

Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa

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Abstract

Although high rates of anthropogenic mortality are often reported for carnivores near reserve borders, the resulting edge effects are rarely quantified, and the consequences on conservation goals are usually unknown. Here, we assess the extent and impact of edge effects on a protected leopard *Panthera pardus* population in the Phinda-Mkhuze Complex (PMC), South Africa. We compared the spatial and demographic characteristics of leopards in two areas of the PMC, one closer to the border than the other. Leopard density declined from the core of the reserve (11.11 ± 1.31 leopards 100 km^{-2}) to the border (7.17 ± 1.12 leopards 100 km^{-2}), and was the lowest in non-protected areas adjoining the PMC (2.49 ± 0.87 leopards 100 km^{-2}), but was not related to prey abundance or inter-specific competition. Radiotelemetry showed that leopards near the border spent a greater proportion of their time outside the reserve and suffered higher annual mortality rates (0.358 ± 0.075) than those closer to the core (0.122 ± 0.065). A Cox proportional hazards model further demonstrated the negative effect of time spent outside the reserve on the survival probability of leopards. Despite an increased risk of mortality, leopards did not avoid non-protected areas, which may have functioned as an ecological trap for predators. Although the overall conservation outcome of the reserve was positive, edge effects clearly weakened the potential of the PMC to protect leopards. Our findings show that high mortality rates of carnivores in areas bordering reserves can extend to protected populations. Management approaches that control human activities on both sides of administrative borders are therefore essential if reserves are to conserve large carnivores effectively.

Introduction

Mammalian carnivores are vulnerable to extinction in fragmented landscapes due to their low densities, extensive spatial requirements and inevitable conflict with people (Purvis *et al.*, 2000; Cardillo *et al.*, 2005). Large, inviolate protected areas therefore remain critical to the persistence of many carnivore populations. However, there is increasing evidence that even protected areas may not effectively conserve carnivores. Using data from 22 intensive studies, Woodroffe & Ginsberg (1998) showed that humans are responsible for the majority of large carnivore deaths inside protected areas. Most mortality occurs when carnivores range beyond reserve boundaries and are killed, accidentally and deliberately, by humans (Castley *et al.*, 2002; Schwartz *et al.*, 2006; Loveridge *et al.*, 2007). The peripheries of reserves may thus function as population sinks and, if mortality in border regions is not balanced by reproduction

and immigration, the resulting edge effect can cause the decline or the extinction of protected carnivore populations (Woodroffe & Ginsberg, 1998).

Although anthropogenic mortality is common at reserve borders, edge effects and their impacts on reserve efficacy are rarely quantified (Revilla, Palomares & Delibes, 2001). Accordingly, we initiated a study to investigate the extent and impact of edge effects on a protected leopard *Panthera pardus* population in the Phinda-Mkhuze Complex (PMC), South Africa. Leopards are subjected to many of the same anthropogenic threats driving carnivore declines globally, have lost an estimated 37% of their range in Africa alone (Ray, Hunter & Zigouris, 2005) and were recently uplisted from Least Concern to Near Threatened in the IUCN Red List (Henschel *et al.*, 2008). Leopards therefore warrant greater conservation concern than often recognized and also act as suitable models for investigating issues that affect the persistence of carnivore populations more widely.

The PMC comprises two adjoining reserves (Phinda Private Game Reserve and Mkhuze Game Reserve) that function as a single protected area for the contiguous leopard population. Leopards are protected inside the PMC but move freely across boundaries into surrounding areas, where they are persecuted (Balme, Slotow & Hunter, 2009b). Although classified as 'specially protected game' by the local conservation authority, Ezemvelo KwaZulu-Natal Wildlife (EKZNW), a quota exists for trophy hunting leopards in the region (Balme *et al.*, in press). Leopards may also be legally destroyed on private land if a landowner possesses a destruction permit issued by EKZNW for removal of confirmed damage-causing individuals (Ferguson, 2006). Finally, large numbers of leopards are killed opportunistically and illegally by landowners because of the perceived threat they pose to livestock (Balme *et al.*, 2009b).

We compared the spatial and demographic characteristics of leopards in two areas of the PMC with different exposure

to edge effects. Specifically, we tested whether leopard density differed in the core and border regions of the PMC and whether the variation was due to ecological or anthropogenic factors. We assessed how the rates and causes of mortality related to the ranging behaviour of individuals and determined whether leopards preferentially selected areas where they were legally protected. Finally, we used these data to evaluate the overall effectiveness of the PMC in conserving leopards.

