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Inbreeding and density-dependent population growth in a small, isolated lion population

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Abstract

In South Africa, more than 30 small, enclosed game reserves have reintroduced lions over the last two decades, which now house more than 500 individuals. There is a high risk of inbreeding in these fragmented, fenced and isolated populations, which may be compounded by a lack of management guidelines. A population of 11 founder lions *Panthera leo* was reintroduced to Madikwe Game Reserve in 1995, and this population has in turn become a source for reestablishing other populations. Only four lineages were reintroduced, founder males were related to founder females, and since 1997, only one male lineage maintained tenure for >9 years, resulting in breeding with direct relatives. Interventionist management to limit lion population growth and inbreeding in Madikwe has taken the form of translocating, trophy hunting and culling of mainly sub adult lions. Despite this management, inbreeding started 5 years after reintroduction. Reproductive performance and thus population growth in Madikwe were dependent on the overall lion population density. When lion density was low, females first gave birth at a significantly younger age and produced larger litters, resulting in a high population growth rate, which decreased significantly when lion density in the park reached carrying capacity, that is, 61 lions. This might have profound consequences for future reestablishment of lion populations when restocking new reserves: our study illustrates the need for founder populations of reintroduced endangered predator species to be as large and genetically diverse as possible, and thereafter new genetic material should be supplemented. The development of such management guidelines is becoming very important as large predator populations become increasingly fragmented and managed as metapopulations.

Introduction

Over the last 30 years, there has been a rapid increase in the number of small ($<1000\,km^2$), enclosed reserves in South Africa, many of which have been established for eco-tourism and for biodiversity conservation (Hayward *et al*., 2007*a*). The development of the eco-tourism industry and the creation of new, privately owned wildlife reserves led to a demand for the reintroduction of lions *Panthera leo* and other large carnivores such as wild dog *Lycaon pictus* and spotted hyena *Crocuta crocuta* (Hofmeyr *et al*., 2003; Lindsey *et al*., 2005; Hayward *et al*., 2007*a*; Hunter *et al*., 2007; Gusset *et al*., 2008; Slotow & Hunter, 2009).

Reintroduction techniques to establish lion populations in new reserves have been developed and the success rates have been very high (Linnell *et al*., 1997; Druce *et al*., 2004; Hayward *et al*., 2007*a*; Hunter *et al*., 2007; Slotow & Hunter, 2009). Well-fenced boundaries to avoid conflict with humans restrict natural migration and recolonization, necessitating managers to manipulate these populations to maintain genetic diversity and regulate population growth rate. To date, only population growth management has been substantively applied (Kettles & Slotow, 2009). In lions, typically such manipulations include controlling pride size and numbers, maintaining paired male coalitions to minimize male–male fighting, capture and removal of mainly sub adult lions, trophy hunting and culling (Kettles & Slotow, 2009; Slotow & Hunter, 2009). Most reintroduced populations are small and will suffer serious genetic problems from inbreeding depression within a few generations unless immigrants from other populations are brought in (Frankham, 2009). Inbreeding depression has been reported in lions in small reserves in South Africa (Trinkel *et al.*, 2008), but also in terrestrial predators both in captivity and in the wild, including grey wolves (Laikre & Ryman, 1991; Liberg *et al.*, 2005), Mexican wolves (Frederickson & Hedrick, 2002), Florida panther (Pimm, Dollar & Bass, 2006) and lion (Packer *et al.*, 1991*b*). In fact, inbreeding has deleterious consequences on all aspects of reproduction and survival (Frankham, Ballou & Briscoe, 2002; Keller & Waller, 2002) and has been shown to be problematic in large mammals, for example, devil facial tumour disease decimating the Tasmanian devil is causing the species to become inbred, potentially hastening its extinction (McCallum, 2008).

In South Africa, 37 reserves have reintroduced lions, which now house over 500 lions (Slotow & Hunter, 2009). However, many of these isolated lion populations display decreased genetic variability (Grubbich, 2001), which may be due to a lack of guidelines on how to manage these populations effectively (Frankham, 2009; Slotow & Hunter, 2009). Without such broader contextualization, these populations may be of limited value for the conservation of this species (Slotow & Hunter, 2009).

Lions were reintroduced into Madikwe Game Reserve in 1995. They formed the second largest population of reintroduced lions in South Africa after the Hluhluwe-Imfolozi Park, and have been a source to reestablish lion populations in more than 15 reserves. Here, we describe the population and breeding dynamics of this reintroduced, intensively managed lion population over 10 years since founding. Specifically, we (1) assess the population dynamics, population growth and inbreeding of this managed lion population; (2) analyse reproductive performance and population growth rate relative to the overall population density. Based on our results, we suggest management strategies to establish and maintain the genetic diversity of isolated lion populations, which could make a substantial contribution to the conservation of this species.

Methods

Madikwe Game Reserve (620 km^2) is situated in North West Province, South Africa (24.79°S; 26.30°E), with a mean annual rainfall ranging from 475 to 520 mm. The major habitats vary from Mixed Kalahari Thornveld and Shrub Bushveld in the north to Mixed Bushveld in the south (Acocks, 1988). The entire perimeter of Madikwe is surrounded by an electrified fence and borders on densely populated rural communities and commercial farms. The reserve was established in 1992, followed by the largest reintroduction of wildlife ever, Operation Phoenix (Hofmeyr *et al.*, 2003). Prey density was >20 prey animals km^{-2}, when lions, wild dogs and spotted hyenas were reintroduced into Madikwe in 1995 and 1996 (Hofmeyr *et al.*, 2003). The carrying capacity for lions in Madikwe was calculated according to Hayward, O'Brien & Kerley (2007*b*), where prey biomass and the lions' preferred prey species were taken into consideration. The carrying capacity was 61 animals, corresponding to a lion density of 0.10 lions km^{-2}, which is comparable to but slightly higher than the average density of lions in Kruger National Park, South Africa (Bauer & Van Der Merwe, 2000).

