Management of reintroduced lions in small, fenced reserves in South Africa: an assessment and guidelines

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Managers of African lions (*Panthera leo*) on reserves where they have been reintroduced increasingly face challenges associated with ecological regulation, genetic degradation and increased susceptibility to catastrophic events. The Lion Management Forum (LiMF) was formed in 2010 to define these challenges and explore possible solutions with the view to developing appropriate management guidelines. LiMF bases its recommendations on the ecologically sound premise that managers should, as far as possible, mimic natural processes that have broken down in reserves, using proactive rather than reactive methods, *i.e.* management should focus on causal mechanisms as opposed to reacting to symptoms. Specifically, efforts should be made to reduce population growth and thus reduce the number of excess lions in the system; disease threats should be reduced through testing and vaccination whenever animals are translocated; and genetic integrity should be monitored. The latter is particularly important, as most of these reserves are relatively small (typically <1000 km^2). An adaptive management framework is needed to implement the guidelines developed here on reserves across the country, with regional nodes addressing more local genetic issues, within an overall national plan. Ongoing monitoring and scientific assessment of behavioural, population and systemic responses of lion populations and responsive modification of the guidelines, should improve management of lions on small reserves in South Africa. This approach will provide a template for evidence-based conservation management of other threatened species. Ultimately 'National Norms and Standards' must be established and a 'National Action Plan' for lions in South Africa developed.

Key words: *Panthera leo*, re-introduction, small reserve management.

INTRODUCTION

In South Africa, lions (*Panthera leo*) were extirpated from much of their historical range by the 1900s (Nowell & Jackson 1996). Three historical populations persisted: Kruger National Park (NP; approximately 1700 individuals; Ferreira & Funston 2010), Kgalagadi Transfrontier Park (TP; approximately 125 individuals in the South African section; Castley *et al.* 2002; Funston 2011) and Greater Mapungubwe Transfrontier Conservation Area (GMTFCA; only a small population of <50 individuals; Funston 2010). Lions re-populated

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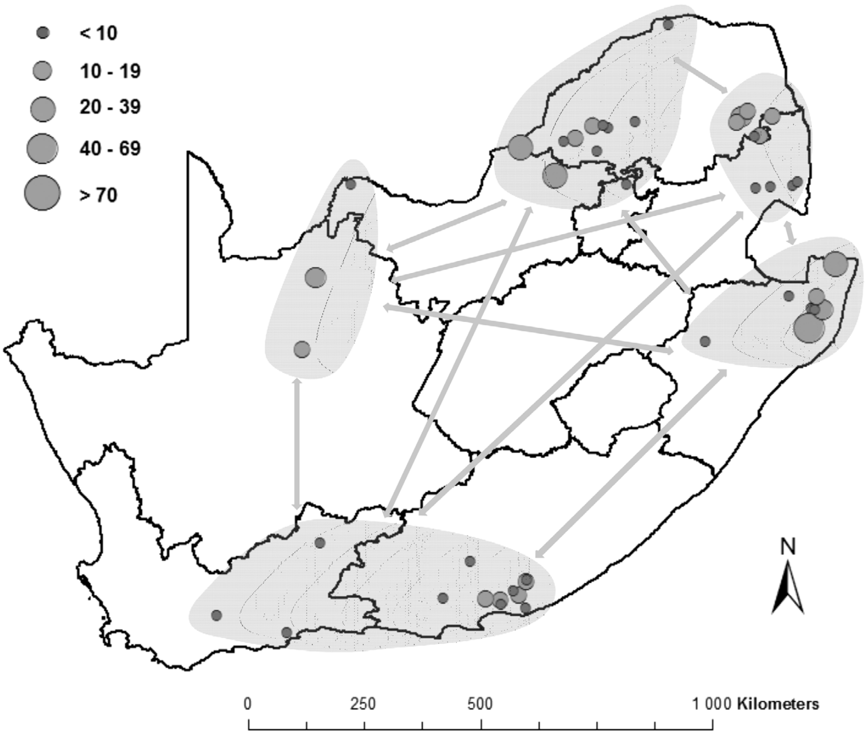

Fig. 1. Location of reserves in South Africa with free-roaming lions and proposed management clusters (shaded areas). The size of the dot represents the number of lions on the reserve as indicated in the legend. Following the proposed management guidelines outlined in this paper we envisage a national network of reserves where translocations between reserves within the clusters occur on a regular basis (as required by each reserve) with less frequent translocations between clusters (indicated by arrows). This should improve the genetic integrity of this population as a whole.

Hluhluwe-iMfolozi Park (HiP) in 1958 with more recent introductions (1999–2001) to improve the overall genetic health of that population (Trinkel *et al.* 2008). The HiP currently has ~200 lions (Grange *et al.* 2012). At least 44 other free-ranging (*i.e.* fending for themselves) lion populations can be found in smaller (<1000 km^2) fenced reserves in South Africa, currently totalling ~500 lions (Fig. 1; updated from Slotow & Hunter 2009). The Kruger NP, Kgalagadi TP, GMTFCA and HiP populations were all recognized by the IUCN in their 2006 report on southern and eastern African lions, with Kruger NP and Kgalagadi TP listed as 'viable' populations, and the GMTFCA and HiP populations listed as 'potentially viable' populations (IUCN/SSC Cat Specialist Group 2006).

All of the reintroduced lion populations are currently intensively managed (Hayward *et al.* 2007a,b; Hunter *et al.* 2007), largely in isolation from each other. The net effect of this is that some believe that these various small and isolated populations are of minimal conservation value at a regional scale (Slotow & Hunter 2009). This has prompted calls to move away from intensive management in isolation towards a managed metapopulation approach (Funston 2008; Slotow & Hunter 2009; Hayward & Kerley 2009; Trinkel *et al.* 2010; Ferreira & Hofmeyr 2014) similar to that developed for African wild dogs (*Lycaon pictus*; Gusset *et al.* 2008). Where possible Hayward *et al.* (2007b) suggest fences could be removed within geographically contiguous areas to increase the size of some areas, presumably reducing the management intensity. However, the extent of human habitation and infrastructure in South Africa would only allow a relatively small proportion of the various reserves to connect.

