Biological Conservation xxx (2009) xxx–xxx

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population

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ARTICLE INFO

Article history:
Received 23 February 2009
Received in revised form 2 June 2009
Accepted 18 June 2009
Available online xxxx

Keywords:
Evidence-based conservation
Trophy hunting
Problem animal control
Human–carnivore conflict
Phinda–Mkhuze

ABSTRACT

There is an extraordinary assortment of technical approaches to conserving carnivore populations, but the effectiveness of conservation activities is rarely evaluated. Accordingly, we initiated a study to assess the impact of several conservation interventions on the dynamics and persistence of a leopard (*Panthera pardus*) population in Phinda Private Game Reserve, South Africa. These included revisions of the statutory systems that regulate problem animal control and trophy hunting, and we instituted a program intended to reduce human–leopard conflict in the region. We compared demographic rates of radiocollared leopards from two sampling periods: a pre-treatment period prior to intervention, and a treatment period after intervention. The average annual mortality rate of the population decreased from 0.401 ± 0.070 to 0.134 ± 0.016, with fewer leopards killed by humans and in intraspecific clashes after intervention. The overall reproductive output of the population increased in the treatment period, although annual cub production was higher in the pre-treatment period. This was mainly due to larger litter sizes prior to intervention, which may have been a strategy used by female leopards to offset high levels of infanticide. Results from camera-trap surveys and a Leslie-matrix model indicated an increase in annual population growth rate (λ) of 14–16% after the implementation of conservation measures. Our findings highlight the importance of addressing both the numerical and functional components of population dynamics when managing large carnivores exposed to hunting or persecution.

1. Introduction

Although protected areas play a critical role in biodiversity conservation, their effectiveness depends on the ecological traits of target taxa (Rodrigues et al., 2004). Where the objective is large carnivore conservation, many reserves are too small or have inadequate resources to meet the extensive spatial requirements of the populations they are intended to protect (Brashares et al., 2001; Linnell et al., 2001). Even in productive habitat, the wide-ranging behaviour of carnivores frequently leads them to cross reserve boundaries where they are killed, deliberately and accidentally, by humans (Schwartz et al., 2006; Loveridge et al., 2007). The resulting edge effect is often sufficient to cause the decline or extinction of protected carnivore populations (Woodroffe and Ginsberg, 1998).

Such trans-boundary issues will likely become more pronounced as landscape alteration increases and parks become more isolated (Harcourt et al., 2001). Consequently, an increasingly important factor in successfully conserving large carnivores is the management of human-mediated mortality adjacent to protected areas (Nawaz et al., 2008). Although a wide variety of methods have been used to foster the persistence of carnivore populations, (Sillero-Zubiri and Laurenson, 2001; Shivik, 2006), the effectiveness of most approaches has rarely been demonstrated. Accordingly, we assessed the impact of several conservation interventions on the dynamics and persistence of a leopard (*Panthera pardus*) population in Phinda Private Game Reserve, KwaZulu-Natal, South Africa (hereafter Phinda). Leopards are protected inside Phinda but are exposed to legal and illegal hunting outside the reserve. High rates of persecution by farmers and trophy hunting in areas surrounding the reserve resulted in higher mortality rates than previously documented for the species (Balme, 2009). We therefore instituted a series of conservation measures aimed at improving the long-term prospects of leopards in the region. These included revisions of the statutory systems that regulate problem animal control and trophy hunting in KwaZulu-Natal (Ferguson, 2006; Balme et al., in press-a), and a conflict mitigation program aimed at limiting damage caused by leopards by improving local husbandry practices (see Section 2).

In this paper, we assess whether these conservation interventions succeeded in alleviating detrimental effects in the Phinda population caused by harvesting in neighbouring non-protected

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doi:10.1016/j.biocon.2009.06.020

areas. We compared demographic rates of leopards in Phinda from two sampling periods: a pre-treatment period (1 April 2002–31 December 2004) prior to intervention, and a treatment period (1 January 2005–31 December 2007) after intervention. We examined how individual leopards adapted to variable harvesting levels to gauge the importance of different demographic processes in either assisting or impeding population recovery. We also assessed the response of local landowners towards the conservation program, and tested whether other biological factors influenced leopard demography in the reserve.

2. Materials and methods

2.1. Study area

Phinda Private Game Reserve (27°44′–27°55′S, 31°12′–32°26′E; Fig. 1) is 220 km^2 and situated in the Maputaland region of northern KwaZulu-Natal, South Africa. The prevailing vegetation is woodland dominated by *Acacia* and *Terminalia* species, interspersed with grasslands and wooded grasslands. Mean monthly temperatures range from 33 °C in January to 19 °C in July. The area receives an average of 550 mm of rain each year, which falls mainly between October and April. Forty-two large mammal species have been recorded on Phinda, including the entire indigenous large carnivore guild (Hunter et al., 2007).

Leopards are fully protected in Phinda but move freely in and out of the reserve into adjoining areas. To the northwest of Phinda is the 440 km^2 public Mkhuze Game Reserve (Fig. 1) where leopards have been protected since the park's inception in 1912 (Gush, 2000). The land to the south and east of Phinda comprises a mosaic of private cattle farms, commercial game ranches, and pastoral Zulu communities, where leopards are legally hunted or killed as pests. Levels of persecution vary markedly among properties. In general, more leopards are killed in game ranching and livestock areas than on communal land, largely because densely populated communal areas have insufficient suitable habitat and prey for the permanent occupation of leopards (Balme, 2009). In contrast, commercial game ranches and cattle farms are suitable for leopards, with low human densities, large expanses of suitable habitat, and significant wild prey populations (Balme, 2009). Land