In 1995 and 1996, 11 lions were reintroduced into Madikwe, three from Etosha National Park, Namibia and eight from Pilanesberg National Park, South Africa. All Pilanesberg lions were originally sourced from Etosha National Park. In general, the lions sourced from Etosha, came from different prides, living in territories that were up to 200 km apart from each other. Thus, lions reintroduced into Pilanesberg and/or Madikwe were unlikely to be closely related to each other. The age of the reintroduced lions ranged from 12 months to 5 years. Lions were identified from whisker-spot patterns (Pennycuick & Rudnai, 1970), natural markings (Packer *et al.*, 1991*b*) and VHF radio collars (Africa Wildlife Tracking, Pretoria, South Africa). Radio collars were fitted to selected individuals so that each group of lions had one collared animal present, with collars being placed onto new groups as they formed. Collars were replaced in a group before they expired. All individuals in the population were individually known, and transponders were implanted under the skin of each individual when first immobilized. Most individuals were also branded with a unique identifier. Individual lions were located one to three times every 10 days. Observations included the identity and number of individuals, the date and location of each lion sighting, the associations between lions and the reproductive status. The extents of lion territories were estimated on the basis of territorial clashes, scent-marking activities and defended kills (Schaller, 1972). Because females hide their cubs until they are 4–6 weeks old (Schaller, 1972; Pusey & Packer, 1987), the initial litter size cannot be known with certainty and birth dates of cubs were estimated. As DNA analysis has shown that behavioural estimates of maternity are highly accurate (Packer *et al.*, 1991*a*), the estimated age of cubs and their association with lionesses were used to assign maternity. Packer *et al.* (1991*a*) also showed that the resident male coalition fathers all cubs in their pride.

The population reintroduced into Madikwe consisted of five females and six males (Table 1, Fig. 1). The females came from two lineages: (1) two sisters (F1/F2); (2) one female (F3) with four 12-month-old cubs (two females F4/F5 and two males M2/3) (Table 1, Fig. 1). Three of the six founder males were related to the founder females: M1 and F1/2 were presumed to be half-siblings as, although of different age, they were caught as sub adults in the same pride in Etosha. The two males (M2/3) were the sons and brothers of F3 and F4/5, respectively. The brother coalitions M4/5 and M6 were not related to any other lions. Prides formed by the founder females were termed 'pride 1a' (F1/2) and 'pride 2a' (F3/4/5). Female offspring of these two lineages, which established their own prides, were termed 'pride 1b', 'pride 1c', etc. and 'pride 2b', 'pride 2c', etc., respectively (Fig. 2a–e).

From 1996 until early 1997, M1 held tenure over both reintroduced female prides (Fig. 2a). The two young brother coalitions, M2/3 and M4/5 (two and two and a half years old), and the lone male M6 did not have access to any females (Fig. 2a). In the beginning of 1997, M1 was ousted

Table 1 Details of lions *Panthera leo* reintroduced in Madikwe Game Reserve between 1995 and 1999

Reintroduction	Group composition	Individual ID	Relatedness among group members	Source population	Date of release
1	Two females	F1/F2[a]	Two sisters	Pilanesberg	July 95
	One male	M1[a]	Brother of F1/F2	Pilanesberg	
2	One female	F3[a]	Mother of F4/F5, M2/M3	Pilanesberg	September 95
	Two females	F4/F5	Daughters of F3	Pilanesberg	
	Two males	M2/M3	Sons of F3	Pilanesberg	
3	Two males	M4/M5	Two brothers	Etosha	January 96
	One male	M6	Unrelated to all	Etosha	March 96
4	One male	M7	Unrelated to all	Pilanesberg	July 98

[a]Originate from Etosha National Park.

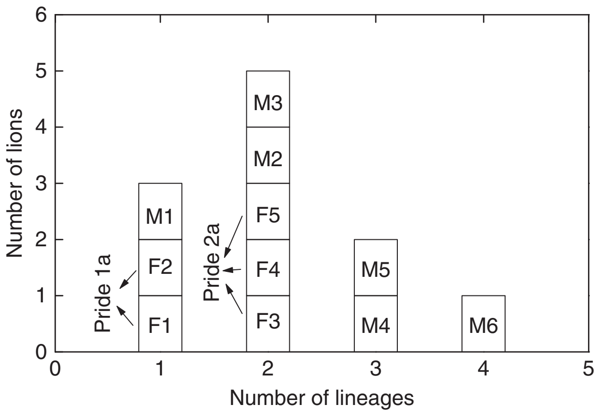

Figure 1 The population reintroduced into Madikwe consisted of five females (F1–F5) and six males (M1–M6) coming from four lineages.

