

Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa

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Over 3000 sightings and fixes of individually identified black rhinoceros (*Diceros bicornis minor*) over a 14-year period provided information on the spatial organization and movements of these introduced animals and their offspring in the Great Fish River Reserve, South Africa. Core home ranges based on 50% adaptive kernel calculations proved useful for depicting spatial associations among individuals and shifts in areas of occupation. The mean home range size (minimum convex polygon) was 11.7 km² and that of core adaptive kernel 6.8 km². Annual and individual variations in home range size were great and social factors clearly affected size. For these and other reasons great caution is recommended in interpretation and inter-population comparisons of home range sizes. Most individuals in this expanding population showed mobility, with home ranges shifting over time. Although clearly exhibiting individual home ranges, most females associated in clusters of three or more individuals. Calves generally moved away from their mothers at the time of her next calving, but some subsequently moved back into their mothers' core home range. In addition to mother-offspring pairs, some females also showed multiple-year associations in these clusters. Male home ranges overlapped, and individuals showed multiple-year associations until they reached approximately nine years of age. Males over age 8 were rarely sighted in the core home range of other similarly aged males.

Key words: behaviour, *Diceros bicornis*, dispersal, home range.

INTRODUCTION

The calculation of home ranges for black rhinoceros (*Diceros bicornis minor*) and comparisons among studies are fraught with a variety of methodological problems. Various studies have differed widely in the methods used, the detail provided with regard to methodology and in the time period and frequency of observations.

For example, Goddard (1967), the first to report on black rhinoceros home ranges, did not use any currently accepted method of calculating home ranges, nor was the number of sightings stated. It is presumed that the home ranges were calculated based on observations over the length of the study, being three years. Such uncertainties contribute to the difficulty in making comparisons with his study.

Kiwia (1989) reported on the home ranges of black rhinoceros in Ngorongoro Crater in 1982, comparing the home ranges with those described

by Goddard (1967). During the intervening years the density of rhinos had declined 80.6% to only 0.06/km². The mean size of home ranges of adults was substantially larger (31.5 km²) at the time of Kiwia's study, and he suggested that this was a response to the much reduced density. However, their methods of calculating home range differed, the number of adult animals in Kiwia's study was small (six), the difference was not tested statistically, and alternative explanations were not considered. The degree of compression and expansion over time of rhinoceros home ranges with changing population density is not yet well understood.

Further complications arose from the fact that researchers calculated home ranges of black rhinoceros by lumping data collected for periods as short as three months (Tatman *et al.* 2000) and as long as three years (Goddard 1967), making these studies difficult to interpret and compare.

Finally, as Linklater (2003) noted, a large proportion of findings regarding black rhinoceros

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behaviour and ecology have been available only in unpublished management reports not subject to peer review. Further, as noted elsewhere, these are often lacking in details regarding methodology

The purpose of this paper, then, is to present such long-term data, with close attention to methodology, particularly to improve understanding of the dynamics of home ranges, individual movements and spatial associations of individuals in an expanding population. The findings will also provide a baseline for comparisons with subsequent data as the population approaches saturation and will assist with planning future rhinoceros removals and other management actions.

METHODS

Study area

The study area lies within the Great Fish River Reserve (GFRR) complex of approximately 44 000 ha located in the Thicket Biome of the Eastern Cape Province, South Africa. It is characterized by dense thickets and clumps of thorny and succulent shrubs. Major plant communities include short succulent thicket, with *Euphorbia bothae* a characteristic and important species (Evans *et al.* 1998). The area is topographically complex with deep ravines and elevations ranging from 95 m a.s.l. on the Great Fish River to 559 m a.s.l. The Great Fish River bisects the reserve and has acted as a barrier to movements of rhinoceros.

Study population

The reintroduction of black rhinoceros into the GFRR complex began in 1986 with the release of four individuals from Hluhluwe/Umfolozo complex in KwaZulu-Natal. In subsequent releases (1989, 1990, 1991 and 1997) 24 additional rhinos were introduced into the GFRR, specifically in the Andries Vosloo Kudu Reserve and the Sam Knott Nature Reserve sectors on the south side of the Great Fish River, an area of approximately 22 000 ha. In addition, from 1990 to 2001 at least 36 rhinos were born in these portions of the reserve. In 2000, 20 additional black rhinos were introduced into the Doubledrift Game Reserve sector on the north side of the Great Fish River. These individuals were not considered in this study.