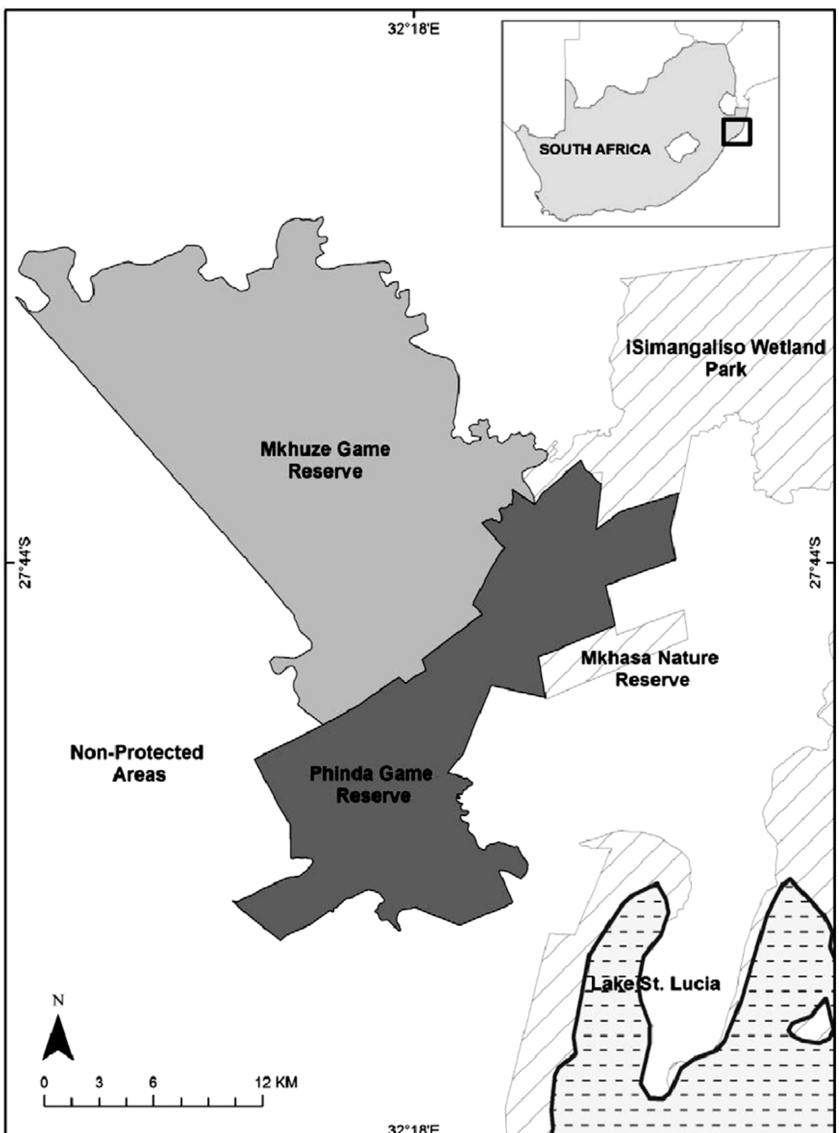

Fig. 1. The study area showing land-use types in the region. Leopards are protected in Phinda Private Game Reserve, Mkhuze Game Reserve, and in hatched areas. White areas comprise mostly cattle farms, game farms, and Tribal Authority land where leopards are exposed to legal hunting and illegal killing. Inset: box indicates region shown.

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management, and the composition and distribution of vegetation types, remained constant in Phinda and surrounding non-protected areas throughout the study (Van Rooyen and Morgan, 2007).

2.2. Conservation interventions and management of leopards in KwaZulu-Natal

Leopards are classified as 'specially protected game' throughout KwaZulu-Natal and fall under the mandate of the statutory conservation authority, Ezemvelo KwaZulu-Natal Wildlife (EKZNW), on both public and private lands. A leopard can be legally killed by a private individual only when they possess a destruction permit or a Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES) permit issued by EKZNW.

Destruction permits are granted by EKZNW for the removal of confirmed damage-causing leopards. In principle, destruction permits are issued only to landowners who demonstrate that a leopard represents a threat to life or property, and that no alternative non-lethal solution is available. However, prior to 2005, destruction permits were regularly awarded on the basis of little evidence and landowners often gained financially from them. Although the skins of leopards destroyed with destruction permits cannot legally be exported from South Africa, property owners have sold the right to shoot perceived problem leopards to local hunters (L.T.B. Hunter & G.A. Balme, Panthera, unpublished data). This likely encouraged landowners to apply for permits even when no problem existed. Destruction permits were also frequently awarded for predation of wild ungulates, especially nyala (*Tragelaphus angasii*), as game ranchers typically perceived large carnivores as competitors.

On our recommendation, EKZNW introduced a series of policy changes in January 2005 intended to prevent misuse of destruction permits and to improve the selective removal of damage-causing leopards (Ferguson, 2006). Under the new system, an EKZNW official inspects depredation events within 24 h of being reported. Once a leopard is verified as being responsible for the damage, an attempt is made to identify the individual by deploying camera-traps (provided by this study) at the site. A destruction permit is granted only when the same leopard is known to be responsible for at least three depredation events within a 2-month period. Although not infallible, this system was designed to increase the likelihood of identifying habitual stock killers. To receive a permit, landowners must additionally demonstrate that they have undertaken to improve husbandry practices to reduce the risk of depredation by leopards (see below). Once a permit has been issued, the offending leopard can be killed only by the landowner or by an EKZNW official. Destruction permits may no longer be sold as commercial hunts to local hunters. Destruction permits are also no longer awarded for the depredation of wild game (Ferguson, 2006).

Removing a problem leopard is only a short-term solution to the loss of livestock, as territorial vacancies are likely to be filled by other leopards that may take to stock-raiding (Rabinowitz, 1986). A preventative management approach that eliminates the source of conflict is often more efficient at mitigating livestock depredation in the long-term and, in principle, reduces the motivation for killing carnivores illegally (Ogada et al., 2003). Accordingly, from January to July 2005 we held a series of workshops with farmers in the region surrounding Phinda to promote the use of alternative husbandry techniques to reduce depredation. Corralling vulnerable animals at night, placing guards with herds during the day, regularly changing grazing paddocks, and rapidly disposing of livestock carcasses were among the management options recommended to landowners. In addition to the workshops, we responded to all reports of depredation events in our study area during the treatment period, and advised landowners on the most appropriate, non-lethal solutions likely to prevent further losses.