Thus, integrated population management may, in most instances, be a better option within a meta-population framework (see Olivier *et al.* 2009), providing potentially important conservation outcomes. Most lion reintroductions in South Africa are for eco-tourism purposes rather than purely ecological reasons (Slotow & Hunter 2009). Any management recommendations must, therefore, account for both the economic and ecological/conservation value of lions and should be guided by area-specific land-use objectives (IUCN/SCC Cat Specialist Group 2006). Practical interpretation and implementation of these diverse requirements provides conceptual as well as logistical challenges.

These challenges prompted reserve managers and scientists to convene a workshop in June 2010 to find innovative solutions for these challenges. That workshop resolved to promote regional linkages, as well as to establish an informal group, known as the 'Lion Management Forum' or LiMF. The aim of this group is to improve the conservation value of lion populations in small reserves through the development of industry norms and standards for lion management following scientifically-based management approaches (Ferreira & Hofmeyr 2014). The forum also committed itself to promote research into areas where information relevant to management was lacking. At two subsequent workshops (one held in Mokala NP in November 2010 and the other at Tshwane University of Technology in Pretoria in August 2011) an experiential approach was used to develop management guidelines and identify areas requiring further research. The purpose of this paper is to provide an integrated output from these three workshops, directed at enhancing lion management and conservation in South Africa. Specifically, we summarize the context of managing lions in small reserves by outlining the challenges managers face, and then provide management guidelines based on published evidence and the expert opinions of workshop participants.

CHALLENGES TO EFFECTIVE MANAGEMENT OF LIONS IN SMALL RESERVES IN SOUTH AFRICA

Keeping lions in small reserves has led to three major challenges: ecological regulation, genetic degradation and increased susceptibility to catastrophic events (especially disease).

Ecological regulation: excess lions and population control

Typically managers define a desired number of lions for their reserve, informed by the reserve's objectives (Vartan 2001; Hayward *et al.* 2007c; Ferreira & Hofmeyr 2014), or based on the available biomass of suitable prey (Hayward *et al.* 2007c). Thus managers either ask 'how many lions do we need' or 'how many lions can we support?' and actively manage numbers accordingly. As lions have high reproductive potential and recover rapidly from disturbances (Smuts 1978; Kissui & Packer 2004), introduction to reserves with abundant, naive prey, inevitably results in an 'excess' number of lions within a short period of time (Kettles & Slotow 2009; Miller & Funston 2014). We use the term 'excess' for lions that exceed the number of desired lions for the reserve and are thus removed by managers. Initially managers mainly used translocation to address overabundance (Kettles & Slotow 2009; Slotow & Hunter 2009), but in more recent years a decrease in the establishment of new reserves has resulted in fewer opportunities for translocation (Hayward *et al.* 2007b; Kettles & Slotow 2009). Euthanasia, and to a lesser degree contraception, have thus become the methods of choice for population control in the last ten years (Kettles & Slotow 2009; Slotow & Hunter 2009; Miller & Funston 2014). From information provided by the workshop attendees it is estimated that about 200 lions were euthanased for this purpose in South Africa from 2010 to 2012.

These are, however, symptomatic approaches that are not designed to address the causal mechanism underpinning rapid population growth. The challenge, therefore, is to determine why lions overpopulate small reserves so readily and then promote simulation of natural processes that regulate population growth in larger reserves (>10 000 km^2) where lion populations are typically stable over extended periods of time (Mills *et al.* 1978; Castley *et al.* 2002; Packer *et al.* 2005; Ferreira & Funston 2010; Funston 2011). Such mechanistic approaches (Ferreira *et al.* 2011) might aid managers to target the cause (*e.g.* disruption of social factors in small areas such as lack of a need to defend cubs against roaming males (Packer *et al.* 1988), which lead to disrupted group structures and increased predation) rather than the symptoms (*e.g.* too many lions) of ecological problems (van Aarde *et al.* 2006).

There is evidence that two density-dependent regulatory mechanisms reduced population growth in the high-density lion population on Madikwe GR (Trinkel *et al.* 2010) with older ages of first reproduction and smaller litter sizes as densities increased (Trinkel *et al.* 2010). However, these effects have not been observed on other small, fenced reserves in South Africa (Miller & Funston 2014). This does not mean that growth rates would continue unchecked on small reserves if densities were allowed to increase, but rather that in the other reserves lion numbers were actively controlled by management (Kettles & Slotow 2009) below densities at which these effects would be expected. This control was necessary due to the smaller size of these reserves and reserve objectives for both lion and prey populations. Such responses precludes density-dependent mechanisms from operating on small reserves and may in fact compound the problem by leading to 'eruptive growth', where populations experience high growth rates and can exceed carrying capacity following culling operations (Caughley 1970; Slotow *et al.* 2008). Even if these two effects could be mimicked in other small reserves, they would probably not be enough to control numbers. For example, even though the growth rate of lions had slowed in Madikwe GR, in 2011 managers had to euthanase 70 lions to bring the population level down (pers. obs. authors). Thus density was likely not the only factor influencing growth rates on Madikwe GR and presumably other small reserves.

The sociality of lions may provide key guidance on the breakdown of regulatory mechanisms. Firstly, lionesses live in groups (prides) for two main reasons: 1) to defend their cubs against roaming males and 2) to defend their groups against other groups of females (Packer *et al.* 1988; Mosser & Packer 2009). Both forms of defence can be violent, sometimes resulting in cubs, subadults and even adults being killed (Mosser & Packer 2009). In most small reserves there are typically 1) few large nomadic males, 2) few other prides, and 3) relatively small prides (Druce *et al.* 2004; Lehmann *et al.* 2008a). Secondly, male lions actively defend their territories and typically only maintain tenure of prides for less than two years (Bygott *et al.* 1979; Funston *et al.* 1998, 2003). Male tenure of prides is often much longer in small reserves than in larger populations, reducing infanticide due to infrequent takeovers (Miller & Funston 2014). The net effect is that ≈87% cubs survive (Druce *et al.* 2004; Hunter *et al.* 2007; Kilian 2003; Lehmann *et al.* 2008a; Miller & Funston 2014). Additionally, no dispersal opportunities exist for subadult lions in small reserves, whereas in large reserves subadult males and some females typically leave their natal prides between two and four years of age. Occasionally young females will remain in their natal pride (Hanby & Bygott 1987; Pusey & Packer 1987). Thereafter they experience high mortality rates, and those that survive either settle far away (Hanby & Bygott 1987; Pusey & Packer 1987) or in nearby prides (Funston *et al.* 2003; Spong & Creel 2001). Thus very few of these natural processes that either induce mortality or dispersal occur on small reserves which leads to the high population growth rates noted.

