Territoriality and spatial patterns of white rhinoceros in Matobo National Park, Zimbabwe

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Abstract

Boundaries associated with reserves or conservation areas may alter spatial patterns of individuals, and may affect the sexes differently in species that exhibit sex-specific patterns of space use. Because of poaching threats, most African rhinos today persist within sanctuaries or reserves with fenced perimeters. We examined spatial patterns of adult white rhinos (*Ceratotherium simum*) in Matobo National Park, Zimbabwe. Matobo Park contains a high-density population of rhinos within a fenced reserve and a lower-density group outside of the fenced area. Adult females in the lower-density group used significantly larger home ranges than those in the high-density group. Overlap among female home ranges was extensive in both groups. Adult male white rhinos establish territories that are exclusive of other males performing scent-marking behaviours, and in Matobo Park, male territories were much larger than those observed in other populations of white rhinos. Additionally, few adult males in the high-density reserve held territories that occupied most available space; two-thirds of adult males were excluded from establishing territories, and followed a non-territorial tactic. In the absence of dispersal opportunities, managers may need to regulate the number of males within smaller reserves. Monitoring of spatial patterns should be undertaken to permit management decisions to be made with an understanding of male behaviour and territorial status.

Key words: *Ceratotherium*, ranges, rhinos, scent-marking, territories

Résumé

Les limites des réserves ou des aires de conservation peuvent modifier les schémas spaciaux des individus et peuvent toucher différemment les sexes dans les espèces qui présentent des schémas spécifiques d'utilisation de l'espace. En raison des menaces de braconnage, la plupart des rhinos africains vivent maintenant dans des sanctuaires ou des réserves clôturés. Nous avons examiné les schémas spatiaux des rhinos blancs adultes (*Ceratotherium simum*) du Parc National de Matobo, au Zimbabwe. Le Parc de Matobo abrite une population très dense de rhinos dans une réserve clôturée et

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un groupe moins dense en dehors de cette zone. Les femelles adultes du groupe moins dense occupaient des espaces vitaux significativement plus vastes que celles du groupe plus dense. Le recouvrement des espaces vitaux des femelles était important chez les deux groupes. Les rhinos blancs mâles adultes établissent des territoires qui excluent tout autre mâle qui présente un comportement de marquage d'odeur et, au Parc de Matobo, les territoires des mâles sont beaucoup plus étendus que ceux que l'on observe chez les autres populations de rhinos blancs. De plus, quelques mâles adultes de la réserve densément peuplée se réservaient des territoires qui occupaient la plus grande part de l'espace disponible; deux tiers des mâles adultes ne pouvaient établir de territoire et utilisaient des techniques non territoriales. Quand il n'y a pas de possibilité de dispersion, les gestionnaires peuvent avoir besoin de réguler le nombre de mâles dans les petites réserves. Il faudrait commencer à contrôler les schémas spaciaux pour prendre des décisions de gestion qui tiennent compte du comportement et du statut social des mâles.

Introduction

Many conservation areas have boundaries that contain target populations and limit the dispersal of individuals. When dispersal is prohibited, population densities of large mammals within reserves often increase (Owen-Smith, 1982), which may affect the use of space by individuals. If spatial patterns differ between adult males and females, the sexes may respond differently to confinement within reserve boundaries. Understanding the factors influencing range use and the potential impacts of restricted dispersal is important for management of rare species within wildlife reserves.

African rhinos are uncommon outside of reserves today because severe levels of poaching have decimated many unprotected populations (Brooks, 1993; Gakahu, 1993; Berger, 1994). Establishment of rhino sanctuaries or intensive protection zones has been a primary focus of recent conservation work for African rhinos (Brett, 1990; Nduku & Martin, 1993; Emslie, 1994). Protection within reserves is likely to be the most viable method of conserving rhinos *in situ*, however, smaller reserves may require management intervention to counter the effects of restricted dispersal on demography and behaviour (Rachlow & Berger, 1998).

Spatial patterns differ between the sexes in white rhinos (*Ceratotherium simum*). Females use undefended home ranges that overlap widely. Mature adult males use non-overlapping territories that are occupied throughout the year, and demarcated with scent-marking behaviours (Owen-Smith, 1971; Pienaar *et al.*, 1993). However, only some adult males in a population establish territories, and others follow a non-territorial tactic (Owen-Smith, 1971; Rachlow, 1997). Young adult males and subadults of both sexes tend to move to the periphery of high-density areas (Owen-Smith, 1982), but such movements are limited in reserves with higher population densities. To gain an understanding of the factors influencing spatial patterns of white rhinos within reserves, we examined how restricted dispersal, population density, and behaviour affected the use of space in adult males and females.