CITES permits are allocated for trophy hunting and the provincial quota varies between 5 and 10 each year (Daly et al., 2005). In principle, CITES permits should be distributed evenly across leopard range in the province but historically, hunting effort has been disproportionately focussed in the region surrounding Phinda (Balme et al., in press-a). To alleviate impacts arising from this and encourage more sustainable trophy hunting of leopards, we recommended a series of revisions to the statutory protocol governing the allocation of CITES permits. Our key recommendations were: (1) limiting the number of CITES permits allocated in KwaZulu-Natal to five each year, (2) allocating applications to leopard hunts to individual properties rather than hunting outfitters, (3) ensuring a more even distribution of permits across the province, (4) linking the likelihood of obtaining a permit to the size of the property, and (5) restricting the trophy hunting of leopards to adult males (Balme et al., in press-a). These changes were implemented by EKZNW from January 2006 onwards.

2.3. Capture and handling

We captured leopards using a combination of free-darting, baited cage-traps, and soft-hold foot snares, and fitted each with a VHF radiocollar (250 g, Sirtrack Ltd., New Havelock North, Zealand) or a GPS collar with a UHF radio-link (420 g, Vectronics-Aerospace, Berlin, Germany). We classified leopards into three age-classes according to the wear and eruption of their teeth and associated behaviour (Stander, 1997): cubs were <1 year old, subadults were between 1 and 3 years old, and adults were >3 years old. We located radiocollared animals from the ground or air and recorded their location to the nearest 50 m using a handheld GPS receiver (Garmin International Inc., Kansas City, USA). GPS collars were programmed to take five fixes daily and we downloaded data remotely to a handheld terminal every fortnight.

2.4. Causes and rates of mortality

We established causes of mortality of radiocollared leopards by direct observation or by post-mortem and evidence collected at the site. Cause of death was rarely ambiguous as radiocollars were fitted with activity-related mortality switches that allowed us to recover most dead leopards within 24 h. Where possible, we also recorded the deaths of uncollared leopards on properties adjacent to Phinda, typically from reports made by local landowners, community members, professional hunters, and EKZNW staff.

We calculated annual mortality rates (AMRs) using the software MICROMORT (Heisey and Fuller, 1985) for the different age and sex classes of collared leopards during the two sampling periods. MICROMORT estimates mortality rates according to the total number of radio-transmitter days for which collared animals are monitored, and the number of deaths occurring during the monitoring interval (Heisey and Fuller, 1985). As leopards only became large enough to collar when they were 10–12 months old, the number of radio-transmitter days for juveniles was calculated from when they were first seen to when they either died or reached 1 year old. We compared the different AMRs in the pre-treatment and treatment periods using the software CONTRAST (Hines and Sauer, 1989), which gives a test statistic distributed as χ^2.

2.5. Reproduction

We calculated the following reproductive parameters for collared female leopards in each sampling period: annual cub production, mean litter size, mean interval between litters, mean age at first parturition, and the relative success of courtship associations. Annual cub (X_p) production in each period was calculated by:

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$$X_p = \frac{N_p^{\text{cubs}}}{N_p^{\text{years}}}$$

where N_p^{cubs} is the total number of cubs born during the period, and N_p^{years} is the total number of radio-transmitter years logged for all adult female leopards in the period. We determined litter size by visual observation once cubs started accompanying their mothers. We also tested for differences in the age of mothers between periods because this can influence the size of litters (Wielgus and Bunnell, 2000). We used a general linear model (GLM) to assess which factor had the greatest impact on litter size: the sampling period in which the litter was born, or the estimated age of the mother. We calculated the relative success of courtship associations by dividing the number of mating bouts observed during each sampling period with the total number of litters born in each period. Courtship associations in leopards are conspicuous, lasting between two and five days, with as many as 300 couplings occurring during this time (G.A. Balme, Panthera, unpublished data). Whenever male and female leopards were found together, we remained with the pair until we could establish whether they were mating. We concluded conception had occurred using visual signs of pregnancy or if a female dramatically localised her movements approximately three months after the mating event, indicating the likely birth of a litter. Although it is possible that we missed some courtship associations, monitoring effort was kept constant throughout the study, which we believe provides a precise index of mating success for comparisons between sampling periods.

The turnover rates of male carnivores can have a significant impact on the reproductive output of populations (Wielgus and Bunnell, 2000; Whitman et al., 2004). As such, we estimated the mean minimum time of territorial tenure of resident male leopards on Phinda during each sampling period. Five of the seven adult males that we monitored became territorial residents during the study and we could determine when tenure began. The remaining two males were already established residents at the onset of the study. Both animals were well known to tourism guides and accurate records of all sightings have been kept since the inception of the reserve (M. Karantonis, CCAfrica, unpublished data). We used the records to establish when these leopards were first seen, and the point at which at least three sightings were recorded per month, which we took as indicating residency. Tenure was considered ended when the leopard either died, was displaced, or when the study ended in December 2007.

2.6. Population growth

We used camera-trap surveys in conjunction with closed capture–recapture models to estimate annual growth (λ) in the Phinda leopard population during the study. We conducted three camera-trap surveys in Phinda: immediately after the pre-treatment period (January–March 2005), towards the end of the treatment period (January–March 2007), and roughly one year after the end of the treatment period (March–May 2009). The methods used to set-up camera-trap stations, their schematic layout, and the analysis of capture data is described in detail in Balme et al. (2009).

In addition to camera-trap surveys, we estimated annual population growth using a simple Leslie-matrix model constructed in Excel (Microsoft, Washington, USA) with the POPTOOLS addition (Hood, 2004). We included survival and reproductive rates of female leopards from four age-classes in the model (<1 years, 1–2 years, 2–3 years, and >3 years). In addition to estimating λ, POPTOOLS calculated sensitivity and elasticity values associated with stage-specific vital rates. Sensitivity is defined as the absolute change in λ given an absolute change in a single demographic element, and elasticity is the proportional change in λ given the proportional change in a single demographic element (Crookes et al., 1998).