Genetic integrity

The choice of lions for reintroduction and supplementation onto reserves in South Africa has seemingly not maintained overall genetic integrity (Slotow & Hunter 2009). There are two main issues: genetic origin and genetic diversity.

Genetic origin

In South Africa, lions have largely been sourced for reintroduction from three main populations: Etosha NP, Namibia, through Pilanesberg NP and Madikwe GR; Greater Kruger NP (*e.g.* Phinda Private GR and Greater Makalali Private GR); and, more recently, from Kgalagadi TP (*e.g.* Tswalu Desert Reserve and Addo Elephant NP; Slotow & Hunter 2009). Northern Tuli Game Reserve, Botswana, was the source of lions for Venetia-Limpopo Nature Reserve (Funston 2010). Many reserves have a mix of origins within their lion populations (Slotow & Hunter 2009).

These southern African lion populations share common ancestors and are considered to be part of the same Ecologically Significant Unit (ESU), but due to decrease in range and isolation of populations, distinct populations have developed in more recent history (Barnett *et al.* 2006; Antunes *et al.* 2008). Using microsatellite data, distinctions can be made between Kruger NP, Namibia (including Etosha NP) and two Botswana (one including the Kgalagadi TP) populations (Antunes *et al.* 2008), which can be viewed as Management Units (MUs). Slotow & Hunter (2009) suggests that this mixing between animals from these MUs may have compromised the genetic integrity of the animals, as they are no longer from a single source population. However, mixing individuals between MUs within an ESU can be useful to reduce inbreeding (Moritz 1999).

Genetic diversity

There are indications that some reserves are facing inbreeding issues (Trinkel *et al.* 2008, 2010). In large open systems, inbreeding is prevented through the social behaviour of lions with young males leaving the pride before they are old enough to challenge for pride tenure within their natal pride

(Packer & Pusey 1987, 1993). In small reserves, important processes that aid this are largely non-functional. Inbreeding has been shown to affect reproductive success in lions (Wildt *et al.* 1987), as well as increased susceptibility to disease (Kissui & Packer 2004; Trinkel *et al.* 2011). Management interventions such as contraception, euthanasia, removal or loss of a key individual could have negative stochastic genetic effects, which might be amplified in small populations. As noted above, by mimicking social mechanisms natural sociality could be restored, possibly improving the genetic situation (*e.g.* reducing inbreeding). Overall genetic diversity is important for the long-term survival of any species (Frankham *et al.* 2009), and it is thus a priority to determine the current status.

Disease

In large reserves, parasites and pathogens play key roles in ecological functioning (Hudson *et al.* 2006), including the regulation of population size and the maintenance of genetic diversity (Altizer *et al.* 2003). In order to embrace these aspects of ecosystem heterogeneity it is important to provide opportunity for processes, including disease dynamics, to play out. However, when these disease-host dynamics are impeded due to human-induced disturbances, conservationists need to make management decisions as to whether it is necessary to try to mitigate the negative effects caused by these changes. Small populations can be severely depleted (Kissui & Packer 2004; Trinkel *et al.* 2011) or even exterminated by an outbreak of a disease (Woodroffe 1999). Although a manager could replace lions that die from disease, these may be key individual/s from a genetic or tourism perspective. Additionally, some diseases may be multi-host diseases (*e.g.* rabies and bovine tuberculosis) and could potentially negatively impact on other species within the reserve.

It is preferable then, that diseases do not break out in lions on small reserves, necessitating vigilance by managers. This is supported by legislative and regulatory requirements governing the control of certain diseases (for example, lions must be vaccinated against rabies before being moved within South Africa; Bishop *et al.* 2003) as dictated by the Animal Disease Act (Anon. 1984). Thus despite the potential of disease to be used as a natural population regulating mechanism, the realities of South African law and small fenced areas negate the effectiveness of diseases.

Therefore, key diseases to control for are: rabies, bovine tuberculosis (BTb) and canine distemper virus (CDV). Rabies, while rare in lions, has been reported on a few occasions in southern Africa (Berry 1993; Bishop *et al.* 2003) and vaccines have been used effectively against a rabies outbreak in wild dogs on Madikwe GR (Hofmeyr *et al.* 2004); BTb is prevalent in the Kruger NP population and adjacent reserves, as well as in HiP (Michel 2002; Michel *et al.* 2006). A CDV outbreak in the Serengeti-Mara in 1994 killed 35 per cent of the lion population (1000 individuals) within six months (Roelke-Parker *et al.* 1996) and in southern Africa in the Kgalagadi TP a number of lion fatalities were reported in 2009 (Zimmermann *et al.,* in prep.).

Lions have coevolved with feline immunodeficiency virus (FIV) (Antunes *et al.* 2008) and some studies suggest that it has no effect on lion populations (Brown *et al.* 1994; Carpenter & O'Brien 1995; Hofmann-Lehmann *et al.* 1996; Packer *et al.* 1999). However, more recent evidence suggests that there may be some effects on wild populations (Roelke *et al.* 2006, 2009), particularly related to the different strains and their impact on other diseases (Troyer *et al.* 2011). Therefore, even though there is no evidence that FIV has negatively impacted lion populations in small reserves in South Africa, it would be useful to monitor the FIV strains within these populations.

Human conflict and compensation

By law (Anon. 2003) all reserves containing lions in South Africa have to be adequately fenced, which greatly reduces lion–human conflict (Hayward & Kerley 2009). Breakouts and subsequent livestock losses are thus a rare occurrence (Hunter *et al.* 2007; Slotow & Hunter 2009). South African legislation dictates that when introducing dangerous species (such as lions) into confined areas, the landowner must insure against breakouts causing property damage (*e.g.* predation of livestock) and/or death or injury to third party persons (Anon. 1991). This liability insurance must be for a minimum of R5 million per incident and should include costs for the relocation of animals to the insured premises and is also extended to include the potential spread of disease (Anon. 1991).