Data collection

Data collection was in accordance with protocols adopted by the Rhino Management Group (RMG) of southern Africa. From the outset all introduced

rhinos were ear-notched prior to release to allow individual identification. Subsequently, 12 rhinos born in the reserve were immobilized and ear-notched as well. Each individual received a number in accordance with the ear notching code. In addition, it was found that naming of the rhinos helped maintain interest and motivation among staff. The ages of most of the rhinos born on the reserve in early years, the subjects of this study, are known to within 1–4 weeks. The age of individuals introduced into the reserve were estimated following RMG criteria based on horn development and size at the time of capture and release.

From the outset game scouts were tasked with locating each rhino at least once a week. This goal was never fully met, especially since the late 1990s, as the number of rhinos increased and the number of scouts declined, frequency of sightings of most individuals was greatly reduced. The dispersal of some individuals into inaccessible portions of the reserve also led to unequal sighting frequencies.

Scouts were trained to use 1:50 000 scale topographic maps overlain with an alpha-numeric grid to record sightings of individually identified rhinos. Each grid cell was 32 ha in area. Within a cell the location was recorded as being in one of five sectors, being the four corners and the centre of the cell. Thus, the location of a sighting was recorded within an area of approximately 6 ha. Initially, plotting by scouts was field-checked and verified. After that, no independent tests of the precision of these locations were made. Obvious errors in identification and location (*e.g.*, when subsequent sightings were mapped across fence lines or topographic barriers) made up only 1–2% of the total sightings.

No data on night-time movements were gathered. Black rhinos are active during darkness and do much of their feeding during the night (Brown *et al.* 2003). Information on limited night-time sightings (Goddard 1967) and from spoors and scrapes of known individuals (Tatman *et al.* 2000) suggests that inclusion of such data does not significantly alter home range depictions.

Data analysis

Sightings of identified individuals exceeded 3000. All data on sightings were transferred to a Geographic Information System (GIS), ArcView (ESRI, California). At the same time a number of GIS layers were developed showing features and

infrastructure of the reserve. Subsequently, all databases and GIS products were converted to TNT-MIPS (Microimages Inc., Lincoln NE) GIS software, which allowed analysis of home ranges.

Home ranges were calculated using two methods. First, we calculated minimum convex polygons (MCP) using the 95% convention. That is, 5% of peripheral fixes were discarded in the process of defining the home range. Adaptive kernel home ranges were also calculated using both the 50% and 95% conventions. In contrast to the MCP method, which plots home ranges solely based on peripheral data points, kernel methods utilize information derived from the placement and density of interior data points. The 50% adaptive kernel provides an estimate of a core use area and is referred to hereafter as the 'core home range'.

Ratios of the 50% to the 95% adaptive kernel home ranges were calculated to estimate the intensity of use of the core areas. We also compared our calculations of home range sizes for selected individuals and years with those previously reported to the RMG. These had been derived from visually plotting sightings over the course of a year, drawing a polygon encompassing all sightings, and using grid cells to estimate area of each polygon.

Unless otherwise stated, the described home ranges are annual ones, based on all sightings made in a single calendar year. In a few cases visual inspection of the adaptive kernel plots revealed distinct groupings of sightings, reflecting portions of a calendar year.

To test the effects of sample size on estimates of home range size, various simulations were run by randomly selecting sightings in sample sizes of 20, 30, 35, 40, and, in one case, 50 and 60, for those individuals that had been sighted 40 or more times in one year. Tests of sample sizes necessary to accurately calculate home range size were performed using nine individuals with 40 or more annual sightings.

We examined time series of sightings and home ranges, together with notes made by staff, to look at shifts in ranges and social interactions. Annual sample size of observations was considered less critical for these largely qualitative purposes and where necessary sample sizes as small as 10 observations were employed.

RESULTS AND DISCUSSION

Home range sizes

In four cases an asymptote in home range size using the MCP convention was clearly reached

with 30 observations. In five others the curve was still showing significant increase at 35 and 40 observations. In light of the above, only cases with sample sizes of 35 or more were used to calculate annual home range size for comparison with other published data. Those with sample sizes smaller than 40 should be considered to slightly underestimate home ranges.

By contrast, Tatman *et al.* (2000) found that reliable estimates of home ranges were obtained with between 20 and 30 fixes. They limited their analyses to individuals with 25 or more fixes. One potentially important difference between our study and that of Tatman *et al.* (2000) is that they estimated home ranges based on data for only three months. Thus, although sample sizes were similar, their observations were in fact far more frequent and represented only seasonal home ranges.