Study area

The PMC is located in the Maputaland region of northern KwaZulu-Natal, South Africa (Fig. 1). The prevailing habitat type is broad-leaved woodland interspersed with grasslands and wooded grasslands, whose composition is similar throughout the reserve and in surrounding non-protected areas (Van Rooyen & Morgan, 2007). The climate

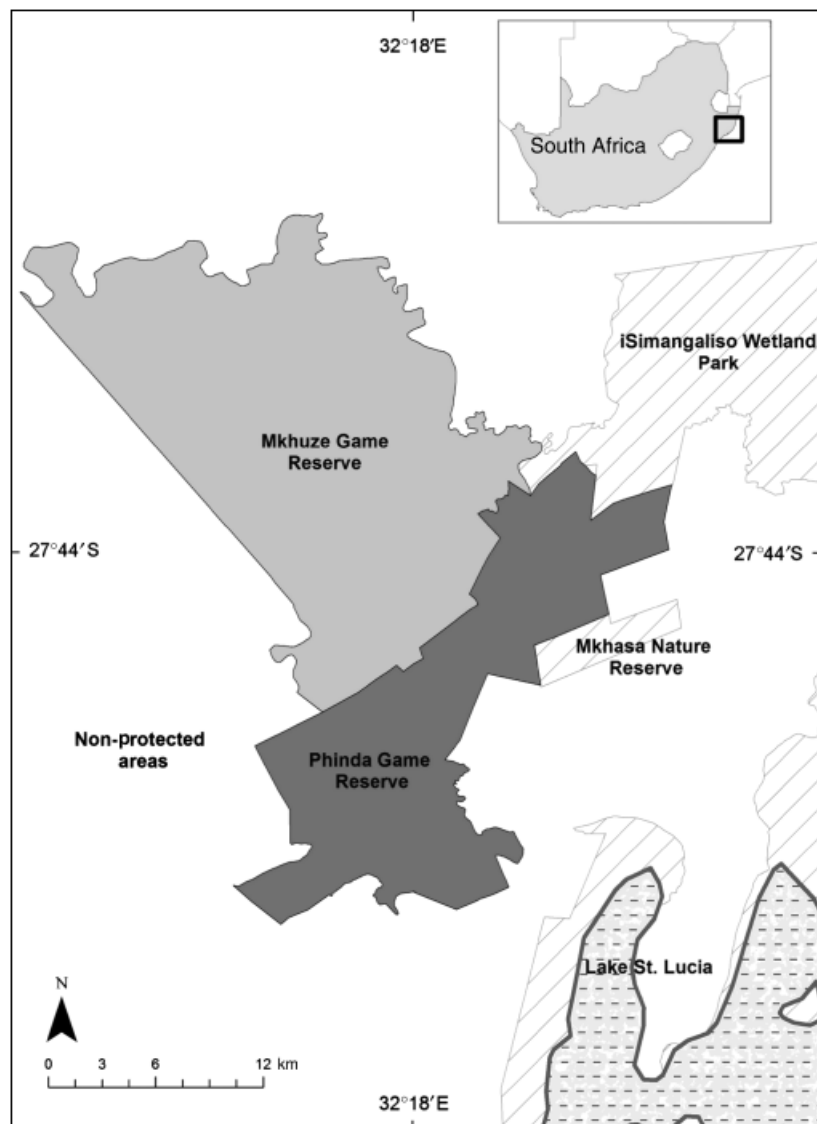


Figure 1 The study area showing land-use types in the region. Leopards *Panthera pardus* are protected in Mkhuze Game Reserve, Phinda Private Game Reserve and in hatched areas. White areas comprise non-protected cattle farms, game farms and tribal authority land where leopards are exposed to legal hunting and illegal killing. Inset: box indicates the region shown.

is warm to hot, humid sub-tropical, with two distinct seasons: a warm, dry winter from April to September and a hot, humid summer from October to March. The average annual rainfall is 550 mm, and the mean monthly temperatures range from 33 °C in January to 19 °C in July.

