6 – 15 females per pride in Phinda.

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![Degree of monitoring intensity applied to reintroduced lion populations](image)

**Figure 2.2** Degree of monitoring intensity applied to reintroduced lion populations
The preferred management techniques for population control where sale of individuals and contraception of females (Figure 2.3), while culling was indicated as the least favoured method of population control.

Some reserves (50%) used the services of a veterinarian at all stages of the reintroduction process and continue to make use of these services post release. This may be excessive in cost as it requires the involvement of external expertise. The other reserves within the study did make use of veterinarian services at some stages of the reintroduction process.

![Figure 2.3](image)

**Figure 2.3** Rankings of preferred management techniques for the control of population growth

Sixty percent of the respondents indicated that they formed part of a metapopulation management approach, however, the specific movement of lions into (immigration) and from (emigration) populations for the purpose of genetic improvement was minimal (10%).
Only 40% of the respondents had undertaken further reintroductions into the population. Recently a large scale reintroduction programme was instituted in Hluhluwe-Umfolozi Park for the specific purpose of gene introduction (Reid, 2002). The population was considered to be suffering from inbreeding effects with records of severe joint swellings, high immuno-incompetence, elevated juvenile mortality, and poor quality of spermatozoa (Stein, 1998). These results, however, were interpreted to be inconclusive by Vartan (2001). The programme initiated involved the introduction of both males and females into the population. The individuals were introduced as male coalitions, newly established pride units, and also involved the introduction of females into existing prides (Reid, 2002).

### 2.3.3 Demographics of reintroduced lion populations

Half of the reserve managers interviewed stated that the birth rate of reintroduced lion populations was medium, while 40% stated that the rate was high. Optimal habitat and an abundance of prey were thought to result in very high reproductive rates for reintroduced lion populations.

Most respondents (70%) indicated that mortality rates of adult lions was low, while cub mortality was low or medium (50% and 40% respectively). This seems to correspond with most lion population studies, where a naturally low adult mortality is experienced coupled with a fairly high birth rate (Packer et al., 1988; Pusey & Packer, 1987; Schaller, 1972). However, where cub mortality in the Serengeti is high, being influenced by food supply and infanticide following pride takeovers (Packer & Pusey, 1983a), cub mortality in the reintroduced populations is low (Killian & Bothma, 2003), as it is in Kruger National Park (Funston et al., 2003).
2.3.4 Financial implications

The overall financial and ecological benefit of the various lion management practices remains relatively unknown. Sixty percent of the reserves questioned introduced lions according to an established budget, while 40% indicated that no budget was established for the programme.

Data regarding the use of these budgets was vaguely indicated. Phinda Game Reserve used the established budget optimally, while Tembe Elephant Park under spent their budget. Shamwari Game Reserve exceeded their budget, but in general most reserves stated that the exact costing of the reintroduction was unknown due to the time lapse from reintroduction to date. In broader financial terms the following costings were applied by the managers to the potential cost of the reintroductions:

• 40% indicated that the final expenditure was unknown
• 20% indicated that the final expenditure was between R10 000 and R100 000.
• 40% indicated that the final expenditure was between R100 000 and R1 000 000.

Initial impact assessments, sourcing and acquirement of lions, veterinarian services, relocation, and introduction costs, as well as the intensive monitoring of the populations post release, result in huge expenses. These seem to be generally unaccounted for in the responding reserves. As this dissertation aimed to establish optimal management techniques it was important to accurately account for the variable costs of different management and monitoring intensities.
2.3.5 *Carrying capacity and reserve size*

Characteristics of an area and specifically area size are important in the reintroduction process. The National Principles, Norms and Standards for the Sustainable Use of Large Predators in South Africa, section 2, stipulates the principles that shall apply when re-establishing large wild predators as:

- enough suitable habitat must be available to accommodate a viable group;
- sufficient suitable prey must be available to sustain the predators through natural hunting;
- adequate fencing as prescribed by the relevant provincial conservation authority must be erected;
- only truly wild or properly rehabilitated large predators may be utilized for re-establishment purposes

In reference to these Norms and Standards, it is ideal that an area should be large enough to acquire a viable population of the species being introduced with the minimum intervention (South African National Parks Management strategy, 2006). A best management approach for lions in medium-sized reserves can only be established when considering all managerial aspects that influence the reserve and it is important that these be considered prior to the re-introduction of lions. One of the key aspects influencing management during the introduction process is the size of the founding population, but we also recommend that reserve size be considered when determining the number of individuals to introduce.

Most reserves introduce lions for the purpose of tourism, however, the management of lions in medium-sized reserves seems to be for ecological and genetic rationale,
focusing on population growth and the curbing of this rapid growth (Hunter et al., in press). The initial problem is, however, related to the number of individuals reintroduced. As a guideline, the relationship between reserve size and carrying capacity was established to determine what size would be required to support a viable lion population (Figure 2.4). Managers will therefore be able to determine upfront, what an acceptable population size will be for a specific reserve size. The equation that defines this relationship is:

\[ A = \frac{N_e}{CC} \]

Where \( A \) = area size

\( N_e \) = effective population size and

\( CC \) = carrying capacity

Figure 2.4  Reserve size required for a minimum viable lion population, with various viable population sizes being given
2.4 DISCUSSION

The survey reconfirmed the findings of Vartan (2001) that lions are specifically re-introduced into medium-sized reserves for the purpose of tourism. The status of “Big 5” is financially beneficial. Reserves do not appear to introduce lions even for secondary objectives, as this was poorly defined in the survey, although the reintroduction of lions does suit objectives related to enhancement of biodiversity. Once lions have been reintroduced reserves appear to manage their populations using a variety of manipulation and management techniques. No management plans are in place for the long term maintenance of a lion population and to date reserves have mainly managed population when the need arises. As a result most reserves are now faced with the dilemma of how to maintain their populations at healthy levels that conform to the tourism objective. Most reserves are not in the position to remove the entire lion population due to tourism demands, especially from the lodge industry. Further to this, management are under constant scrutiny from the public when it comes to some forms of population manipulation. Culling and hunting are least preferred by not only reserve management, but also by the public (Cotterill, 1997). Reserves need to be cautious when opting for these forms of population control.

The health of a population does depend on the founder population, as well as the introduction of new genes from time to time, usually through immigration of individuals. Most introduced founder populations are from differing bloodlines to increase the heterozygosity of the population. The size of the lion population introduced is often related to the size of the reserve and the resources available, although it would appear that reserves are now introducing smaller founder
populations in an attempt to decrease the rate of population growth, and the time period in which new individuals would need to be introduced in order to bring in new genes (e.g. Welgevonden, Kilian & Bothma, 2003). This may have serious genetic ramifications in years to come.

In most cases, the genetic integrity of established lion populations, as well as tourism benefit, dictate the management and manipulation procedures. In terms of the genetic integrity of a population, many reserves attempt to manipulate population structure and demography in order to maintain the genealogies. It is clear that the intense focus on the dynamics and genetic status of each lion population is important to managers.

In order to best manage lion populations, reserve managers need to clarify the stated goals and objectives for introducing the lions and then manage accordingly. As tourism is the general goal and objective in medium-sized reserve in South Africa, when introducing lions, this would be expected to constitute the overall driving factor in lion population management. The importance to reserve managers should be that tourists are satisfied with their sightings of lions.

Lion densities do play a role in the satisfaction of tourist expectation. Optimal viewing and the likelihood of seeing lions are associated with lion density (Cotterill, 1997). Managers can, however, calculate the number of lions and therefore the correlating density that can be introduced depending on the size of the reserve. Thereafter it will be vital that management monitor the achievement of the tourism objective and adapt as necessary. Carrying capacity should be established such that the reserve can sustain a viable lion population while reducing, as far as possible,
conflict between lions and people. Lion ranging patterns, prey biomass, reserve size, topography, geography, habitat type and landscape features will play a role in the establishment of a viable population size.

The survey established that there is a need for a pragmatic management approach that can be implemented in South African reserves, and that most managers welcome the prospect of another form of management that may allow for a less intensive approach (Mr E Leibniz, pers. comm.)
CHAPTER 3

FINANCIAL CONSEQUENCES OF MONITORING AND MANAGING LIONS ON MEDIUM-SIZED RESERVES.

3.1 INTRODUCTION

Cost efficiency has been the focus of a number of studies on conservation planning (Moran et al., 1997; Ando et al., 1998), however, research into the cost efficiency of the monitoring and management of single species is lacking. Here, specifically the cost-efficiency of the monitoring and management of lions in Pilanesberg National Park was investigated as a case study. Pilanesberg was chosen as many of the methods of lion monitoring and management for medium-sized reserves were pioneered here (van Dyk, 1997; 2000). Importantly lions were introduced into the Pilanesberg National Park to contribute to the tourist experience thereby generating income for the tourism industry in the region (van Dyk, 2000).

Over the last decade the Pilanesberg lion population has been both intensively monitored and managed (manipulated), with population dynamics being manipulated and controlled. Male coalitions are strictly maintained at two individuals and prides are limited to three or four adult lionesses. Pilanesberg consider larger prides and coalitions to be disadvantageous, as the lions would then be more likely to hunt larger,
more valuable prey species such as disease free buffalo, giraffe and rhinos (van Dyk & Slotow, 2002).

With tourism being the primary objective for the introduction of lions, Pilanesberg management established that ‘sighting satisfaction’ (frequency and quality of sightings) of the lions was the key objective of management (van Dyk, 2000). Therefore the number of times lions were seen by tourists was monitored. However, the reserve managers were also concerned with the effect of the lions, and other large carnivores, on their prey populations, and this was also monitored. An additional concern was the genetic composition and integrity of the lion population. The population was thus managed according to intensive manipulative techniques largely developed by van Dyk (1997, 2000).

The Pilanesberg monitoring and management strategy for lions was based on the decision that each individual animal was an important feature of the population, and the management and monitoring was therefore designed to recognize individuals and assess each individual’s contribution to the population (van Dyk, 2000). In order to facilitate this form of management, the lions needed to be intensively monitored and thus needed to be accustomed to vehicles and people.

Specially designed bomas were constructed to acclimatize the lions to the new surroundings, habituate lions to electrified fences, and to bond pride/coalition members (van Dyk, 1997). Lions were initially held in the Pilanesberg boma in order to facilitate this familiarization. As a result of this period in the boma lions became habituated to vehicles and people. Habituation of lions to vehicles was deemed
essential in Pilanesberg National Park for the purpose of post release monitoring and management. Habituated lions are easier to immobilize for the purposes of changing of collars, branding, are more easily identified at kills and are better suited to tourism activities (van Dyk, 1997).