Tests of sample size on 50% adaptive kernel home ranges yielded different results. In general these sizes changed proportionally less with increased sample size and asymptotic curves were not apparent. In several cases small samples of annual observations yielded slightly higher home range calculations than did the larger data sets, presumably due to different weightings of the sub-samples. With the exception of one individual, no significant correlation between sample size and core home range was demonstrated.

Home range sizes are shown in Table 1 for individuals with 35 or more sightings in a year. The mean home range (MCP) size was 11.7 km² and that of core adaptive kernel 6.8 km². The ratio of core 50% adaptive home range areas to 95% areas averaged 0.21. That is, rhinos on average spent about 50% of their time in 21% of their home range. There was a significant difference between the mean size of these core (50% adaptive) kernel home ranges and that expected if use of home ranges was uniform (paired *t*-test, $P < 0.01$). Home range sizes were highly variable and because of the small sample sizes no attempt was made to compare among years or classes of individuals.

The ratio of 0.21 may be compared with the 0.12 ratio reported by Linklater *et al.* (2000) for horses in New Zealand and 0.08 for spotted turtles (Lewis & Faulhaber, 1999). Thus, while black rhinos used core areas intensively, the relatively large ratio in the black rhinoceros indicates that they tended to concentrate activities in a somewhat greater portion of their home range. Their mobility was

Table 1. Annual home ranges (km²) for individuals with 35 or more observations in one year.

Individual	Year	Age at end of year	MCP 95%*	Core adaptive kernel 50%	Ratio core to 95% kernel	Visually plotted polygon**
Alpha	1993	5 yr, 4 mo	13.0	9.2	0.24	
Boris	1996	~11	18.3	8.0	0.16	20.1
Boris	1999	~14	15.3	8.7	0.19	21.5
Dumile	1993	2 yr, 9 mo	12.7	9.9	0.28	
Hlathi	1997	3 yr, 10 mo	1.7	1.8	0.27	
Jumbluti	1992	~21	13.2	6.0	0.20	20.5
Jumbluti	1993	~22	11.4	4.8	0.18	12.4
Khataza	1992	~30	6.2	3.2	0.17	12.0
Khataza	1993	~31	13.7	9.5	0.22	10.5

*MCP = minimum convex polygon.

**As reported to RMG. For years prior to 1995 the reporting year did not coincide with the calendar year. See text for further details.

often characterised by 'probes', isolated outlier sightings in areas made prior to actual shifts in home ranges.

When the MCP home ranges in this study are compared with visual estimates of home range polygons previously reported to the RMG (Table 1) it may be seen that the MCP areas were almost all substantially smaller, ranging from 52% to 91% of the visually plotted RMG home ranges, except for one anomalous case in which the MCP was the larger of the two estimates. While statistical testing of these differences was not feasible it seems clear that the differences were greater than would be expected if due solely to the exclusion of 5% of observations (outliers) in the MCP calculation. Thus, use of visually derived estimates, as reported by Adcock *et al.* (1998) and Adcock (1997), for example, must be treated with caution. Further, many of these reported observations are based on small sample sizes.

As noted above, the number of annual sightings was insufficient for accurate home range size calculation for most individuals. One approach to dealing with this problem of small sample size is to lump sightings made over more than one annual cycle. There is very little discussion in the literature of the effects of duration of sampling periods, and none with regard to black rhinos. Powell (2000: 68) noted, '...a home range must be defined for a specific time interval (*e.g.*, a season, a year, or possibly a lifetime). The longer the interval, the more data can be used to quantify the home range, but the more likely that the animal has changed its cognitive map since the first data were collected'. In the dynamic situation existing in the GFRR with a relatively new, reintroduced population still expanding into unoccupied black rhinoceros

habitat, it appeared that, indeed, individuals' cognitive maps were changing rapidly and that durations of more than one year thus provided misleading results.

Adaptive kernel core areas were considered most useful for display of overlaps in home ranges and for demonstrating movements. This is the case in part because core area estimates were found to be less sensitive to sample size and also because peripheral observations outside the core area often preceded shifts in home range.

