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External Research

Mortality in a protected Leopard population, Phinda Private Game Reserve, South Africa: A population in decline?

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Abstract
We investigated the causes and rates of mortality in a protected Leopard population in the Phinda Private Game Reserve, South Africa. Data from 16 radio-tagged Leopards and their cubs were used to determine the causes of mortality and annual mortality rates for various age and sex classes in the population. Intra-specific strife accounted for the greatest number of deaths followed by human-related mortality. Males died mainly as a result of human activity whereas females died from natural causes. The mortality rate for males was significantly higher than for females, and the annual mortality rate for the population was higher than any previously recorded in Leopards. Rapid turnover of adult males due to human persecution may have reduced recruitment into the population because social instability prevented females from raising cubs. If the present rates of mortality and recruitment are maintained, Phinda may represent a population sink for Leopards with poor conservation and tourism prospects.

Introduction
Mammalian carnivores are vulnerable to local extinction in fragmented landscapes due mainly to their low densities, large ranges and inevitable conflict with humans (Noss *et al*., 1996; Woodroffe & Ginsberg, 1998). Outside protected areas, accidental or intentional killing by people drives local extinction of large carnivores or reduces their numbers, and it is a matter of fact that many human-dominated landscapes will always be unsuitable for some large carnivores. As such, large, inviolate protected areas remain critical to the conservation of top carnivores.

However, there is increasing evidence that even protected areas may not effectively protect large carnivores. Using data from 22 intensive studies of carnivores *inside* protected areas, Woodroffe and Ginsberg (1998) demonstrated that 74% of known-cause deaths were directly caused by people. They showed that high levels of persecution of carnivores along the border regions of protected areas were sufficient to create population sinks. The impact of such sinks was greatest in small reserves with high perimeter:area ratios where the wide-ranging behaviour of carnivores leads them to cross reserve boundaries frequently and suffer high rates of human-caused mortality. Irrespective of population size, those carnivores that suffered most from human-caused mortality along reserve boundaries were the species most likely to disappear from reserves (Woodroffe & Ginsberg, 1998).

In 2002, we initiated the Munyawana Leopard Project to assess the impact of human-caused deaths on a protected Leopard *Panthera pardus* population in the Phinda Private Game Reserve, Kwa-Zulu Natal, South Africa. Leopards are fully protected in Phinda and in the Mkhuze Game Reserve on its western boundary (Figure 1). However the land to the south and east of Phinda comprises a mosaic of pastoral Zulu communities, livestock farms and private game farms where Leopards are often killed as perceived or real problem animals, or by commercial trophy hunting operations. Despite electrified game-fencing along most borders, Leopards move freely between adjacent properties and, because Phinda is long and narrow, few individual Leopards have their entire home range within the boundaries of the reserve (Balme & Hunter, unpub. data). The result is that most individual Leopards considered protected on Phinda are actually exposed to high levels of hunting due to frequent movements off the reserve.

In this paper, we present the results of the first 29 months of the study, addressing three main questions:
1. What are the causes of mortality to Leopards in the Phinda population?
2. What is the annual mortality rate of the Phinda Leopard population for different age and sex classes?
3. Does Phinda effectively protect Leopards?

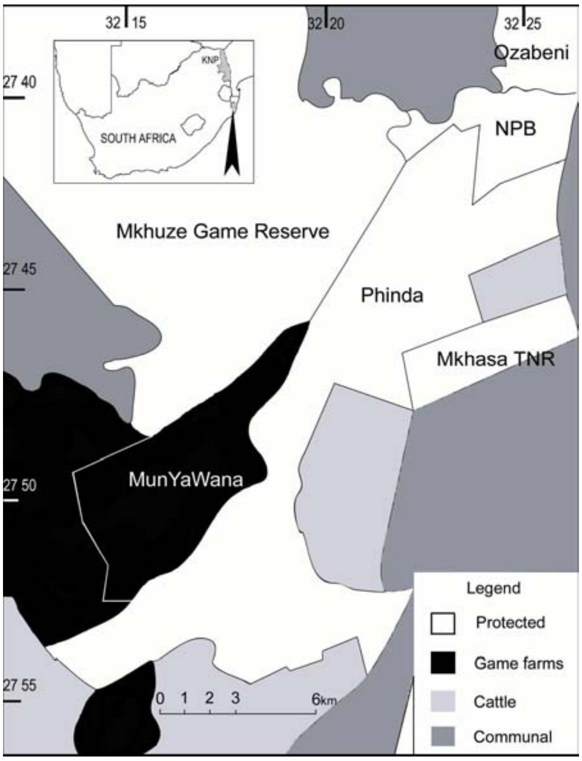

Figure 1: The study site showing land-use types in the region (*Inset*: arrowhead indicates region shown). Leopards are legally protected in areas shown in white but the degree of protection actually offered them varies widely; Leopards are best protected in Phinda and Mkhuze Game Reserve. Leopards are persecuted on game farms though harvest rates depend on individual landowners. The MunYaWana area is now contiguous with Phinda and although Leopards are occasionally hunted there, this is likely to diminish or cease entirely. Cattle areas are indicated where livestock is present though these areas also have significant game populations; these areas are hostile to Leopards. Leopards appear to be killed rarely on communal land though these areas have insufficient habitat and prey for permanent occupation.