Effect on biodiversity/prey populations

The impact of predation by lions on ungulate (prey) populations appears to be more acute in small reserves (*e.g.* Hunter 1998; Mills & Shenk

1992; Tambling & Du Toit 2005; Hayward *et al.* 2007c; Lehmann *et al.* 2008b). The possible explanations for this include that prey populations are often not completely established prior to the introduction of predators (*e.g.* Operation Phoenix in Madikwe GR; Hofmeyr *et al.* 2003). However, there are several incidences of established populations that declined dramatically once lions were introduced (Hunter 1998; Mills & Shenk 1992; Tambling & Du Toit 2005; Hayward *et al.* 2007c; Lehmann *et al.* 2008b). Clearly some of these were precipitated by inappropriate management interventions, typically the continued removal or supplementation of prey (Peel & Montagu 1999; Louw *et al.* 2012), and inappropriate lion reintroductions (Tambling *et al.* 2013).

Managers prioritize stocking rates, which is a bottom-up process, as indicators, and when prey populations decline, they tend to respond by reducing the numbers of lions, restocking prey or both (Louw *et al.* 2012). In essence, conservation managers tend to ignore temporal and spatial variability that characterize larger savanna ecosystems (see Mills *et al.* 1995; Owen-Smith & Mills 2008). There are several reasons for this, but key amongst these seems to be that tourism demands (or expectations) encourage managers to be relatively risk averse. For example, a removal proposal of a large dominant male to initiate pride takeovers may contrast with the tourism value of that particular animal resulting in no removal. The potential cascade effects that lions may have on other predators and/or keystone species on smaller reserves must also be kept in mind by managers. For example, very few small reserves with lions seem to be able to sustain reasonable numbers of the more threatened predators such as cheetahs (*Acinonyx jubatus*) or wild dogs (van Dyk & Slotow 2003; Hayward *et al.* 2007a,b).

MANAGEMENT GUIDELINES

Key principles of the management approach

The free-ranging lion populations within South Africa potentially present an important conservation resource, at the provincial, national, and continental scale. In order to highlight and safeguard this resource, a comprehensive holistic management approach needs to be taken (Ferreira & Hofmeyr 2014). The approach for lions should be process-based focusing on the cause of a problem (*e.g.* social dynamics disrupted), rather than responding to the symptoms (*e.g.* there are too many lions; van Aarde *et al.* 2006). Such approaches hinge on an ecological understanding of systems (Gaylard & Ferreira 2011) and preferably aim to restore processes. When restoration is not viable, specifically in small reserves, interventions should simulate the outcomes of natural processes (Ferreira & Hofmeyr 2014). Consequences at different levels, such as individual (health, welfare, aggression, reproduction), population (size, composition, social arrangement, spatial arrangement, genetics, disease), ecological (predator–prey relations, predation landscape, inter- and intra-guild dynamics, predator refugia), socio-economic (consumptive use, non-consumptive use) and political (ownership, conflict, participation) must all be considered (Biggs *et al.* 2008).

Ideally, lion managers should restore all of the above population regulating mechanisms that are currently lacking. Most small reserves are typically isolated and surrounded by landscape uses that are not conducive to the dropping of fences to increase the reserve area and/or are not easily reconciled with the presence of lions. Thus, to be effective, managers may, at times, need to mimic the outcomes of the natural processes occurring in large, fenced or open systems that have failed on small reserves. Such simulation of processes can be targeted at the reproductive, survival and dispersal schedules of lions, and, to achieve scaling efficiencies, should be framed within a management plan involving a network of reserves, *i.e.* a metapopulation approach (see *e.g.* Gusset *et al.* 2008). One approach may be to have four or five regional nodes within which translocations occur more regularly, with less frequent translocation between the nodes (see Ferreira & Hofmeyr 2014 and Fig. 1). This would simulate natural dispersal and gene flow, and result in a genetically sound population into the future. In Tables 1, 2 and 3 we summarize guidelines developed by the LiMF for reproductive schedules, survival and dispersal schedules, and managing disease issues. These tables also indicate gaps in the knowledge base, where further research is required. Guidelines as developed so far are expanded upon below.

One particular challenge that conservation managers often face is choosing appropriate tools, technologies or approaches. Given that management strategies have inherent focal objectives – for lions these are more often than not associated with tourism products (Slotow & Hunter 2009) – but also associated other values, reserve

Table 1. Guidelines for the manipulation of reproductive schedules of lions on small reserves[1]: intervention *vs* process being simulated.

Natural process being simulated	Female contraception[2]			Removal
	Chemical	Unilateral 'tube-tying'	Sterilization[3]	Culling
Increase age of first reproduction – female	Y		(Y)	
Increase interval between births	Y		(Y)	
Decrease litter size		Y	(Y)	Partial litter
Decrease age of last reproduction			Y	Y

[1]An initial population reduction may be required before these options are explored to keep future population growth under control.
[2]Please note, vasectomies are not recommended as they do not simulate a natural process – see text for details.
[3]See text.
(Shaded) Experimental – assessment required.

managers usually need to compromise other values and objectives (*e.g.* Ferreira *et al.* 2011; Ferreira & Hofmeyr 2014). Risk–benefit analyses (Mentis 2010) are particularly useful to help address this challenge. Such analyses recognize that several events or outcomes may take place or result if a specific tool, technology or approach is applied.

An event or outcome may carry risks, benefits or both for the achievement of a suite of objectives. Objectives differ between different land-uses: Managers of State-owned protected areas assign more weight to purist conservation objectives, while managers of ecotourism destinations see tourism experiences, a key driver of revenue generation, as the primary objective. The risks or benefits that an event or outcome carries is the product of the effect or impact it will have on an objective and the likelihood that the event or outcome will actually realize. For example, a reserve may be considering introducing new male lions to simulate a pride takeover. This could result in infanticide during the takeover process and serve as a benefit associated with the reserve objectives of simulating natural population control. If this does take place then the impact on achieving biodiversity objectives is high, but the likelihood that it will happen is lower (*e.g.* Tambling *et al.* 2013). The benefits associated with achieving biodiversity objectives will be influenced by this uncertainty.

The proposed introduction, however, may disrupt pride dynamics and fragment females resulting in

Table 2. Guidelines for manipulation of survival and dispersal schedules of lions on small reserves: intervention *vs* process being simulated.