2.7. Public response

We conducted interviews from January to December 2007 with landowners on 18 private properties that were outside protected areas but within ranging distance of leopards collared on Phinda. These 18 properties comprised 92% of the non-protected area utilised by radiocollared leopards and, together with Phinda and Mkhuze, accounted for 85% of all mortality records (Balme, 2009). We questioned landowners about the physical features of their properties, the presence of leopards on their land, previous problems experienced with leopards, the number of leopards removed from their properties, and their perceptions on the new protocols for managing leopards in KwaZulu-Natal. This was part of a more exhaustive process covering all socio-economic aspects relevant to leopard conservation in the province (L.T.B. Hunter and G.A. Balme, unpublished data), but we include here only the results relevant to the persecution of leopards on properties surrounding Phinda.

2.8. Prey availability

We assessed whether the availability of prey affected leopard demography in Phinda. We used a road strip sampling technique to estimate the abundance of the six primary prey species (nyala, impala *Aepyceros melampus*, grey duiker *Sylvicarpa grimmia*, red duiker *Cephalophus natalensis*, reedbuck *Redunca arundinum*, and warthog *Phacochoerus aethiopicus*) of leopards in Phinda (see Balme et al. (2007) for detailed description of methodology). Surveys were conducted every year throughout the study in July and December, allowing us to determine whether prey numbers varied seasonally. Annual biomass of available prey was calculated using abundance estimates and mean weights of prey species from Skinner and Chimimba (2005). We used repeated measures Analysis of Variance to determine whether the size of prey populations and available prey biomass changed throughout the study.

2.9. Interspecific competition

Changes in interspecific competition may have also affected our comparison of leopard biology between the two periods. We evaluated the relative abundance of other large carnivores in Phinda to assess levels of interspecific competition during the pre-treatment and treatment periods. Lion (*Panthera leo*) numbers in Phinda were carefully monitored by reserve staff and the population size was known with certainty throughout the study (Hunter et al., 2007). In contrast, we had no independent density estimates of spotted hyenas (*Crocuta crocuta*). We therefore used relative abundance indices (RAI) estimated from camera-trapping data (O'Brien et al., 2003). We tallied the number of photographic captures of spotted hyena taken during each survey, and calculated an RAI defined as the number of frames taken per 100 trap-days. Although African wild dogs (*Lycaon pictus*) and brown hyenas (*Hyaena brunnea*) compete with leopards (Creel et al., 2001), both species are transient in the region and are unlikely to exert significant effects on leopards. Cheetahs (*Acinonyx jubatus*) were widespread in Phinda at low densities; however, leopards dominated in all observed interactions between the two species and cheetahs are unlikely to affect the status of leopards in the reserve (Hunter, 1998). In addition to evaluating abundance, we compared the proportion of leopard kills kleptoparasitised by other predators in each sampling period.

We calculated all analyses and statistical comparisons using SPSS 15.0 (SPSS, Chicago, USA), and present means ± SE throughout.

3. Results

3.1. Capture and handling

We captured and radiocollared 35 leopards on Phinda between April 2002 and December 2007. In addition, we recorded seven cubs that either died before they were old enough to collar ($n = 4$) or were >1 year old at the end of the study ($n = 3$). In total, we monitored 26 leopards in the pre-treatment period and 28 leopards in the treatment period. Collared leopards were located every 2.85 ± 0.29 days (range = 1–8 days) and tracked for an average of 757 ± 97 days (range = 16–1791 days). We recorded 13,056 daily locations during the study and observed radiocollared leopards on 1669 occasions.

3.2. Causes and rates of mortality

Twenty of the 42 leopards that we monitored during the study died (Table 1). We also recorded the deaths of 11 uncollared leopards on properties surrounding Phinda. In general, more leopards were killed by humans ($n = 19$) than died of natural and unknown causes ($n = 12$). This result may have been biased by an increased likelihood of detecting uncollared leopard deaths that were anthropogenically related. Nevertheless, unbiased data from radiocollared individuals confirmed human activity as an important cause of leopard mortality in the region.

The number of leopards harvested both legally and illicitly decreased after we implemented interventions (Table 1). Farmers without destruction permits illegally shot six leopards during the pre-treatment period, and two leopards died in poachers' snares in Mkhuze Game Reserve. The two illegal mortalities in the treatment period were leopards that died from ingesting the insecticide Temik® (aldicarb) laced into a carcass by poachers in Phinda. With the exception of one unsexed juvenile and a single adult female that was poisoned, all leopards killed illegally were males.

Four destruction permits were issued to three properties in our study area during the pre-treatment period, resulting in the removal of three leopards (one male shot, one male and one female translocated). Only one destruction permit was awarded in the treatment period and the problem leopard disappeared before it could be destroyed. Thirteen CITES permits were issued to five properties surrounding Phinda in the pre-treatment period, resulting in six leopard deaths (four females, two males), and four CITES permits were issued to three properties in the treatment period, causing two leopard deaths (two males).

The number of leopards killed through intraspecific conflict also declined after 2005 (Table 1). During the pre-treatment period, six leopards died because of clashes with conspecifics. One subadult female was killed by an adult female and another by an adult male. A resident male leopard also died from injuries sustained in a fight with a younger immigrant male. Additionally, we observed one case of infanticide when three 4-month-old cubs were killed by a newly established male that was not their sire. We only recorded one case of intraspecific mortality in the treatment period when a resident male leopard killed an adult female. A post-mortem revealed that this female (F11) was reproductively senescent, having not reproduced since raising one litter to independence in 2003.

Interspecific conflict accounted for a single leopard death in each of the two sampling periods (Table 1). A subadult male died from septicaemia arising from wounds inflicted by a spotted hyena in the pre-treatment period, and lions killed a subadult male in the treatment period.

The average annual mortality rate of the radiocollared leopard population was 0.241 ± 0.069 with high variability during the study (Fig. 2). AMRs were higher in all cohorts in the pre-treatment period compared to the treatment period (Table 2); the difference was significant in juveniles ($\chi^2_1 = 41.595$, $P < 0.001$), subadult males ($\chi^2_1 = 28.548$, $P < 0.001$), subadult females ($\chi^2_1 = 14.867$, $P < 0.001$), and adult males ($\chi^2_1 = 4.560$, $P = 0.033$). All cubs born during the treatment period ($n = 14$) survived to independence. It is possible that we missed some early juvenile deaths since we only counted cubs large enough to accompany their mothers. Nevertheless, the age that we first determined litter size remained constant throughout the study (3.00 ± 0.45 months, range = 1–6 months; $U = 6.500$, $Z = -1.434$, $P = 0.150$), therefore comparisons between sampling periods should not be affected by our inability to detect pre-emergence mortality.

