Role of delinquent young "orphan" male elephants in high mortality of white rhinoceros in Pilanesberg National Park, South Africa

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We describe white rhinoceros (*Ceratotherium simum*) mortality at Pilanesberg National Park, South Africa, focussing on mortality caused by African elephant (*Loxodonta africana*). We reconstructed records from a range of historical sources, and estimated that up to 49 rhino were killed by elephant. There was confirmed mortality in 1994 and 1996, and based on patterns, we suggest a set of rhino mortality from elephant in 1992. Both sexes and all age classes were victims. There was no significant bias to older animals, but given the rhino population structure, there was a significant bias towards males in adult deaths. The culprits were identified as young male elephants that entered musth about 10 years younger than expected, and maintained musth for a full term at first occurrence. We attributed this to the lack of a mature bull hierarchy in the park, because these elephants were the product of translocation of young animals (<10 years old) remaining from culls in Kruger National Park. We emphasise the need for accurate monitoring and record keeping, and a focus on individual identification of key species in small reserves.

Key-words: Conservation Ecology, *Ceratotherium simum*, *Loxodonta africana*, rhinoceros, small population management.

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Introduction

South African conservation agencies are renowned for their contribution to the conservation of endangered species, particlularly Megaherbivores such as white (*Ceratotherium simum*) and black rhinoceros (*Diceros bicornis*). Many innovations have originated in southern Africa, particularly in the ability to immobilise and transport large individuals. The "flagship" success story is saving the white rhinoceros from extinction (see Owen-Smith 1981 for graphical representation of recovery).

An original population of fewer than 100 white rhinoceros remained in Umfolozi Game Reserve in KwaZulu-Natal, South Africa. The Natal Parks Board (now KwaZulu-Natal Nature Conservation Service) protected and nurtured this population to the extent that there were surplus animals that could be translocated to other areas. Such translocations began in the 1960s to other reserves in South Africa, such that there are now a number of substantial populations of this species in southern Africa, most of them in small (< 1000 km^2) fenced reserves.

Such small reserves are not only established to protect the rhinoceroses, but these animals provide an important financial foundation to such reserves. A vigorous growing population of rhinoceros provides excellent viewing potential, and excess animals that can be allocated to hunting quotas or to live auctions (the 2000 value was about US$25 000 per individual!).

Pilanesberg National Park houses one of the five key populations of the southern white rhino (Brooks & Brooks 2000). In addition to the importance of this population for conservation, rhino provide a key component to the annual income of the reserve, and increase the long-term viability of conservation as a land-use practice for the reserve.

This paper describes a novel situation in Pilanesberg, where elephant were identified as a major source of mortality of white rhino. This situation is not unique to Pilanesberg, and has been identified from Borakalalo National Park, Hluhluwe-Umfolozi Park, Itala Game Reserve, Letaba Ranch, Mabula Lodge, Shamwari Game Reserve (Gus van Dyk *pers. comm.* with managers of reserves). In most reserves the numbers involved have been low, excepting 43 rhino (including 5 black rhino) killed in Hluhluwe-Umfolozi park (D. Balfour, Ecologist, Hluhluwe-Umfolozi Park, *pers. comm.*). The aim of this paper is to document this phenomenon, and to highlight issues pertinent to management of rhino in small populations.

Methods

Pilanesberg National Park (25°8'S–25°22'S; 26°57'E –27°13'E) is situated in the remains of an extinct volcano. It comprises 500 km² of very hilly savanna terrain. The habitat consists of *Acacia* and broad-leaf bushveld which ranges from thickets to open grassland patches. There is one major river system running southeast through the central part of the park, and a large dam in the centre of the park, with a number of smaller dams scattered throughout the reserve. Rainfall is approximately 630 mm/y, and falls in summer. Winters are cold (minimum temperature 1–5 °C), and summers very hot (mean maximum temperature 28–31 °C). The park was proclaimed in 1979 and since then about 6 000 individuals from a range of species were reintroduced to the park. Two hundred and forty eight white rhinoceros were introduced from Hluhluwe-Umflozi Park in KwaZulu Natal between 1979 and 1982. Between 1984 and 1999 at least 275 have been removed from Pilanesberg. On 15 May 1996 the white rhinoceros population was estimated. This was based on introduction records and an aerial survey focussed on white rhinoceros population structure and mortality detection in April 1996. The estimated population was 166, comprising 47 adult males, 60 adult females, 51 subadults, and eight juveniles (unpublished memo, Northwest Parks and Tourism Board—then Bophutatswana Parks Board—copy lodged with Gus van Dyk, Field Ecologist, Pilanesberg National Park). The rhinoceros population was estimated as 171 from the annual census in spring 1996 (Brockett 1997).