We selected 140 km² within the 220 km² Phinda Private Game Reserve as our 'border' study area (hereafter Phinda). This site was located on the southern boundary of the PMC, adjacent to a mosaic of non-protected areas (hereafter NPAs) made up of livestock farms, private game ranches and Zulu tribal authority land, where leopards are legally hunted and persecuted as pests. Forty-four large mammal species (excluding small rodents and bats) occur on Phinda including all indigenous large carnivores (Hunter *et al.*, 2007). We selected 130 km² in the centre of the 440 km² Mkhuzi Game Reserve as our 'core' study area (hereafter Mkhuzi). Mkhuzi is a state-managed reserve with habitat and mammal fauna comparable to Phinda, except that lions *Panthera leo* are absent.

Methods

Population monitoring

Between 2002 and 2007, we captured 20 leopards in Phinda and 17 leopards in Mkhuzi using a combination of free darting, baited cage-traps and soft-hold foot snares. All leopards were fitted with a VHF radiocollar (Sirtrack, Havlock North, New Zealand) or a GPS collar with a UHF uplink (Vectronic-Aerospace, Berlin, Germany). All capture and handling protocols were approved by the Animal Welfare Ethics Committee at the University of KwaZulu-Natal (Balme, 2009). 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 leopards on average every 3 days from the ground or air, and recorded their position to the nearest 50 m using a hand-held Global Positioning System receiver (Garmin International, Kansas City, MO, USA). We calculated the proportion of locations that individuals were found outside the reserve (PLOR) and used a general linear model to determine whether age, sex or location (Phinda or Mkhuzi) affected PLOR.

We used camera-trap surveys to estimate leopard population density in Phinda, Mkhuzi and in the NPAs to the south of the PMC. We surveyed all three sites in 2005 and we additionally surveyed Mkhuzi in 2008 following the methods we evaluated earlier in Balme, Hunter & Slotow (2009a). We used 30 stations per survey, each comprising paired cameras (Deercam, Park Falls, WI, USA), that is, 60 cameras in total. Each site was sampled for 40 days and we grouped two successive trap-days together to form a single sampling occasion, resulting in 20 sampling occasions per survey. We compiled capture histories for individual leopards in the program CAPTURE (Rexstad & Burnham, 1991), and used the model selection function to determine which estimator best fit the data in question and tested for popula-

tion closure. We calculated the size of the effectively sampled area by adding a circular buffer to each camera-trap station equal to half the mean maximum distance moved (HMMDM) by leopards photographed more than once. We calculated leopard density by dividing the population abundance estimated by CAPTURE for each site with the corresponding sampled area.

Prey availability and interspecific competition

We used photographic rates to compare prey availability among the different sites. We calculated relative abundance indices (RAI) for the six principal prey species of leopards in the region (Balme, Hunter & Slotow, 2007): nyala *Tragelaphus angasii*, impala *Aepyceros melampus*, grey duiker *Sylvicapra grimmia*, red duiker *Cephalophus natalensis*, reedbuck *Redunca arundinum* and warthog *Phacochoerus aethiopicus*. The RAI was defined as the number of independent photographs (captures) taken of each species per 100 trap-days (O'Brien, Kinnaird & Wibisono, 2003). We calculated relative biomass indices (RBI) for each survey area using the mean weights of prey species from Skinner & Chimimba (2005).

We also used photographic rates as a proxy for levels of interspecific competition at the three sites. Leopards lost similar numbers of kills to lions and spotted hyenas *Crocuta crocuta* (Balme *et al.*, 2007); hence, we combined the captures of these two species to calculate the RAI of interspecific competitors in Phinda. Because lions were absent in Mkhuzi and the NPAs, we used captures of only spotted hyenas to determine the RAI of competitors in those areas. Although African wild dogs *Lycan pictus* and brown hyenas *Hyaena brunnea* are known to compete occasionally with leopards (Creel, Spong & Creel, 2001), both species occur at very low densities in the region, and we have no records of any kind of interactions between them and leopards. Accordingly, we believe that their influence on leopards was insignificant.

Abundance indices should share a monotonic relationship with absolute density when used in spatial or temporal comparisons (Conroy, 1996). To test this, we compared the RAIs of the six prey species, lions and hyenas with independent density estimates in Rowe-Rowe (1992), Balme *et al.* (2007), Hunter *et al.* (2007) and annual counts of ungulates from Mkhuzi derived using ground-based distance sampling (EKZNW, unpubl. data).