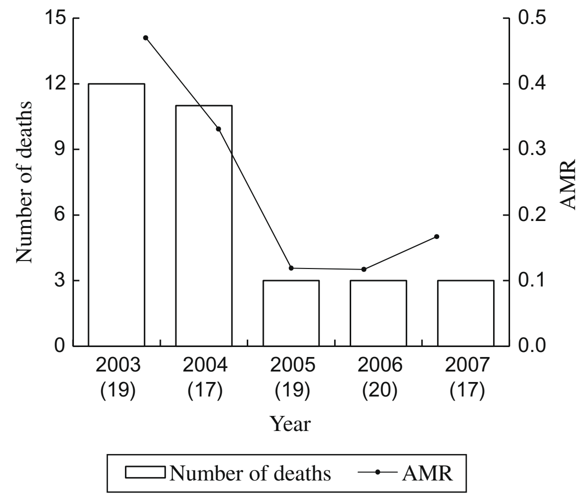

Fig. 2. Annual mortality rates (AMR) of radiocollared leopards in Phinda Private Game Reserve, and the total number of leopards killed in Phinda and surrounding properties in KwaZulu-Natal, South Africa, 2003–2007. The number of leopards monitored each year in Phinda is given in parentheses.

3.3. Reproduction

We monitored the reproductive behaviour of 11 radiocollared female leopards in Phinda for a combined 23.29 female-years

Table 1
Causes of mortality of collared and uncollared leopards in Phinda Private Game Reserve and surrounding properties in KwaZulu-Natal, South Africa, during the pre-treatment and treatment periods, 2002–2007.

Causes of mortality	Pre-treatment period			Treatment period		
	Collared	Uncollared	Total	Collared	Uncollared	Total
Intraspecific	6	–	6	1	–	1
Interspecific	1	–	1	1	–	1
Human – legal	2	5	7	1	1	2
Human – illegal	3	5	8	2	–	2
Unknown	1	–	1	2	–	2
			23			8

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(Table 3). During this time, a minimum of 25 cubs were born in 16 litters. Litter size was greater in the pre-treatment period than in the treatment period ($U = 6.000$, $Z = -2.733$, $P = 0.008$) and results from the GLM showed that only the period in which the litter was born was significant in influencing litter size ($F_{1, 11} = 16.667$, $P = 0.045$). The only inter-litter interval we recorded during the pre-treatment period involved the female leopard (F12) who lost her cubs to infanticide when they were 4 months old. All females in the treatment period successfully raised their cubs to independence. The mean time between the independence of a litter and the birth of a new one was 3.8 ± 0.73 months (range = 1–5 months). This was considerably less than the 11 months that F12 took to replace her litter, even though we recorded her mating from one month after the infanticide event. Female leopards gave birth for the first time at a later age in the pre-treatment period compared to the treatment period ($U = 0.001$, $Z = -1.964$, $P = 0.050$).

We recorded 44 courtship sessions involving six adult female leopards and seven males (Table 4). Although the number of mating sessions observed per individual was similar for the two sampling periods (pre-treatment period: 3.50 ± 0.96, treatment period: 3.83 ± 1.30; $t_5 = -0.226$, $P = 0.830$), the relative success of mating bouts differed ($t_5 = -2.566$, $P = 0.050$). When we removed the senescent female F11 from the analysis, the difference was more pronounced (19% success rate in the pre-treatment period compared to 69% in the treatment period; $t_4 = -6.448$, $P = 0.003$). The mean minimum length of territorial tenure of male leopards was shorter in the pre-treatment period than the treatment period ($U = 1.000$, $Z = -2.033$, $P = 0.042$).

3.4. Population growth

The number of individual leopards photographed during camera-trap surveys varied between 13 and 16 (Table 5), with capture frequencies ranging from 1 to 7 captures per individual (2.84 ± 0.284). Capture selected M_h, which allows for heterogeneous capture probabilities among individuals (Otis et al., 1978), as the most appropriate model for all surveys, and population clo-

Table 2
Annual mortality rates (AMRs) of collared leopards in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, recorded during the pre-treatment and treatment periods, 2002–2007.

Sex and age	Pre-treatment period				Treatment period			
	AMR	SE	RD[a]	Deaths	AMR	SE	RD	Deaths
Juvenile	0.574	0.089	1713	4	0	0	3236	0
Subadult male	0.801	0.066	733	3	0.111	0.111	2631	1
Subadult female	0.345	0.030	1731	2	0.071	0.071	2499	1
Adult male	0.396	0.087	2116	3	0.267	0.020	3572	3
Adult female	0.149	0.149	2839	1	0.130	0.069	5660	2
Total male	0.538	0.023	2849	6	0.205	0.035	6203	4
Total female	0.144	0.144	4570	3	0.161	0.031	8159	3
Total subadult	0.518	0.048	2464	5	0.195	0.034	5130	2
Total adult	0.252	0.122	4955	4	0.185	0.045	9232	5
Total	0.401	0.070	9132	13	0.134	0.016	17,598	7

[a] Number of radio-transmitter days.

Table 3
Reproductive and demographic characteristics of leopards in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, during the pre-treatment and treatment periods, 2002–2007.

	Pre-treatment period			Treatment period		
	x	SE	N	*x*	SE	*n*
Annual cub production (# cubs/female/year)	1.41			0.90		
Inter-litter interval (months)	15.00	15.00	1	16.2	1.45	7
Litter size	2.2	0.20	5	1.3	0.14	11
Annual litter production (# litters/female/year)	0.64			0.71		
Mating success (# litters/# mating bouts)	0.19			0.39		
Age at first parturition (months)	45.3	1.73	3	33. 7	1.85	3
Male tenure (months)	32.0	19.00	4	45.4	16.13	4

Table 4
The number of courtship sessions and litters recorded for collared female leopards in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, during the pre-treatment and treatment periods, 2002–2007.