from both prides. M2/3 took over pride 1a; M4/5 took over pride 2a. M6 was killed by a Cape buffalo *Syncerus caffer* in 1997. In 1998, two females born in pride 2a established a new pride (pride 2b) in the vicinity of their natal area, which was also taken over by M4/5. M1 was pushed back into areas where no females resided, and after being on his own for about 1 year, was joined by his two sons (Fig. 2b). During 2000, M4/5 shifted their territory out of pride 2a's area, and took over pride 1b, consisting of two females, which established a territory close to their natal pride. As a result, by the end of 2000, M1 and his sons held tenure of both prides 2a and 2c, comprising three females in total. M2/3 remained with pride 1a (Fig. 2c). In 2001, M1 died from old age and his two sons were trophy hunted. By the end of 2002, M4/5 were holding tenure over three prides (1b, 1c, 1d) consisting of five females. M4/5 expanded their territory and forced pride 1a associated with M2/3 to move out of their area. As a result, M2/3 were moving into the territory of their natal pride 2a (Table 1, Fig. 1). To prevent inbreeding, park management decided to trophy hunt M2/3 in 2003. In 2002, two young brother male coalitions born in Madikwe and fathered by M2/3 and M4/5 (sons 'a') and one lone male (M7), translocated into Madikwe in 1998 to supplement new genes into the existing population, were attempting to access females. Finally, the sons of M2/3 and M7 took over pride 2b and pride 2c, respectively. Sons 'a' of M4/5 were in an area where no females were resident (Fig. 2d). In 2005, M7 and the sons of M2/3 were trophy hunted. Towards the end of 2005, M4/5 controlled six prides (pride 1b–1g) consisting of 10 females. Three other two-male coalitions, all fathered by M4/5 (sons 'b', 'c', 'd'), had limited access to females (Fig. 2e).

Population growth rate and reproductive performance, including age of first reproduction, inter-birth interval and litter size, were determined for two different time periods: (1) from 1995 until the end of 2000, when lion numbers increased; (2) from 2001 until the end of 2005, when lion numbers were kept constant. Inbreeding coefficients were calculated using the software package FSpeed 2. To measure the effect of inbreeding on reproductive performance, mean litter size was calculated for (1) inbred pairings, that is, females mating with known related males; (2) pairings involving unrelated individuals. Population stability was maintained by management interventions such as removing sub adults by translocation to other reserves, trophy hunting of mainly adult males and culling. The population growth rate was calculated according to the following equation, where Pl (x) is the number of lions in year x, $\mathrm{Pl}_{\mathrm{rem}}$ (x) is the number of lions removed in year x and Pl ($x-1$) is the number of lions in year $x-1$.

$$\text{Population growth rate} = [\mathrm{Pl}(x) + \mathrm{Pl}_{\mathrm{rem}}(x)]/\mathrm{Pl}(x-1)$$

To determine the available biomass per lion over the years, prey density and prey biomass in Madikwe were derived from a model designed for the description of predator–prey systems in which the prey has an age-specific vulnerability to predation (Steward, 2006). In this model, seven of the most abundant and most relevant ungulates in terms of showing the effects of predation in Madikwe (Hayward *et al.*, 2007*c*) were chosen for the modelling process. These were warthog *Phacochoerus africanus*, blue wildebeest *Connochaetes taurinus*, greater kudu *Tragelaphus strepsiceros*, impala *Aepyceros melampus*, zebra *Equus burchelli*, hartebeest *Alcelaphus buselaphus* and eland *Taurotragus oryx*.

Statistical analyses were performed using the MINITAB 15 software. The Student *t*-test was used to calculate differences in the population growth rate, age of first reproduction, inter-birth interval and litter size.

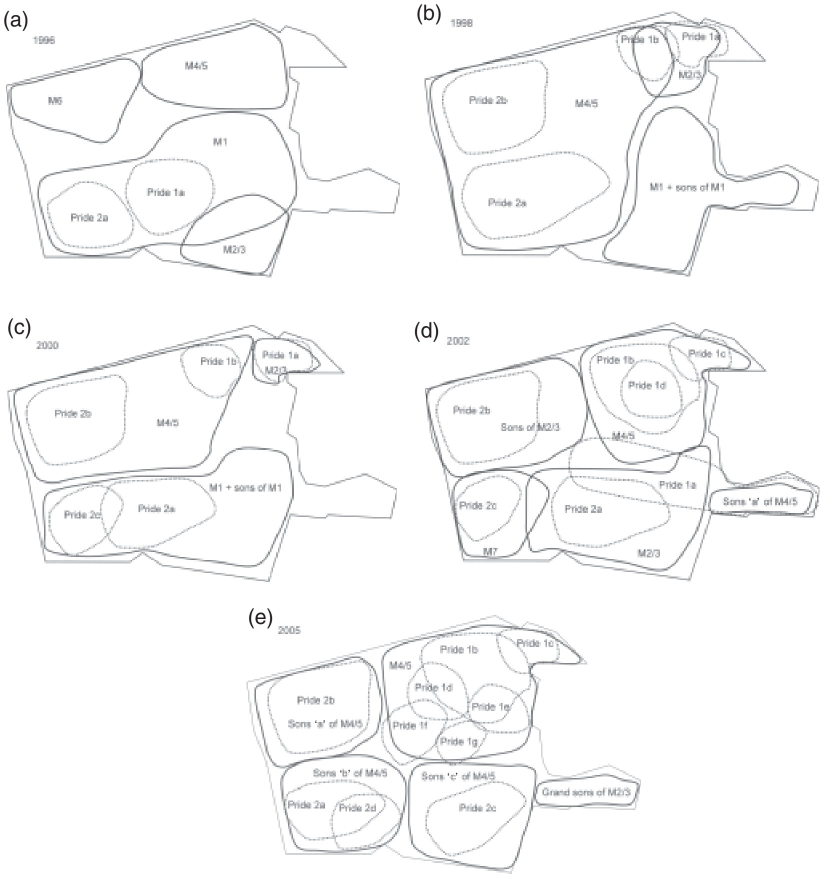

Figure 2 (a–e) Approximate ranges of reintroduced lions in the Madikwe game reserve from 1996 until the end of 2005. All female prides consisted of two females, except pride 2c, which consisted of only one female.