Mortality and survival

We estimated survivorship for leopards in Phinda from 2002 through 2004 during a period of heavy persecution adjacent to the PMC when we expected potential edge effects to be the strongest (Balme *et al.*, 2009b). We excluded data from Phinda after 2004 as we began a programme of conservation interventions in 2005 in NPAs adjacent to Phinda that affected leopard mortality and survival (Balme *et al.*, 2009b). We estimated survivorship of radiocollared leopards

in Mkhuzi from 2005 through 2007. Although this period overlaps with our intervention programme, the Mkhuzi population was distant from the intervention programme, and it remained both stable and at capacity throughout the study (see 'Discussion'). Hence, despite consecutive study periods, we believe that differences in leopard survivorship between Phinda and Mkhuzi relate to spatial rather than temporal factors.

We calculated cause-specific and annual mortality rates for all radiocollared leopards using the Trent–Rongstad maximum likelihood estimator in the program MICROMORT (Heisey & Fuller, 1985). Radiocollars were fitted with mortality switches and we found most dead leopards within 24 h. We compared the mortality rates among different age and sex classes of leopards in Phinda and Mkhuzi. In addition, we assessed seasonal and annual variation in mortality during the study. Comparisons between rate estimates were performed in the program CONTRAST, which yields a test statistic distributed as χ^2 (Hines & Sauer, 1989).

We used Cox proportional-hazards regression (Cox & Oakes, 1984) to evaluate the effect of different variables on the survival probability of leopards. Age, sex and PLOR were incorporated into the model and sequentially removed using a backward stepwise elimination process based on the Wald statistic. Interactions between variables were excluded because of data limitations. We tested the assumption of proportional hazards using the approach described by Grambsch & Therneau (1994).

We assessed whether leopards discriminated between the PMC and adjoining non-protected areas using compositional analysis (Aebischer, Robertson & Kenward, 1993). A leopard was considered to have access to non-protected land if its home range (calculated as a 100% minimum convex polygon) overlapped the border of the PMC. For these individuals, we calculated the proportion of each animal's home range inside the reserve and used this to determine a log ratio of its available home-range area within the PMC. We compared this with the log ratio of its utilized home-range area in the PMC, calculated from the proportion of daily locations found in the reserve. A significant difference between these log ratios would indicate that each leopard was either selecting or avoiding the PMC (Aebischer *et al.*, 1993).

Dispersal direction

We classified a disperser as a subadult that established a home range after becoming independent with <5% overlap of its natal range or that died outside its natal range (Sweaner, Logan & Hornocker, 2000). We calculated dispersal direction as the angle from the arithmetic centre of a leopard's natal range to the arithmetic centre of its independent range or mortality site. We used Raleigh tests (Zar, 1999) to ascertain whether dispersal direction was uniform or random for subadults in Phinda and Mkhuzi.

We performed all analyses and statistical comparisons using SPSS 15.0 (SPSS Inc., Chicago, IL, USA), and present means \pm SE throughout. Ratio data were normalized using an arcsine square-root transformation.

Results

Population monitoring

Radiocollared leopards in Phinda spent less time inside the protected area than those in Mkhuzi ($F_{1,7} = 16.369$, $P \leq 0.001$; Fig. 2). Only three of the 20 leopards captured in Phinda resided solely within the PMC compared with 13 of 17 leopards monitored in Mkhuzi that used the reserve exclusively. There was no difference between male and female leopards for the time spent outside the PMC ($F_{1,7} = 1.695$, $P = 0.203$), although all males from Phinda were found off the reserve on at least one occasion. Subadult leopards spent a greater proportion of their time outside the PMC than adults ($F_{1,7} = 5.326$, $P = 0.028$).

We photographed between three and 13 individual leopards during camera-trap surveys (Table 1), with capture frequencies ranging from 1 to 10 captures per individual (3.38 ± 0.45). CAPTURE selected M_h , allowing for heterogeneous capture probabilities among individuals (Otis *et al.*, 1978), as the most appropriate model for our data, and population closure was confirmed in all surveys. Estimated capture probabilities per occasion (\hat{P}) were relatively consistent across surveys (range 0.11–0.18), resulting in population estimates ranging from three leopards in the NPAs to 16 leopards in Phinda. The mean maximum distance moved by leopards photographed on more than one occasion (MMDM) was similar for all surveys (mean 4.23 ± 0.38 km, range 2.22–7.59 km; Kruskal–Wallis Test: $\chi^2_2 = 0.203$, $P = 0.925$), yielding effectively sampled areas of 121–223 km². The estimated leopard population density in 2005 in the NPAs (2.49 ± 0.87 leopards 100 km⁻²) was approximately one-third the density in Phinda (7.17 ± 1.12 leopards 100 km⁻²) and less than one-quarter of that in Mkhuzi (11.11 ± 1.31 leopards 100 km⁻²).

