Animal Conservation. Print ISSN 1367-9430

Translocating lions into an inbred lion population in the Hluhluwe-iMfolozi Park, South Africa

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Keywords
lion; *Panthera leo*; translocation; inbreeding; population dynamics.

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Received 13 November 2007; accepted 24 January 2008

doi:10.1111/j.1469-1795.2008.00163.x

Abstract

A fundamental problem in conservation biology is the risk of inbreeding in fragmented and declining populations. In the Hluhluwe-iMfolozi Park (HiP), a small, enclosed reserve in South Africa, a large lion *Panthera leo* population arose from a founder group of five individuals in the 1960s. The HiP lion population went through a persistent decline and showed indications of inbreeding depression. To restore the genetic variation of the inbred HiP lion population, new lions were translocated into the existing population. Translocated females formed stable associations and established enduring pride areas with other translocated lionesses, but did not bond into native female prides. The translocated male coalition was more successful in gaining and maintaining residence in a pride than the translocated lone male that split off on his own from the male coalition. Litter size and cub survival was about twice as high for pairings involving at least one translocated parent than for pairings of two native lions. It is therefore possible to infuse new genes rapidly and successfully into a small, isolated lion population. Such translocations may become an important adaptive management tool as lion populations become increasingly fragmented.

Introduction

In recent 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. 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*. Reintroductions are now well-practiced techniques that are used to establish lion populations in new reserves (Killian & Bothma, 2003; Druce *et al*., 2004; Hunter *et al*., 2007). While reintroduction is an attempt to re-establish a species within its historical range, translocation refers to the addition of individuals taken from the wild to an existing population (IUCN/SSC, 1998). Translocations will become increasingly important in the future, as little or no dispersal of medium-sized to large vertebrates can occur within small fenced reserves, resulting in inbred populations (Packer *et al*., 1991*a*; Kissui & Packer, 2004) that will need to be actively managed to maintain genetic diversity (Grubbich, 2001).

In the Hluhluwe-iMfolozi Park (HiP), South Africa, a lion population established from a small group of founders in the 1960s started showing conspicuous signs of inbreeding by the early 1990s (Maddock *et al*., 1996; Stein, 1999). Lions at HiP showed little genetic variation and cub mortality was found to be higher than elsewhere in the wild (Stein, 1999). Records of abscesses, a generally poor condition and post-mortem evidence of reduced immune-competence were all thought to be associated with inbreeding in HiP lions (Stein, 1999). HiP management decided to introduce new lions into the existing population to increase genetic diversity, but there was no precedent for weighing the potential costs and benefits of alternative translocation strategies. Given the costs of immobilization and transport, one clear consideration is economic. In polygynous species such as lions, each translocated male that becomes a member of a small cohort would provide a more extensive infusion of fresh genetic diversity into a population than would a single translocated female. On the other hand, lions form complex social groups that are subject to considerable social disruption from intra-sexual competition through infanticide and eviction of young animals.

Lions live in permanent prides consisting of related adult females, their dependent offspring and a coalition of breeding males (Packer *et al.*, 1988). When new males first take over a pride, they kill or evict the dependent offspring of the prior coalition so as to mate with the pride females (Packer & Pusey 1987). In contrast to the potential impact of translocated males, adding new females to a pre-existing population will not be nearly as disruptive, provided there are unoccupied areas in the reserve. Although females are territorial (McComb, Packer & Pusey, 1994), they mostly compete against each other for high-value landscape features (Mosser, 2008) and only occasionally kill each others' cubs (Packer & Pusey 1987).

We therefore tested the advantages and disadvantages of three different types of translocation into HiP. First, we translocated a pride along with its resident coalition. Second, we translocated a pride of females. Third, we attempted to bond new females into pre-existing HiP prides. In this paper, we compare the reproductive success and mortality of each type of translocated lion with the HiP lions and describe how the new lions affected the native HiP lion population.

Materials and methods

Study area

HiP (900 km^2) is situated in KwaZulu-Natal, South Africa (between 28°00′ and 28°26′S, 31°43′ and 32°09′E), with a mean annual rainfall ranging from 608 to 709 mm. The major habitats vary from semi-deciduous forest in the north of Hluhluwe to open savanna woodland in the southern iMfolozi. Most of the area is covered with woodland savanna interspersed with shrub thicket. Topography is extremely rugged with altitudes ranging from 40 to 560 m above sea level. Perennial surface water is available on the major river systems, and ephemeral streams and waterholes often retain water until well into the dry season. Major rivers are the Black Umfolozi, the White Umfolozi and the Hluhluwe. The entire perimeter of HiP is fenced and borders on highly populated rural communities. As a result of the high human population density bordering the HiP, any lions that break out of the reserve have to be destroyed. New lions were translocated into HiP in different areas, that is in the northern Hluhluwe and in the iMfolozi.