Five African elephants (*Loxodonta africana*) were introduced initially from Addo Elephant National Park in 1979, three of which died, and one was removed, leaving one young male (5-6 years old in 1979). This male may still be present in the population, or may have been removed among culls of unidentified individuals (see below). Additional elephant were introduced from Kruger National Park in 1981 (13 juvenile males and 5 juvenile females), 1983 (13 juvenile males and 11 juvenile females) and 1993 (19 males and 17 females), and from Namibia in 1982 (one juvenile male and one juvenile female). At the time of the introduction, the technology of translocations was such that elephants of a maximum shoulder height of 2 m (age 8–10 years) could be translocated live. The elephants that were translocated were the result of culling operations, and were thus orphans. In 1982 two 19 year old females were introduced. These were tame elephants that were returned from the USA to Africa, and released into the wild. These two older females assumed the role of matriarchs in the Pilanesberg herds. The first young elephant was born in 1989, indicating that males were breeding at the age of about 18 years old. The elephant population on 15 May 1996 was estimated as 29 females and 22 males, with about 30 calves, giving a total population of 81 (unpubl. internal memo, North West Parks and Tourism Board, copy lodged with Gus van Dyk, Field Ecologist, Pilanesberg National Park). Twelve males were classified as >14 years old. Six males had been culled prior to this date (see results).

Rhinoceros horn database

Pilanesberg National Park staff keeps records of all rhinoceros horn found in the park. Such horns are usually found by game-scouts who patrol the park on foot. When a carcass was found the front and rear horn were collected and handed in to the Warden for lodging in a safe location. The measurements of the horns were recorded in master file. Unfortunately, no biological information was noted in this file, and details such as individual identity, cause of death and location were missing in most cases. The date of collection was recorded in most cases, and we used this date for our analysis. The actual date of death was an undetermined time before this date. The type of analysis we make is not likely to be biased in one or other direction by this uncertainty.

All black rhino horn data were removed from the database prior to analysis since none in Pilanesberg have been killed by elephant and this analysis concerned only white rhino. In the database, each horn is recorded on a separate line. In most cases it was clear which were the associated front and rear horn, and these data were combined into one record. In some instances it was not clear which back horn was associated with which front horn. In this case we used the record for the front horn only. We assumed that any horn length > 292 mm was that of a front horn (smallest record allocated in this manner = 368 mm). This is based on an analysis of the lengths of the known back horns, which had a maximum length of 292 mm ($n = 94$). This yielded 118 mortality records between 1987 and 1999.

This database was used to generate an expected level of mortality in years when elephants were not killing rhino, and particularly, to reveal rhino mortality from elephants for 1992, when elephants were not thought as responsible (see results).

Direct verification of carcasses

From 1994 onwards it was suspected that elephants may be the culprits, and carcasses were checked for wounds caused by elephants (large puncture wounds in shoulder and neck) and for sign of elephant around the carcasses. There are two sources of these data. The 1994 data were sourced from an electronic mortality database at Pilanesberg National Park (captured by G. Redman, University of Natal, from monthly and quarterly reports of reserve staff which are lodged with the Warden, Pilanesberg; the electronic database is now lodged with Ray Schaller, Ecological Services, North West Parks and Tourism Board). The 1996 data were sourced from an internal report generated in May 1996 (unpubl. memo, North West Parks and Tourism Board, copy lodged with Gus van Dyk, Field Ecologist, Pilanesberg National Park), and three additional records from the same electronic mortality database captured by G. Redman (see above). These data provided dates, exact locations (counting blocks for 1994, GPS coordinates or map-grid references for 1996), and ages and sexes for most records. These data provided the absolute minimum number of elephant caused rhino mortality.

There were therefore two sources of information, the horn database and the verified carcasses. We combined these two databases to check for overlap for the period 1994 to 1996 (no carcass data were available for 1992). We went through each record and we combined 10 records where we could match dates in the two databases. We then checked all remaining records for commonalities, counted the number of records that should exists in the horn database at that time, and removed excess records from the combined dataset. This left over a dataset that contained all the recorded incidents of mortality from elephants, plus additional records that existed in the horn database, but that were not in the direct observation database. These are carcasses that were found, but that the cause of death was not noted. These databases have been lodged with Ray Schaller, Database Manager, Ecological Services, North West Parks and Tourism Board.