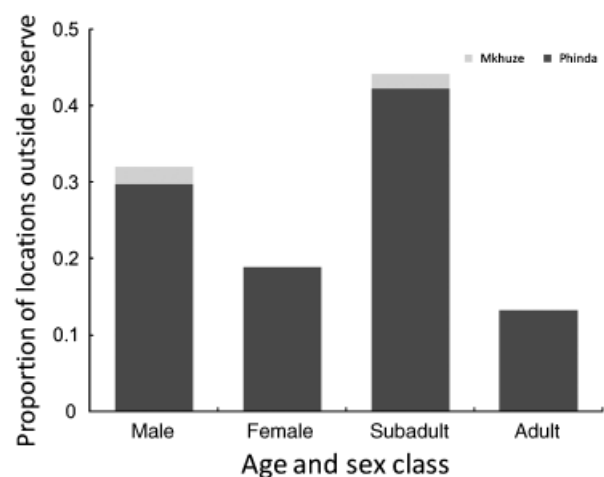


Figure 2 Mean proportion of daily locations found outside the reserve for different age and sex classes of radiocollared leopards *Panthera pardus* in Phinda Private Game Reserve and Mkhuzi Game Reserve, KwaZulu-Natal, South Africa, 2002–2007.

Table 1 Results of camera-trap surveys conducted in the Phinda Private Game Reserve, Mkhuze Game Reserve and adjoining non-protected areas (NPAs), KwaZulu-Natal, South Africa, 2005–2008

Survey area (year)	Number of leopard captures	Number of individuals captured	Closure test			CAPTURE abundance	Buffer width (km)	Effectively sampled area (km ²)	Density (number of leopards 100 km ⁻²)
			<i>z</i>	<i>P</i>	<i>P</i> -hat				
Mkhuze (2005)	48	13	0.437	0.669	0.17	14 ± 2.89	2.02	126	11.11 ± 1.31
Mkhuze (2008)	37	12	-0.265	0.395	0.11	17 ± 4.29	2.31	158	10.76 ± 1.79
Phinda (2005)	39	13	0.087	0.535	0.12	16 ± 2.97	2.33	223	7.17 ± 1.12
NPAs (2005)	11	3	-0.514	0.171	0.18	3 ± 0.23	2.16	121	2.49 ± 0.87

NPA, non-protected area.

Prey availability and interspecific competition

We obtained 9649 independent photographs from 52 species (41 mammals, 10 birds and one reptile). We photographed the six principal leopard prey species on 6297 occasions (Table 2). There was a significant difference in the frequency that different species were captured at the three sites (Friedman's test: $\chi^2_2 = 11.952$, $P = 0.035$). Nyala were the most regularly photographed species in Phinda and the NPAs, comprising roughly half of all captures, while impalas comprised nearly 60% of photographs taken in Mkhuze. Phinda had the highest estimated RBI (11 401 captures/100 trap-days kg), followed by Mkhuze (7330 captures/100 trap-days kg) and the NPAs (6052 captures/100 trap-days kg).

We obtained similar lion ($n = 25$) and spotted hyaena ($n = 24$) photographs in Phinda, resulting in a combined RAI of 4.17 captures/100 trap-days. The RAI of spotted hyaena in Mkhuze and the NPAs was 4.58 captures/100 trap-days and 0.66 captures/100 trap-days, respectively.

There was a close positive relationship between the RAIs calculated from the camera-trap data and independent density estimates for the eight species of interest ($F_{1,12} = 67.934$, $P < 0.001$, $r^2 = 0.850$; Fig. 3). Accordingly, we believe that the results of the RAI reflect real differences in the abundance of leopard prey and interspecific competitors between the three sites.