Home range shifts and rates of movement after release

Two females, Nodwebile and Khataza, captured in separate KwaZulu-Natal reserves, were both released in the GFRR in 1986. Khataza was estimated to be 24 years old at the time of release. Nodwebile was a subadult, 3–4 years old. Until the end of 1987 the two maintained small home ranges within 2.5 km of the release site. Subsequently, both individuals shifted westward where they maintained larger home ranges, also overlapping. Overall, the home range of Khataza shifted slowly westward a total of 7.3 km over the course of 12 years until her death in 1998 (Fig. 1). Nodwebile also shifted her core home ranges westward, but maintained linear home ranges extending approximately 7 km back toward the release area.

Although these two females demonstrated coordination in their dispersal patterns, as Shrader & Owen-Smith (2002) correctly pointed out, the dispersals of black rhinoceros are generally solitary ones in contrast to the dispersal of companions observed in white rhinoceros (*Ceratotherium simum*).

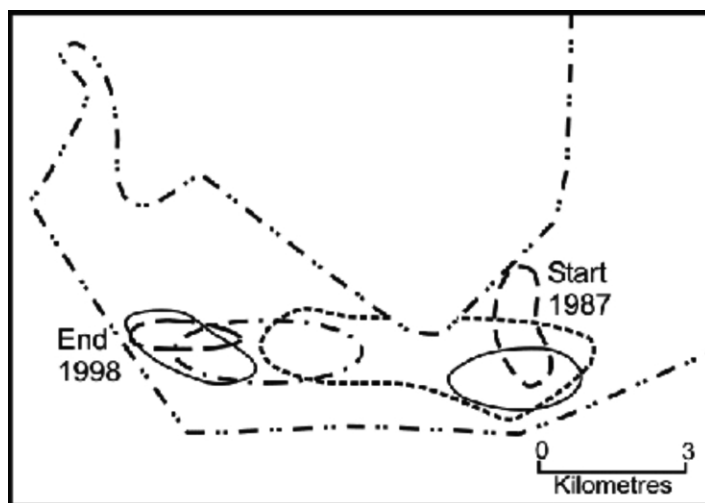


Fig. 1. Shifts in core home range of Khataza, 1987–1998; — · — · — represents boundary fence.

Gertrude, two years old when released in 1992, initially maintained a home range of approximately 4.4 km², bounded on three sides by a large hairpin meander of the Great Fish River. Starting in 1994, but especially in 1995 onwards, she made a number of exploratory probes southward, with sightings occurring 6 km outside her original home range (Fig. 2). Her home range subsequently shifted southward 8 km at a rate of approximately 2 km annually. Commencing in 1998 she settled in

a new area, with a core home range centred nearly 13 km from the original release site and only 1.5 km² in extent. The establishment of this new home range coincided with the birth of her first calf. After 1997 she was never observed back in her original home range.

The male Jumbluti (20–21 years old) was released in January 1992. Within less than a month he made a rapid shift approximately 12 km and established a home range within an area already

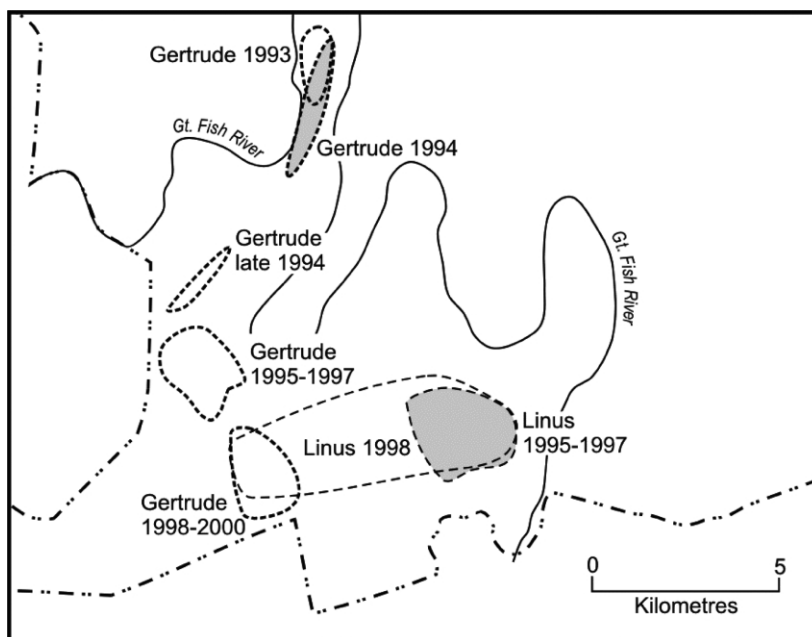


Fig. 2. Shifts in core home ranges of Gertrude and Linus; — · — · — represents boundary fence.