Natural process being simulated	Removal Translocation/culling/hunting	Introduction Translocation[1]
Decreased cub survival	Partial litter – culling	
Male takeover/infanticide – 1 pride	Before introduction of new male(s)	After removal of current male(s)
Male takeover/infanticide – 2 or more prides	After takeover occurs or to prompt a takeover if existing 'extra' males are not succeeding and are required for genetic reasons	Before removal ideally have 'extra' males on the property the whole time to promote pride stability and natural takeovers
Emigration/immigration of young males	Y	Y, usually at breeding age (see takeovers)
Emigration/immigration of young females	Y	(Y) – not required often

[1]There is currently limited scope for translocations, but some are essential for maintaining genetic diversity.
(Shaded) Experimental – assessment required.

Table 3. Guidelines for diseases of concern and recommended actions for lions on small reserves.

Disease	Vaccine available	Test available	Sample required	Comments
Rabies	Y	Y on post-mortem	Post-mortem	Vaccination legally required
Tuberculosis	N	Y	Skin test – multi-day	Test should be done before translocation
Canine distemper	Y	Y	Serum	Test to see if animal has been exposed
Echinococcosis (tapeworm)	–	Y	Faecal	Zoonotic concern
Feline immunodeficiency virus	N	Y	Serum	Monitor strains in the population

a reduced tourism experience when visitors see single lions more often than a pride of lions. The introduction thus carries risks associated with tourism and revenue objectives. If this outcome happens, the impact on tourism and revenue objectives will be high. The likelihood that the outcome will happen though is very low if one assumes that tourists' experience of lions are largely determined by whether they see large males or not (pers. obs. authors). In this case the risk to tourism and revenue objectives may be low. The benefits associated with biodiversity objectives traded-off against the low risks associated with tourism and revenue objectives provide a manager with confidence to proceed with the proposed intervention.

The complete risk–benefit profile associated with the application of a tool, technology or approach is the sum of all consequences for objectives. Operational elements usually comprise costs and logistics, and use a similar structure to assess influence on managers' ability to achieve objectives. By adding cost profiles to the profiles for objectives, the complete risk–benefit–logistic-cost profile can be generated for a management option. Options are prioritized according to the value of these profiles with the largest one the most favourable option to use given the suite of objectives a manager seeks to achieve and the costs and logistic implications.

Reproductive schedules

The main objective of any free-ranging contraception programme should be to control reproduction with minimal disruption of the social structure and behaviour of the animals involved. A number of factors need to be taken into consideration when selecting the contraceptive method. These include 1) safety to the animal – a number of drugs used have potentially negative side-effects on the animals (see below); 2) effect on social structure and behaviour of the animal – *e.g.* hormone-dependent characteristic changes such as mane loss in lions and reduced dominance of males (Munson 2006); 3) reversibility – the choice of reversible or irreversible methods of fertility control depends on the management requirements (Munson *et al.* 2005); 4) cost – including equipment for surgery or drugs and need for repeat treatments; and 5) logistics – remote delivery or immobilization required to contracept the animal and the feasibility of capturing/locating the animals on a regular basis for repeated contraception.

Reproductive control of male lions

Vasectomies have been applied to zoo lions since the 1970s (Robinson *et al.* 1975) as well as to free-ranging lions (Kettles & Slotow 2009; Slotow & Hunter 2009). In our view, however, vasectomies do not simulate a natural regulatory process in lions. We are not aware of any study that describes free-ranging male lions that become sterile. Therefore, vasectomies are not recommended as part of the options for management interventions of free-ranging lion populations.

A vasectomy of a lion is relatively easy to perform (Slotow & Hunter 2009) and although not encouraged should reduce conception rates depending on how many males have been targeted and the social dynamics of those males. There are potential social consequences of vasectomies. Females may change their associations and ranging patterns and seek out non-vasectomized, non-pride males (if present in the population) and conceive even though the pride males are vasectomized (pers. obs. authors). Incidences of mating may increase because females do not conceive – a potential advantage for reserves with ecotourism as a primary objective. However, continuous mating when all males are vasectomized may also carry some social consequences for prides, given the disruptive impact of consortship on general pride behaviour and dynamics. Lion mating incidences can last two to six days, during which time hunting is reduced (Schaller 1972; Packer & Pusey 1983).

If this occurs frequently, it may have negative consequences for other pride members. Furthermore, if the vasectomized males are replaced with fertile males at some point, then all the females may breed at once leading to an immediate population explosion, and consequentially a cohort of young lions that will have to be simultaneously removed between two and four years later.

Vasectomy of male lions may also have potentially serious consequences on the reproductive health of the lionesses. Lionesses, like many other felids, are reflex ovulators, only ovulating after repeated coitus with a male lion (Bakker & Baum 2000). In the case of a vasectomized lion, mating still occurs resulting in reflex ovulation but an infertile mating may, over time, result in the lioness developing cystic endometrial hyperplasia-pyometra, infertility, uterine infection, uterine cancer, mammary tissue cancer or diabetes mellitus (Munson 2006).

Vasectomies, therefore, may have limited value primarily because of the health risks to the females, but also unknown consequences at ecological and social levels, and unknown effects on tourism experiences. Thus far, no studies have reported that vasectomization has reduced population growth rates, and there is clear evidence that it has increased rates of inbreeding (Trinkel *et al.* 2010).

Chemical contraceptives could be used in males. However, the side-effects in a male are similar to those after a gonadectomy: potential for weight gain and loss of mane and dominance in males (Munson 2006). Therefore, it is not recommended in male lions because of this disruption to pride social structure and the negative impact on tourism.

Reproductive control of female lions

Controlling the lifetime reproductive output of a lioness can be achieved through manipulating four reproductive parameters: 1) the age at which females first have cubs; 2) the interval between births; 3) the age at which females have their last cubs; and 4) litter size. Making use of hormonal- or immuno-contraceptives is a popular option for dealing with the first three parameters, but more invasive options are also available. We consider each reproductive parameter separately.