Mortality and survival

Twelve of the 37 leopards that we monitored during the study died, for which the cause of death was certain in 10 cases (Table 3). An equal number of leopards were killed by humans ($n = 5$) as died from natural causes ($n = 5$). The rates of anthropogenic mortality ($\chi^2_1 = 3.919$, $P = 0.477$) and natural deaths ($\chi^2_1 = 3.919$, $P = 0.477$) were higher in Phinda than in Mkhuze. Most (80%) anthropogenic mortality was illegal; two adult males were caught in poachers' snares inside the reserve and two subadult males were illegally killed on farms. The only legally killed leopard was an adult male shot during a trophy hunt outside the PMC. An adult male and three subadult females were killed by conspecifics, and one subadult male died from wounds inflicted by a spotted hyaena. The mean distance at which leopards were

killed outside the reserve ($n = 3$, all from Phinda) was 7.63 ± 4.58 km (range 1.21–16.50 km).

There was a significant difference in the average annual mortality rates of the two study populations, and mortality was higher in all cohorts in Phinda compared with Mkhuze, except for adult females (Table 4). We recorded no variation in annual (Phinda: $\chi^2_2 = 0.212$, $P = 0.897$; Mkhuze: $\chi^2_2 = 0.038$, $P = 0.981$) or seasonal (Phinda: $\chi^2_4 = 1.929$, $P = 0.748$; Mkhuze: $\chi^2_4 = 1.062$, $P = 0.905$) mortality rates during the study.

The assumption of proportional hazards was met for all covariates tested in the Cox regression, indicating that the model was appropriate for our data. The only significant predictor remaining in the model after backward elimination was PLOR, that is, time spent off the reserve (Wald = 6.480, $B = 2.425 \pm 0.953$, $P = 0.011$). An odds ratio of 11.3 suggested that leopards spending more time off the reserve had less chance of surviving. Because leopards moving outside the reserve experienced elevated mortality, they may be expected to avoid adjacent non-protected areas. However, results from the compositional analysis revealed no difference between the log ratios of leopards' available and utilized home-range areas within the reserve ($t_{20} = 1.179$, $P = 0.252$).

Dispersal direction

Five of nine subadult leopards captured in Phinda dispersed during the study (three males, two females). Dispersal direction was not randomly distributed ($z = 3.726$, $P = 0.015$), with leopards moving south and east into the NPAs or remaining in Phinda. Six of eight subadults captured in Mkhuze dispersed (five males, one female). In contrast to the pattern in Phinda, the dispersal direction was random ($z = 0.525$, $P = 0.611$). Two adult males also shifted their home ranges from the centre of Mkhuze to Phinda during the study.

Discussion

Despite equivalent legal protection, leopards near the border of the PMC lived at lower densities and suffered higher mortality rates than those closer to the reserve's core. Interspecific competition was similar in the two areas, while prey availability was greater near the border than at the

Table 2 Number of captures, relative abundance indices (RAI) and relative biomass indices (RBI) of six leopard prey species photographed in camera-trap surveys in the Phinda Private Game Reserve, Mkhuzi Game Reserve and adjoining non-protected areas (NPAs), KwaZulu-Natal, South Africa, 2005

Species	Phinda			Mkhuzi			NPAs		
	Captures	RAI ^a	RBI ^b	Captures	RAI ^a	RBI ^b	Captures	RAI ^a	RBI ^b
Impala	509	42.42	1697	1211	100.92	4036	327	27.25	1090
Nyala	1686	140.50	8430	470	39.17	2350	757	63.08	3785
Grey duiker	61	5.00	83	72	6.00	99	271	22.58	373
Red duiker	76	6.33	75	42	3.50	41	128	10.67	126
Reedbuck	7	0.58	29	11	0.92	45	27	2.25	113
Warthog	290	24.17	1088	202	16.83	757	151	12.58	566
Total	2628	219.00	11 401	2008	167.33	7330	1661	138.42	6052

^aNumber of captures/100 trap-days.

^bNumber of captures/100 trap-days kg.

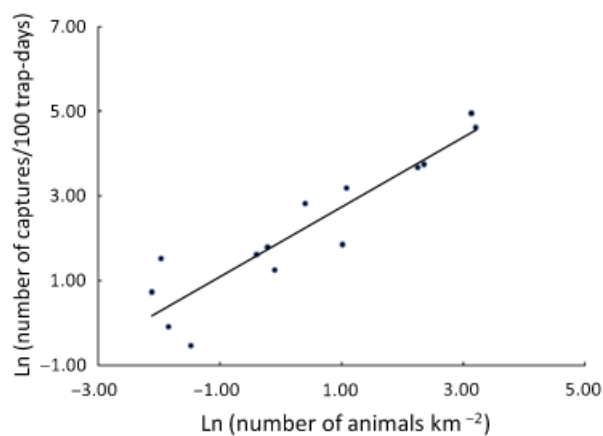


Figure 3 Relationship between independent density estimates (number of animals km⁻²) and the corresponding relative abundance indices (RAI; number of captures/100 trap-days) calculated from camera-trap data in the Phinda-Mkhuzi Complex, KwaZulu-Natal, South Africa ($r^2=0.850$). Data are for lion, spotted hyaena and the six main prey species of leopards. Both density and RAI are log-transformed.