We classified ages according to classification in the above records. These are based on the following criteria: juveniles < 2 years old; sub-adults 2–6 years old; adults > 6 years old.

Total mortality database

A printed table exists showing the total mortalities of rhino in Pilanesberg National park from 1992 to the end of April 1996. This was attached to an internal report on rhino mortalities from elephants (unpublished memo, North West Parks and Tourism Board, copy lodged with Gus van Dyk, North West Parks and Tourism Board). The source of these data are unknown, but are assumed to be correct estimates based on carcasses. The original data from which this table was generated were not seen. These data do provide cause of death where known.

Elephant musth patterns

We noted direct observation of musth in individually identified elephants from March 1996. Elephants were identified using unique ear, trunk, tusk, and tail markings, and a master identikit file was produced. Musth was defined as a combination of temporal streaming, swollen temporals, urinal dripping, and posture (Poole 1987).

Mapping

Data were mapped using Arcview (ESRI). Locations for 1994 carcasses were given as counting blocks rather than exact locations. We estimated locations as the centre of counting blocks. The 1996 locations had exact GPS readings, or 500m grid block references associated with them. For these locations we generated an active kernel "home range" (Worton 1989) (65 % kernel) to indicate the area covered by these deaths. This 65 % probability range incorporated all of these locations. Female elephant herd locations were extracted from a historical database for the period April 1996 (R. Slotow & G. van Dyk, unpubl. data) when most rhino mortality occurred, and we generated a 95 % kernel range for these data to indicate the area in which the females were known to be active at the time. Note that the females may well have moved outside of this area and not been detected, so this is a minimum area of activity, and simply provides an indication of the ranging pattern of female elephants.

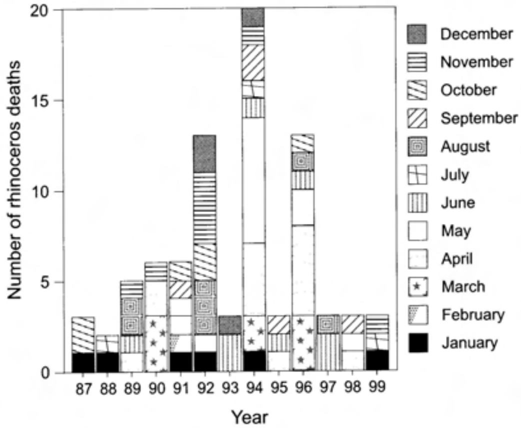

Fig. 1. Temporal distribution of white rhino mortality in Pilanesberg National Park from the horn database. These data are from the horn database of North West Parks and Tourism Board, and include only records of confirmed front horns, or if the horn did not have a confirmation, we then used only records of horn length >292 mm (see text). Note the three peaks in mortality in 1992, 1994, and 1996. The peaks in 1994 and 1996 are ascribed to elephant caused mortality. We speculate that the 1992 peak in mortality was also caused by elephants. Note that data vary from Fig. 2 which were based on carcass records.

Results

Horn database

Mortality was consistent from 1987 through 1999, with between two and six rhino deaths being recorded for each year excepting 1992, 1994, and 1996 (Fig. 1). The median mortality in all years excluding 1992, 1994, and 1996 was 3 (mean 3.7). However, there were marked increases in mortalities in 1992, 1994, and 1996 (Fig. 1). Using the other years as an estimate of expected mortality, there were a total of 37 excess rhino deaths in 1992, 1994, and 1996 (Table 1). Note that we are inferring that the mortalities in 1992 were from elephants based on the nature of the peak being similar to those in 1994 and 1996. There is one comment in the horn database that the cause of death could be elephant (26 October 1992).

In 1992 most of the mortalities occurred in the latter four months of the year. However, in both 1994 and 1996, the mortalities occurred mainly between March and June (Fig. 1). In other years, mortalities were spread through the entire year, with at least 1 mortality in each month, and the highest mortalities occurring in March (16 %) and May (16 %). These two months do coincide with the periods of highest mortality in 1994 and 1996.