In order to manipulate the lion population towards the objectives for the Pilanesberg reintroduction, an ongoing post release monitoring programme, especially in the first 12 months, was also seen as vital (van Dyk, 1997). Methods of monitoring included daily radio-tracking and locating all groups, and hot branding each individual to facilitate identification. The intensity of the monitoring and management of the lion population also involved ongoing veterinary care and individuals injured in natural processes such as pride takeover events were removed from the population and treated in a holding facility. Although very expensive this management technique has been widely applied in most reserves with reintroduced lion populations in South Africa. Even individuals injured while hunting are removed from the population and treated in holding facilities (Kilian & Bothma, 2003).

In an effort to obtain funding to maintain such intensive monitoring and management, the North West Parks and Tourism Board appealed to companies to fund prides within the reserve (Maoka, unpublished). It was envisaged that companies adopt one out of the five prides in the reserve, and fund the monitoring and management of that pride on an annual basis. It was estimated that the annual cost of the Pilanesberg lion monitoring programme was R 150 000 or R 30 000 per pride. This figure included vehicle kilometre usage, radio-telemetry equipment, immobilizing drugs and darts, basic assistance to visiting biologists as well as some genetic finger printing (Maoka,
unpublished). The costing did not, however, cover the cost of salaries for monitoring staff, fence maintenance, and security.

The aim of this study was to establish the cost of the monitoring and management process utilized by most reserves in South Africa. We used the Pilanesberg National Park as a case study, focussing on a two year period of intensive management, 2000 and 2001. Further to this we will establish alternative techniques to apply, utilizing the same concept of monitoring but with reduced intensity. Reduced intensity implies less time spent in the field, fewer numbers of collars within the population, and the removal of some management interventions. The removal and reduction of these aspects will be correlated into financial terms and be calculated accordingly. This should result in a reduced cost approach to apply in the monitoring of lion populations in medium-sized reserves. We also investigate the costs and purpose of the habituation process and the necessity thereof.

Once the methods and specific programmes of lion population monitoring and management conducted by the Pilanesberg management have been established the aim is to provide a cost analysis of this programme. The specific aim of the ensuing comparative analysis and costing is to determine whether a less expensive method of monitoring can be achieved.

Different monitoring and management techniques are thus proposed, and cost analyses provided for each. A costing for each individual adult lion within the population (n = 29) was determined, as it was felt that this would allow managers the
opportunity to incorporate financial constraints when deciding on the number of lions to introduce and then to allow in a population.

In establishing a cost effective monitoring and management programme, it was determined that the overall goals and objectives of the reintroduction should be maintained and achieved. As this study only considers the financial implications of managing and monitoring a lion population, the financial impact of the lions on their prey population are not considered here. The costs incurred for the specific purpose of feeding in the boma, during the habituation process were, however, taken into account. Costs associated with upgrading of the perimeter fence and holding facilities were also not included in these calculations, as they are components of management prior to release, and not of population management or monitoring.

3.2 METHODS

The North West Parks & Tourism Board pioneered many of the current monitoring and management strategies in use in South Africa today and as such were asked to provide more extensive data. This data spanned the duration of the reintroduction from the establishment stage to the current date. Changing personnel prevented the collection of initial reintroduction data, but it was established that various different monitoring strategies have been applied to the lion population since the initial introduction. Little data were available regarding the initial post-release phase 1993 – 1998, however, during the period 1998-2002 an intensive monitoring and management phase was implemented. A less intensive approach was applied from 2002 to date. For this reason it was decided to calculate costs in two phases, these
being; a) initial costs incurred prior to the release of the lions into the park, specifically the cost of habituation; and b) monitoring costs for a two year period within the intensive monitoring stage (2000 & 2001).

Financial and budget records were not available for study. Costs were thus calculated according to the number of veterinary or ecological operations carried out within a given period. These operations were indicated in management reports during the given period. The costs of these activities were then calculated according to current fees charged by practicing wildlife veterinarians and experts operating in the field (Dr A Uys, *pers. comm.*; Dr P Bartels, *pers. comm.*).

The overall expense of the monitoring process incurred during the habituation process (1993) and during the intensive monitoring period (2000 & 2001) was calculated at current price indexes. The use of current pricing enables the calculation of an up-to-date assessment of an intensive monitoring and management approach that can be applied today.

3.2.1 Capture and relocation process

Pilanesberg National Park introduced 19 lions from the Etosha National Park in Namibia. The cost of this process included immobilization costs for all animals as well as translocation costs from Namibia to South Africa. The lions introduced into the Pilanesberg National Park were donated to the programme by the Namibian Wildlife Authority, however, an estimated R15 000.00 per lion was applied in this
study as most reintroduction programmes in other reserves will be required to pay for the animals.

3.2.2 Habituation process

For the purpose of estimating the costs incurred during this stage of the reintroduction process we needed to establish the appropriate time period that the animals were held in the boma. According to van Dyk (1997) the time period that lions were held in the boma until deemed successfully habituated varied from 6 weeks to 4 months, but that an ideal time period in most circumstances was six to eight weeks. We therefore calculated costs according to an eight week habituation process. Costs were calculated for a single pride or coalition held in a boma for a period of eight weeks. Managers could therefore calculate the total cost depending on the number of prides and coalitions they wish to introduce.

The most expensive management component of the habituation process was the cost of feeding. Pilanesberg routinely fed whole, ungutted carcasses, on a twice weekly basis. Smaller animals such as warthog and impala were fed specifically to avoid the need to clean the boma and these animals are normally almost entirely consumed. Vehicle expenses were also calculated as part of the feeding component for the driving required to find animals to hunt for lion food.

In order to habituate the lions to vehicles, work was carried out around the boma. The vehicle would be driven around the boma on a regular basis as well as be left unattended for periods of time outside the boma.
As a result of the habituation process all darting undertaken on individuals within the population could then be conducted from a vehicle. This reduced costs significantly as no helicopter-assisted capture was needed once the lions were released into the park.

Calculations for the habituation process included;

1. One full time student salary
2. Applicable percentage of field ecologist salary
3. Vehicle usage
4. Prey species – feeding

3.2.3 Intensive monitoring stage (2000-2001)

At the onset of the reintroduction process Pilanesberg management established that they would manage the lion population intensively, promoting the use of individual animal recognition. As such, all adult individuals were branded and transponders implanted. The average population size over the two year intensive monitoring period was 60 individuals, comprising an average of 30 adults and 30 subadults and cubs (Momberg, 2004). A costing per adult individual as well as for the entire adult population (n = 29) was undertaken.

In most instances, management did conduct various activities such as branding and collaring in combination, and the number of immobilizations was thus calculated accordingly. Data gathered from the North West Parks & Tourism Board showed that between 13 and 18 radio collars were in use in the population during the 2 year period. For calculation purposes the total number of collars in use was included as this depicts the total number of immobilizations undertaken. Collars which were recorded
as not working were also included in the total number of 18, as these animals were immobilized in order to collar. The working status of the collar was thus irrelevant. Telemetry equipment, such as the radio and antennae were calculated as a once-off cost. Daily monitoring was undertaken during which various prides and coalitions were tracked.

Other additional activities were conducted, specifically the treatment of injured lions. Male lions injured in territorial fights and takeovers were removed from the population and treated. They were held in the boma for a recovery period before being released back into the population or sold (van Dyk, 2000). Data acquired showed that these treatment activities occurred in both 2000 and 2001. The calculations, therefore, incorporated one such activity per year.

A calculation was also made to include the ongoing genetic testing that was undertaken in order to maintain a stud book or gene database. It was assumed that genetic banking and testing would be undertaken in association with work undertaken on individuals when collaring and branding. A total of 29 genetic tests were therefore done in the two year period.

Calculations for the monitoring process (2000 & 2001) included;

1. One full time student salary
2. Applicable percentage field ecologist salary
3. Veterinary care – re: dartings, brandings,
4. Immobilization costs – re: capture drugs
5. Cost of telemetry equipment (once off)
6. Cost of collars  
7. Vehicle usage – daily kilometre, petrol consumption  
8. One immobilization, treatment and care activity / year – injured animal  
9. Genetic testing  
10. Blood sampling, testing and banking for each darting  

3.2.4 Less intensive monitoring approach  
A second calculation was undertaken where some monitoring actions were excluded and a less intensive management approach adopted. As the main purpose for introducing lions in most reserves is for their tourism value, the key measurable variable should be how often they are sighted and viewed by tourists. The recognition of individual lions could therefore be regarded as not being essential, with pride and coalition recognition being sufficient. As such branding of individuals would not be necessary.  

A single female within each pride and a single male within each coalition would still be radio-collared. The number of collars in the population would also be kept to a minimum. Each pride or coalition would only be tracked twice a week. The monitoring cost is calculated for the entire population and for each adult individual. Management would not intervene to treat injured individuals, with natural processes being allowed to take their course.  

Calculations for a less intensive monitoring approach included;  

1. Applicable percentage of student salary
2. Applicable percentage field ecologist salary
3. Immobilization costs – re: capture drugs
4. Cost of collars
5. Vehicle usage
6. Genetic testing

3.2.5 Extensive monitoring approach

In this case scenario an extensive or “hands off” approach was proposed. For an extensive and low budget monitoring approach to be successful, the participation of tourists, lodge / hotel guides and management staff would be important. Most reserves in South Africa have a number of lodges and hotels established within the boundaries of the reserve. These tourism facilities make up a large percentage of reserve revenue. These facilities also employ personnel to guide tourists on bush excursions within the reserve. Often the guides can provide detailed and useful information on predator dynamics within the reserve and frequently monitor lions (prides and coalitions) whilst viewing them with tourists. An extensive monitoring approach proposes that the sightings and data collection be gathered opportunistically by reserve management and on an on-going basis by persons frequently traversing the reserve, such as lodge guides. This data could then be collected from all lodges and hotels on a weekly or monthly basis.

As the information would mainly be based on individual/group recognition radio-collars would not be necessary, and individuals would not be branded. Guides would be encouraged to develop their own identikits and use the locality and group composition of known individuals to identify other individuals, prides and coalitions.
Thus here an entire adult population cost analysis only was included. Management intervention regarding injured individuals would be avoided and natural processes allowed to take their course.

Calculations for an extensive monitoring approach include;

1. Applicable percentage of student salary
2. Applicable percentage field ecologist salary
3. Vehicle usage (only to and from lodges)
4. Genetic testing

3.2.6 Cost analysis designation

The costing analysis and calculations for the specified components of the various monitoring intensities were established according to information gathered from Pilanesberg National Park, as well as from external consultants and managerial reports. The student salary was based on a gross salary of R2000 / month. The time allocation pertains to the hours of a normal working day spent by a student who undertakes all issues regarding the reintroduction.