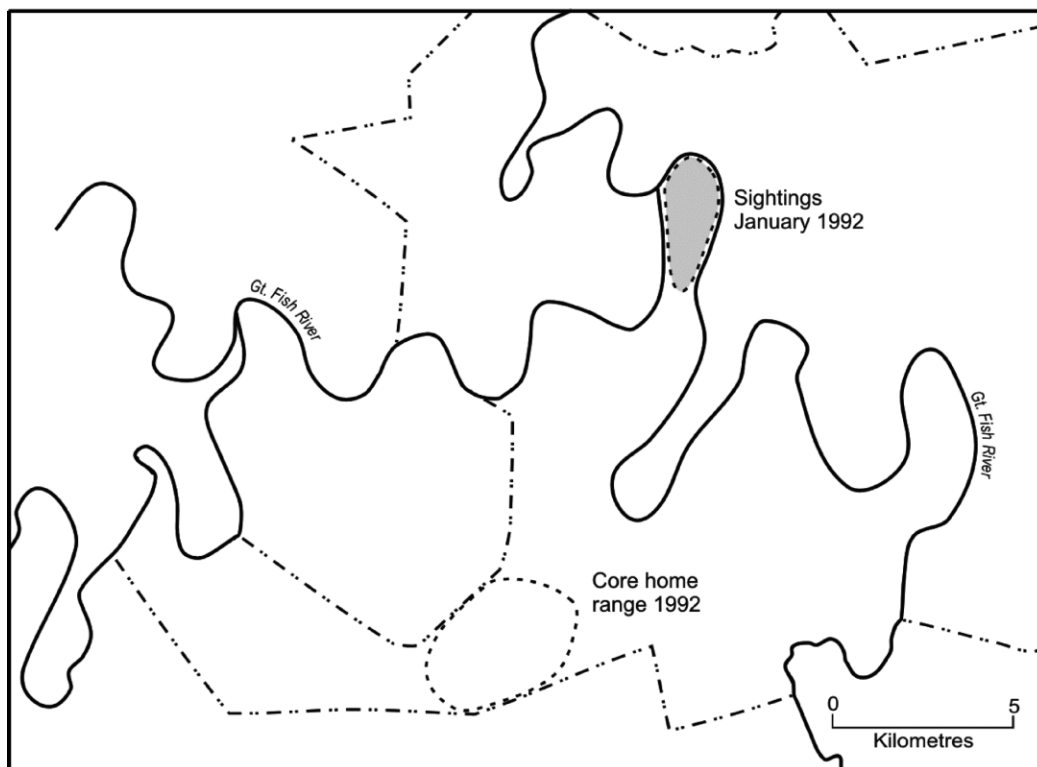


Fig. 3. Movement and core home range of Jumbluti, 1992; — · · — represents boundary fence.

occupied by other rhinos. On 20 February 1992 he was observed mating with Khataza and thereafter remained in approximately the same area (Fig. 3).

As described above, in this medium-sized reserve, most individuals shifted their home ranges measurably within a year or two after release. The longest such post-release movement we recorded was 12 km. Because of the dangers of releasing further adult males close to the home ranges of resident males this information may be helpful for managers of similar reserves contemplating successive introductions to select release sites and space out releases in order to minimize conflict between resident and newly released animals.

Home ranges of males

The core home ranges of all males four years and older in the southern sector of the reserve, as they occurred in 1998, are shown in Fig. 4.

Two of these males had maintained roughly congruent home ranges since 1990 until late 1994, when both were approximately nine years old. At that time, Boris shifted his home range approximately 16 km to the west, but Linus continued to

retain his home range (Fig. 5).

This shift by Boris brought him into the home ranges of three younger males still associated with the general area where they were born. At the ages of 7 and 8, one of these, Dumile, described earlier, continued to maintain a small core home range within that of Boris. This range gradually shifted westward but in 1998 it was still about 50% within that of Boris's. At age 9 in 2000, Dumile shifted his home range largely west of that of Boris, then in 2001 he disappeared. Although thought dead, sightings of him were confirmed after more than a year in a new area centred approximately 13 km from his former home range.