Methods:

Detail of the study site and general methodology can be found in Hunter (1998) and Hunter *et al*. (2003). Between April 2002 and October 2003, we captured 16 Leopards and fitted them with VHF radio-collars. We attempted to locate every radio-collared animal at least once daily and recorded their location to the nearest 50m using a hand-held GPS receiver. From April 2002 to August 2004, we logged a total of 6527 transmitter-days following Leopards.

We aged Leopards by the wear and eruption of teeth (Stander, 1997), and classified them into three age classes to investigate age-related mortality: juveniles under one year old, sub-adults one to three years old, and adults over three years old. All sub-adults were independent from the mother but showed little or no territorial behaviour, while all adults displayed frequent territorial behaviour such as territorial vocalising and scent-marking (Balme & Hunter, unpub. data). All juveniles were dependent on the mother.

We established causes of mortality by direct observation or by post-mortem and evidence collected at the site such as tracks in the surrounding substrate. We usually found dead Leopards within 24 hours of their death and the cause was rarely ambiguous. We considered three Leopards which disappeared outside Phinda to have been killed by people. Although this is speculative, in all cases the animal disappeared and its radio-collar abruptly stopped transmitting within 24 hours of moving into an area known to be hostile to Leopards. We were unable to search for missing Leopards on these properties to confirm their fate. However, we searched for radio-collar signals from their boundaries or from the air, a technique which had always yielded a signal in similar attempts made while the Leopard was living. Further, radio-collars did not fail during the study and had they, Leopards with faulty collars would almost certainly have been re-sighted given that all our collared animals during life were seen consistently by game drives at Phinda (Balme & Hunter, in prep.). The highly probable explanation in these cases is that the radio-collars were destroyed by people after the animal was illegally killed.

We calculated annual mortality rates (AMRs) after Ferraras *et al*. (1992) using the formula:

$$\frac{\text{number of deaths}}{\text{number of radio-transmitter days}} \times 365$$

We calculated the AMR for the population, and separately for males, females, all adults and all sub-adults using age/sex-class specific data (i.e. number of deaths and radio-transmitter days). We did not have sufficient observations to calculate the juvenile mortality rate. We compared differences between age and sex classes using non-parametric statistics (Siegel, 1956).

Results:

Causes of mortality

Eight radio-collared Leopards died during the study, for which the cause of death was certain or probable in seven cases (Table 1). Intra-specific conflict and anthropogenic deaths were equally important causes of mortality for adults and sub-adults combined, both claiming three individuals. Natural causes (excluding other Leopards) were responsible for one and possibly two additional deaths.

Age & Sex	Human		Intra-specific		Inter-specific		Unknown	
	AMR	DEA	AMR	DEA	AMR	DEA	AMR	DEA
Adult male	0.497	2	0.248	1	0	0	0	0
Adult female	0	0	0	0	0	0	0.160	1
Sub-adult male	0.484	1	0	0	0.484	1	0	0
Sub-adult female	0	0	0.361	2	0	0	0	0
Total	**0.168**	**3**	**0.168**	**3**	**0.056**	**1**	**0.056**	**1**

Table 1: Cause of death (DEA) and cause-specific annual mortality rates (AMR) for different age and sex categories.

Sex & Age	AMR	RD	IND	DEA
Adult male	0.745	1469	4	3
Adult female	0.160	2280	5	1
Sub-adult male	0.968	754	3	2
Sub-adult female	0.361	2024	5	2
Total male	0.821	2223	7	5
Total female	0.254	4304	9	3
Total adult	0.389	3749	9	4
Total sub-adult	0.526	2778	8	4
Total	**0.447**	**6527**	**16***	**8**

Table 2: Annual mortality rates (AMR), number of radio-transmitter days (RD), number of monitored individuals (IND) and number of deaths (DEA) for different age/sex classes of leopards (*Total shows number of individuals radio-tracked during study. Classes combined may exceed this number because some individuals were tracked while belonging to different age classes.)

Intra-specific clashes killed one adult male and two sub-adult females. M1 was a resident territorial male when killed by the adult male, M5. The sub-adult female F10 was killed by an uncollared adult female leopard when almost three years old and displaying the first signs of territorial behaviour (‘sawing’ and scent-marking). The sub-adult female F15 was 20 months of age when killed by a male Leopard, the sub-adult M14. Additionally, although we have not included juvenile deaths in the estimation of mortality rates, three juveniles were killed by the adult male M13 that had recently become established and was not their sire.