The HiP lions

The native lion population of HiP descends from five individuals: a male who entered the park on his own in 1958 and two females with two cubs who were introduced into the reserve in 1965 from Kruger National Park, South Africa. The population increased to 140 individuals in 1987 (Maddock *et al.*, 1996). During the course of a herbivore reintroduction program, nearly all lions of the northern part of the park were shot between 1988 and 1992, with the result that no lions subsequently established permanent residence in the Hluhluwe area (Maddock *et al.*, 1996). In 1999, the HiP population consisted of about 80 lions (D. Balfour *et al.*, unpubl. data).

Translocation of lions

Between August 1999 and January 2001, 16 new lions were translocated into HiP from the Pilanesberg National Park ($n = 9$) and the Madikwe Game Reserve ($n = 7$), South Africa. The lions were sourced from Pilanesberg and Madikwe because: (1) they originated from Etosha National Park in Namibia, thus maximizing the genetic distance from the HiP population; (2) they were free from bovine tuberculosis *Mycobacterium bovis* (bTB); (3) they were already habituated to tourism activities; (4) the North West Parks and Tourism staff had experience in translocating lions; (5) the lions were available as a free donation. The age of the translocated lions ranged from 17 to 32 mos, and represented a number of different bloodlines (Table 1). All lions were captured by darting with 5 mg kg^{-1} of zolezapam-telitamine (Zoletil, Virbac, Carros, France) while feeding at a carcass. They were transported to HiP by air while immobilized with Zoletil. Upon arrival, they were kept in

Table 1 Details of lions *Panthera leo* released in the Hluhluwe-iMfolozi Park between 1999 and 2001

Release	Group composition	Individual ID	Relatedness among group members	Source population[a]	Date of release
1	Two females	F1	Two sisters	Pilanesberg (2)	August 1999
		F2			
	Two males	M1	Two brothers	Pilanesberg (2)	
		M2			
	One female	F3	Unrelated to all	Madikwe (1)	
	One male	M3		Madikwe (1)	
2	Two females	F4	Unrelated	Pilanesberg (1)	June 2000
		F5		Madikwe (1)	
3	Two females	F6	Unrelated	Pilanesberg (1)	September 2000
		F7		Madikwe (1)	
4	Four females	F8/F9	Unrelated to all	Pilanesberg (1)	January 2001
		F10/F11		Madikwe (3)	
	Two females	F12/F13	Two sisters	Pilanesberg (2)	

[a]Numbers in parentheses represent number of individuals originating from Pilanesberg and Madikwe.

0.5–1 ha acclimatization bomas with electric boundary fencing for 4–6 weeks. In the second and third release, native females were confined in the bomas with the translocated females in an attempt to bond them as pride mates. Before release from the bomas, VHF radio collars (Africa Wildlife Tracking, Pretoria, SA) were fitted to selected females ($n = 7$) and males ($n = 2$).

First release: Three male and three female lions were translocated as a mixed-sex pride to the northern part of HiP, where no resident lions had occurred since 1992. The intention was that these six lions should establish a female pride with an attendant male coalition.

Second release: Two females that were unfamiliar with each other were released into a boma located within a native pride range in the western iMfolozi, together with two of the eight females from that native pride. The intention was to bond translocated females into the existing lion population, making them part of an established pride.

Third release: Two females that were unfamiliar with each other were released into a boma located just outside a native pride range in the western iMfolozi, together with one female of a native pride comprising about eight animals. The intention was to bond translocated females into the existing lion population, making them part of that pride.

Fourth release: Six females were released into the southern iMfolozi with the intention that they should establish one pride. No native prides used that area.

Field data collection and observations of new and native lions

New lions were identified from whisker-spot patterns (Pennycuick & Rudnai, 1970), natural markings (Packer *et al.*, 1991*a*), radio collars and ear tags. Every translocated individual was located one to three times every 10 days. Our observations included the identity and number of individuals, the date and location of each lion sighting, the associations between new and native lions, body condition and reproductive status. The dense vegetation and therefore limited visibility in HiP made observations of behavioral interactions between resident and translocated lions impossible. Birth dates of cubs were estimated, but initial litter size cannot be known with certainty, because females hide their cubs until they are 4–6 weeks old (Schaller, 1972; Pusey & Packer, 1987). The estimated age of cubs and their association with lionesses were used to determine maternity, because DNA analysis has shown that behavioral estimates of maternity are highly accurate (Gilbert *et al.*, 1991). Packer *et al.* (1991*b*) also showed that the resident male coalition fathers all cubs in their pride. Reproductive success, defined as litter size and cub survival to first birthday, was measured from the date of the first release (August 1999) until the end of December 2004.