The ecologist salary was based on a gross salary of R10 000 / month. As the ecologist is required to oversee a number of various ecological aspects throughout a reserve, a time allocation dependant on intensity or specifically required work regarding the lions was adhered to.

Vehicle usage was calculated according to per kilometre rate as specified by the Automobile Association of South Africa (AA). The distances were calculated
according to an average that would be suitable when driving to find prey species to
hunt or when tracking the lions using telemetry. Petrol consumption calculations were
made according to records relating to the 4X4 status as well as consumption figures
published by manufactures.

Costs associated with veterinarian operations, immobilizations, translocations,
collaring and branding were prescribed at current prices (Dr A Uys, *pers. comm.*). The
costs analysis of genetic testing, blood sampling, testing and banking were based on
current costs (Dr P Bartels, *pers. comm.*).

### 3.2.7 Costs versus benefits

A cost benefit analysis is a technique for assessing the viability of a new expenditure
project (Curry, 1994), and should be conducted on an annual basis by reserve
management. The main motivation for the reintroduction of lions into medium-sized
reserves is tourism (Vartan, 2001; van Dyk, 2001). Lions are an important component
of an “African Safari” (van Dyk, 1997), and most tourists are prepared to pay extra
(Cotterill, 1997) for the opportunity of seeing these majestic animals. Most medium-
sized reserves in South Africa incorporate a number of different tourism amenities,
ranging from day trips and self drives, camping and caravaning to luxury lodges
offering guided drives and exclusivity. Some reserves such as the Pilanesberg
National Park offer this broad range of activities, while others such as the Madikwe
Game Reserve offer only exclusive lodge facilities. The status of a “Big 5” game
reserve attracts tourists to these reserves (Vartan, 2001), however, the financial gain
differs greatly depending on the facility on offer. Madikwe and other game reserves,
which focus primarily on the up market tourism sector, are paid large concession fees as well as bed night fees by the operating lodges.

Reserves such as Pilanesberg and Marakele National Parks cater more for day tourists, camping and caravanning tourists, and therefore rely on the monies generated from this lower financial generating form of tourism. The overall financial benefit of reintroducing lions to a reserve will therefore depend on the type of tourism on offer to the particular reserve. Management will therefore have to monitor the expenditure versus income.

Lions have been shown to have a benefit to photographic tourism in two ways as they increase occupancy rates, and allow for higher rates to be charged per person per bed night (Cotterill, 1997). A questionnaire survey revealed that an amount of US$44.00 extra could be charged in the exclusive lodges for the privilege of seeing lions (Cotterill, 1997). Lindberg (2006) found in an analysis of visitor and resident surveys that visitors are not very price-responsive. He concluded that fees could be increased to generate more revenue.

Tourism generates a range of positive impacts such as economic upliftment through job creation and increased income, fee revenue and protection of habitat and biodiversity (Lindberg, 2006). Lions may also have an ecological benefit to a reserve as they aid in maintaining the health of prey species populations. Predators also regulate ungulate populations, preventing the tendency of these populations to increase beyond the carrying capacity (Schaller, 1972).
The costs and benefits involved with lion management involve a delicate balancing act. The expenses of introducing and maintaining a lion population should form part of the financial component of a management plan, and adaptive management is important. However, it has been shown that the presence of lions and the “Big 5” status can outweigh the financial expenditure of maintaining the population (Cotterill, 1997).

3.3 RESULTS

3.3.1 Costs of monitoring strategies
The results associated with the analysis of the monitoring of lions in the Pilanesberg clearly show that a substantial amount of money is spent using the current monitoring programme (Figure 3.1). The current intensive monitoring approach remains the most expensive option, with a less intensive approach and an extensive approach potentially being respectively more cost efficient (Figure 3.1).

The costs involved with the capture and relocation process are dependant on the number of lions initially acquired, as well as the translocation distance. Here the cost was based on the combined purchase and translocation for a single animal, which was R 18 250 (Table 3.1). From this reserve managers could calculate the cost of the purchase, capture and translocation of lions, in accordance with the size of founding population they wish to initially introduce.


### Table 3.1  Estimated costs of capture and relocation process for the introduction of lions

<table>
<thead>
<tr>
<th>Description</th>
<th>Item</th>
<th>Cost (R)</th>
<th>Population</th>
<th>Per lion</th>
</tr>
</thead>
<tbody>
<tr>
<td>19 reintroduced lions</td>
<td>15,000.00</td>
<td>285,000.00</td>
<td>15,000.00</td>
<td></td>
</tr>
<tr>
<td>Immobilization costs / lion</td>
<td>750.00</td>
<td>14,250.00</td>
<td>750.00</td>
<td></td>
</tr>
<tr>
<td>Translocation (average) / lion</td>
<td>2,500.00</td>
<td>47,500.00</td>
<td>2,500.00</td>
<td></td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td><strong>18,250.00</strong></td>
<td><strong>346,750.00</strong></td>
<td><strong>18,250.00</strong></td>
<td></td>
</tr>
</tbody>
</table>

The habituation process is relatively expensive, estimated at R 26 400 / pride or coalition per eight weeks (Table 3.2), but is recommended in order to make future work with the animals easier and thus cheaper.

![Figure 3.1](image_url)  Total estimated costs for the various monitoring approaches for lions in medium-sized reserves

49
Table 3.2 The estimated costs associated with the initial habituation process when reintroducing lions

<table>
<thead>
<tr>
<th>Description</th>
<th>Item</th>
<th>Cost (R)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Pride / coalition</td>
<td>Per lion (pride of 3 females)</td>
<td>Per lion (coalition 2 males)</td>
<td></td>
</tr>
<tr>
<td>Feeding costs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 warthogs</td>
<td>850.00</td>
<td>6,800.00</td>
<td>2,266.67</td>
<td>3,400.00</td>
<td></td>
</tr>
<tr>
<td>8 impalas</td>
<td>650.00</td>
<td>5,200.00</td>
<td>1,733.33</td>
<td>2,600.00</td>
<td></td>
</tr>
<tr>
<td>Vehicle expenses</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hunting (50km)</td>
<td></td>
<td>1,600.00</td>
<td>533.33</td>
<td>800.00</td>
<td></td>
</tr>
<tr>
<td>Habitation</td>
<td></td>
<td>800.00</td>
<td>266.67</td>
<td>400.00</td>
<td></td>
</tr>
<tr>
<td>Student salary - full time (per month)</td>
<td>2,000.00</td>
<td>4,000.00</td>
<td>1,333.33</td>
<td>2,000.00</td>
<td></td>
</tr>
<tr>
<td>Applicable % field ecologist salary (per month) – 40%</td>
<td>4,000.00</td>
<td>8,000.00</td>
<td>2,666.67</td>
<td>4,000.00</td>
<td></td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td>7,500.00</td>
<td>26,400.00</td>
<td>8,800.00</td>
<td>13,200.00</td>
<td></td>
</tr>
</tbody>
</table>

The cost analyses for the varying monitoring intensities showed a definite increase in expenditure as the level of monitoring intensity increased. An intensive monitoring approach, as utilized by the Pilanesberg management in this case study, is certainly the most expensive option (Table 3.3). The cost for monitoring the total population (n = 19) over a two year period, is R393 450.
### Table 3.3  Estimated costs of intensive monitoring stage over a two year period (2000-2001)

<table>
<thead>
<tr>
<th>Description</th>
<th>Item</th>
<th>Cost (R) Population</th>
<th>Per lion (29 adults)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cost of telemetry equipment (once off)</td>
<td></td>
<td>12,000.00</td>
<td>413.79</td>
</tr>
<tr>
<td>Running costs / year</td>
<td>500.00</td>
<td>1,000.00</td>
<td>34.48</td>
</tr>
<tr>
<td>Immobilization costs / lion (29 adults)</td>
<td>750.00</td>
<td>21,750.00</td>
<td>750.00</td>
</tr>
<tr>
<td>Cost of collars / collar (18 collars)</td>
<td>2,500.00</td>
<td>45,000.00</td>
<td>1,551.72</td>
</tr>
<tr>
<td>Veterinary care / hour</td>
<td>500.00</td>
<td>9,000.00</td>
<td>310.34</td>
</tr>
<tr>
<td><strong>Daily monitoring</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vehicle usage (520 days)</td>
<td></td>
<td>104,000.00</td>
<td>3,586.21</td>
</tr>
<tr>
<td>Student salary – full time (per month)</td>
<td>2,000.00</td>
<td>48,000.00</td>
<td>1,655.17</td>
</tr>
<tr>
<td>Applicable % field ecologist salary (per month) – 50%</td>
<td>5,000.00</td>
<td>120,000.00</td>
<td>4,137.93</td>
</tr>
<tr>
<td>One immobilization, treatment &amp; care activity</td>
<td>12,000.00</td>
<td>24,000.00</td>
<td>827.59</td>
</tr>
<tr>
<td>Genetic testing / individual</td>
<td>300.00</td>
<td>8,700.00</td>
<td>300.00</td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td><strong>23,550.00</strong></td>
<td><strong>393,450.00</strong></td>
<td><strong>13,567.24</strong></td>
</tr>
</tbody>
</table>

Less intensive monitoring approaches were estimated to be far more cost effective and would probably still achieve the reserve goals and objectives. A semi intensive (or less intense) monitoring approach is, therefore, probably the most efficient approach to adopt. The costs involved with monitoring the entire population, as based on the case study, is R 191 100 (Table 3.4).