With regard to the 1992 mortalities: two 18 year old male elephants were introduced to Pilanesberg National Park during 1992. These bulls came from Mabula Lodge, and were removed from Pilanesberg on 16 march 1993. The reason they were removed is that these individuals were a "nuisance". In addition, two elephants were culled on 27 March 1993. These bulls were responsible for killing a tourist. Any of these four individuals are possible candidates for the cause of mortalities of rhino in 1992. It is unknown if any of these animals displayed symptoms of musth as such details were not recorded at that time.

Verified elephant caused mortality

There were 11 records in 1994 and 12 records in 1996 of confirmed elephant caused mortality. At these carcasses there were signs of trauma caused by massive wounds behind the shoulder or the neck, or else at older carcasses, there was a large amount of evidence of elephants around the carcass, including spoor and trampling. In some cases elephants were seen in the vicinity. There is one record in 1992 from the horn database of elephants being the most likely cause of death. However, in 1992 elephants were not thought of as being the culprits, and so carcasses were not examined in detail for cause of death.

The known elephants caused mortality occurred mainly over the period February to May, both in 1994 and 1996 (Fig. 2). Two deaths occurred outside this period, in late 1996. This pattern is probably a result of few individual elephants being responsible for the mortality, since only the oldest of the young males would have been reproducing with females, and possibly entering musth (see methods for breakdown of population). The deaths during 1994 are probably the result of a single elephant that was subsequently culled (see below). The deaths from early 1996 are most probably all from elephant Bull #1 that was also culled (see below). The two deaths from late 1996 were probably from elephant Bull #18 that was not culled. A large number of rhino deaths that were not confirmed as elephant-caused (Fig. 2 open bars) occurred within the period when verified elephant-caused mortality also occurred (Fig. 2 closed bars). Most of these deaths were probably caused by elephant as well. However, at least two of these in 1996 were probably caused by territorial rhino fights, as wounds were noted under the front chest of the animals. The deaths in 1995 (Fig. 2) were probably natural mortality from intraspecific fights.

Age-sex classes of elephant caused mortality

We analysed the database of 20 verified elephant caused deaths to examine patterns in age and sex of rhino carcasses. In four cases the age was not noted, but the horn measurements were present. We classified three of these as adult (front horn lengths 510 mm, 610 mm, and 690 mm) and one as a juvenile (front horn length 30 mm). There was one case of a record of a female for which we could not match the horn dimensions.

Elephants were killing predominantly adult rhino, with 16 out of 22 (73 %) aged carcasses being adults (Table 2). However, this is not significantly different from what is

Table 1
Total white rhino mortality in Pilanesberg National Park in 1992, 1994, and 1996 and mortality attributed to elephants

Source	Horn Database	Horn Database	Horn Database	Unknown Spreadsheet	Direct Verification			
Year	Observed mortality	Estimated non-elephant mortality[a]	Estimated mortality from elephant	Total Rhino Mortality[b]	Total confirmed mortality from elephant[d]	Estimated mortality from elephant[e]	Estimated mortality from elephant[f]	Best guess mortality from elephant[g]
			1	2	3	(1+2+3)	(1+3)	
1992	13	3	10	16	1	13	n/a	13
1994	20	3	17	23	11	20	16	17
1996	13	3	10	10[c](22)	12	19	19	19
Total	46	9	37	59	24	45		49

[a] Median value of 3 from all years excluding 1992, 1994, and 1996 was used (mean was 3.7)
[b] Based on a spreadsheet produced for a May 1996 internal report. The original source of the information is unknown. This includes all rhinoceros mortality.
[c] Value for 1996 is until the end of April. There were at least five additional deaths after April 1996 (from direct verification), and we have separated a total of 22 records of rhino mortality for 1996.
[d] Based on recorded incidents of direct verification of elephant inflicted wounds, or tracks around old carcasses. We consider this a minimum value as it is unknown as to whether this is a complete dataset.
[e] This is a best estimate using the total mortality values (2) minus the direct verification elephant mortality values (3), and the estimated elephant mortality from the horn database (1) as a guide.
[f] This is a best estimate of elephant caused mortality combining the direct verification elephant caused mortality (3) with the horn database (1). This involved assessing each individual record in each database, and removing replication (see text).
[g] This is an estimate based on all the information in the proceeding columns. This is a realistic rather than a conservative estimation.