Results

Out of the founder population of 11 lions, four females and five males reproduced successfully; two animals died before they reproduced. By the end of 2005, 105 cubs had been born. Of these, 16 females and eight males (four two-brother coalitions) were kept in Madikwe and reproduced. Female prides were kept at a low size (one or two lionesses per pride) through management intervention, and similarly, males were reduced to a coalition size of two. Between 1995 and 2000, the period when lion density was increasing, there was a significant difference in the females' mean age of first reproduction (Table 2): eight females first reproduced at a mean age of 2.8 ± 0.4 years (range: 2.3–3.6 years), whereas between 2001 and 2005, the period when lion density was kept constant at about 0.10 lions km^{-2}, eight females first reproduced at a mean age of 3.8 ± 0.7 years (range: 3.0–4.9 years) (Student's *t*-test, $t = 3.33$, $n_1 = 8$, $n_2 = 8$, $P = 0.01$). There was no significant difference in inter-birth intervals (Student's *t* test, $t = 1.32$, $n_1 = 9$, $n_2 = 17$, $P = 0.20$) between the two time periods, but litter size (Student's *t* test, $t = -2.27$, $n_1 = 19$, $n_2 = 28$, $P = 0.03$) was significantly larger from 1995 to 2000 (Table 2).

Table 2 Reproductive performance of females from 1995 until the end 2000, when lion *Panthera leo* density was increasing and from 2001 to 2005, when lion density was kept close to carrying capacity by management interventions

	1995–2000	2001–2005
Mean age of first reproduction (years)	2.8 ± 0.4 (n=8)	3.8 ± 0.7 (n=8)
Mean inter-birth interval (years)	1.8 ± 0.4 (n=9)	2.0 ± 0.5 (n=17)
Litter size	3.4 ± 0.9 (n=19)	2.5 ± 0.7 (n=28)

Age of first reproduction (P=0.01) and litter size (P=0.03) of reintroduced females differed significantly between 1995–2000 and 2001–2005.

Whereas litter size was dependent on the overall lion population density, inbreeding did not have any effect on litter size during the period of this study: there was no significant difference in the litter size between inbred pairings (litter size = 3.0) and pairings involving unrelated individuals (litter size = 2.8) (Student's *t*-test: $t = -0.667$, $n_1 = 10$, $n_2 = 25$, $P = 0.51$). Males ($n = 4$ is not; $n = 10$) became resident in their first pride when they were 3.5 ± 0.4 years old (range: 2.8–4.1 years). Coalitions of two males ($n = 4$) remained in individual prides (usually one or two) for 4.1 ± 2.4 years (range: 1.9–6.3 years). However, one male coalition (M4/5) held tenure over a succession of prides for >9 years and produced cubs with 15 out of 20 breeding females. M4/5

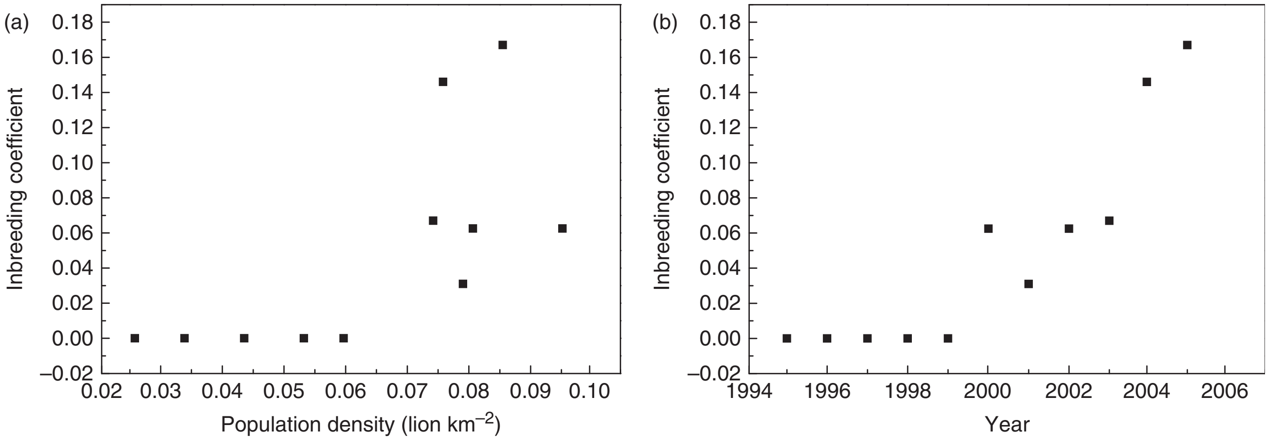

Figure 3 (a and b) The average inbreeding coefficient of the cubs born each year that were kept in Madikwe to reproduce was increasing with increasing population density from 2000 to 2005.