Native lions were individually fitted with VHF radio collars (Africa Wildlife Tracking, Pretoria, SA) ($n = 11$), and pride members were given a unique color ear-tag. All native adults were individually recognized with young lions being immobilized and individually identified as they matured (from about 6 months old). In addition to tracking the native lion population at least once every 10 days, the native HiP lions were surveyed by call-ups (Mills, 1985; Ogutu & Dublin, 1998) at 31 stations situated 5–10 km apart scattered throughout the park, and within the home ranges of all known lions. Each year, between 2000 and 2004, intensive call-ups were performed over a 16- to 21-day period, using tape recordings of spotted hyenas *Crocuta crocuta* mobbing lions, lions squabbling at a kill and the bleats of a distressed wildebeest *Connochaetes taurinus* calf or a bleating buffalo *Syncerus caffer* calf with breaks of 5 min between each play-back until the lions arrived at the calling stations. Information collected when tracking the native lions population and at each call-up included the number, age and sex of responding lions, body condition and reproductive status.

The mean litter size and cub survival were calculated for (1) inbred pairings, that is native females × native males and (2) 'out-crossed pairing', that is pairings involving translocated females × native males and native females × translocated males. Statistical analyses were performed with the MINITAB 15 software. The Student *t*-test was used to calculate differences in litter size and cub survival. A P-value < 0.05 was considered to be statistically significant.

Lions that died or were euthanized due to poor body condition, that is suffering from malnutrition, were tested for bTB by histopathological examination (Bengis *et al.*, 1996).

Result

Pride formation of new lions

During their time in the boma, the lions associated with each other without any overt signs of aggression. The translocations were designed so as to encourage the females to form four separate prides, but they instead split into six prides comprised of related and/or unrelated lionesses (Table 2). While the holding period fostered enduring associations between unrelated translocated females, the translocated females separated from the native female(s) immediately after being released from the boma (second and third release). However, one translocated female (F4) separated from another translocated female (F5) and established a new pride with a 2-year-old HiP female that she met for the first time after leaving the boma.

Except for two females that died within the first 3 mos of their release (F2, killed while hunting buffalo; F5, euthanized after breaking out of HiP), all translocated females established stable pride ranges over the study period. Translocated females associated with both translocated and HiP males.

The three males in the first release split into two groups: a coalition of two brothers, M1/M2, and one lone male, M3, who was unrelated to the male coalition (Table 1). After their release into the Hluhluwe area, M1/M2 as well as M3 remained with the translocated females until entering two native prides 1.5 years later (Table 2). No cubs were killed when M3 took over the native pride, because this pride did not have dependent cubs at that time. By the beginning of

Table 2 Pride formation of translocated females and associations between translocated and native lions *Panthera leo*

Release	Pride composition	Pride size	Association with males	Association period between males and females[a]
1	F1/F2[b]	1[b]	M1/M2	08/99–12/00
			M1/M2	Since 07/03
	F3	1	M3	08/99–04/01
			M1/M2	Since 07/03
2	F4/F5	2[b]	Native males[c]	07/02–03/04
	Native female		M4/M5/M6/M7	
3	F6/F7	2	Native males	07/01–06/04
			M8/M9	
4	F8/F9/F10	3	Native males[c]	Since 08/02
			M4/M5/M6/M7	
	F11/F12/F13	3	Native males	Since 08/02
			M8/M9	
–	Native pride 1	4	M1/M2	Since 09/01
–	Native pride 2	3	M3	05/01–01/04
–	Native pride 2	3	M1/M2	Since 06/04

[a]Association period until the end of 2004.
[b]The translocated females F2 and F5 died within 3 months after their release; F4 established a new pride with one native lioness.
[c]The native males M6 and M7 died during 2003; M6 and M7 were extremely emaciated.

2004, M1/M2 and their male offspring controlled four prides (two prides established by translocated females and two by native HiP prides), after M3 was ousted from a native HiP pride and killed. When the male coalition M1/M2 took over the two native prides, they killed seven dependent cubs. Two native HiP male coalitions became resident in the four translocated prides established by the second, third and fourth releases (Table 2).