centre of the PMC, suggesting that exposure to anthropogenic mortality originating outside the PMC was the principal factor affecting the vital rates of leopards. As few leopards monitored on Phinda had home ranges entirely within the reserve, many individuals were vulnerable to persecution on adjacent non-protected land, reflected both by elevated anthropogenic mortality and by reduced probability of survival.

Despite an increased risk of mortality, leopards did not avoid non-protected land. Prey abundance in the NPAs was comparable to that in Mkhuzi, and interspecific competition was lower in the NPAs than in Phinda or Mkhuzi. Therefore, besides high anthropogenic mortality, the NPAs represented suitable leopard habitat and may have functioned as an ecological trap, that is, an area with disproportionate mortality that would otherwise provide suitable resources (Delibes, Goana & Ferreras, 2001; Schlaepfer,

Runge & Sherman, 2002). Additionally, the removal of leopards from non-protected areas may have created vacancies, attracting leopards from surrounding areas. The dispersal direction of subadult leopards in Phinda was not random, with most dispersers moving off the reserve into NPAs. High mortality rates among adult male leopards in Phinda also attracted males from Mkhuzi to depopulated border areas, presumably because of increased access to mating opportunities (Bailey, 2005). This 'vacuum effect' has been documented previously in carnivores and may cause edge effects to reach the interior of even very large protected areas (Castley *et al.*, 2002; Loveridge *et al.*, 2007).

Both natural and anthropogenic mortality were higher in Phinda than in Mkhuzi. Persecution of leopards in NPAs may have increased intraspecific conflict in Phinda by disrupting social stability (Tuystens & Macdonald, 2000). Leopards live in a complex land tenure system that is highly dependent on the stability of long-term relationships (Bailey, 2005). Although both male and female leopards defend home ranges against same-sex intruders, interactions between familiar neighbours are more tolerant than between unknown individuals (the 'dear enemy' effect; Ydenberg, Giraldeau & Falls, 1988). Elevated turnover would likely increase contact between unfamiliar individuals and promote intraspecific strife, including elevated levels of infanticide (Swenson *et al.*, 1997; Wielgus & Bunnell, 2000; Whitman *et al.*, 2004). Although male leopards provide no parental care, the sire's presence limits incursions by immigrant males that threaten cub survival. We witnessed one case of infanticide in Phinda following the illegal killing of an adult territorial male outside the PMC. The resulting vacancy was rapidly filled by a transient male from Mkhuzi, who killed three 4-month-old cubs sired by the previous resident. Further, reproductive performance of the Phinda population between 2002 and 2004 was poor, with only three of 11 cubs born to radiocollared females surviving to adulthood (Balme *et al.*, 2009b). In Phinda, mortality rates exceeded the number of leopards born into the population, and so high levels of immigration would be required for densities to remain stable. Yet, even if this occurs, it may depress reproduction if it encourages constant incursions by

Table 3 Cause-specific annual mortality rates (AMR) and number of recorded deaths of radiocollared leopards in Phinda Private Game Reserve and Mkhuze Game Reserve, KwaZulu-Natal, South Africa, 2002–2007

Cause of mortality	Phinda			Mkhuze			χ^2	<i>P</i>
	AMR	SE	Deaths	AMR	SE	Deaths		
Natural	0.179	0.055	4	0.042	0.042	1	3.919	0.047
Anthropogenic	0.179	0.055	4	0.042	0.042	1	3.919	0.047
Unknown	0.048	0.048	1	0.042	0.042	1	0.008	0.925

Table 4 Annual mortality rates (AMR), number of radiotracking days (RD) and number of recorded deaths of different age and sex classes of radiocollared leopards in Phinda Private Game Reserve and Mkhuze Game Reserve, KwaZulu-Natal, South Africa, 2002–2007

Age and sex class	Phinda				Mkhuze				χ^2	<i>P</i>
	AMR	SE	RD	Deaths	AMR	SE	RD	Deaths		
Subadult male	0.801	0.066	733	3	0.195	0.195	1396	1	8.665	0.003
Subadult female	0.345	0.030	1731	2	0.118	0.118	1671	1	3.922	0.048
Adult male	0.396	0.087	2116	3	0.082	0.082	3603	1	6.898	0.009
Adult female	0.149	0.149	2839	1	0		1757	0	1.000	0.317
Total	0.358	0.075	7419	9	0.122	0.065	8427	3	5.654	0.017

new males that kill cubs (Whitman *et al.*, 2004; Balme *et al.*, 2009b).