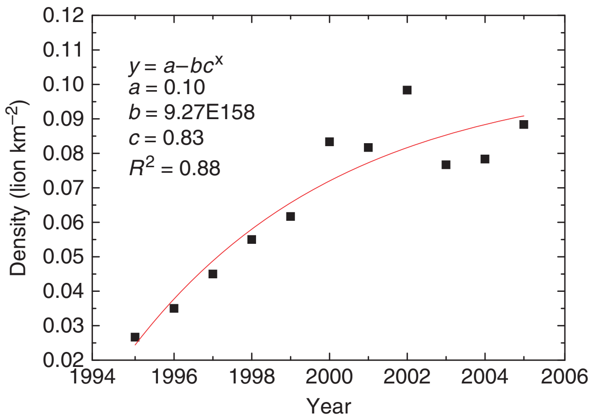

Figure 4 The lion density was increasing from lion reintroduction in 1995 until the end 2000, whereas from 2001 to 2005, the lion density was kept close to carrying capacity by management interventions.

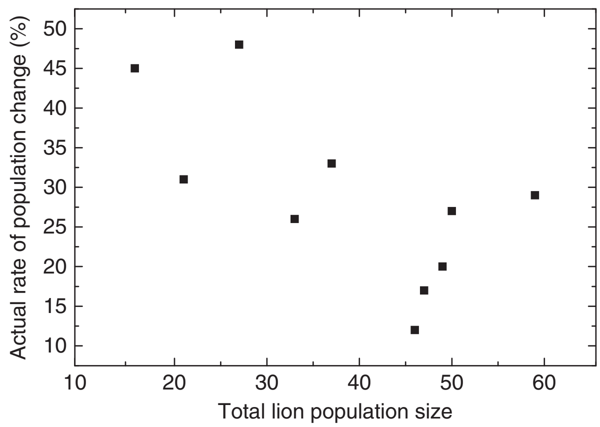

Figure 5 Annual rate of population change as a function of the total lion population size from 1995 until the end of 2005.

controlled up to six prides comprising 10 females, all of them from the same lineage (Fig. 2e). Since 2003, M4/5 have produced offspring with their daughters and grand daughters. In total, M4/5 sired a minimum of 57 cubs, followed by M2/3 ($n = 17$) and M1 ($n = 10$). Four male coalitions born in Madikwe fathered 21 cubs, all from matings with their mothers, sisters, grand mothers or half-sisters by their father. As a result of numerous incestuous matings, the average inbreeding coefficient of cubs born each year that were kept in Madikwe to reproduce increased with increasing population density from 0.0 in 1999 to 0.167 in 2005 (Fig. 3a and b).

Between 1996 and the end of 2000, the lion population increased, while from 2001 until the end of 2005, the lion population was kept constant by management interventions and totalled between 49 and 59 individuals, that is, 0.08–0.10 lions km^{-2} (Fig. 4). To reduce the lion population, 35 mainly sub adult animals were captured and removed to other small reserves, 16 were trophy hunted and seven individuals were culled. Sixteen lions died naturally. There was a significant difference in the population growth rate between the two time periods: from 1996 to 2000, the population growth rate was 1.38 ± 0.09 and from 2001 to 2005 the growth rate was 1.22 ± 0.11 (Student's t-test, $t = -2.61$, $n_1 = 5$, $n_2 = 6$, $P = 0.03$). As a result, a decrease in the annual rate of population change as a function of the total lion population size was observed (Fig. 5). Prey biomass increased from 1995 to 2000 and from 2002 to 2005. The decline in prey biomass in 1999, 2001 and 2002 was caused by removals of prey, in particular zebra and wildebeest, to other small reserves (Fig. 6). The available biomass per lion, however, decreased until 2000, whereas from 2001 onwards, the biomass per lion remained constant (Fig. 7).

Discussion

Madikwe Game Reserve reintroduced lions and other large carnivores for eco-tourism and biodiversity conservation. From a tourism perspective, the reintroduction of lions into

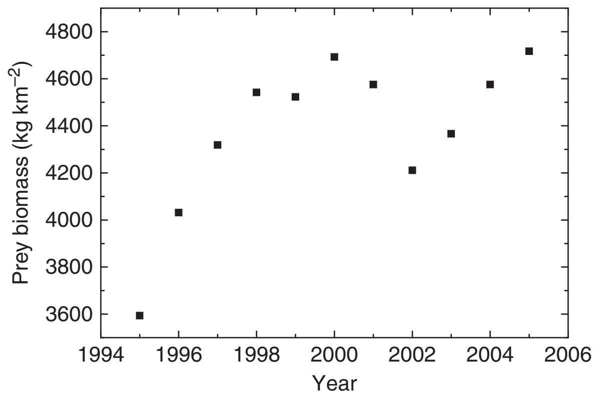

Figure 6 Prey biomass was increasing from 1995 to 2000 and from 2002 to 2005. The decline in biomass in 1999, 2001 and 2002 was caused by management interventions, that is, by removal of prey into other small reserves.

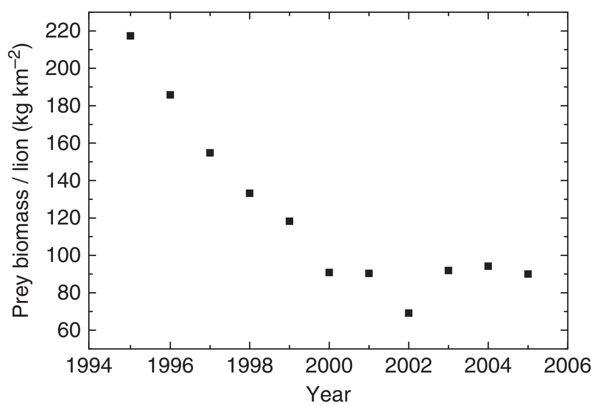

Figure 7 Prey biomass per lion was decreasing from 1995 to 2000, whereas from 2001 until 2005, prey biomass per lion remained constant.