Population dynamics of translocated and native HiP lions

Litter size and cub survival

Seven of the 11 surviving translocated females reproduced successfully; two disappeared before giving birth, and two did not give birth before the end of 2004. The seven breeding females first reproduced 23.1 ± 6.2 mos after release (range: 17–36 mos) at a mean age of 50.5 ± 7.1 mos (range: 41–61 mos). One lioness was pregnant when translocated and lost her litter about 3 weeks after release.

There was no significant difference in either litter size ($P = 0.49$) or cub survival ($P = 0.87$) between pairings involving translocated females × native males ($n = 5$) versus native females × translocated males ($n = 8$). However, 'out-crossed' pairings (translocated females × native males and native females × translocated males) produced significantly larger litters and higher cub survival than 'inbred pairings' (native females × native males) (Table 3).

Table 3 Mean litter size and mean cub survival of 'inbred' and 'out-crossed' pairings from 2000 until the end of 2004

	Sample size	Number of cubs	Litter size	Cub survival
Inbred pairings	13	20	1.5	0.31
Out-crossed pairings	13	40	3.1[a]	0.67[a]

[a]Litter size ($P < 0.01$) and cub survival ($P = 0.02$) of out-crossed pairings differ significantly from those of inbred pairings.

Mortality of adult lions

By the end of 2004, eight of the 16 translocated lions (seven females, one male) had died. One female was destroyed after escaping from HiP, two other females disappeared and were presumed dead and a fourth female was euthanized because she was emaciated; she tested negative for (bTB). Three other females died from natural causes.

Over the same time, nine of 84 native HiP lions died from bTB and 15 were euthanized because they suffered from severe malnutrition and thus were extremely emaciated. Many of them had developed large abscesses on their foreleg elbows. At least 40 more emaciated animals disappeared and are assumed to have died. In contrast to the poor health condition of many native animals, all translocated lions with the exception of one female, were in excellent body condition.

The HiP lion population

The native HiP population consisted of about 84 lions in 2000 but crashed to only 20 native individuals and their offspring by 2004, corresponding to 32% of the total population (Fig. 1). F1 offspring of translocated and native HiP lions totalled 29 individuals by the end of 2004 (47%), and the translocated lions and their offspring totalled 13 individuals (21%) (Fig. 1).

Discussion

Overall, the translocations into the existing lion population in the HiP were very successful. Of the three translocation techniques, only the attempts to integrate females into pre-existing prides were unsuccessful, although one of the females in this subset did ultimately join a native HiP female that she encountered after leaving the boma. The goal of this technique was to minimize social disruption by providing the incoming females with a set of companions who grew up in HiP, but we cannot recommend it for future translocations. Female pride mates are almost always close relatives (Packer *et al.*, 1991*a*) that live in a familiar pride area (Pusey & Packer, 1987). In our study, it appeared as if a cohesive social bond had developed between all translocated female lions while they were still in the boma, but many individuals separated after release. Thus, the newly established prides were much smaller than intended, consisting of only one to three females. Similar observations were made with re-

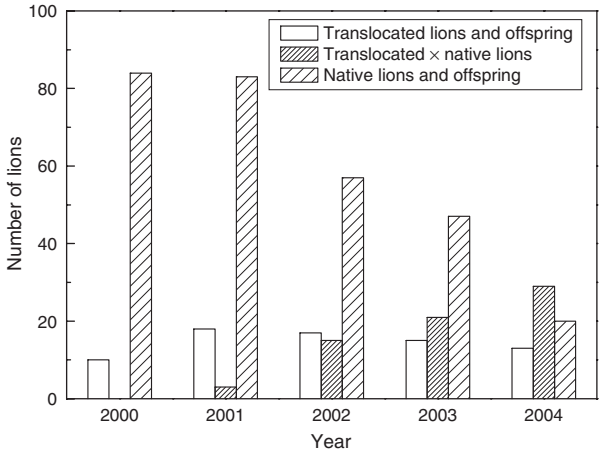

Figure 1 Number of translocated lions *Panthera leo* and their offspring, number of F1-offspring between translocated and native Hluhluwe-iMfolozi Park (HiP) lions and the number of native HiP lions alive each year between 2000 and 2004.

introduced lions in another small reserve in South Africa (Killian & Bothma, 2003): five lions were re-introduced and although they remained in the boma for 3 months, they split into two groups upon release. The pride sizes established by translocated females in HiP might reflect important environmental parameters, with females living as solitaries in the dense vegetation of the northern Hluhluwe and prides of two and three in the open habitat in the southern iMfolozi. Native HiP females also form larger prides in the open habitat of the southern iMfolozi while living in smaller prides in the thick vegetation of northern Hluhluwe (Trinkel *et al.*, 2007).