Individual	Pre-treatment period		Treatment period	
	# of courtship sessions	# of litters	# of courtship sessions	# of litters
F6	3	1	3	2
F8	1	0	3	2
F9	4	0	4	3
F11	5	1	10	0
F12	7	2	1	1
F16	1	0	2	1
Total	21	4	23	9

Please cite this article in press as: Balme, G.A., et al. Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. Biol. Conserv. (2009), doi:10.1016/j.biocon.2009.06.020

Table 5
Results of camera-trap surveys conducted in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, 2005–2009.

Survey	Number of leopard captures	Number of individuals captured	MMDM[a] (km)	Closure test		P-hat	Capture abundance	Density (number of leopards/100 km^2)
				Z	P			
2005	39	13	4.43	0.087	0.535	0.12	16 ± 2.97	7.17 ± 1.12
2007	38	16	4.73	0.552	0.709	0.09	21 ± 4.36	9.42 ± 1.93
2009	53	16	4.78	−0.357	0.361	0.11	25 ± 6.92	11.21 ± 2.11

[a] Mean maximum distance moved by leopards photographed on >1 occasion (Balme et al., 2009).

Table 6
Annual survival rates of different aged female leopards and annual female cub production used in Leslie-matrix models to determine the annual population growth rate (λ) of the leopards in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, 2002–2007.

Time period	Annual survival rate				Annual cub production	Λ
	<1 year	1–2 years	2–3 years	>3 years		
Pre-treatment period	0.426	0.496	1.000	0.851	0.758	0.978
Treatment period	1.000	0.781	1.000	0.879	0.484	1.136
Entire study	0.764	0.656	1.000	0.868	0.575	1.071

sure was confirmed in all cases. The mean maximum distance moved by leopards photographed on more than one occasion (MMDM) was similar for all surveys (4.66 ± 0.42 km, range = 2.24–10.13 km; Kruskal–Wallis Test: $\chi^2_2 = 0.456$, $P = 0.756$). We therefore added a circular buffer of 2.33 km (0.5 × MMDM) to each camera-trap station, yielding an effectively sampled area of 223 km^2. The resulting density estimates for the Phinda leopard population increased by 56% from 2005 to 2009, with an estimated annual population growth rate (λ) of 14%.

Only adult female leopards (⩾3 years) contributed towards reproduction in the Leslie-matrix model (Table 6). Ten (54%) of the 19 cubs that we sexed were female, resulting in a sex ratio at emergence close to parity (1 male: 1.11 females). Hence, the annual production of female cubs per female-year was 0.758 (1.414 × 0.536) for the pre-treatment period and 0.484 (0.903 × 0.536) for the treatment period. We assumed that survivorship of male and female cubs to independence was equal throughout the study.

Our Leslie-matrix model predicted that the annual growth rate of the Phinda leopard population improved by 16% after the change in management regime (Table 6). During the pre-treatment period, we estimated that the population was declining at 2% per year ($\lambda = 0.978$). This improved to a 14% annual population increase ($\lambda = 1.136$) in the treatment period. The population growth rate calculated for the entire study was positive, with an estimated 7% increase every year ($\lambda = 1.071$).

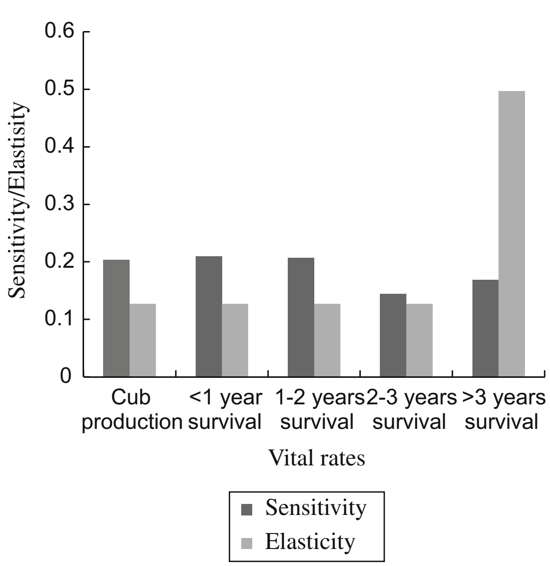

Fig. 3. Sensitivity and elasticity of annual population growth (λ) associated with stage-specific vital rates for leopards in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, 2002–2007.

Results from the sensitivity analyses performed by POPTOOLS emphasised the importance of adult female survival in determining population growth (Fig. 3). The sensitivity and elasticity values associated with mean survivorship of the juvenile and subadult stages, as well as annual cub production, were at least three times lower than those associated with the adult class. In other words, a 10% decrease in adult survival would require at least a 30% increase in fertility, juvenile survival, or subadult survival, to return the population to its original growth rate.

3.5. Public response

The average size of properties on which interviews were conducted was 11.05 ± 2.73 km^2 (range = 1.20–40.00 km^2) and the total amount of land owned by all respondents combined was 198.98 km^2. All properties had more than one land-use. Most of the sampled area comprised unmodified habitat dedicated to combined cattle and game ranching (79%), with the remainder occupied by crops (10%) and timber (11%). Landowners reported evidence of leopard occupancy on 15 of the 18 properties. Five of these properties complained of livestock depredation by leopards. Accurate records of stock losses were not kept but estimated annual losses due to leopards appeared low, averaging 1.36 ± 0.38% (range = 0.55–2.8%) of total herd size (446 ± 341, range = 59–1810). Four of the five properties altered husbandry practices in response to leopard depredation and this lowered losses in all instances. Corralling calves at night stopped losses on one farm completely, and reduced losses on another farm by 90%, and rotating grazing paddocks after a depredation event reduced losses on two farms by 63% and 81%, respectively.