Madikwe was very successful: lions were easy to reintroduce, they reproduced successfully and were frequently seen by tourists. Besides tourism, the translocation of excess individuals to other small reserves and trophy hunting provided additional income. However, the benefit for conservation is questionable as it is clear that substantive close breeding has occurred despite the interventionist management approach. When considered in the context that Madikwe is the second largest population of reintroduced lions, and fourth largest overall in South Africa, this casts significant doubt over the conservation value of the lion subpopulations in the other 30-odd reintroductions. Only five females from two lineages were reintroduced, founder males were related to founder females and since 1997, there has only been one unrelated male lineage in Madikwe that maintained tenure for $>$ 9 years, breeding with direct relatives.

The genetic diversity depends mostly on the size and the genetic diversity of the founder population, and thereafter on the rate at which new genes are supplemented into the population (Shaffer, 1987; Simberloff, 1988). However, the managers of Madikwe only introduced one new individual into the population in order to reduce costs and in an attempt to curtail population growth. This was compounded by the relatedness of individuals, as the founder population only contained four different lineages. Reintroduced lion population growth in these small reserves has been very high because of a high resource base (lack of starvation) and in most cases no infanticide (Killian & Bothma, 2003; Druce *et al.*, 2004; Hayward *et al.*, 2007*a*; Hunter *et al.*, 2007; Trinkel *et al.*, 2008; Slotow & Hunter, 2009).

An interesting aspect of our results is the apparent density-dependent effect on population growth, with reproductive performance, and thus population growth depending on the overall lion population density. When lion density was low, females first gave birth at a significantly younger age and produced larger litters. With increasing lion numbers, the age of first reproduction in Madikwe lionesses increased to be similar to that in large populations in southern and eastern Africa (i.e. those at carrying capacity; Smuts, Hanks & Whyte, 1978; Packer *et al.*, 1988). To our knowledge, this is the first time that density-dependent effects on litter size in lions have been recorded. Our results might indicate a population-level response to territory vacancies and per capita food availability. Similar inversely density-dependent effects have been reported for grey wolf *Canis lupus*, with litter sizes increasing with declining density due to higher availability of food (Rausch, 1967; Sidorovich, Tikhomirova & Jedrzejewska, 2003; Sidorovich *et al.*, 2007).

Given that Madikwe has one of the largest reintroduced populations, and that inbreeding could not be avoided, there are concerns about all small reintroduced populations in South Africa (Slotow & Hunter, 2009). Lion population sizes in these small reserves range from two in recently introduced populations up to 68 lions, with 20 reserves with ≥ 8 lions (January 2007 data from unpublished survey data reported in Slotow & Hunter, 2009). Although inbreeding took place, our study was too short for demographic changes to establish in the population. In fact, lions were shown to display conspicuous signs of inbreeding only after >20 years (Maddock *et al.*, 1996; Trinkel *et al.*, 2008).

However, to mitigate against inbreeding, firstly, as large as possible a founder population, with as many unrelated lineages, should be introduced (Frankham, 2009). When the founder population is close to carrying capacity, our data indicate that the relative growth rate should be lower.

Despite the management intervention in Madikwe, which was mainly to limit population growth, the reluctance of managers to remove the founder male lineages, which were key tourism animals, led to very high rates of close breeding. The ultimate consequences of frequent close breeding include impoverishment of genetic diversity (Packer *et al.*, 1991*b*) and ultimately in lions to lowered resistance to disease and reduced population growth rates (Kissui & Packer, 2004; Trinkel *et al.*, 2008). Only one new male was released into the population, who was not very successful as he sired only two cubs, because he could not successfully compete with the existing male coalitions. To introduce new genetic material, new lions, preferably paired young adult male coalitions, should be brought in, and existing males should be removed (Druce *et al.*, 2004; Trinkel *et al.*, 2008; Kettles & Slotow, 2009; Slotow & Hunter, 2009).

Finally, such an intervention to introduce new lineages should ideally be conducted in the context of a broader meta-population management plan, as in African wild dogs (Davies-Mostert, Mills & Macdonald, 2009), and should consider the longer-term conservation potential for this, and other populations (Slotow & Hunter, 2009). Such a meta-population approach has already been applied successfully for the reintroduction and management of wild dogs in South Africa (Akçakaya, Mills & Doncaster, 2006; Gusset *et al.*, 2008). In the short term, captive-breeding tools such as the use of studbooks can be helpful in reducing inbreeding. For example, a studbook is maintained in Madikwe and many other small populations, and when lions were removed from Madikwe, they were selected based on their known relatedness (e.g. daughters rather than mothers were removed). However, in the longer term, a major genetic intervention is still required, such as introduction on new bloodlines. Maintenance of studbooks is also resource intensive and costly (monitoring and immobilization).