An extensive monitoring approach may not be the most efficient or effective monitoring method. However, this method is the most cost effective at R 84 000 for the monitoring of the entire population over a two year period (Table 3.5).
### Table 3.4  Estimated costs involved in a less intensive monitoring approach

<table>
<thead>
<tr>
<th>Description</th>
<th>Item</th>
<th>Pride / coalition</th>
<th>Per lion (29 adults)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cost of telemetry equipment (once off)</td>
<td></td>
<td>12,000.00</td>
<td>413.79</td>
</tr>
<tr>
<td>Running costs / year</td>
<td>500.00</td>
<td>1,000.00</td>
<td>34.48</td>
</tr>
<tr>
<td>Immobilization costs / lion (10 adults)</td>
<td>750.00</td>
<td>7,500.00</td>
<td>258.62</td>
</tr>
<tr>
<td>Cost of collars / collar (10 collars)</td>
<td>2,500.00</td>
<td>25,000.00</td>
<td>862.07</td>
</tr>
<tr>
<td>Veterinary care / hour</td>
<td>500.00</td>
<td>5,000.00</td>
<td>172.41</td>
</tr>
<tr>
<td>Bi-weekly monitoring</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vehicle usage (208 days)</td>
<td></td>
<td>41,600.00</td>
<td>1,434.48</td>
</tr>
<tr>
<td>Student salary – part time (per month)</td>
<td>1,000.00</td>
<td>24,000.00</td>
<td>827.59</td>
</tr>
<tr>
<td>Applicable % field ecologist salary (per month) – 30%</td>
<td>3,000.00</td>
<td>72,000.00</td>
<td>2,482.76</td>
</tr>
<tr>
<td>Genetic testing / individual</td>
<td>300.00</td>
<td>3,000.00</td>
<td>103.45</td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td>8,550.00</td>
<td>191,100.00</td>
<td>6,589.66</td>
</tr>
</tbody>
</table>

### Table 3.5  Estimated costs involved in an extensive monitoring approach

<table>
<thead>
<tr>
<th>Description</th>
<th>Item</th>
<th>Population</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vehicle usage (drive to lodges) – 500 km/month</td>
<td></td>
<td>12,000.00</td>
</tr>
<tr>
<td>Student salary – full time (per month)</td>
<td>2,000.00</td>
<td>48,000.00</td>
</tr>
<tr>
<td>Applicable % field ecologist salary (per month) – 10%</td>
<td>1,000.00</td>
<td>24,000.00</td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td>3,000.00</td>
<td>84,000.00</td>
</tr>
</tbody>
</table>
3.4 DISCUSSION

Although the primary objective for the Pilanesberg lion reintroduction programme was that of tourism, monitoring was promoted for other key factors in order to satisfy a broad spectrum of objectives (van Dyk, 1997). As this reintroduction was essentially the first of its kind, the results and outcomes of the programme were critical for the future of other lion reintroductions. The tourism objective was easily obtained through the presence of the lions in the reserve, as this status attracted more tourists (Cotterill, 1997). Tourist satisfaction and thus the sighting potential of lions are key to the attainment of the objectives of the reintroductions process. The intensive post release monitoring facilitated further population studies as well as satisfied stipulations in terms of breakouts and human safety.

Most reserves introduce and maintain lions for the specific purpose of tourism, however, with the introduction of these large carnivores come various other management requirements. Most managers believe the management of lions needs to be intensive, promoting a programme whereby all individuals in the population can be identified and monitored. However, in order to achieve this, substantial amounts of money are required (van Dyk & Slotow, 2002).

Van Dyk (2001) stated that often the cost of maintaining a lion population exceeds the direct financial return from the animals. His assumption was based on the intensive management and monitoring strategy adopted in 2000 and 2001. However, with the established lower financial expenditure through slight alterations in monitoring and
management, a more cost effective alternative has been forwarded. This less intensive monitoring approach should still allow sound management of lion populations.

Monitoring of large carnivore is an important management technique as it provides important information on the population and thus enables better management. In applying a less intensive monitoring approach the basic fundamental of research and monitoring should still be adhered to. Data recording and archiving as well as analysis and interpretation of the acquired data are essential (van Dyk & Slotow, 2002). The reduction in costs from less time in the field tracking and recording data should not result in reduced accuracy and efficiency. However, the cost of intensive monitoring should be considered as an important management component. Some reserves in South Africa monitor and track their lion population as often as twice daily. This policy of intensive monitoring is possibly excessive and is probably only sustainable in very small reserves. Thus a combination of current and new techniques could be better applied to facilitate the management and monitoring of a lion population, while achieving the tourism goal and objective and optimising expenses.

Irrespective of the monitoring approach adopted, the outcomes should be the same. The objective of the reintroduction and the maintenance of the population should be achieved. As this is aimed at the satisfaction of tourists and their sightings of lions it is not the genetic stability of the population, the exact ranging patterns or paternity, and maternity that is essentially important. These are certainly management considerations but should not form the focus of managerial actions. Further to this, if generating income for the reserve is a reason for the introduction then expenditure should not exceed the income where the lion population is concerned.
We recommend the implementation of the habituation process as this further facilitates a better sighting of lions for tourists and indirectly aids the monitoring process. A combination of the habituation process and a less intensive monitoring approach would probably better suit most reserves where lions are reintroduced for the purpose of tourism and financial gain. This is already becoming the approach of choice in certain reserves (Mr H Kilian, *pers. comm.*). The use of adaptive management will be essential to any reserve and effective monitoring is an important step in this process (van Dyk, 1997).

An entirely extensive monitoring approach may not be suitable for use in medium-sized reserves as the degree of monitoring accuracy by tourists and lodge personal is questionable. This option does require further investigation.

An excellent alternative to the extensive monitoring approach and the reduction in monitoring costs incurred by the reserve is to enlist in the services of external parties such as Universities and Technikons to conduct research and therefore the monitoring of the population (van Dyk & Slotow, 2002).

Effective monitoring is essential to managers of medium-sized reserves and used in combination with responsible genetic management and a sound management approach, the conservation of large carnivores such as lions can be successfully achieved. Responsible management of these large carnivores is essential, although the expense of this management need not outweigh the benefits.

Mr H Kilian, Welgevonden Game Reserve, PO Box 433, Vaalwater, South Africa
The monitoring of lion populations is certainly an important management aspect and facilitates a variety of vital managerial decisions. Goals and objectives for maintaining a lion population as well as the monitoring thereof should be clearly stated. The profits and expenditures related to the population should be carefully monitored. It is, therefore, recommended that a lower level of monitoring and management intensity be incorporated that can sustainably achieve the goals and objectives and retain efficiency. A monitoring strategy could thus be implemented whereby costs are reduced, but where the benefits of good monitoring are not lost completely. With this reduction in costs of monitoring, the profits and benefits of lions within the reserve will further enhance the desirability of introducing large predators such as lions in medium-sized reserves.
CHAPTER 4

GENETIC CONSEQUENCES OF VARIOUS LION
MANAGEMENT STRATEGIES

4.1 INTRODUCTION

The ever-increasing tourism industry in South Africa has resulted in a growing demand for large predator sightings, with many reserves finding it necessary to reintroduce large predators, most importantly lions (Vartan, 2001). Lions are especially suited to reintroductions as they have a wide habitat tolerance and select a wide range of prey species (van Dyk, 1997). However, reintroductions into medium-sized reserves tend to be followed by exponential population growth as a result of abundant prey species and little or no inter or intra-specific competition (Druce et al., 2004a; Kilian & Bothma, 2003). Furthermore, prey species appear to be more susceptible to predation as a result of lower vigilance levels in the presence of reintroduced large carnivores (Hunter & Skinner, 1998). Thus, it would appear that the population dynamics of reintroduced lion populations differs from those of established populations, as there is a lack of initial social pressure. This results in earlier breeding ages, high cub and subadult survival rates, and inevitably inbreeding (Kilian & Bothma, 2003).
All medium-sized reserves in South Africa are fenced. Exponential population growth coupled with dispersal restrictions quickly lead to managerial problems, potentially including reduced genetic integrity through inbreeding.

The genetic integrity of lion populations in medium-sized reserve has been the focus of two studies (Vartan, 2001; Reid, 2002). Reserve managers focus to a large extent on this managerial aspect, and have managed this aspect intensively (van Dyk, 1997). Though most reserves have applied a highly intensive manipulation regime to avoid genetic depression, inbreeding seems to persist. Twelve years after the reintroduction of lions into the Pilanesberg National Park, the population has thus begun to show reduced genetic variation when compared with outbred populations (Grubbich, 2001). The lion population in Hluhluwe-Umfolozi Park is also currently thought to be experiencing high levels of inbreeding. van Dyk & Slotow (2002) concluded that as a result of only three founder bloodlines (one male from Mozambique, two related females and offspring [i.e. with a second male bloodline] from Kruger National Park), the present lion population displays strong indications of inbreeding depression, including sperm abnormalities, low reproductive rate and health problems. Stein (1998) found evidence of a declined reproductive performance due to decreased heterozygosity.

In order to maintain the health and viability of each lion population, manipulation and monitoring techniques are applied (van Dyk, 1997). To date, lion introduction programmes in South Africa have typically focused on introducing small groups (usually less than 10 individuals), concentrating primarily on introducing individuals that are as unrelated as possible. In order to avoid inbreeding depression, the
reintroduced population size is recommended to be no less than 50 breeding adults (Soule, 1980; Erwens et al., 1987; Goodman, 1987). However, relatively little is known about the minimum viable population of large mammal species (Schaffer & Samson, 1985; Erwens et al., 1987; Schaffer, 1987).

Managers also apply various techniques in order to curb population growth and the resultant inbreeding events. Current strategies include manipulation of prides and coalition size. This technique decreases the potential of aggressive fighting between various groups and prevents single coalitions dominating multiple prides (van Dyk, 1997).

In this chapter an attempt is made to establish the time that it would typically take before close breeding starts to occur. From this, the expected time duration can be predicted to advise management when new animals should be introduced into the population in order to avoid inbreeding. The dissertation aims to model a ‘real’ reintroduction process based on data from completed reintroductions and documented reintroduction techniques. This will essentially result in a probable outcome of resultant population dynamics. The study proposes management techniques and time lines to be incorporated in the management plan to aid in the management of a genetically healthy lion population. The importance to management in ‘knowing’ the time-line to inbreeding and the time period involved will allow management decisions to be made prior to the onset of inbreeding problems.
4.2 METHODS

Computer simulations were used to establish the potential time frame before close breeding is likely to occur. This was achieved through modelling hypothetical populations using a complex lion demography model (SimSIMBA Version 2.01) (Whitman et al., 2004). The genetic trends were then analysed with a gene drop programme (GenoPro Computer Simulation), which traced the complete ancestry of each individual within the prides. The demographic model ignored environmental stochasticity, so the maximum number of territories and maximum pride size was held constant for a given set of simulations. Population dynamics were measured and were based on the social and territorial behaviour of lions.

Here the model was used to simulate population growth and breeding outcomes for varying numbers of prides within a reserve (one to five prides). The model requires that certain parameters are specifically set while others are fixed. Model parameters included survival statistics, cub production and coalition configuration. Required parameters were set according to data extracted from medium-sized reserves.