The large core home range of the male Emthini at age 7 in 1999 encompassed that of Boris. At the same time more than 50% of 29 sightings of the similarly aged male Hlathi were within the core home range of Boris. Hlathi at age 8 continued to spend 50% of his time in the area occupied by Boris. Thus, young males were frequently sighted in the core home ranges of males that were nine years and older and their core home ranges overlapped considerably, as shown in Fig. 4. By contrast, of 73 sightings of males over age 8 in the

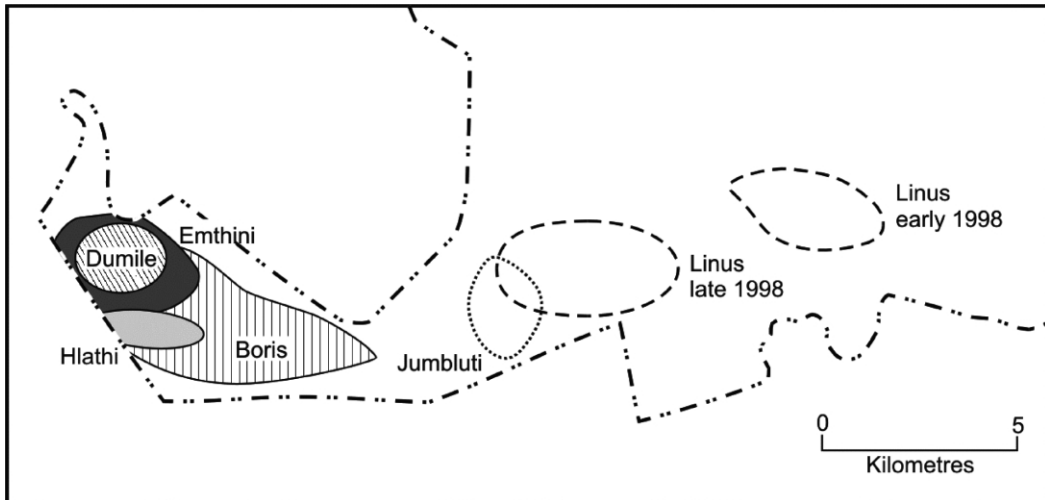


Fig. 4. Core home ranges of six males, 1998; - - - represents boundary fence.

period, 1999–2000, only two were within the core home ranges of other such males.

The departure of the male Dumile apparently provided a space into which the younger male, Emthini, moved. This space occupies a relatively confined 'cul-de-sac' formed by the narrow westward extension of the reserve boundary fencing. Whether this cul-de-sac represents a feature that promotes male – male conflict by restricting movements is not clear.

Our observations thus demonstrate that younger males, up to the ages of 7 or 8, behave as 'satellite bulls' (Estes 1993), apparently being allowed to roam and associate with an older male. Bertshinger (1997) also noted that males do not

have territories until age 9; Adcock (1997) indicated that this occurred at age 10 in the Pilanesberg National Park.

The male, Linus, released in 1989 at an estimated age of four years, initially displayed a compact home range of 7.7 km². During the period 1994–1996 his home range decreased slightly to 5.2 km². Although he was sighted a few times to the west of this home range these were treated as outliers. However, in 1998–2000 more sightings in the same direction resulted in a pronounced expansion of his home range to 15.4 km². In this case Linus continued to go back to locations used in earlier years.

The westward probes of Linus and the expansion

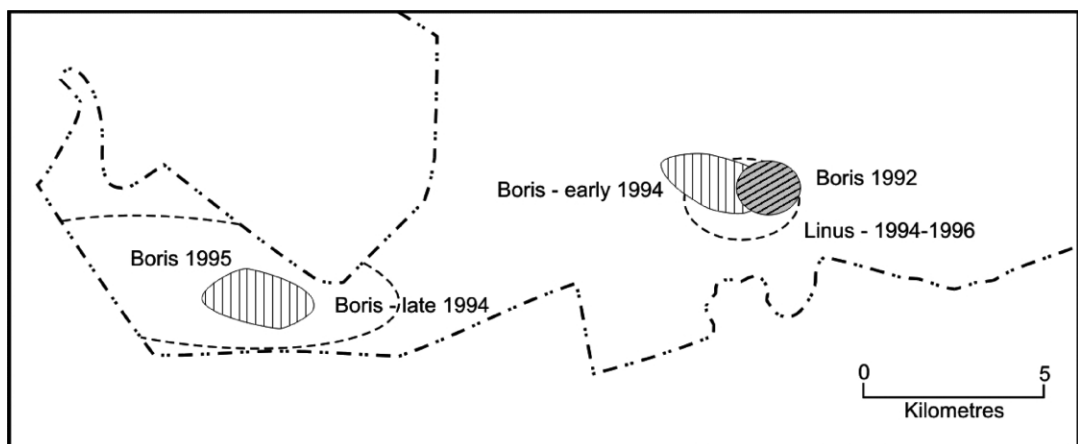


Fig. 5. Core home ranges of Boris and Linus, 1992–1996; - - - represents boundary fence.