Gonadotropin releasing hormone (GnRH) agonists are considered to be the safest reversible contraceptives and are recommended for carnivores (Asa *et al.* 2005). Specifically deslorelin (Suprelorin®, Peptech Animal Health, Sydney) mimics an ovariectomy in females and castration in males by suppressing the reproductive endocrine system and preventing the production of pituitary and gonadal hormones (reviewed by Ponglowhapan 2011). In the first few weeks following implantation, deslorelin actually stimulates the reproductive system and can result in oestrus, but downregulation then follows and oestrus is stopped (reviewed by Ponglowhapan 2011). In trials on African carnivores (including lions), no mating was observed with treated females (Bertschinger *et al.* 2002). The hormonal effects are reversed when the hormones within the implants are depleted or the implant is removed and regular oestrus should resume (Bertschinger *et al.* 2001, 2008; however, see below).

Increasing age at first reproduction can be achieved using chemical contraceptives (specifically deslorelin implants) on lionesses before they have a chance to mate and reproduce. Determining the age at which to do this may prove somewhat challenging as the age of first reproduction can be as young as 26 months on small reserves (Miller & Funston 2014). Managers may need to carefully monitor when females appear to be coming into oestrus for the first time, or err on the side of caution and contracept females at two years of age.

Increasing the interval between births can also be achieved through the use of contraceptives (deslorelin implants). Again, this may not always be successful as some lionesses have reproduced as little as 7 months after the birth of a surviving litter, but the average is still 26 months (Miller & Funston 2014). In Bertschinger *et al.*'s study (2008), the average interval from time of treatment to conception following the application of a 3 × 4.7 mg dose of deslorelin contraceptive was 30.1 months with a range of 15–40 months (n = 7). Thus, should a manager want to prolong the contraceptive period, a new implant should be administered at 24-month intervals (every 2 years). Prolonged use of deslorelin implants for up to eight years have produced no visible or measurable side effects (Bertschinger *et al.* 2008). However, concerns have been raised over some apparent side effects, with a small number of lionesses showing severe weight gain and a failure to return to normal cycling (pers. obs. authors). Most reports are anecdotal, but this would appear to be more prevalent in lionesses that have had repeated deslorelin implants (pers. obs. authors). Another factor to bear in mind is that the time to return to cycling seems to correlate with the number of implants (years) given, for example animals treated consecutively for three years may take up to 36 months to cycle again (pers. obs. authors).

There are some potential social consequences of these interventions. One such consequence is the fragmentation of prides into smaller groups or singleton females (pers. obs. authors). Whatever the cause, fragmentation can cause shifts in predator–prey relations and intraguild dynamics, notably additional predation of prey species (Lehmann *et al.* 2008b). However, fragmentation could have a tourism benefit in that the lions are more spread out, increasing the chances of them being seen. The pros and cons of fragmentation must be carefully considered and the reasons behind it more fully explored.

Decreasing the age at last reproduction may be more difficult to achieve as a targeted demographic parameter. Lionesses can continue to have cubs up until death at a maximum of 16 years of age (in the scientific literature) and litter size has been observed to decrease at 14 years of age (Packer *et al.* 1998). Lionesses on small reserves often live longer than 16 years of age and have litters right up until death (pers. obs. authors). Therefore, there may be a case for sterilizing or euthanasing older females to control population numbers.

Decreasing litter size is a challenging but attractive option, which might be successfully achieved through unilateral tubal salpingectomy, unilateral hysterectomy or unilateral ovario-hysterectomy. These techniques involve various levels of intervention varying from simply tying off a fallopian tube to the removal of an entire uterine horn with or without its associated ovary. The theory behind the procedure is to limit the uterine space available for implantation and hence the resultant litter size. There is evidence that this technique works in mice (Finn 1963). Studies are needed to ascertain whether simple unilateral salpingectomy ('tube-tying') will result in the desired effect or if a unilateral hysterectomy or ovario-hysterectomy will be required to physically restrict uterine space before managers see the desired reduction in litter size.

This new, experimental technique in lions was performed for the first time on a free-ranging wild 17-month-old lioness in 2011 with 20 completed procedures expected by early 2013. Although invasive in terms of surgery, these procedures are readily performed in the field and to date the lionesses operated on have shown rapid recovery and returned to normal pride and hunting behaviour within a day (pers. obs. authors). There are no external sutures and the wound is only 2.5 cm long on the ventral midline. Follow-up is planned to determine the effectiveness of the procedure and to ensure that there are no behavioural changes associated with the procedure. While the procedure is more expensive than conventional hormonal contraception, it need only be performed once in a lifetime. The procedure has ethical advantages as it should reduce the need for the future removal of cubs and even though it reduces lifetime reproductive potential of the female, she will still have cubs that are more likely to be allowed to survive, thus ensuring that her genes are passed on. There is, however, the risk of complications during surgery. These ethical considerations must be included in a risk–benefit analysis before deciding on a course of action. There is also an implant that can be used to block one fallopian tube that is available for humans (Duffy *et al.* 2005) that may be applicable to lionesses as well (although it has yet to be attempted) and require less invasive surgery.

A cautionary note when managing small populations where there are only a handful of adult breeding females must be considered: if a large percentage of the lionesses are contracepted and something happens to one or a few of the reproductive females, such as death, then the potential for the population or pride to recover is limited in the short term.

We advocate that chemical contraception is the best option currently available to reserve managers for controlling population growth. It can be used to mimic the longer inter-birth intervals and older ages of first reproduction seen in open systems such as Kruger NP. Deslorelin implants have been shown to be effective and safe over a period of eight years (Bertschinger *et al.* 2008). The key point though is that chemical contraception should be applied selectively to simulate natural population regulation mechanisms seen in large lion populations. Further research is required and should focus on 1) collating information from all experiences with lion contraceptions, and 2) robustly evaluating surgical methods to reduce litter size. Several initiative are under way to address these needs.

Survival and dispersal schedules

Manipulating male takeovers through replacement of pride males

Artificial removal of pride males provides an opportunity to mimic the outcomes of lion interactions associated with changes in male tenure of prides and defence of cubs and territories (Packer *et al.* 1988; Mosser & Packer 2009) that seemingly occur at substantially lower incidences in small reserves (Trinkel *et al.* 2010). A removal will result in new pride males and subsequent genetic diversification (assuming new males are introduced at the same time). There may or may not be infanticide or death of young lions as a result depending on the timing and size of the reserve. Several reserves, most notably the Greater Makalali Private GR, have successfully replaced their pride males multiple times over the years to prevent inbreeding (Kettles & Slotow 2009). Madikwe GR, on the other hand, has experienced extensive inbreeding since the introduction of lions in 1995, with one male coalition retaining tenure for nine years (Trinkel *et al.* 2010). On small reserves with only one pride it will usually be necessary to remove the existing male(s) before introducing a new one/s (*e.g.* Druce *et al.* 2004; Kettles & Slotow 2009), while on larger reserves with two or more prides, it may be possible to introduce new males and allow a natural takeover to occur (*e.g.* Trinkel *et al.* 2008) although it may not always work out as expected (Tambling *et al.* 2013). We recommend frequent replacement of males as it would more closely mimic natural turnover rates.