The model distinguished between sex and age classes and monitored individuals by social and reproductive status. Female lions were organised into ‘prides’ that defended spatially arranged and interconnected territories. Male lions were divided into three classes namely subadult, nomadic, and pride residents (territorial males). Subadults and nomads wander through all territories, forming related coalitions or lone males may join up to form unrelated coalitions.
Survival statistics were established for coalitions in terms of coalition, nomadic and subadult survival probability. Further data were recorded for second time nomadic males and single pride males with neighbours. Group lioness survival rates were also incorporated into simulations. Cub survival rates dependant on age (0-6 months, 6 months to one year and older than a year) and a survival probability for abandoned cubs were also considered.

Five simulations were run for a period of twenty years. Each simulation represented a reserve with an increasing number of prides from one through to five prides. Each breeding pride contained three adult females and was defended by a paired male coalition. Pride and coalition size were initially set at these sizes, as this composition is typical for most lion reintroductions in South Africa. Van Dyk (1997) stated that the introduction of smaller groups consisting of three females and a coalition of two males made management of the pride easier and also promoted higher genetic variation in the population as five different blood lines could be introduced.

The model did not allow for breeding between subadults and nomads with females. Competition for pride residence was determined by a competition matrix that weighted overall competitive strength according to male age and coalition size. During a takeover event infanticide occurred and cubs were killed based on an age-specific probability.

Cub production was based on a production histogram and was simulated using a random number for each eligible female that drew her litter size from a distribution. This was established according to the number of litters produced by a female, where
first time litters and subsequent litters were distinguished. A probability index for the abandonment of a single cub was also incorporated. A sex distribution matrix was established and considered events such as pride takeovers.

Males within a pride were assigned to subadult coalitions (two years of age) and nomadic coalitions (three years of age). Females were either recruited into their natal pride or wandered through the reserve seeking a vacant territory. Should a vacant territory not be available the females died. Recruitment into the pride depended on the number of adult females already in the pride and the specified upper limit for that pride. This study specified an upper limit of three adult females, but a maximum of two additional females can temporarily exceed the upper limit. There was no such similar upper limit specified for male coalitions. All females began breeding at the age of three years.

The model ran each scenario for 100 replicates, the results presented here being the mean of these replicates. Each model step represented a time period of six months during which all statistics were updated.

Genetic sequences were also produced from the data generated by the model. These are graphically depicted in Appendices 3-7. The gene flow sequences tracked the lineage of each pride and record information, specific to each lion in the population. Aspects recorded included, paternity and maternity, date of birth and death, fecundity, coalition formation, time lines, and events of close breeding between related individuals. The construction of these sequences forms a complete pedigree of the lion populations within each of the reserves.
4.3 RESULTS

4.3.1 Single Model Run

The model was initially run with a single iteration in order to establish a generic genetic composition and map of each of the various prides. Within the time duration of ten years, the genetic sequences indicated F1 mating (sire / daughter or dame / son), F2 mating (grandfather / granddaughter), and brother / sister mating (see Appendix 3-7) in several of the pride size simulations.

4.3.1.1 Single pride:

The model run resulted in two females being recruited into the pride, and within the ten-year period a total of eight breeding females were established within the reserve, three of which were outside the main pride in a ‘vacant’ territory. This secondary pride was established by dispersing females from the original pride and was defended by a coalition of three related males. This resulted in close breeding events within the population (brother / sister mating). In reality, however, there would be no vacant territories available in a reserve that could only accommodate one pride. This was a constraint of the model, but the important result, suggesting close breeding fairly early on (4 years), remains valid, and was compounded by the original coalition defending their territory for eight years. This resulted in these males mating with the two lionesses that were recruited into the pride, who were their own progeny (Appendix 3). Within a ten-year period the population size fluctuated between 11 and 34 lions.
4.3.1.2 Two prides:

In the two-pride reserve, the first pride remained stable with three breeding females, but in the second pride two related lionesses were recruited. Thus within a ten-year period there was also a total of eight breeding females in the two pride reserve (similar results to the single pride reserve due to the way the model works). All other females dispersed from the natal pride (n = 27), and were assumed to have died (n = 6), and all dispersing males formed coalitions (n = 17) or died (n = 17).

With the recruitment of related females into the prides, and extended tenure length of coalitions, events of close breeding were increased (Appendix 4a and 4b). However, new genes were added to the population when dispersing males from one of the prides joined the coalition from the adjoining territory. In the event of pride takeovers, infanticide occurred and all cubs below a certain age were killed. Within the following year, new cohorts were born to the new coalition. However, with only two prides in the reserve there was an increased possibility that new coalitions were directly related to the pride, and that close breeding events would occur. In the event that a coalition defended the territory for an above average period of time, the possibility of further close breeding, F2 incidents, increased. Within a ten-year period the population size fluctuated between 16 and 37 lions.

4.3.1.3 Three prides:

All prides within the reserve recruited related females during the ten-year period resulting in fifteen breeding females throughout the ten-year run. All other females (n = 29) dispersed from their natal prides or died (n = 13). All dispersing males formed coalitions (n = 49) or died (n = 27).
Three unrelated females established a prides in the reserve, adding to the genetic diversity of the population (Appendices 5a-c). Here tenure length was shorter thus decreasing the chances of close breeding within the population. Pride takeovers occurred within all the prides with resulting infanticide. With a larger population, there was an increased possibility that the new pride males were unrelated to the pride and so enhanced the genetic diversity of the population. However, with numerous pride takeovers, in close succession, the overall genetic potential of the population was reduced as an excessive amount of cubs were killed in infanticide events. Within a ten-year period the population size fluctuated between 28 and 66 lions.

4.3.1.4 Four prides:
All prides within the four pride population recruited related females into the pride during the ten-year run, resulting in a total of nineteen breeding females being in the population at the end of the run. The average tenure length within this population was five years, however, with the early recruitment of related females into the prides (n = 6) close breeding (breeding between closely related individuals) occurred (Appendices 6a-d). A subsequent takeover and resultant infanticide served to introduce new genetic material, and importantly kill some of the close bred individuals before maturity was reached. Some pride coalitions lost males within their tenure, however, nomadic males then joined the pride male thus introducing new genetic material. Within the ten-year period some close bred (F1) individuals reached sexual maturity but no F2 or brother / sister mating occurred. Within a ten-year period the population size fluctuated between 40 and 70 lions.
4.3.1.5 Five prides:

In the five pride reserve all prides recruited related females during the ten-year period, resulting in twenty-three breeding females in the population by the end of the run. Territorial male tenure length within this larger population was more stable throughout the simulation (five years). However, most coalitions lost a pride male during the tenure due to territorial fighting. This resulted in pride males either being ousted by larger coalitions or joined by wandering nomads. Incidents of infanticide were noticeably less in the five pride reserve, as the timing of takeovers coincided with the dispersal of subadults. In two of the five prides, incidents of close breeding occurred, as cohorts of cubs formed large coalitions and ousted their fathers (Appendices 7a-e). Another incidence of close breeding occurred due to the death of an entire coalition of pride males and the resultant takeover of the territory by males born in that pride.

Due to the larger size of the population, the possibility of unrelated individuals and coalitions taking over prides and increasing the genetic variation of the population was greater. Throughout the ten-year period most cubs reaching sexual maturity were genetically more heterogeneous, and so contributed to the overall genetic stability of the population. Within a ten-year period the population size fluctuated between 47 and 95 lions.

Data extrapolated from the model outcomes established a mean rate of inbreeding which is presented in Table 4.1.
Table 4.1 The rate at which inbreeding can be expected to occur in various pride size reserves based on a single model run for each reserve

<table>
<thead>
<tr>
<th>Number of prides</th>
<th>Mean interval for F1 mating (years)</th>
<th>Mean interval for F2 mating (years)</th>
<th>Mean interval for brother / sister mating (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.0</td>
<td>6.5</td>
<td>8.5</td>
</tr>
<tr>
<td>2</td>
<td>6.0</td>
<td>9.0</td>
<td>10.0</td>
</tr>
<tr>
<td>3</td>
<td>8.3</td>
<td>&gt; 10</td>
<td>&gt; 10</td>
</tr>
<tr>
<td>4</td>
<td>7.8</td>
<td>&gt; 10</td>
<td>&gt; 10</td>
</tr>
<tr>
<td>5</td>
<td>9.2</td>
<td>&gt; 10</td>
<td>9.6</td>
</tr>
</tbody>
</table>

It can clearly be seen that there was a decreasing occurrence of close breeding events as the number of prides in each reserve increased. This allows for the establishment of a time relationship that could act as a guide to managers, as to when new individuals should be introduced into a specific pride size population in order to avoid close breeding (Figure 4.1). A regression line was fitted to the data and found to be strongly linear ($R^2 = 0.8678$), the equation being:

$$y = 1.22x + 3.4$$

Where $y$ is the time period for the introduction of new genes

$x$ is the number of prides

This showed a direct relationship between the time relationship for the introduction of new genetic material into a population and the number of prides within the reserve.
Figure 4.1  Time relationship depicting when the first inbreeding events would probably occur in various pride size reserves and thus when new genetic material should probably be added.

4.3.2 Multiple Model Run

The model was then run multiple times for each pride size reserves in order to establish population characteristics that influenced management of the species. Here the model was run for twenty years with 1000 replicate simulations. The data from the multiple runs was not as easy to interpret as for the single runs due to the random generation of input variable resulting in quite wide variability in the results. It was nevertheless an important exercise and allowed some verification of the single run results. One of the outcomes was that the mean population size varied quite widely over the twenty-year period.

4.3.2.1 Pride size

In the single pride reserve, the population size was again larger than would be expected due to the model not allowing a single territory only. In this run, the second
vacant territory was re-colonised by the sixth year on average. In all simulations, an increase in the population occurred when prides reached maximum size, due to recruitment of breeding females. Average population size, represented as the number of individuals within the population, was 15.8 individuals in a single pride, 18.4 for a two-pride reserve, 40.4 for a three-pride reserve, 52.3 for a four-pride reserve and 71.4 for a five-pride reserve. On average, the number of breeding females per pride was 3.5.

4.3.2.2 Male coalitions

The initial parameter stipulated male coalition size at two individuals per coalition, as this is typical in most medium-sized reserves. However, coalitions that developed thereafter in the modelling framework were not manipulated in terms of size. Males dispersing from the natal pride formed large coalitions were possible, with some coalitions reaching four to five members, however, as a result of pride challenges and resultant fighting, coalition size was reduced before coalitions took over prides. Interestingly, it was found that mean territorial male coalition size throughout the five reserves was 2.02 individuals per coalition (Figure 4.2). This is also typical of average male coalition size recorded in typical savanna ecosystems; e.g. 2.0 in Kruger National Park (Funston et al., 2003). This suggests that the current manipulation techniques used by managers in medium-sized reserves, of maintaining paired coalitions only, may not be necessary. They would probably tend to establish themselves, although at times larger coalitions will occur.
As the number of territorial males averaged about two males per coalition per pride, the number of territorial males in each reserve increased proportionally to a mean maximum of 10.2 territorial males in the five pride reserve (Table 4.2). There was a similar increasing relationship for non-territorial males, but they were always less numerous in the various pride size reserves (Table 4.2). On average territorial males made up 14.2% of the population, while non-territorial males made up 8.0% of the population, in each pride size reserve.