of his home range to the west coincided in time with the southern movements of Gertrude and the establishment of her new home range in 1998. This was evident by plotting the sightings of Linus over the new home range of Gertrude established in 1998. In the years 1991–1995 there were 67 sightings of Linus. None of these were made in the area to be subsequently occupied by Gertrude (Fig. 2). In December 1996, Gertrude and Linus were observed together in the area that was to become Gertrude's home range. In the years 1998–2000, after Gertrude had established her new home range, seven of 31 sightings of Linus were within the area. Thus, the expansion of the home range of Linus, described above, clearly appeared to be a social response to the presence of Gertrude.

Spatial separation of mothers and offspring

Our data provide insights into the dynamics of spatial relations between mothers and their offspring. The best documented examples are described below.

The male, Dumile, born to Khataza in March 1991, retained a home range generally congruent with that of his mother up to 1993 (84 sightings). In 1994 Dumile was first sighted outside the home range of his mother. The separation process continued rapidly with Dumile shifting to the west so that in 1995, their core home ranges were separated by approximately 1 km overall. In 1994/95, 63% of 37 sightings of Dumile were outside of the MCP home range of Khataza. From 1997 to 2000, 18% of sightings were within the MCP home range of his mother. However, Hlathi, her next born (1994) and also a male, continued to show a core home range congruent with hers in 1997. By 1998 Hlathi was ranging widely with only eight of 32 sightings within the core home range of Khataza. His core home range encompassed that of his mother but was nearly twice the size. Sightings of Hlathi distant from his mother's core home range were prior to her death in that year.

The female, Alpha, born to Khataza in 1988, demonstrated a similar separation process but at a later age. In 1991 and 1992, following the birth of Khataza's next calf, Alpha maintained a core home range encompassing her mother's but nearly twice as large (6.3 vs 3.3 km²). At age 6 Alpha continued to maintain a core home range largely overlapping with Khataza. Alpha gave birth to her first calf in early June 1994 within her mother's core home range, but she and Khataza

were not sighted together for the remainder of the year. Subsequently, their core home ranges showed no overlap.

Basari, born in 1990 and the first calf of Nodwebile, maintained a congruent home range with her up to 1993. In that year her core home range encompassed her mother's and exceeded it (8.0 vs 4.7 km²). In 1994 her core area split into two disjunct sections or peaks. However, the unusual pattern could not be clearly related to the birth of Nodwebile's next calf, Julia. In 1995 her home range overlapped substantially with that of her mother and about 50% of observations lay within that core area. This general pattern of close spatial association continued until 2000.

Julia, was born in July 1994 to Nodwebile. In 1997, Nodwebile gave birth again, subsequently only two of seven observations of Julia were within the core home range of her mother, both before Nodwebile's estimated birthing date. But in 1998 Julia again showed a core home range overlapping 75% with that of her mother. In January 1999, Nodwebile gave birth again, following that only four of 19 sightings of Julia were within her mother's core home range. Their core home ranges were then 2.6 km apart.

Female Celiwe born to R160 in 1990 showed a core home range in 1993 that overlapped her mother's by approximately 75% but was somewhat larger. By 1995, only approximately 20% of her home range overlapped with that of her mother. However in 1998 her home range again largely encompassed that of her mother but was twice as big (14.1 km² vs 6.7).

Goddard (1967) first reported that females would not tolerate their former calf after a new offspring arrived. While our data confirm that these separations usually occur they also demonstrate that such disassociations are generally of a temporary nature. Strong overlap of core ranges was typically restored in the months following the birth of a younger sibling. That is, typically offspring ranged separately for some time and later moved back into closer association with their mothers. Schenkel & Schenkel-Hulliger (1969) also made brief reference to such re-associations in some East African populations.