Table 2
Age-sex classes of rhino mortality caused by elephants[a]

Age	Sex	1994	1996	Total
Adult	Male	4	6	10
Adult	Female	1	3	4
Adult	Unknown	1	1	2
Total adult		6	10	16
Sub-adult	Male	2	0	2
Sub-adult	Female	1	0	1
Total sub-adult		3	0	3
Juvenile	Male	1	0	1
Juvenile	Female	1	0	1
Juvenile	Unknown	0	1	1
Total juvenile		2	1	3
Unknown	female	0	1	1
	Total male	7	6	13
	Total female	3	4	7
Grand Total		11	12	23

[a] These data are all verified carcasses that can be attributed to fights with elephants.

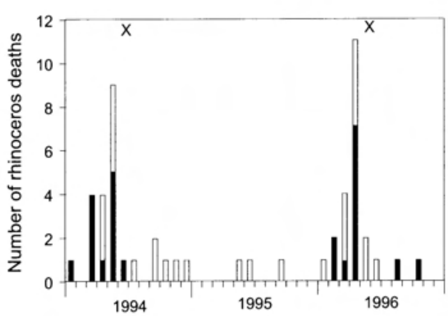

Fig. 2. Temporal pattern in rhino mortality caused by elephant from the carcass database. We illustrate all the carcasses confirmed as killed by elephant (shaded bar) and additional carcasses for which cause of death is unknown (open bar). Given the large number in 1994 and 1996, we believe that most of those are also a result of elephant fights. Small tick marks on the x-axis separate months. X's mark elephant culling events, with 3 bulls being culled in May 1994, and one bull in June1996. Note that data vary from Figure 1 which were based on the horn database.

expected given the rhino population breakdown in 1996 (65 % adult - see methods for population breakdown) ($\chi^2 = 0.66$, $df = 1$, $P > 0.05$). Mortality was not limited to adults, with 3 sub-adult and 3 juveniles also confirmed as being killed by elephants. Elephants killed significantly more males than expected, with 10 out of 14 (71 %) sexed adult carcasses being male (65 %) (expected = 47/107 = 44 %) ($\chi^2 = 4.3$, $df = 1$, $P < 0.05$).

Spatial distribution of elephant caused mortality.

Elephant caused mortality was distributed throughout the reserve (Fig. 3). The 1994 mortality was estimated as the centre of counting blocks, and are thus only an indication of the approximate area of the park in which the mortality occurred (there are 23 blocks in the park). Mortality in 1994 was restricted to the western third of the park. The three March 1994 carcasses (Fig. 3 filled squares) were widespread, whereas the May 1994 carcasses were more localised. The 1996 mortality was spread over most of the park. Carcasses in August and October 1996 were from a different elephant (Bull #18) to those in February to April (Bull #1). Although Bull #1 killed some rhino in the western sector of the park, most of his activity was limited to the eastern half (Fig. 3).

We have some information on the distribution of the female elephants over the period from February to April 1996. These data are not complete, since the entire park was not sampled equally, but they do indicate that the eastern sector of the park was frequented by the female elephants over the period of greatest rhino mortality (Fig. 3). There may be an apparent association between the rhino mortality and the distribution of the female elephants because male elephants in musth tend to follow the female elephant groups (R. Slotow & G. van Dyk, unpubl. data). If this was the case for Bull #1, then the encounter rate with rhino would be higher in the area where the female herds were present.

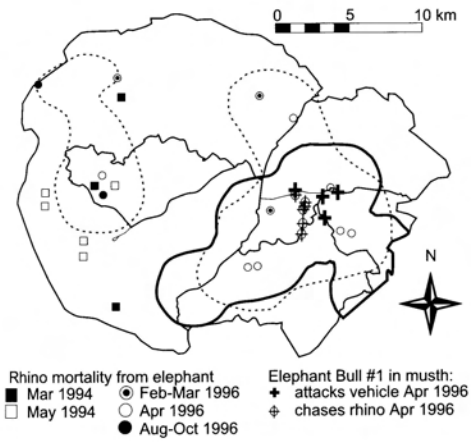

Fig. 3. Spatial patterns of rhino mortality caused by elephant. We show a 65% kernel distribution of the carcasses for 1996 (shaded), and a 95% kernel range for sightings of female elephants during 1994 (area enclosed by heavy black line). All 1994 locations are estimates based on counting blocks, and are thus approximate locations. Thin black lines are the border and main roads.

Note that in addition to the relatively high frequencies of mortality in the east, there were also a number of incidents observed between elephant Bull #1 and rhinoceros (Fig. 3). These are discussed in detail below.