**Table 4.2** The average number of territorial and non-territorial males in each different pride size reserve

<table>
<thead>
<tr>
<th>Number of prides</th>
<th>Number of territorial males in each reserve</th>
<th>Number of territorial males in each reserve (per pride)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.8 (1.8)</td>
<td>1.8 (1.8)</td>
</tr>
<tr>
<td>2</td>
<td>3.2 (1.6)</td>
<td>3.2 (1.6)</td>
</tr>
<tr>
<td>3</td>
<td>6.9 (2.3)</td>
<td>6.9 (2.3)</td>
</tr>
<tr>
<td>4</td>
<td>6.5 (1.6)</td>
<td>6.5 (1.6)</td>
</tr>
<tr>
<td>5</td>
<td>10.2 (2.0)</td>
<td>10.2 (2.0)</td>
</tr>
</tbody>
</table>
Pride tenure was predictably longer in a single pride reserve, but the excessively long average tenure of 16.5 years was an unexpected result (Figure 4.3), and suggests some problem inherent in the model. Within the other reserves, pride male tenure stabilized at an average of 5.5 years. However, this is also much longer than average tenure recorded in the Kruger National Park, where males typically defended prides for about two years before abandoning the territory (Funston *et al.*, 2003). As expected, there were some cases in which coalitions maintained more than one pride simultaneously.

![Figure 4.3](image-url)  
**Figure 4.3** Average tenure length of territorial male coalitions in each pride size reserve

### 4.3.2.3 Cub production

Across all reserves an average of 12.2 cubs / year were produced, with the maximum number of births being in a five-pride reserve 22.6. The proportion of cubs killed in infanticide events over the twenty-year period, as a result of pride takeovers, averaged 30.3% across all the reserves. However, within the two-pride reserve, 65.7% of the
cubs were killed. This excessive amount of deaths was directly related to a large number of closely spaced pride takeovers in this population.

4.3.2.4 Rate of inbreeding

From data extrapolated from the multiple model runs, the mean rate of inbreeding was established for each reserve size (Table 4.3).

<table>
<thead>
<tr>
<th>Number of prides</th>
<th>Mean interval for F1 mating (years)</th>
<th>Mean interval for F2 mating (years)</th>
<th>Mean interval for brother / sister mating (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6.5</td>
<td>&gt;20</td>
<td>6.5</td>
</tr>
<tr>
<td>2</td>
<td>7.8</td>
<td>&gt;20</td>
<td>8.5</td>
</tr>
<tr>
<td>3</td>
<td>7.1</td>
<td>&gt;20</td>
<td>&gt;20</td>
</tr>
<tr>
<td>4</td>
<td>6.4</td>
<td>19</td>
<td>10.8</td>
</tr>
<tr>
<td>5</td>
<td>8.9</td>
<td>&gt;20</td>
<td>&gt;20</td>
</tr>
</tbody>
</table>

This data was then depicted on an interval graph and shows an increasing time span with increasing reserve size, suggesting when on average new males should be introduced into the reserve (Figure 4.4). A regression line was fitted to the data and was found to be fairly strongly linear ($R^2 = 0.4056$) but not as strong as the single model runs. The equation that defined the line was:

$$ y = 0.7825x + 5.4175 $$

Where $y$ is the time period for the introduction of new genes

$x$ is the number of prides

However, there was less confidence when using a multiple run simulation. This may be a result of the average effect of 1000 replicate runs, in which minimum and
maximum estimates are ‘pulled’ toward the average and thus decrease the confidence levels.

\[ y = 0.7825x + 5.4175 \]

\[ R^2 = 0.4056 \]

**Figure 4.4** Time relationship for the introduction of new genes in the multiple runs

### 4.4 DISCUSSION

The results of the single model runs for the various reserves were easier to interpret than those of the multiple replicate runs. The most important finding was the establishment of a strong linear relationship between the number of prides in a reserve, and the interval when inbreeding is likely to start occurring. In establishing a potential time parameter suggesting when inbreeding is likely to first occur, this can now be calculated ahead, and plans made to introduce new individuals to a population in order to maintain the gene pool. In so doing, close- or inbreeding could possibly be largely avoided without intensively manipulating the population. This may negate the need for current typical management strategies such as manipulating pride composition, coalition size, and which males are in tenure with each pride. Strategic
removal and addition of new males could thus be as effective, and certainly more cost effective, than typical current management manipulations and interventions. Importantly it was also established that territorial male coalition size tended to average towards two individuals without any management intervention. In the model runs, subadult male coalitions tend to be comprised of three or more individuals, but lost coalition members as a result of fighting, especially when challenging pride males. This aspect of the model, therefore, very closely replicates the patterns observed in large free roaming populations (Funston et al., 2003).

Unlike male coalitions, the number of adult females in each pride was capped at three individuals by the model, with up to two additional lionesses being allowed to be members of a pride for a limited time period. The high reproductive rates observed in the model corresponded very closely with those recorded in medium-sized reserves (Kilian & Bothma, 2003; Druce et al., 2004a), and the Serengeti (Packer et al., 1988), whose population demographic variables were used to parameterise the model (Whitman et al., 2004). These reproductive rates are, however, much higher than those recorded in the Kruger National Park, where high cub survival rates and longer residence of subadults are believed to result in much longer birth intervals (Funston et al., 2003). It thus remains an untested experiment to see what would happen to birth rates and population growth rates in medium-sized reserves if populations were not intensively managed.

Results presented in Packer’s et al. (2005b) stable state hypothesis, show that while lion populations have the potential for very rapid expansion under suitable ecological conditions, they invariably tend to overshoot their carrying capacity by as much as 30-
40% before settling at lower levels into a tighter oscillation around the ecological capacity. If this pattern indeed characterises lion population growth, it could be expected that the lack of intra- and interspecific competition (Funston, 2004b; Killian & Bothma, 2003), and reduced vigilance of ungulates (Hunter & Skinner, 1998), will lead to rapid initial expansion of lion populations in medium-sized reserves. Inevitably, managers must realise that ungulate numbers will decline to some extent when large carnivores are introduced. The presence of large carnivores should be viewed as altering the carrying capacity for the reserve, rainfall and forage levels no longer being the only determinants. Unfortunately these sorts of experiments have to date not been allowed.

From the multiple model runs the findings discussed above were reconfirmed, but with greater variability due to the higher number of replicate runs and the averaging process. A possible anomaly with the model was the long tenure periods calculated for territorial male coalitions. Extended male tenure has been reported in certain trophy hunted lion populations (Yamazaki, 1996), but given the fact that all prides were defended by male coalitions, and subadult males were continually being produced in accordance with expected ratios and group sizes, this result remains puzzling. It could be that because each population was closed, thus allowing for no subadult male dispersal, the fight matrices built into the model (Whitman et al., 2004) may have resulted in higher subadult male mortality rates through intra-specific competition than would normally be expected. This would have given rise to longer territorial male tenure if the odds of winning a contest were stacked in favour of older more experienced males.
It is, therefore, suggested that in reserves with reintroduced lion populations, where the primary goals and objectives are that of tourism, that the introduction of new individuals at least once every ten years will probably sufficiently reduce the probability of inbreeding (Beier, 1993), and thus largely negate the need for intensive management of paternity. It should, however, be recognised that individuals remaining in the population will continue to contribute to the genetic status of the population unless removed.

In establishing the time line before which close breeding events are likely to occur, managers can now establish in advance when to introduce new individuals, as well as from where the individuals should be acquired, the number they wish to introduce and the technique of reintroduction. We further recommend that this analysis be used in conjunction with other management techniques, such as monitoring, that will promote a pragmatic approach to the management of lions. A dynamic approach should be used in which adaptive management is crucial. In summary we forward two management approaches that can be used with the genetic analysis and monitoring options by managers when maintaining a lion population for the purpose of tourism.
CHAPTER 5

SUMMARY AND MANAGEMENT IMPLICATIONS AND APPROACHES: METAPOPULATION VERSUS SINGLE POPULATION MANAGEMENT

INTRODUCTION

Most medium sized reserves in South Africa have reintroduced lions with the specific purpose of improving tourism potential as the stated goals and objectives. However, once the reintroduction process is complete, management tend to find that in their view, a need soon arises to manage several other aspects of the lion and prey populations. Little research attention has been given to these aspects as a whole in medium-sized reserves where lions have been reintroduced (Hunter, 1998; Peel & Montagu, 1999), and specific advice and protocols are largely non-existent (Funston, 2004b).

One of the initial problems faced by management is the impact of these large carnivores on their ungulate prey base. Most prey species are limited by predation, especially in smaller systems where they are forced to be resident through fencing and
occur in low numbers (Caro & Fitzgibbon, 1992). Managers need to recognize that declines in prey numbers are affected by many factors, predation being only one of these. Ungulate populations should be allowed to vary within established minimum viable population size to acceptable upper limits (South African National Parks Management strategy, 2006).

Reintroduced lion populations initially tend to undergo rapid population increases, usually due to a lack of inter- and intraspecific competition and an abundant food supply. As a result of high population growth rates, the genetic integrity or health of the population soon comes into question, with related individuals mating more frequently than would be expected in normal lion populations. Twenty-five individuals are often referred to as the minimum viable population (MVP) for a generic large carnivore reintroduction programme (East, 1981; Fuerst & Maruyama, 1986). However, no reserve in South Africa has ever introduced that many lions, with most having completed reintroduction programmes with fewer than ten individuals (Vartan, 2001). This could potentially lead to these populations becoming genetically compromised in much shorter periods of time than would normally be expected and thus forcing management intervention at a very early stage of the reintroduction process. These problems could be exacerbated by the fact that many of the more recent lion reintroductions come from genetic stock in Pilanesberg and Madikwe, which have already been shown to suffer from some reduced genetic variation compared to outbred populations (Grubbich, 2001). The success of most lion reintroductions, as measured by reproduction rate (Kilian & Bothma, 2003; Druce et al., 2004a), has also affected the genetic integrity of these lion populations, as the
potential for inbreeding occurs earlier than expected as a result of rapid population growth from a small founder stock.