Management goals for reserves such as the PMC that act as reservoirs for harvesting in adjacent areas typically require populations to be at, or close to, carrying capacity (Cougar Management Guidelines Working Group, 2005). Hayward, O'Brien & Kerley (2007) demonstrated a close relationship between leopard density and the biomass of preferred prey ($y = -2.248 + 0.405x$; $r^2 = 0.833$; $P \leq 0.001$), and predicted the carrying capacity of leopards in several protected areas. Using the same approach, the predicted carrying capacity is 10.61 leopards 100 km⁻² in Mkhuze and 12.21 leopards 100 km⁻² in Phinda. The Mkhuze estimate is similar to the density from our camera-trap survey (11.11 leopards 100 km⁻²); however, the Phinda estimate is considerably higher than ours (7.17 leopards 100 km⁻²). This suggests that, although leopards were adequately protected in the core of the PMC, edge effects kept the population well below carrying capacity nearer the border. While it is unlikely that leopards will disappear completely from the reserve, given the proximity of other protected populations (e.g. Hluhluwe-Imfolozi Park, iSimangaliso Wetland Park), the overall effectiveness of the PMC was clearly weakened by persecution in border regions and associated effects on vital rates.

The most effective options for combating such effects are increasing the size of the protected area or decreasing the number of people living outside its boundaries (Woodroffe & Ginsberg, 1998; Harcourt, Parks & Woodroffe, 2001). However, with the rapid expansion of local human populations, both are unlikely. A suitable alternative is the implementation of conservation measures on both sides of the administrative border (Forbes & Theberge, 1996). In 2005, a new management strategy was instituted in KwaZulu-Natal

to reduce edge effects and improve the conservation prospects of the province's leopard population (Balme *et al.*, 2009b). The new strategy revised the statutory systems that regulate problem animal control and trophy hunting, and we also instituted a programme to reduce human–leopard conflict in the region. (Ferguson, 2006; Balme *et al.*, 2009b; Balme *et al.*, 2010). These interventions appeared to alleviate edge effects, as demonstrated by increases in density and reduced mortality near the border. While density estimates of the buffered Mkhuze population remained essentially constant from 2005 (11.11 ± 1.31 leopards 100 km⁻²) to 2008 (10.76 ± 1.79 leopards 100 km⁻²; Table 1), the Phinda population increased by over 56% (2005: 7.17 ± 1.12 leopards 100 km⁻², 2009: 11.21 ± 2.11 leopards 100 km⁻²; Balme *et al.*, 2009b). Annual mortality in the Phinda population after our interventions (0.134 ± 0.016) decreased to near parity with that in Mkhuze (0.122 ± 0.065; Balme *et al.*, 2009b).

As human populations continue to increase around protected areas, approaches that manage human activities on both sides of administrative borders will be essential if conservation of wide ranging taxa is to succeed (Wittemyer *et al.*, 2008). Relatively resilient, large carnivores such as leopards can act as surrogates for conservation outcomes that benefit other species (Sergio *et al.*, 2008). At our site, activities that mitigate edge effects for leopards would favour cheetahs *Acinonyx jubatus*, wild dogs and spotted hyaenas, although implementation would need to occur on a large scale to benefit cheetahs and wild dogs, given their more demanding area requirements (Woodroffe & Ginsberg, 1998). Similar potential surrogates include cougars *Puma concolor* and black bears *Ursus americanus* in the Americas, and striped hyaenas *Hyaena hyaena* and leopards in Asia. Understanding the impact of edge effects on their

populations and devising appropriate mitigation strategies might hold promise for buffering, maintaining or restoring landscapes that are suitable for more endangered species such as jaguars *Panthera onca*, tigers *Panthera tigris*, grizzly bears *Ursus arctos* and grey wolves *Canis lupus* (Woodroffe, 2001).

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