The elephant side of the story

The staff at Pilanesberg had detected the sudden increase in rhinoceros mortality in early 1994. By May 1994 staff had become convinced that elephants were the culprits, and the three elephant males closest to the carcasses were culled. This ended the mortality at that time (Fig. 2). We do not know what the musth condition of these culled elephants was. One of these males was probably the culprit responsible for the 1994 mortality, and possibly for the as yet undetected 1992 mortality.

When rhinoceros mortality from elephants were detected in March 1996, a helicopter survey was commissioned, and a process of individual identification of elephants was initiated. Bull #1 was identified as chasing rhinoceros, and was noted as being in full musth at the time. This is the first documented record of musth in Pilanesberg elephants (observed by G. van Dyk on 23 March 1996). A number of incidents of this individual chasing rhinoceros were documented (24 and 26 April 1996, and three incidents on 15 June 1996) (see Fig. 3 for locations). Bull 1 was also documented as near the breeding herd of elephants while in musth. Bull 1 was noted as being in musth for 3 months, until the end of June, when he was culled (27 June 1996) to prevent further rhinoceros mortality. He had been in musth for at least 3 months and was between 20 and 22 years old.

There was a lull in rhinoceros mortality, but then more carcasses were detected in late 1996. At this time Bull #18 was noted as being in musth on 18 August 1996. He may have been in musth and undetected for an unknown period before this. He was located on 4 September 1996 during the aerial count, and was near the most recent rhinoceros mortality, and was in full musth. Although a decision to cull him was taken, staff were unable to locate him alone, and in a suitable location for culling. The mortality ceased, and given that alternative management strategies were being developed, his culling was postponed indefinitely.

Elephant Bull #20 was the next elephant seen in musth and associated with rhinoceros. This elephant had regularly been seen interacting passively with rhinoceros, and moved in the company of rhinoceros (over previous years). Bull #20 was occasionally photographed mock mating (mounting) rhino. However, in mid-1997 the encounters between Bull #20 and rhinoceros increased in intensity and frequency, and Bull #20 was seen aggressively chasing a rhinoceros on 16 April 1997 (although he was not in musth at that time). A management decision was taken to cull Bull #20 at this time. However, he left his usual area, and was seen only twice until July 1997. Both of these times he was with other elephants, and the decision to cull was postponed. He disappeared in July 1997, and was not seen again until early August 1997.

He was seen chasing a rhinoceros cow in the wilderness area in the northwest of the park. The cow's horn had been ripped from her head. The elephant was tracked and culled, and it proved to be Bull #20 who was in full musth. We do not know how long Bull #20 had been in musth, since this is the only documented record of this elephant being in musth.

Discussion

A solution to the problem

The young "orphan" male elephants of Pilanesberg were entering musth at a young age (18 years old), and that they are staying in musth for abnormally long periods (3–5 months) for such young animals (Slotow *et al.* 2000). This is symptomatic of a lack of a stable bull hierarchy in which they could develop their experience with the heightened aggression associated with musth (Slotow *et al.* 2000). Six older elephant males were introduced from Kruger National Park to Pilanesberg National Park in February to March 1998. The result of this introduction is a significant reduction in the duration of musth periods of the now subordinate Pilanesberg "orphans" (Slotow *et al.* 2000). A consequence of this is a complete lack of mortality from elephants despite the fact that seven Pilanesberg "orphan" elephants have entered musth since early 1998.

Mortality patterns

Mortality in white rhinoceros is typically in the order of about 1–3 % (this study "normal" years: 3/166 = 1.8 %; Owen-Smith 1981, 1988). Annual mortality in years of high elephant caused mortality reached up to 12 % (20/166). The most common cause of death in "normal" populations is intraspecific conflict between territorial males, getting stuck in the mud, and drought conditions (Owen-Smith 1988; Rachlow *et al.* 1998), and were the causes of "normal" mortality in Pilanesberg (G. Van Dyk *pers. obs.;* unpubl. records).