There is little evidence as to whether the effect of inbreeding poses a threat to the future of lions as a whole, but there is concern as to the long-term viability of smaller, isolated populations (Kissui & Packer, 2004). Lowered genetic variation within populations reduces the opportunity for adaptation, resilience to disease outbreaks, and may result in reduced reproduction or survival, thereby reducing the viability of the population (Madsen, Stille & Shine, 1996).

It is thus strongly advised that all these aspects be carefully considered before a lion reintroduction project is commenced, and that plans for addressing population increase, security, impact on prey populations and genetic considerations, to name a few, are in place before the need to implement them arises.

As it was established that most reserves reintroduce lions for the specific purpose of increasing tourism potential, it was incumbent on this study to establish management strategies that would best fulfil these primary goals and objectives, although it would be unwise to totally ignore broader conservation goals and objectives. The management of lions in medium-sized reserves has been shown to be complex, and a variety of management aspects need to be applied to successfully conserve these populations. The question really is, should these reserves be allowed to manage their lion populations purely for tourism and financial gain, or should they be held accountable for also improving the conservation status of the species?
In support of the latter, managers should be aware that the dynamics of specific animal populations cannot be separated from those of associated populations or from the environment as a whole (Smuts, 1978b). However, aspects of this dissertation suggest that a management style can be developed which both incorporates the tourism objectives as well as includes the ecological aspects of a reserve, and the conservation of all species therein including the lion population.

Aspects that are considered vital to the management of a reintroduced lion population were investigated, and strategies have been forwarded that incorporate financial expenditure as a guideline for sound or pragmatic management. Other than the important evaluation of cost expenditure on introduction, monitoring and management, a quite different genetic management strategy is proposed that could probably be successfully integrated into a lion management plan, even where the primary goals and objectives are simply that of tourism.

Faced with the diversity of responses to genetic change, a conservation manager should use appropriate monitoring to judge whether erosion of genetic variation is actually affecting population viability. When necessary, the manager should also consider how best to avert or remedy erosion of variation. Like most conservation problems, the solutions to genetic problems are easier, if action is taken early in the process of decline, when the existence of a number of individuals and populations allows choice of various management strategies (Young & Clarke, 2000).

Lande (1988) argued that for wild populations, demographic factors may usually be of more importance than genetic factors in assessing the requirements for long term
species persistence. However, genetics and demography, and their interactions are important in the extinction process and only by the integration of these two fields can we hope to achieve effective conservation management and the long-term population and species survival (Young & Clarke, 2000). There is therefore, a need for a combined management approach, which involves both demography and genetics.

Using the recommended time relationship graphs, presented in Chapter 4, managers could predict when new males need to be introduced so as to prevent inbreeding in the population. It would probably be necessary to combine this with strategic removal of individuals that have already contributed to the population. From these findings, it could be argued that much of the artificial manipulation of pride and coalition structure, and thus who mates with whom, in current management strategies, is an excessive and possibly unnecessary level of management intervention that approaches micro-management. It is thus argued that by merely strategically introducing new males at the appropriate time, and removing specific individuals ahead of time, most of the genetic concerns in small isolated lion populations could be alleviated. Most species have natural mechanisms designed to largely reduce the rate at which close breeding occurs, and with new males being introduced to the reserve when necessary, the chance of close breeding would be substantially reduced.

Depending on the objectives of the reserve, and the relative conservation value of each reintroduced lion population, their management could possibly be divided into two separate management strategies, namely a metapopulation or a single population management approach. While some reserves in South Africa have to date managed
their lion populations according to a loosely defined metapopulation approach, about as many are merely managing each population as a single entity.

Reserves managers, perhaps in conjunction with species conservation consultants, need to decide which of the two different management approaches should be applied. It is further recognised that the financial implications of lion reintroductions influence management styles, and as such a cost analysis for each approach has been incorporated. The basic premise of each approach is discussed below.

**Metapopulation management approach**

Metapopulation theory implies that populations with independent dynamics are spatially structured into assemblages of local breeding populations with small amounts of immigration taking place (Hanski & Simberloff, 1997). The basic concept in the South African situation would require a number of medium-sized reserves with lion populations, with the immigration and emigration of individuals between these areas being facilitated or simulated by managers. The metapopulation strategy recognizes that recolonization characteristics significantly affect the genetic structure within and among local population subunits. The predictions of the theory models of metapopulation have been supported by studies of real metapopulations, reinforcing the assumptions that genetic diversity within and among local population subunits is strongly influenced by characteristics and methods of dispersal (Hanski & Simberloff, 1997).

Population dynamics, under this management approach, allow for some manipulation in order to achieve various management objectives. There is potential with this form
of management to exchange animals between reserves in order to reduce the potential loss of genetic diversity in small populations. Artificial dispersal opportunities created by management can, and do, facilitate immigration and emigration. Even modest rates of immigration can counter the effects of inbreeding depression, loss of diversity by drift, and demographic and environmental stochasticity (Simberloff, 1988; Hooper, 1971; Richter-Dyn & Goel, 1972; Schaffer, 1987). This approach thus seems a sensible and a viable management option available to maintain a healthy lion population. This approach would, however, require a detailed and up-to-date study book of all populations through continual monitoring thereof as well as the immobilization, veterinary involvement, and logistical co-ordination for successful genetic exchange. The establishment of a management liaison committee would also be required in order to facilitate the movement of individuals to and from reserves.

Metapopulation management has been applied in the management of wild dog populations in medium-sized reserves in South Africa, resulting in an increase from 19 individuals in 3 packs in 1997, to 54 individuals in 10 packs prior to denning in 2002 (Lindsey, 2003). The target population size for the wild dog metapopulation was achieved in just over half the time that was expected (Mills et al., 1998). However, Lindsey et al. (2005) established that while the metapopulation approach was very successful for the conservation of wild dogs, it was the most expensive approach that could be used to conserve wild dogs in South Africa, and required a large amount of funding when undertaken outside large extensive reserves.

The cost of the approach does depend on the number of reserves participating in the metapopulation approach. A liaison committee, or person, would need to be employed
to maintain records of individual movements, stud-books, and communications between reserves. The salary of this person would need to be equally shared by the participating reserves. For the purpose of this analysis it was assumed that ten reserves would participate in the metapopulation approach, each with 15 adult lions, and that in order to maintain accurate stud books, an intensive monitoring approach would be the monitoring programme of choice in each reserve. Individual animals will not be sold to reserves participating in the approach, but swapping of same sex individuals would be done. Financial gain need not be the desired outcome of this approach, but rather the conservation of the species in South Africa, through the maintenance of a healthy genetic population at the minimum expense to each role player.

The cost of management aspects such as fencing costs, vehicle costs and such were not included in the overall costs, as these would vary vastly from one reserve to the next, and it is assumed that these aspects are included in each reserves budget for the overall management of all species within the relevant reserve.

Costs incurred for each reserve on an annual basis would thus include;

1. Cost of liaison officer (logistical co-ordinator, facilitator, record keeper)
   R 20 000

2. Costs of monitoring program per year for 15 adult lions (Chapter 3)
   R 101 752

3. Facilitated immigration / emigration (cost / animal)
   R 3250
The total financial expenditure incurred per year would vary from one reserve to the next depending on the number of immigration/emigration operations they wish to conduct. However, for this management approach to be successful each reserve participating in the metapopulation approach would probably spend a minimum of about R 125 000 per year.

The adoption of the metapopulation approach would require the coordinated participation of a number of reserves throughout South Africa. These reserves would form sub-units of the entire South African lion population, and could possibly ensure a wider genetic variability. The University of Natal established a lion project in 1996, with the main aim of beginning the unification of numerous efforts to reintroduce lions in South Africa (Hunter, 1999). This project has already gathered important information vital in establishing a metapopulation management approach in terms of a genetic register. Seven reserves are included in the register, namely Phinda, Pilanesberg National Park, Makalali, Madikwe, Welgevonden, Ligwalagwala and Entabeni. The collection of this population genetic data is essential in providing a foundation for long-term research and management that will enable reserves to safely exchange lions and maintain a healthy population. This shows that some reserves are already attempting a management approach that could possibly be adapted to that of a more formal metapopulation approach.

The logistical, financial, and time implications of the metapopulation approach, however, may force many reserves to opt for the single population management approach.
**Single population management approach**

The concept of this management approach is that each reserve, in which free roaming lions have been reintroduced, are considered to be separate units to each other. As each reserve is managed as an ‘island’ population, the genetic integrity of the population should ideally be carefully managed in order to avoid inevitable inbreeding.

With the analysis of population genetics conducted in this study, and the establishment of a time relationship advising when new genetic material should be introduced, management could predict at which time to introduce new animals. This form of management would not require extensive communication between other reserve bodies, provided lions of good genetic quality can be regularly sourced. No liaison committee would need to be established, and the participation of other reserves would be irrelevant to each reserve’s management strategy. Communications between other reserves, could of course, be conducted at the discretion of the reserve management especially with respect to trading of new individuals (buying and selling). Management could also incorporate hunting into the management strategy and use this aspect for the generation of funds. As the most successful method of gene introduction is to introduce new males, hunting or sale of coalitions that need to be removed could be considered.

A less intensive monitoring approach could probably be implemented, as precise knowledge of the population would be less important than the objective of tourism. This would thus further reduce the overall cost of the management approach. The movement of individuals to and from the reserve could be maintained at minimal
levels, as time relationships can be consulted as to when new individuals need to be introduced in order to curb inbreeding. The time parameters established in this study are surprisingly similar in comparison to those of Beier (1993) on immigration levels of cougars, who found that as few as between one and four animals per decade could significantly decrease the risk of inbreeding depression in small isolated populations.

This form of management may yet prove to best suit reserve managers, and may be a more financially viable method of lion management in medium-sized reserves. This approach importantly demonstrates that lion populations in medium-sized reserves, where the primary goal and objective is that of tourism, can be maintained using a less intensive management approach. The populations genetic status need not be compromised through this less intensive management and monitoring approach, and managers could probably still attain the desired goals and objectives of the reserve.

The costing of this management approach, as with the costing for the metapopulation approach, did also not take into consideration aspects such as fencing costs, vehicle costs and the like. Again this is calculated for 15 adult individual lion in the reserve.

Costs incurred for a reserve on an annual basis would include;

1. Costs of monitoring programme (Chapter 3)
   Less intensive monitoring approach  R 49 425

2. Costs associated with sale and translocation of animals
   Translocation of animal  R 3250

3. Costs associated with acquisition of new individuals (cost / animal)
   R 15 000
Thus the maximum financial expenditure incurred, excluding a derived profit from sales or hunting, for a reserve planning to manage a lion population according to the single population management approach are just a little more than 50% (R 67 675) of those required for a metapopulation management approach.