The Madikwe lion population is one of the largest sources of Etosha lions outside the Etosha National Park. As the availability of lions from Etosha is very limited, we recommend to source lions from other large reserves such as the Kruger National Park or the Kgalagadi Transfrontier Park as both have large and genetically diverse lion populations (Smuts *et al.*, 1978; Mills, 1995). The reluctance of managers to introduce lions from areas other than Etosha is mainly due to the fact that Etosha lions are free from feline-immuno-deficiency virus (FIV). Although in fact Etosha lions are FIV free (W. Killian, pers. comm.), the disease was shown not to have any negative effects on wild lion populations (Packer *et al.*, 1999). The presence of bovine tuberculosis within the Kruger lion population represented another argument not to source lions from the Kruger National Park. However, lions can be screened easily for bovine tuberculosis before introduction (Keet *et al.*, 1996). Another reason for the reluctance of bringing in new lions and thus supplementing new genes into Madikwe was the managers' concern of the lions' impact on their prey. In Madikwe, however, decreasing zebra and wildebeest populations, with their decline starting 4 years after lion reintroduction, were mainly found to be the result of excessive removals of these prey species to other small reserves (Steward, 2006). Further, we have to stress that the removal of male coalitions and their exchange with new males would not result in any additional pressure on the lions' prey base. Consideration should be given to introducing male lions from the Kruger and/or Kalahari origin, which are now available (Slotow & Hunter, 2009), and potentially to removal of all male lions in the population at regular intervals to create a population with the highest potential to contribute to lion conservation in the region. Similar recommendations are likely to apply to other small reserves in South Africa having lions. This is of considerable importance as lions are listed as vulnerable both globally (IUCN, 2009) and nationally (Friedman & Daly, 2004).

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References

Acocks, J.P.H. (1988). *Veld types of South Africa*. 3rd edn. South Africa: Botanical Research Institute.

Akçakaya, H.R., Mills, M.G.L. & Doncaster, C.P. (2006). The role of metapopulations in conservation. In *Key topics in conservation biology*: 64–84. Macdonald, D.W. & Service, K. (Eds). Oxford: Blackwell Publishing.

Bauer, H. & Van Der Merwe, D. (2000). Inventory of free-ranging lions *Panthero leo* in Africa. *Oryx* **38**, 26–31.

Davies-Mostert, H.T., Mills, G.L. & Macdonald, D.W. (2009). A critical assessment of South Africa's managed metapopulation recovery strategy for African wild dogs and its value as a template for large carnivore conservation elsewhere. In *The reintroduction of top-order predators*: 10–42. Hayward, M.W. & Somers, M.J. (Eds). Oxford: Blackwell Publishing.

Druce, D., Genis, H., Braak, J., Greatwood, S., Delsink, A., Kettles, R., Hunter, L. & Slotow, R. (2004). Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *Koedoe* **47**, 103–118.

Frankham, R. (2009). Genetic considerations in reintroduction programs for large terrestrial predators. In *The reintroduction of top-order predators*: 371–387. Hayward, M.W. & Somers, M.J. (Eds). Oxford: Blackwell Publishing.

Frankham, R., Ballou, J.D. & Briscoe, D.A. (2002). *Introduction to conservation*. Cambridge: Cambridge University Press.

Frederickson, R. & Hedrick, P. (2002). Body size in endangered Mexican wolves: effects of inbreeding and cross-lineage matings. *Anim. Conserv*. **5**, 39–43.

Friedman, Y. & Daly, B. (Eds.). (2004). *Red data book of the mammals of South Africa: a conservation assessment: CBSG southern Africa*. South Africa: Conservation Specialist Group (SSC/IUCN), Endangered Wildlife Trust.

Grubbich, J.D. (2001). *Genetic variation within and among fragmented populations of South African lions Panthera leo:*

implications for management. MSc thesis, University of Pretoria, Pretoria.

Gusset, M., Ryan, S.J, Hofmeyr, M., van Dyk, G., Davies-Mostert, H.T., Graf, J., Owen, C., Szykman, M., Macdonald, D., Monfort, S., Wildt, D., Maddock, A., Mills, M.G.L., Slotow, R. & Somers, M. (2008). Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. *J. Appl. Ecol*. **45**, 100–108.

Hayward, M.W., Adendorff, J., O'Brien, J., Sholto-Douglas, A., Bissett, C., Moolman, L.C., Bean, P., Fogarty, A., Howarth, D., Slater, R. & Kerley, G.I.H. (2007*a*). Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. *Open Conserv. Biol. J*. **1**, 1–11 (Online DOI: 10.2174/1874-8392/07). Available at http://www.bentham-open.org/pages/content.php?TOCONSBJ/2007/00000001/00000001/1TOCONSBJ.SGM.

Hayward, M.W., O'Brien, J., Hofmeyr, M. & Kerley, G.I.H. (2007*b*). Testing predictions of the prey of lion derived from modeled prey preferences. *J. Wildl. Mgmt*. **71**, 1567–1575.

Hayward, M.W., O'Brien, J. & Kerley, G.I.H. (2007*c*). Carrying capacity of large African predators: predictions and tests. *Biol. Conserv*. **139**, 219–229.

Hofmeyr, M., Davies, R., Nel, P. & Dell, S. (2003). Operation Phoenix – the introduction of larger mammals to Madikwe Game Reserve. In *Madikwe game reserve: a decade of progress*: 8–20. Brett, M. (Ed.). Rustenberg, South Africa: North West Parks & Tourism Board.

Hunter, L., Skinner, J.D., Pretorius, K., Carlisle, L.C., Rickelton, M., Walker, C. & Slotow, R. (2007). Reintroducing lions *Panthera leo* to northern Kwazulu-Natal, South Africa: short-term biological and technical successes but equivocal long-term conservation. *Oryx* **41**, 196–204.

IUCN. (2009). *IUCN Red List of Threatened Species, Version 2009.2*. Available at http:// www.iucnredlist.org (accessed 03 November 2009).

Keet, D.F., Kriek, N.P.J., Penrith, M.L., Michel, A. & Huchzermeyer, F. (1996). Tuberculosis in buffaloes (*Syncerus caffer*) in the Kruger National Park: spread of the disease to other species. *Onderstepoort J. Vet*. **63**, 239–244.