Human-related deaths killed three males. Two adult males M5 and M13 were established territorial males at the time of their disappearance on properties adjacent to Phinda. The sub-adult male, M7 was last located on private property near the town of Hluhluwe, approximately 11km south of Phinda’s southern boundary, when his signal disappeared.

One Leopard was killed by another carnivore. The sub-adult male, M4 died from septicemia arising from severe bite wounds on the neck, shoulders and hindquarters. We found evidence at the site of a prolonged fight between the Leopard and an adult Spotted Hyaena *Crocuta crocuta* which was consistent with the bite marks. We do not know the cause of death of the adult female F2 whose carcass we examined approximately two weeks after death when decomposition was advanced.

Mortality rates

The average annual mortality rate (AMR) of the population between April 2002 and August 2004 was 0.447 (Table 2). The mortality rate for males was significantly higher than for females ($p = 0.004$, df = 1). Sub-adult males (0.968) had the greatest annual mortality of any cohort, followed by adult males (0.745). Adult females had the lowest mortality rate (0.160) with only one death recorded for the study period.

Discussion:

Causes of mortality

Leopards at Phinda were killed chiefly by other Leopards. Two deaths (M1 and F10) were the result of territorial clashes between same-sex pairs. Leopards are known to defend their territories from same-sex intruders sometimes leading to fatalities (Le Roux & Skinner, 1989) though the proportion of deaths here caused by other Leopards is higher than reported in other detailed studies (Bailey, 1993; Stander *et al.,* 1997). The killing of sub-adult female F15 by a sub-adult male (M14) is unusual, particularly as these animals had met on previous occasions. F15 was not reproductively mature and M14 typically rebuffed curious approaches from her in past encounters we observed, but his aggression was largely demonstrative and never escalated to physical contact. A similar instance of a male Leopard killing a younger female was documented at Londolozi Private Game Reserve, South Africa (Hes, 1991). Males might regard young, reproductively unavailable females as competitors for food resources and attack them as such, though it is unclear why it happened later rather than sooner in this case.

All radio-tagged Leopards that died due to human-related causes were males. Males are more desirable to trophy hunters due to their larger size, and males also utilise larger home ranges and cover greater daily distances than females, increasing their chances of moving off the reserve into areas where they can be hunted (Mizutani & Jewel, 1998; Hunter & Balme, unpubl. data). Importantly, as far as we know, males killed outside Phinda were not shot legally by international hunters with CITES permits. Nonetheless, all three deaths occurred during the legal trophy hunting season between April to November. This may be due to Leopards being mistaken for another legally hunted species but more likely they are killed intentionally by South Africans. Leopards are persecuted intensely by various landowners in the region and there is little chance of prosecution for illegal killing. We do not know whether the risks for Leopards are elevated during the legal hunting season. It is likely that opportunistic killing of Leopards occurs year-round though increased numbers of local hunters seeking other species in the area during the legal season might result in more Leopards killed then.

Bailey (1993) reported that starvation (mainly of sub-adults) accounted for the greatest proportion of Leopard deaths in Kruger National Park (KNP). He suggested that sub-adults were more likely to starve due to a related set of factors that included a lack of hunting experience, loss of condition due to increased parasitic infestations, competition for resources with other predators, and seasonal changes in prey abundance and availability of cover. We found no evidence of starvation contributing to Leopard deaths at Phinda. One individual, M7 was emaciated at capture but this was due to serious injuries, probably incurred from a conspecific. His condition improved dramatically post-capture and he made a full recovery. He was clearly foraging successfully for 12 months following capture until February 2004 when he was killed outside Phinda.

The only adult female to die during the study probably succumbed to natural causes. At the time of her death, she was due to give birth and we made no effort to approach her, assuming she was localised with newborn cubs. By the time we decided to investigate, autolysis of the carcass was too advanced to determine a cause but there was no evidence to suggest her death was related to human activity. We found no snares and the site was not close to a boundary where the risk of snaring at Phinda is greatest. She may have died due to complications arising from birth. This is considered unusual in felids (Apps & Du Toit, 2000) but is occasionally recorded: for example, an otherwise healthy Lioness *Panthera leo* in Pilanesberg National Park died from secondary septicemia due to dystocia (G. van Dyk, *Pers. comm.*).