The three translocated males split into a pair and a singleton. As in other studies (Bygott, Bertram & Hanby, 1979; Packer *et al.*, 1988), the pair was more successful than the solitary, gaining residence in a pride more easily and maintaining residence for longer. Thus, even though the lone male and the pair sired similar numbers of offspring per male, cub survival was significantly higher for the pair than for the singleton. From our results, we suggest translocation of males in groups (i.e. in pairs) that are large enough to compete successfully against native males, but not so large that the coalition will divide after being released into the new reserve (i.e. trios).

Reproductive performance after the translocations provides compelling evidence that the native lions suffer from adverse effects of inbreeding. Fertility and cub survival were significantly higher in the out-crossed pairings and similar to lions translocated to the Phinda reserve (Hunter *et al.*, 2007). Despite our initial concerns about infanticide by translocated males, only two native HiP prides (consisting of four and five females) were taken over by the new males; thus, social disruption only affected about 10% of the HiP females' cubs.

The high adult mortality of the native HiP lions may also be linked to inbreeding in that inbred lions appear to be especially susceptible to infectious disease (Packer *et al.*, 1991*a*; Kissui & Packer, 2004), in this case bTB. Following the translocation of new lions into HiP, the native population crashed from 84 to 20 individuals. Most of the surviving lions descended from at least one translocated parent, and we predict that these descendants will soon replace the entire native stock. Thus, continued management will be essential to prevent future inbreeding. While new females should be retained for the rest of their reproductive lives, the translocated male coalition should eventually be replaced (Druce *et al.*, 2004). This pair is likely to enjoy a long tenure, sire a large number of half-siblings and full cousins and produce another genetic bottleneck. However, male replacement is sufficiently disruptive to require continued detailed knowledge of the HiP lion population so as to optimize the timing of any further male translocations.

We have demonstrated that new blood can be rapidly and successfully introduced into a small isolated lion population. Social disruptions were relatively minor (with $<10\%$ of cub mortality due to male infanticide), and translocated males produced three times as many cubs as each translocated female. On the other hand, translocated females established stable prides, and persistent (at least over the study period) out-bred bloodlines.

In South Africa, more than 30 fenced, small game reserves exist (Vartan, 2002; Killian & Bothma, 2003; Druce *et al.*, 2004; Hunter *et al.*, 2007). Lion populations closed to dispersal and immigration as a result of anthropogenic barriers may benefit from new genetic material via translocations. With biodiversity in mind, however, there are intentions to increase protected areas with the potential for connectivity that will have allowance for gene flow (D. Hofmeyr, pers. comm.). Besides these 'unnatural' situations where populations are fenced, there are natural reserves, for example the Ngorongoro Crater, East Africa, where little or no dispersal of medium-sized to large vertebrates can occur, resulting in an inbred lion population (Packer *et al.*, 1991*a*; Kissui & Packer, 2004). Translocations are likely to become an important adaptive management tool as populations of lions and other large carnivores, for example wild dog *Lycaon Pictus*, become increasingly fragmented, and will require active management (Akçakaya, Mills & Doncaster, 2006).

Acknowledgements

We thank the HiP management staff, who were an integral part of the project from its inception to completion, and who spent many hours (particularly at night) working on the introduction and monitoring that followed. This innovative project would not have been possible without Gus van Dyk, Dave Balfour and Pete Hartley. Many of the ideas behind the introduction approaches were from discussions with Gus van Dyk. We thank Dave Balfour, S. van Rensburg, O. Howison and R. Howison from Ezemvelo KZN Wildlife Hluhluwe Research Centre for logistical support, and providing access to EKZN Wildlife data. We acknowledge

North West Parks and Tourism Board for donation, capture and housing of lions. This project was funded by: THRIP grant to N. Ferguson, NRF grant to R. Slotow, UKZN funding to R. Slotow, The Green Trust (WWF-SA) grant to M. Somers, NSF, Walt Disney Foundation and MGM Grand Hotel grants to C. Packer, Wild about Cats, Hluhluwe Tourism Association, Bateleurs and Wildlife Conservation Trust (KZN). We thank the staff and interns who provided assistance and information. W. Trettnak and P. Fleischmann are thanked for making valuable comments on this paper.

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