Keller, L.F. & Waller, D.M. (2002). Inbreeding effects in wild populations. *Trends Ecol. Evol*. **17**, 230–241.

Kettles, R. & Slotow, R. (2009). Management of free-ranging lions on an enclosed game reserve. *S. Afr. J. Wildl. Res*. **39**, 23–33.

Killian, P.J. & Bothma, J.du P. (2003). Notes on the social dynamics and behaviour of reintroduced lions in the Welgevonden Private Game Reserve. *S. Afr. J. Wild. Res*. **33**, 119–124.

Kissui, B.M. & Packer, C. (2004). Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proc. Roy. Soc. Lond. Ser. B* **271**, 1867–1874.

Laikre, L. & Ryman, N. (1991). Inbreeding depression in a captive wolf (*Canis lupus*) population. *Conserv. Biol*. **5**, 33–40.

Liberg, O., Andren, H., Pedersen, H.C., Sand, H., Sejberg, D., Wabakken, P., Akesson, M. & Bensch, S. (2005). Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biol. Lett*. **1**, 17–20.

Lindsey, P.A., Alexander, R., Du Toit, J.T. & Mills, M.G.L. (2005). The potential contribution of ecotoursim to African wild dog *Lycaon pictus* conservation in South Africa. *Biol. Conserv*. **123**, 339–348.

Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R. & Swenson, J. (1997). Translocation of carnivores as a method for problem animal management: a review. *Biodivers. Conserv*. **6**, 1245–1257.

Maddock, A., Anderson, A., Carlisle, F., Galli, N., James, A., Verster, A. & Whitfield, W. (1996). Changes in lion numbers in Hluhluwe-Umfolozi Park. *Lammergeyer* **44**, 6–18.

McCallum, H. (2008). Tasmanian devil facial tumour disease: lessons for conservation biology. *Trends Ecol. Evol*. **23**, 631–637.

Mills, G.M.L. (1995). Notes on wild dog (*Lycaon pictus*) and lion (*Panthera leo*) population trends during a drought in the Kruger National Park. *Koedoe* **38**, 95–99.

Packer, C., Altizer, S., Appel, M., Brown, E., Martenson, J., O'Brien, S.J., Roelke-Parker, M., Hofmann-Lehmann, R. & Lutz, H. (1999). Viruses of the Serengeti: pattern of infection and mortality in African lions. *J. Anim. Ecol*. **68**, 1161–1178.

Packer, C., Gilbert, D.A., Pusey, A.E. & O'Brien, S.J. (1991*a*). A molecular genetic analysis of kinship and cooperation in African lions. *Nature* **351**, 562–565.

Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Cairns, S.J., Hanby, J.P. & Borgerhoff-Mulder, M. (1988). Reproductive success in lions. In *Reproductive success*: 363–383. Clutton-Brock, T.H. (Ed.). Chicago: University of Chicago press.

Packer, C., Pusey, A.E., Rowley, H., Gilbert, D.A., Martenson, J. & O'Brian, S.J. (1991*b*). Case study of a population bottleneck: lions of the Ngorongoro crater. *Conserv. Biol*. **5**, 219–230.

Pennycuick, C. & Rudnai, J. (1970). A method of identifying individual lions, *Panthera leo*, with an analysis of the reliability of the identification. *J. Zool. (Lond.)* **160**, 497–508.

Pimm, S.L., Dollar, L. & Bass, O.L.J. (2006). The genetic rescue of the Florida panther. *Anim. Conserv*. **9**, 115–122.

Pusey, A.E. & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour* **101**, 275–310.

Rausch, R.A. (1967). Some aspects of population ecology of wolves. *Am. Zool*. **7**, 253–265.

Shaffer, M.L. (1987). Minimum viable populations: coping with uncertainty. In *Viable populations for conservation*: 69–86. Soule, M.E. (Ed.). New York: Cambridge University Press.

Schaller, G.B. (1972). *The Serengeti lion*. Chicago: University of Chicago Press.

Sidorovich, V.E., Stolyarov, V.P., Vorobei, N.N., Ivanova, N.V. & Jêdrzejewska, B. (2007). Litter size, sex ratio, and age structure of grey wolves, *Canis lupus*, in relation to population fluctuations in northern Belarus. *Can. J. Zool.* **85**, 295–300.

Sidorovich, V.E., Tikhomirova, L.L. & Jedrzejewska, B. (2003). Wolf *Canis lupus* numbers, diet, and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. *Wildl. Biol.* **9**, 103–111.

Simberloff, D. (1988). The contribution of population and community biology to conservation science. *Annu. Rev. Ecol. Syst.* **19**, 123–131.

Slotow, R. & Hunter, L.T.B. (2009). Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: African lion in South Africa. In *The reintroduction of top-order predators*: 43–71. Hayward, M.W. & Somers, M.J. (Eds). Oxford: Blackwell Publishing.

Smuts, G.L., Hanks, J. & Whyte, I.J. (1978). Reproduction and social organization of lions from the Kruger National Park. *Carnivore* **1**, 17–28.

Steward, A.E. (2006). *Modelling predator–prey relationships with re-established large carnivore populations*. MSc thesis, University of Pretoria, Pretoria.

Trinkel, M., Ferguson, N., Reid, A., Reid, C., Somers, M., Turelli, L., Graf, J., Szykman, M., Cooper, D., Haverman, P., Kastberger, G., Packer, C. & Slotow, R. (2008). Translocating lions into an inbred lion population in the Hluhluwe-iMfolozi Park, South Africa. *Anim. Conserv.* **11**, 138–143.