Manipulating other lion survival/dispersal rates

Translocation can be used to simulate other natural processes that may not occur in small reserves. For example, removal of subadults could be used to mimic emigration and euthanasing part of a litter would simulate cub mortality. The latter would have the added management benefit that the mother would not come back into oestrus as long as she had at least one cub remaining, resulting in slower birth rates; however, the ethics and potential public outcry surrounding the euthanasia of lion cubs may negate the usefulness of this option. Euthanasia can also be used to remove problem animals (*e.g.* ones that repeatedly break out), as well as sick or inbred individuals.

Method of removal

Managers have three options for removing animals: translocation, euthanasia or hunting. With the decrease in translocation opportunities, translocation has largely become a tool to assist with gene flow between populations in the form of supplementation, rather than as a population control method. However, along with hunting and euthanasia, translocation is still a method that can be used to remove excess lions. When translocations do occur, they should follow a broad metapopulation-based plan outlining which reserves will need lions when. There also needs to be an accreditation process for reserves in terms of the handling of lions in order to ensure that the lions which come onto the reserve meet the tourism requirements of the reserve (*e.g.* habituated to vehicles) and have not been mistreated. For example, the boma conditions and feeding within the bomas should meet a minimum industry-wide standard, further developing on the guidelines set out by van Dyk (1997; summarized in Box 1).

Trophy hunting of lions is legal in South Africa and is used on some reserves as a management tool (Kettles & Slotow 2009; Slotow & Hunter 2009). The economic benefit that results from hunts can then be reinvested into the conservation initiatives of the reserve. However, not all reserves are allowed to hunt due to legislation (*e.g.* protected areas in KZN, SANParks), and even those that can legally hunt may choose not to due to ethical concerns (Kettles & Slotow 2009) and potential negative consequences for tourism. Photo-tourists often see hunting as a negative activity, with hunting being the least preferred option for lion removal in a poll by Vartan (2001). If a reserve does choose to implement hunting, it should only be applied as an intervention that simulates a natural population process and not exploited purely for financial gain. Thus, trophy hunting can be used to remove excess mature lions if it fits within the ethos of the reserve.

Euthanasia is already used (Kettles & Slotow 2009) and was considered a viable method of management intervention by the majority of reserves polled in 2007 (Slotow & Hunter 2009). The method of euthanasia is critical as euthanasia in the presence of other pride members could cause stress. If the animals are to be shot this should ideally be done when only a small subgroup of a pride is present. Another option is to first anaesthetize the target individuals, and then euthanase them either chemically or with a rifle once separated from the pride.

Managers should be cautious to use euthanasia as a quick fix, rather than addressing the underlying cause of overpopulation. This is indeed a growing tendency in small reserves in South Africa (Miller & Funston 2014), as fewer translocation opportunities exist and contraception options are neither fully understood nor applied. Group members also report that euthanasia causes conflict

Box 1. Boma recommendations (summarized from van Dyk 1997)

It is essential that all lion introductions involve a holding period within a boma before release onto the reserve. This allows the lions to recover from the stress and trauma of the capture and transport and from the drugs used in the relocation. It provides time for acclimatization to new surroundings and possibly new pride members. In the case of lions captured from unfenced areas, it allows them to learn to respect electric fences.

Fence: Bonnox or diamond mesh; inward folding half metre apron, pegged and rock-packed; inside electrification at least five live strands using large bobbins, with three in the lower metre; outside electrification.

Roads: Three metre road/clearing inside and outside of fence; for access and as a firebreak.

Location: Centrally located, preferably near a main road, but not visible to tourists, to allow ease of access and habituation to traffic noise. For larger reserves where more than one pride may be released, having a second boma in a different part of the reserve could reduce confrontation following a second release.

Habitat: Open grassland for good visibility with a few small thickets for shade, shelter and cover.

Size: 60 m × 80 m is large enough for a small pride; extension should be made to the length only if possible to ensure a maximum distance of 30 m from the fence to any animal – a reasonable distance for a darting from outside the boma if required.

Water: A 1 m × 1 m shallow (<30 cm deep) trough with raised edges (to prevent fouling by sand and vegetation), located close to the fence for easy visibility from outside the boma and away from the feeding/immobilizing areas. Filling can be controlled by a ball valve or, preferably, from outside the fence. It should be easily drained and cleaned (although cleaning should be avoided during the habituation period to prevent stress to the lions). It is ideal if the trough is empty when animals are drugged.

Parasites: Lions should be treated for internal and external parasites to reduce the stress on the animals and limit the build-up of parasites within the boma over time.

Introduction into boma: Immobilized lions should be placed in shade and allowed to wake up quietly. A carcass should be provided and the animals should not be disturbed for at least the first 24 hours. Long-acting tranquilizers (*e.g.* Clopixol Acuphase®) have been used on wild-caught lions to aid the habituation to fences as well as to introduce non-related lions to each other.

Feeding method: Extreme care should be taken to ensure lions do not form an association between food and people or vehicles. A screen (not covering more than two sides of the boma) should be used to block any visual cues related to feeding. One successful approach is to hoist carcasses up to a tower (from behind the screen) and allow them to slide down a cable into the boma (or even better, lower the carcass in to reduce the disturbance). Feeding repeatedly in the same place can allow for darting from behind the screen as well. More recent developments include a fenced and screened 'feeding camp' that is attached to the boma. A carcass can then be placed in the closed feeding camp and the gate to the main boma opened from outside the boma. The carcass can be chained to the feeding camp to assist in darting or left unchained to allow the lions to drag the carcass into the main boma for less stressful feeding. The feeding camp is both cheaper to build and easier to use than the original hoisting tower method. If darting from outside the boma without compromising habituation is not an option, a carcass containing a sedative, such as Dormicum® can be used. A dose of 150 to 300 mg per lion has been used successfully to sedate lions to make them more approachable and easier to dart. Extreme caution should be exercised when approaching sedated lions as they lose their fear of humans and are unpredictable.