Eight (44%) of the landowners that we interviewed supported the new guidelines for managing damage-causing leopards in KwaZulu-Natal (Ferguson, 2006), two (11%) felt they were fair but believed a destruction permit should be granted after the first rather than the third depredation event, three (17%) believed the new process was too stringent, and five (28%) declined to comment. Perceptions were similar for the revised protocol governing the trophy hunting of leopards in the province (Balme et al., in press-a). Seven (39%) landowners agreed completely with the

Table 7
Mean density (animals/km^2), total population size, and biomass (kg/km^2) estimates for six leopard prey species in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, during the pre-treatment and treatment periods, 2002–2007.

Species	Pre-treatment period				Treatment period				Mean confidence intervals for counts (%)
	Mean density	Population size	SE	Biomass	Mean density	Population size	SE	Biomass	
Impala	10.98	1495	335	439	14.61	1990	289	584	15
Nyala	23.59	3213	462	1414	19.65	2675	411	1178	12
Grey duiker	0.71	97	3	12	0.77	105	5	13	3
Red duiker	2.75	375	51	33	2.31	315	32	27	9
Warthog	3.26	444	109	146	4.16	567	171	187	16
Reedbuck	0.23	31	2	11	0.16	22	4	8	7
Total				2056				1998	

new model, two (11%) felt that the allocation of CITES permits should be linked to the control of damage-causing leopards, two (11%) preferred the old process, and seven (39%) showed no interest in hunting leopards.

3.6. Prey availability

We conducted 10 road strip surveys in Phinda during the study comprising 51 transect counts and covering 1785 km. The road strip method appeared to provide reasonable population estimates for each species, with confidence intervals ranging from 3% to 16% (Table 7). The size of prey populations on Phinda ($F_{4,\,20} = 0.443$, $P = 0.776$) and available prey biomass ($F_{4,20} = 0.361$, $P = 0.833$) remained constant throughout the study. There was also no marked seasonal change in prey abundance, with similar wet and dry season counts ($t_5 = 0.500$, $P = 0.638$).

3.7. Interspecific competition

Lion numbers remained stable on Phinda for the duration of the study ($U = 2.000$, $Z = -1.091$, $P = 0.275$). In the pre-treatment period, mean lion density on the reserve was 12.90 ± 0.95 lions/100 km^2 (range = 11.33–14.61 lions/100 km^2). In the treatment period, mean density was 11.41 ± 0.70 lions/100 km^2 (range = 10.47–12.77 lions/100 km^2). Results from the camera-trap surveys suggested spotted hyena abundance was also similar for the two sampling periods. In the 2005 survey, we obtained 25 photographs of spotted hyena, resulting in a RAI of 2.08 frames/100 trap-days, while in 2007 we obtained 30 photographs of hyenas, producing a RAI of 2.50 frames/100 trap-days.

There was no difference in the number of leopard kills lost to other scavengers between the two sampling periods ($Z = -0.577$, $P = 0.564$, $n = 20$). In the pre-treatment phase, five kills were taken by spotted hyenas, four by bushpigs (*Potamochoerus larvatus*), and two by lions (7.8% of total kill record for the period, $n = 141$). In the treatment period, three kills were lost to spotted hyenas, two to bushpigs, and four to lions (7.3% of total kill record, $n = 124$).

4. Discussion

The conservation interventions we introduced from 2005 onwards appeared to foster positive demographic changes in the Phinda leopard population. Estimated population growth increased, annual mortality dropped, and the reproductive output of the population improved. Leopard population density increased and, by the end of the study, it was similar to that estimated in the adjacent Mkhuze Game Reserve (11.11 ± 1.31 leopards/100 km^2; Balme, 2009). Mkhuze's larger size and more rounded shape buffered its leopards from edge effects caused by anthropogenic mortality in surrounding areas, and the population was regulated primarily by intrinsic factors (Balme, 2009). Interspecific competition, habitat quality, and prey biomass were comparable in Phinda and Mkhuze, so we believe the Phinda leopard population was close to its optimum size in 2009 when densities approached parity. At this time, leopard density in Phinda was also close to the carrying capacity predicted for the reserve using biomass of preferred prey species (12.21 leopards/100 km^2; Hayward et al., 2007).

There were no marked changes in prey availability or interspecific competition during the study, suggesting that our intervention program was the principal factor driving population recovery. The number of leopards harvested legally and illegally decreased significantly after 2005. The revised trophy hunting protocol successfully alleviated hunting pressure in our study area, and EKZNW's new strategy for managing damage-causing leopards reduced the number of animals legally removed through problem animal control. The number of leopards killed illegally may have been expected to increase if landowners perceived that the new legislation governing leopard management was not in their best interests. However, this was not case, with eight illegal leopard deaths in the pre-treatment period and only two in the treatment period. While it is possible that our ability to detect illegal mortalities decreased in the treatment period, this seems unlikely. The number of illegally killed radiocollared leopards also declined after intervention and was independent of reporting rates, as we accounted for all deaths of collared leopards while radiotracking.

It is more likely that increased tolerance among landowners contributed to the reduction in illegal kills. Most leopards killed illegally during the pre-treatment period were shot as perceived threats to livestock. Reducing the risk of stock depredation or providing incentives that could compensate for potential losses should therefore foster tolerance towards leopards (Treves and Karanth, 2003). The workshops held with farmers provided several alternative non-lethal means for defending livestock from predators. Although we have limited data on the relative frequencies of stock losses between the two sampling periods (mainly because few depredation events occurred in the treatment period), improved husbandry appeared to reduce the risk of depredation. The new protocol for managing damaging-causing leopards also ensured farmers had a structured, transparent framework for dealing with livestock depredation (Ferguson, 2006). The more even distribution of CITES permits across the region also gave a larger proportion of landowners the opportunity of hosting a hunt, and hence the chance to benefit financially from having leopards on their land (Balme et al., in press-a). Results from our interviews with landowners bordering Phinda suggested that most supported the change in leopard management.