DISCUSSION

Reserve managers need to decide what genetic, monitoring and management methods and techniques to incorporate into the management of reintroduced lion populations. A range of options are available that can be used across the range of reserves in South Africa, and under varying situations. It was established that most reserves have similar goals and objectives for the reintroduction of lions, but that they have differing resources available to manage them. Private game reserves may have more funding available to use for lion management, than provincial or national parks.

This need not undermine the success of a reintroduction programme. Expenditure can be reduced while monitoring and management of the lion population is not necessarily undercut. With appropriate management of lion populations in terms of their genetic composition and the monitoring approach utilized, lions can be financially viable in medium-sized reserves.

The metapopulation approach, while somewhat more expensive, aims at the conservation of the species as a whole in South Africa. As the basic concept of this approach already exists in South Africa, the application of this management approach could be easily modified and applied in other reserves where lions have been
reintroduced. While managing each reintroduced lion population as its own discrete entity, under the single population management approach is probably more cost effective it would probably not greatly benefit the conservation status of the species as a whole. Thus, although contrary to conservation goals, this strategy does make greater financial sense and in many respects, is the approach being most closely followed in most reserves in South Africa with reintroduced lion populations.

Following the management trends and developments across a wide range of reserves in South Africa with reintroduced lion populations, it is clear that many are already changing their attitude towards management. Some reserves have already begun implementing a more “hands-off” approach, Pilanesberg National Park and Madikwe Game Reserve have implemented less intensive monitoring, with Madikwe now only radio-collaring males coalitions and not prides, and Welgevonden Game Reserve has removed all radio-collars from the population relying on sightings to maintain the monitoring programme. South African National Parks, Conservation Services Division (2006), have recently introduced a lion management strategy (Marakele National Park), where contraception and other manipulative technique will only be used in exceptional cases, as the interference with functional biodiversity is considerable, highly invasive and the long term effects of which are unknown.

While a small amount of movement of individuals between various reintroduced lion populations still occurs, very few homes for excess individuals are currently available. Reserve managers all attest to the fact that there is an insufficient ‘market’ for the sale of excess lions. Reserves also find that they need to carefully consider the sale of individuals to zoos, and more specifically to lion-hunting operations, as the public
perception of these operators may negatively affect the image of the reserve. Thus both hunting and culling of lions has resulted in management and moral complexities.

This study has forwarded the various advantages and disadvantages of two alternate management approaches, as well as provided important managerial considerations, vital in the management of reintroduced lion populations. The choice of which management approach to choose is largely dependent on the available funds, as well as overall goals and objectives for each reserve. These two management approaches provide managers of medium-sized reserves with a decision making tool that could promote the management of lions in South Africa, incorporating population viability, genetic integrity, and financial implications of lion management and monitoring. This further provides managers with the necessary means to better understand management of lion populations, as well as the ability to manage more pragmatically.
REFERENCES


Sunderland, Massachusetts.


Appendix 1  
Questionnaire

ESTABLISHMENT OF A BEST MANAGEMENT PRACTICE FOR THE MANAGEMENT OF LIONS IN MEDIUM SIZED RESERVES.

1. What are the goals and objectives of the reserve in terms of reintroduced lion populations?

2. Was a specific set of objectives established for the reintroduction of lions, if so what were they?

3. What is the size of the reserve? What areas surround the reserve?

4. How many lions were introduced? Please specify sex and age ratio.

5. Please specify origin of lions.

6. Why were the lions introduced from this population?

7. What ecological studies were initially undertaken?

8. State the time-lapse since the introduction.
   1-3 years
   3-5 years
   5-10 years
   More than 10 years

9. What initial impact or effect was noticed post release?
10. How was the lion population monitored post release?

11. What is the current size of the population?

12. Have other individuals been introduced post-initial introduction?

13. What has the lion birth rate been? Possible explanations?
   - Low
   - Medium
   - High

14. What has the lion mortality been? Possible explanations?
   - Low – cub mortality
   - Low – adult mortality
   - Medium – cub mortality
   - Medium adult mortality
   - High cub mortality
   - High adult mortality

15. At what stages in the project are the services of a vet employed?
   - Pre-release
   - Release
   - Post release
   - All of the above

16. Are lion numbers maintained or manipulated? If so how is this achieved?

17. What is the average size of male coalitions and prides?

18. What is the current standard of your fence?
   - Non-electrified
   - Electrification
   - Trip wire in place and spaced bobbins
   - Bonnox on lower fence

19. Have any breakouts been reported?
20. What is the break out policy?

21. Is financial compensation for stock or life loss accounted for in the policy and budget?

22. Was the reintroduction budget optimally used?

23. Did management
   - Exceed budget
   - Under spend

24. Approximately how much did the operation cost?
   - R 10 000 – R 100 000
   - R 100 000 – R 1 000 000
   - In excess of R 1 000 000.

25. Which do you consider more cost effective?
   - Daily monitoring
   - Veterinary services
   - Fence patrols
   - Hunting
   - Sale

26. What is the expected or concluded cost of the reintroduction to date?

27. What degree of monitoring is currently undertaken in the reserve?
   - Highly intensive (Vet, daily monitoring, manipulation etc.)
   - Moderate (Daily monitoring)
   - Extensive (No vet, monitoring or manipulation)

28. On a scale of 1 – 5 (1 = 1st option) how do you rank the following management techniques?
   - Hunting
   - Vasectomy of male lions
   - Culling
   - Contraception of female lions
   - Sale of sub-adults & males

29. Is your lion population managed according to a metapopulation approach? If so to which other reserves have genetic swapping occurred?
30. What is the perceived carrying capacity for lions on the reserve?
## Appendix 2 Questionnaire recipients and respondents

<table>
<thead>
<tr>
<th>Reserve</th>
<th>Size (ha)</th>
<th>Manager</th>
<th>Contact details</th>
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<tr>
<td><strong>Private Reserves</strong></td>
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<tr>
<td>Welgevonden Game Reserve</td>
<td>33000</td>
<td>Erwin Liebnitz</td>
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<tr>
<td>Karongwe Game Reserve</td>
<td>8500</td>
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</tr>
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</tr>
<tr>
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<td>Kevin Pretorius</td>
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</tr>
<tr>
<td>Shamwari Game Reserve</td>
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<tr>
<td>Venetia-Limpopo Nature Reserve</td>
<td>30000</td>
<td>Warwick Mostert</td>
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<td><strong>Provincially Managed</strong></td>
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<tr>
<td>Madikwe Game Reserve</td>
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</tr>
<tr>
<td>Pilanesberg National Park</td>
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<td>Mandy Momberg</td>
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</tr>
<tr>
<td>Hluhluwe-Umfolozi Park</td>
<td>96000</td>
<td>Sue van Rensberg</td>
<td><a href="mailto:vanerss@kznwildlife.com">vanerss@kznwildlife.com</a></td>
</tr>
<tr>
<td><strong>South African National Parks</strong></td>
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<tr>
<td>Marakele National Park</td>
<td>65000</td>
<td>Nicholas Funda</td>
<td><a href="mailto:nicolasF@parks-sa.co.za">nicolasF@parks-sa.co.za</a></td>
</tr>
<tr>
<td>Marakele Contractual National Park</td>
<td>23000</td>
<td>Bradley Schroder</td>
<td><a href="mailto:marakeleptyltd@lantic.net">marakeleptyltd@lantic.net</a></td>
</tr>
</tbody>
</table>
Appendix 3  Gene flow sequence of a pride in a single pride reserve.
Appendix 4a  Gene flow sequence of a two-pride reserve. (Pride 1)
Appendix 4b  Gene flow sequence of a two-pride reserve. (Pride 2)
Appendix 5b  

Gene flow sequence of a three-pride reserve. (Pride 2)
Appendix 5c

Gene flow sequence of a three-pride reserve. (Pride 3)
Appendix 6a  Gene flow sequence of a four-pride reserve. (Pride1)
Appendix 6b  
Gene flow sequence of a four-pride reserve. (Pride 2)
Appendix 6c  Gene flow sequence of a four-pride reserve. (Pride 3)
Appendix 6d
Gene flow sequence of a four-pride reserve. (Pride 4)
Appendix 7b  
Gene flow sequence of a five-pride reserve. (Pride 2)
Appendix 7c  Gene flow sequence of a five-pride reserve. (Pride 3)
Appendix 7d  Gene flow sequence of a five-pride reserve. (Pride 4)

New Bloodline

2000
Coalition 4

2000
Female 10

2000
Female 11

2000
Female 12

2003
Coalition 8

2003
Female 26

2003
Female 16

2003
Cub 30

2003
Coalition 8

2006 - 2006
Cub 70
Infanticide

2006 - 2006
Cub 71
Infanticide

2006 - 2006
Cub 72
Infanticide

2006 - 2006
Cub 73
Infanticide

2007
New Bloodline

2007
Cub 84

2007
Cub 85

2007
Cub 86

2007
Coalition 7 New Bloodline

2009
Cub 171

2009
Cub 172

2009
Cub 173
Coalition 21

2009
Cub 174

2009
Cub 175

2009
Cub 176
Coalition 21

2009
Cub 177

2009
Cub 178
6m

2009 - 2010
Cub 179

2009 - 2010
Cub 180

2009 - 2010
Cub 181

2009 - 2010
Cub 182

2009
Cub 183

2011
Cub 223

2011
Cub 224

2011
Cub 225

2011
Cub 226

2012 - 2012
Cub 240

2012 - 2012
Cub 241

2012 - 2012
Cub 242

2012
Cub 237

2012
Cub 238

2012
Cub 239

2006
Cub 66
Infanticide

6m

2006 - 2006
Cub 67
Infanticide

6m

2006 - 2006
Cub 68
Infanticide

6m

2006 - 2006
Cub 69
Infanticide

6m

2006 - 2006
Cub 72
Infanticide

6m

2006 - 2006
Cub 73
Infanticide

6m

2006 - 2006
Cub 70
Infanticide

6m

2006 - 2006
Cub 71
Infanticide

6m

2008 - 2008
Cub 66
Infanticide

6m

2008 - 2008
Cub 67
Infanticide

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2008 - 2008
Cub 68
Infanticide

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2008 - 2008
Cub 69
Infanticide

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2008 - 2008
Cub 72
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Cub 73
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2008 - 2008
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2008 - 2008
Cub 72
Infanticide

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2008 - 2008
Cub 73
Infanticide

6m
Appendix 7e  Gene flow sequence of a five-pride reserve. (Pride 5)