Mortality rates and the future of the Phinda population

Our results agree with other detailed studies of African Leopards in demonstrating sex dependent mortality. Similar to Bailey's (1993) study of Leopards in Kruger National Park, males at Phinda suffered higher mortality rates than females. However, there are some significant contrasts. The AMR of the Phinda Leopard population is high, with effectively half the population dying each year, many of them directly or indirectly due to human factors. This is considerably higher than mortality rates recorded for the protected population in the KNP, South Africa where all deaths were natural (see Table 2: KNP adult AMR = 0.185, subadult AMR = 0. 320; Bailey, 1993). In particular, the AMR of Phinda males is close to three times that of Kruger males (AMR = 0.250; Bailey, 1993) though differences between the methods used to calculate mortality rates may have given rise to some of the discrepancy.

High levels of mortality among adult males at Phinda may have had an additive effect on mortality in the population by lowering the reproductive success of females. Although male Leopards provide no parental care to cubs, the presence of the sire allows mothers to raise cubs with a reduced risk of infanticide by foreign males (Hunter *et al*., in press). There are few reliable observations of infanticide in leopards (see: Ilani, 1986; 1990; Scott & Scott, 2003) but new males entering the population are likely to kill existing cubs. We saw this once during the study period, following the illegal killing of M5. The resulting vacancy was rapidly filled by the male M13 who killed the 4-month old cubs of F12 (which M5 probably sired). Although we observed infanticide only on this occasion, there was limited evidence of successful reproduction in general. During the 29-month study, we observed consorting pairs on 18 occasions involving seven adult females, multiple males and 305 actual matings, yet only seven cubs in three litters were born. Only two cubs are still alive at the time of writing, one of them still dependent on its mother.

That few cubs were produced during the study may be a further consequence of high turnover among males. In Lions, high levels of infanticide further impact reproductive output by reducing the rate at which females conceive (Packer & Pusey, 1983). Lionesses display a period of reduced fertility immediately following the take-over of a pride by a new male coalition. This presumably allows females to assess the fitness of new males and postpone conception until the males are established and the threat of another take-over is reduced. Rapid turnover of male Leopards at Phinda might be driving female Leopards into a reproductive dead-end in which cubs are killed at high rates and subsequent conception is delayed. In an isolated Leopard population in the Judean Desert, Israel, infanticide was the chief reason that not a single individual was recruited into the adult population during a five-year period (Ilani, 1986; 1990).

At Phinda, human persecution of males outside the reserve is a possible ultimate cause. Whitman *et al.* (2004) demonstrated that excessive trophy hunting of male Lions under a certain age reduced the chance of population persistence because Lionesses failed to raise cubs to independence due to the constant cycle of infanticide and delayed conception. We do not yet have sufficient data to draw the same conclusion here;

however there are coarse patterns that warrant concern. Only one individual born into the population reached independence and became established on Phinda during the study period and, at the time of writing, she is still too young to reproduce. In contrast, eleven individuals died, four of which were breeding residents. For a population to remain stable, birth and mortality rates need to be equivalent, and immigration and emigration rates need to be comparable (Eltringham, 1979). At Phinda, deaths far exceeded the number of Leopards being born in the population so high levels of immigration will need to occur for densities to remain stable. We do not yet have a clear picture of immigration and emigration at Phinda to assess this. However, even if immigration is balancing mortality, it may be depressing reproduction if it encourages constant incursions by new males that kill cubs.

It is possible that the study period represents a temporary period of unusually elevated social flux in Leopards that will eventually stabilise. We do not yet know whether male territorial tenure is reduced across the population, or that the low success rates of female reproduction observed here are permanent. Continued monitoring (the project will proceed until at least the end of 2006) will investigate whether the population attains greater stability in the future.

In the meantime, we need to consider the possibility that Phinda Leopards are in a state of ongoing instability. Geographically narrow, and located between the (presumably) well-protected population in Mkhuze Game Reserve to the west and the private and communal lands to the south and east where Leopards are persecuted, Phinda might represent a population sink for Leopards, despite their fully protected status on the reserve. There is little reason to think that levels of killing of Leopards adjacent to Phinda will decline. Indeed, with the recent (October 2004) CITES approval granted to South Africa to double its quota of Leopard trophies to 150, legal off-take will increase in the area. Assuming that levels of illegal killing remain the same, the patterns described here are likely to persist or possibly worsen.

Provided a well-protected source population (Mkhuze) persists, it is unlikely that Leopards will disappear from Phinda. However, at the very least, ongoing social perturbation will affect the tourism potential of the species on the reserve. Regular replacement of known, viewable animals with shy immigrants and a lack of cubs are two immediate consequences already evident. To address these problems and the potentially more serious conservation implications for the species will require a coordinated approach from all stakeholders with an interest in the Leopard. The formation of the Munyawana Leopard Conservancy (Hunter *et al*., 2003) represents a beginning toward this end. However, to date there is little evidence that this has fostered greater tolerance for the Leopard in the region outside protected areas where the species is already valued.

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