The higher number of leopards killed by conspecifics in the pre-treatment period may have been related to high harvest rates during that period. Manipulation or exploitation of carnivore populations can elevate levels of social flux with concomitant increases in intraspecific strife (Stoner et al., 2006). Leopards live in a complex land tenure system that is highly dependent on the stability of long-term relationships (Bailey, 2005). An increase in turnover and immigration rates could increase the likelihood of contact between unfamiliar individuals and promote intraspecific strife. High turnover among adult males may also result in increased infanticide (Swenson et al., 1997; Wielgus and Bunnell, 2000). Although male leopards provide no parental care, the continued presence of the sire prevents incursions by immigrant males that pose a threat to cub survival. We observed infanticide only on one occasion, though cub survival was poor during the pre-treatment period, becoming markedly higher during the treatment period when the overall reproductive output of the population also improved. Female leopards gave birth at a younger age, spent a greater proportion of their time with dependent young, and produced more litters after intervention. The relative success of mating bouts also increased in the treatment period. Packer and Pusey (1983) proposed that infanticide in lions lowers the rate at which females conceive. Lionesses display a period of reduced fertility immediately following the takeover of a pride by a new male coalition, apparently allowing females to assess the fitness of new males and postpone conception until the threat of further takeovers has diminished (Packer and Pusey, 1983). Female leopards in Phinda appeared to adopt a similar strategy. The success of mating bouts was significantly lower in the pre-treatment period when male turnover was comparatively high. When the territorial tenure of males increased, so did mating success.

Female leopards at Phinda may have compensated for high harvest rates and elevated social instability in the pre-treatment period by producing larger litters. Knowlton (1972) reported that coyotes (*Canis latrans*) had larger litters when population abundance was reduced by intensive control, and an exploited grizzly bear population (*Ursus arctos*) in British Columbia also had larger litter sizes than nearby undisturbed populations (McLellan, 1989). It seems unlikely that the size of litters would greatly influence the susceptibility of leopard cubs to infanticide. Furthermore, high levels of anthropogenic mortality in the Phinda population would have reduced density-dependent restraints on reproduction. Hence, the selective benefits realised by female leopards producing larger litters should presumably outweigh the associated metabolic costs, though it did not result in increased reproductive output by females in this case. It must be noted that we had a small sample size for the number of litters recorded during the study ($n = 16$); however, radiocollared leopards comprised a significant proportion (>80%) of the overall population (Balme et al., 2009), which reduced the possibility of sampling bias.

The increase in population growth predicted by the Leslie-matrix model after our interventions was similar to that estimated by the camera-trap surveys. Similarly rapid recovery rates have been documented for several other carnivore populations released from high levels of control (Mills et al., 1998; Lindzey et al., 1992; Logan and Sweanor, 2001). In all cases, there were large protected populations nearby that could provide individuals for replacement or recolonisation. Rapid recovery was assisted in our study area by the close proximity of a large source population of leopards in Mkhuze Game Reserve. Male leopards are effective dispersers and transients from Mkhuze replaced four of the six adult males killed in Phinda within three months (G.A. Balme, unpublished data). These animals buffered the population from decline but also contributed towards social instability that we believe contributed to low reproductive success during the pre-treatment period.

The sensitivity and elasticity values calculated by our matrix model demonstrated the importance of adult female survivorship for population recovery. A number of felids have been shown to be resilient to disturbance if the reproductive female life-stage remains unaffected (Crookes et al., 1998; Gaona et al., 1998; Whitman et al., 2004). The same is likely to be true of leopards although there appears to be a critical level at which the effects associated with high male mortality (i.e. increased infanticide and lowered reproductive rates) cause a population to decline regardless of female survival. This was presumably the case at Phinda during the pre-treatment period when we predicted the population would decline despite low female mortality. The subsequent increase in population growth in the treatment phase was likely due to increased survival amongst the juvenile and subadult cohorts of the population, as adult female mortality remained relatively constant. These parameters were related to lowered adult male mortality and improved social stability.

Our results highlight the importance of addressing both the numerical and functional components of population dynamics when managing carnivores exposed to hunting or persecution. Simply increasing abundance, for example, by artificially translocating individuals, may not be sufficient to guarantee population persistence and will almost certainly fail if high rates of anthropogenic mortality remain in place. Management strategies that avoid high levels of social flux should therefore be encouraged, even for large carnivores widely considered able to withstand disturbance (Robinson et al., 2008). For carnivore species with more specialised breeding systems, such as lions, cheetahs, wild dogs or spotted hyenas (Mills, 1990; Caro and Kelly, 2001; Whitman et al., 2004; Rasmussen et al., 2008), the ability to respond to human perturbation may be even less flexible, and the need for such strategies even more pressing.

Our study is notable in experimentally evaluating the consequences of conservation practises for a large carnivore, addressing a significant omission in many similar projects (Pullin et al., 2004; Sutherland et al., 2004). We have demonstrated positive outcomes for a leopard population due to our interventions, which have since been incorporated in the statutory management plans for the species in the province (Ferguson, 2006; Balme et al., in press-a). While our treatment was clearly beneficial for leopards, it entailed simultaneously changing three key factors, making it difficult to discern the relative importance of each. *In situ* conservation projects will rarely have the luxury of experimentally evaluating how individual factors affect the target species and indeed, they may be inter-related in such a way as to exclude such an approach; in our study, changing problem animal policy would likely have failed if not combined with an attempt to reduce leopard–livestock conflict. However, where possible, attempting to evaluate the outcome of each change would be very valuable, providing an empirical basis on which to adjust interventions should problems arise, while also possibly enhancing the efficacy and cost-efficiency of intervention programs.

Acknowledgements

This study was funded by A. Hartog, Panthera, and the Wildlife Conservation Society (WCS). G.B. was supported while writing this paper by a Panthera/WCS Kaplan Graduate Award and received a NRF bursary from Grant # FA2004050400038. We are indebted to CCAfrica for allowing us to conduct research on Phinda and thank all those who assisted with fieldwork, particularly T. Dickerson, V. Mitchell, K. Pretorius and J. Mattheus. We are grateful to all at EKZNW who helped implement the new leopard management strategy, and to the various professional hunters, game ranch managers, farmers, and landowners who agreed to adopt it in the field. The manuscript was improved by comments from three anonymous reviewers. S. Nijhawan (Panthera) prepared the map of the study area.

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