Home ranges and associations of females

Home ranges of females tended to overlap and occur in clusters containing three or more individuals. Three such clusters, as they occurred in 1998, are illustrated in Fig. 6. Each of the clusters

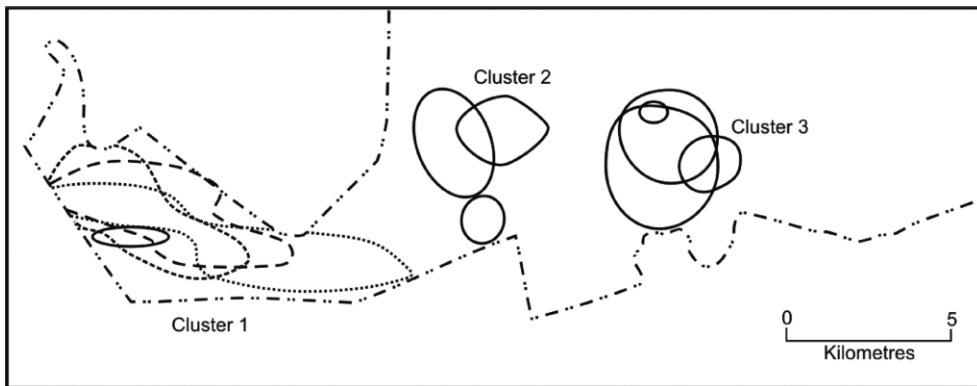


Fig. 6. Core home range clusters of females in 1998. Cluster 1: Home ranges of Khataza, Nodwebile, Basari (born to Nodwebile, 1990) and Julia (born to Nodwebile, 1994), Cluster 2: Alpha (born to Khataza 1988), Gertrude and Ivy (born to Alpha 1994), Cluster 3: Burdetski, R160 and Celiwe (born to R160, 1991). — · · — Represents boundary fence.

contained at least one mother–daughter pair but females with no known relationship consistently occurred together in such clusters as well. The association over several years of two unrelated females, Khataza and Nodwebile, has already been described. Similarly, the core home ranges of R160 and Burdetski (both females) overlapped significantly each year from 1992 until 1999, when they separated by less than 2 km.

The greatest overlap of home ranges occurred in short succulent thicket dominated by ‘noors’ (*Euphorbia bothae*), a preferred forage species. These individuals also showed the largest core home ranges. The generally low height of this vegetation type facilitates sightings of rhinos but may also promote aggregations of individuals. It is not uncommon for four or more individuals to be sighted together in this area (pers. obs., D. Brown, pers. comm.). Goddard (1967) was also of the opinion that aggregations of several individuals occurred more frequently in open habitats.

Conway & Goodman (1989) and Joubert & Eloff (1971) both noted associations of adult and younger individuals, referring to these as ‘clans’. These so-called clans were reported to be associations of animals sharing the same waterhole in an arid environment. Some of the home ranges in Ndumo Game Reserve were described by Conway & Goodman (1989) as group home ranges, presumably equivalent to the clusters reported herein. Our long-term observations suggest that reference to group home ranges may be misleading because the home ranges are individual ones, dynamic in size and location, even while associations of individuals persist. Individual ranges at Ndumo

were similar in size to the MCP home ranges we report.

CONCLUSIONS

Our study, dealing as it does with a newly established population, demonstrated a dynamic situation with home ranges of almost all individuals shifting from year to year, often by distances of a few kilometres. The availability of long-term data on the movements of identifiable individuals clearly demonstrates that both the location and the sizes of home ranges are also strongly influenced by social interactions. Thus any attempt to relate home range size to ecological carrying capacity or habitat quality must be made with care and should not be based on short-term data. This is most clear with regard to home ranges of mature males. However, the female home ranges associated with Cluster 1 (Fig. 6) suggest that in an area of several overlapping home ranges individuals may in fact exhibit larger home ranges than elsewhere. The extent to which home ranges are elastic or compressible as population density increases will become more evident as this study continues.

Our observations also demonstrate that associations of females, even those not involving mothers and offspring, may persist for several years. Furthermore, dispersal (from release areas) and movements of black rhinoceros have involved loose coordination of more than one female.

The 50% adaptive kernel provided a clear visual representation of changing home ranges and for that reason alone it is recommended as a useful tool. Occasionally, its application yielded multiple peaks instead of a single unitary home range.

Exploration of the sightings associated with each peak proved to be useful also for identifying shifts in core use areas within the annual cycle. Such clues are lacking in MCP displays. It is hoped that these core area depictions will also prove useful for analyses of habitat use patterns in black rhinos.

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