Interactions between elephants and rhinoceros are well known in conservation circles, although not well documented in the literature (but see Berger & Cunningham 1998). Such interactions are typically associated with waterholes, and may involve either rhinoceros or elephants displacing one or the other through chases. However, other than one at Addo-elephant park (a black rhinoceros killed by female elephants) and one in Kruger National Park (Pienaar 1970) there are no documented cases resulting in mortality outside the small reserves that have introduced elephants (see list in introduction). Some unique aspect to these reserves must be the factor that results in escalations of conflicts to such high levels that death is possible. There are several possibilities:

1. The high densities of rhinoceros and elephant in these reserves lead to a high encounter rate, and thus greater probability of escalation. This would imply that mortalities would occur in larger "natural" populations, although at a reduced rate. In other words, this should have been extensively documented previously from other locations.
2. Water is a limiting resource, and thus the value of fighting over it increases. Water is widely distributed throughout Pilanesberg in both the wet and dry season, with no location in the reserve being further than about 2.5 km from a water-source. Access to water is thus unlikely to be a limiting factor on either rhinoceros or elephant biology.
3. Abnormal patterns of musth in Pilanesberg males. We have argued in the results for an association between musth patterns in the young orphan males and rhinoceros mortality. These include direct evidence of musth males chasing and wounding rhinoceros, and indirect evidence of temporary cessation of mortality after culling of musth males. Further, no mortality has occurred since the experimental reduction in musth behaviour of males subsequent to the introduc-

tion of a structured male hierarchy (Slotow *et al.* 2000).

We believe that elephants are killing rhinoceros, and that this is an abnormal behaviour that is associated with musth in young males. We do not know what the mechanistic basis of this is. Apparently, older elephants can cope with the physiological and behavioural consequences of musth in the presence of rhinoceros. We speculate that there is an experiential component to "dealing" with musth.

Under normal circumstances, there is a gradual acquisition of musth in an individual (Poole 1987). We suggest that this gradual increment in the duration and frequency of high levels of hormones, particularly testosterone (Poole *et al.* 1984; Rasmussen *et al.* 1996), allows each individual to experience gradual escalation of conflicts while under the influence of musth. The conflicts that we refer to here are intraspecific contests rather than interspecific ones. Male elephants in musth typically encounter other male elephants in musth, and contests ensue with a loser normally backing down without serious injury. The loser subsequently drops out of musth, particularly after repeated encounters (Poole 1987). These repeated defeats may allow cognizance with, or experience with, the rules of escalated conflict while under the influence of heightened testosterone.

The young males in Pilanesberg that have entered musth would not have encountered defeat while in musth. We suggest that encounters between rhinoceros and elephant are common, and are often initiated by rhinoceros (e.g. see Berger & Cunningham 1998). Young "orphan" musth males may respond to such challenges by beserker behaviour, and pursue rhinoceros despite submissive surrender on the part of rhinoceros (i.e. de-escalation), with a result of wounding or death to the rhinoceros.

Rhinoceros mortality consists of adult males, adult females, and also some juveniles. We speculate that the females and juveniles are killed in instances when adult females are attempting to defend their young against threats from elephants. The adult males may be territorial males that are defending their prime resource (possibly water), rather than beta-males (see Owen-Smith 1975 for description of rhinoceros territorial behaviour) that are less likely to defend a spatially explicit resource.

Management implications

The mortality that we have documented here is important in two regards:

1 Such mortality directly impacts the ability of conservation agencies to conserve megafauna in limited space. A cumulative total of almost 1/3 of the rhinoceros population size has been killed by elephants over the years! This was under conditions where elephants were well below their planned population size (about 120 individuals for Pilanesberg).
2 Mortality removes assets from the reserve that can be sold to contribute to the conservation budgets of agencies. The average value of white rhinoceroses at live auctions in 2000 was SAR176 801 each (Anon. 2000) (= about US$25 000) or about R8 663 249 (US$1 250 000) for 49 rhinoceroses, which is more than the annual budget of Pilanesburg National Park. This excludes any lost productivity from females.

This study has highlighted two important points for managers of small reserves to consider:

1 The value of detailed record keeping with continually updated output, which should be externally reviewed in the manner that companies are externally audited. Such a procedure would have detected the 1992 increase in mortality.
2 The value of knowledge of individual animals. The link between musth and mortality was solidified after Elephant Bull #1 was identified and all the incidents could be linked to this individual. Knowledge of the entire population of selected important species is feasible. Such knowledge tends to be associated with external research projects (e.g., this

study, elephants in Amboseli National Park (Poole 1987), Addo Elephant National Park, (Whitehouse & Hall-Martin 2000), and managers of small reserves are encouraged to solicit external research projects that can provide them with such knowledge, and to require such aspects to be incorporated into outputs of existing and new research projects.

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