Feeding frequency: Animals should not be overfed in the boma. Twice weekly feedings are recommended to allow the lions to experience hunger which should lead to them testing the fence and 'learning' about electrification.

Food: Whole, ungutted carcasses should be used to prevent any nutritional problems from developing. Smaller animals (such as impala or warthog) are preferred to prevent the need to clean the boma during the habituation.

Vehicle habituation: Habituation to vehicles while in the boma is essential for effective post-release monitoring, future immobilizing (*e.g.* for collar changes/removals) and tourism viewing. Including a road around the boma in the design facilitates this as vehicles can be driven around the boma with increasing frequency during the habituation process. An unoccupied vehicle can also be left outside the boma for extended periods. There should be no need to drive a vehicle within the boma at any time. There should be no exposure to humans on foot at any time to reduce stress and prevent loss of inherent fear of humans on foot.

Release from the boma: There is no set length of time for holding lions in a boma before release onto the reserve. Younger lions tend to habituate faster than older lions. Six to eight weeks is probably sufficient in most cases, but if the lions are not thought to be sufficiently bonded, habituated or fence-aware, a longer time may be required. Lions have been held in a boma for up to four months on Pilanesberg NP with no apparent adverse effects on hunting ability or fitness. Lions should be allowed to leave on their own and not chased out of the boma, it is not important that they all leave at once. A carcass can be dragged through the entrance of the boma and chained to a tree outside the boma to entice the lions out (it is important to chain it or the lions may drag it back into the boma). If other lions are known to be in the area, the release should be delayed until they have moved off.

with the tourism operators in the reserves, and has the potential to attract criticism from the general public similar to that of trophy hunting (pers. obs. authors). Euthanasia should be used as a last resort and reserve managers should apply other population control methods, in a similar manner to that outlined in the Norms and Standards for the Management of Elephants in South Africa (DEAT 2008), wherever possible. Euthanasia may be minimized by having a network of reserves communicating on a regular basis, whereby a particular reserve might take some excess animals from another reserve when needed for genetic purposes (see above).

There are many ethical concerns regarding euthanasia and contraception. Having put up fences and reintroduced lions, humans have a responsibility to manage these lion populations ethically on both an individual and a population level. Due to the high cub survival rates and the challenges and ethics associated with mimicking naturally lower cub survival, it may be best to reduce the number of cubs being born (while still allowing as many females as possible to breed). This can be done through reducing litter size and/or limiting the number of litters a female has through a contraception programme as outlined above. This should reduce the number of 'excess' lions while still allowing animals to reproduce and pass on their genes. Older animals that have had a chance to breed may still need to be removed from (through euthanasia or hunting) to mimic process in natural systems. Any euthanasia should be done as ethically as possible (see description above).

Genetic integrity

Bjorklund (2003) calculated that a minimum of 50 prides with unlimited dispersal is required for the genetic viability of a lion population. If all of the reserves in South Africa with lions were managed collectively, this minimum would be exceeded and translocation could be used to mimic the natural movement of individuals, thus ensuring the genetic integrity of the population as a whole. A similar approach is being implemented for the management of the wild dogs in South Africa (reviewed by Gusset *et al.* 2008; Davies-Mostert *et al.* 2009). At present, a full understanding of the genetic status of lions in small reserves in South Africa is not known. A study is under way to determine the heterogeneity of the populations and to assess the origin and degree of relatedness of lions in the various small reserves following which recommendations will be made. A studbook is also being established to aid in this aspect of lion management. DNA samples (blood, tissue or hair) should be collected from animals whenever they are immobilized to aid in decisions regarding genetic management (as suggested by Hayward *et al.* 2007b).

Disease

Sound management does require knowledge of the disease status of source or destination populations. Consequently, it is important to define the disease profiles of lion populations. Animals should be tested for known diseases and available vaccinations administered whenever possible (*e.g.* when immobilized for other purposes). When translocating animals, this would include vaccination for rabies, canine distemper, feline herpes and feline calici viruses. Additionally, a BTb skin-test should be done if they are being moved from an area where BTb is known to occur. Lions should be treated for tapeworms (to prevent measles). FIV serotypes should also be determined for use in linking to other disease outbreaks. FIV serotypes can also aid in historical genetic origin studies (as done by Antunes *et al.* 2008).

SYNTHESIS AND MANAGEMENT IMPLICATIONS

The management guidelines outlined here are intended to aid managers in overcoming the challenges of managing lions in small reserves. If applied to current populations they should address the issues of ecological restoration, genetic degradation and increased susceptibility to catastrophic events outlined earlier in this paper. These guidelines are the first step in developing a national management plan that would see integrated practices implemented within a network of reserves across the country.

Participation should be enabling, and follow agreed norms with accreditation for compliance at different levels of engagement within the national strategy. The overall plan would have to be centrally supported around databases and models. These should include first and foremost a sound ecological process based set of guidelines supported by establishing features such as a studbook (which has been established, although it is not complete) and using risk–benefit analysis inclusive of ethical, financial and logistical constraints.

These guidelines are a starting point that will be updated with continuous, critical assessment based on results from implementation across reserves (experiential learning). Thus, the effectiveness of these guidelines will only be realized if reserves work together and learn from each other's experiences (Slotow & Hunter 2009). The LiMF serves as a platform for this communication and collaboration. We are currently developing a management framework/guideline for decision-making. We envisage an adaptive management framework as is explained in Biggs *et al.* (2008) in which various aspects of the proposed guidelines are implemented on reserves across the country together with appropriate monitoring and follow up to allow for a scientific assessment of the outcomes. This would involve behavioural, population and systemic responses that would then be used to improve the guidelines, and ultimately, lion management on small reserves in South Africa.

Official 'Norms and Standards' should follow in line with the government's 'Norms and Standards for Biodiversity Management Plans (BMP)' (DEAT 2009) and include all lions in South Africa, not just those in small populations. A BMP would also satisfy the recommendations of the IUCN/SSC Cat Specialist Group (2006) that all nations with lions develop their own National Action Plan to ensure the successful conservation of lions in Africa.

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