Methods

Study area and population

The study was conducted in 1994–95 in Matobo National Park, which encompasses over 425 km^2 of the Matobo Hills in south-western Zimbabwe. Most of the 52 white

rhinos in Matobo Park were contained within a 105-km^2 fenced area known as the Whovi Game Park. A group of nine rhinos exists outside of the fence in the Hazelside Area of Matobo Park. All adults and most subadults were individually identified by ear-notching patterns. We fitted sixteen adults with radio-collars and followed each individual at least weekly. Other rhinos were located either visually or by following spoor with the help of a National Parks tracker. All locations were recorded in UTM co-ordinates using a 1:50 000 topographic map and/or a hand-held global positioning system.

Ages were known or estimates available from previous monitoring work in Matobo Park (Rachlow, 1997). The youngest age of a territorial male during this study was 9 years. However, considering that males are likely to become sexually mature at around 6 years of age (Owen-Smith, 1988; Bertschinger, 1994), we classified all males $\geq$ 6-years-old as adults, and those from 6 to 10 years of age as young adults. The youngest age at first reproduction for females in Matobo and in Umfolozi, South Africa, was 6.5 years (Owen-Smith, 1988) and hence, we classified females $\geq$ 6-years-old as adults.

Spatial use

Location data were used to estimate range use for all adults. Only one location per day was included in home range analyses for each individual, and the mean sampling interval between locations for all adults ($n = 30$) was 8.4 $\pm$ 0.8 days. We used two methods for estimation of home range sizes because territorial males move about their ranges in different patterns from females and non-territorial males. Territorial males delineate their ranges with marking behaviours, and rarely wander outside of these ranges (Owen-Smith, 1971). Thus, the minimum convex polygon (MCP) approach (Mohr, 1947) for calculating a home range adequately describes the area used by territorial males. However, females and non-territorial adult males do not demarcate their ranges, and hence, are likely to move beyond the outermost locations that we observed. For this reason, an adaptive-kernel (ADK) method (Worton, 1989, 1995) was used to estimate the size of the areas used by females and non-territorial males. This method tends to produce a larger home range estimate than the MCP method because it calculates a probability density function for the home range of an individual based on the distribution of observed locations. Although the ADK method likely reflects the size of the area used by non-territorial males more accurately, we used the MCP estimates for all males (territorial and non-territorial) in the analyses to avoid a bias stemming from methodological differences. For purposes of comparison with other studies, results from both methods are reported for non-territorial males and females in the Tables.

The CALHOME home range analysis program (Kie *et al.*, 1996) was used to estimate home ranges. When constructing an ADK estimate, CALHOME chooses a smoothing parameter assuming that the location data are normally distributed, and a measure of goodness-of-fit is provided based on least-squares cross-validation (LSCV) scoring (Worton, 1989). However, location data rarely meet the assumption of normality, and if clumped, a better LSCV may be obtained using a smaller smoothing parameter. Following the recommendations of Worton (1989), we decreased the smoothing parameter to 80% of the predicted optimum, and then ran a second ADK analysis. We used and reported the analysis for each animal that resulted in the best fit to

Table 1. Territory sizes of adult males expressing scent-marking behaviours calculated using the 100% minimum convex polygon (MCP) method. Territory sizes are reported before and after a shift in territory structure that occurred in the fenced Whovi Game Park. Estimates are in hectares, and sample sizes equal the number of locations per individual.

	ID	*n*	100% MCP (before)	*n*	100% MCP (after)
Whovi Game Park	M-05	20	1733	36	1852
	M-07	36	5041	–	dead
	M-09	21	1462	44	1921
	M-25	37	establishing	60	1733
Hazelside Area	M-31	33	3619	–	no change

the data based on minimising the LSCV score (providing that it did not cause the home range to become fragmented). Home range polygon data from CALHOME were imported into a geographical information system (IDRISI) for analyses of range overlap (Eastman, 1995).

Behavioural data

We conducted observations during daylight between 05.00 and 19.00 hours, concentrating on the early morning and late afternoon periods when rhinos were most active. We recorded scan-samples of focal groups at 5-min intervals to quantify activity patterns (Altmann, 1974). All occurrences of male scent-marking behaviours (urination and defecation) were recorded. Observations were suspended if the rhinos were disturbed by our presence and exhibited increased vigilance behaviour for > 5 min, or when a focal group was out of sight for > 5 min. Mean values are reported $\pm$ standard errors, and *p*-values of < 0.05 were used to determine statistical significance.

Results

Male territoriality

Data on rates of territorial marking behaviours were recorded during 205 h of observations of adult males ($n = 14$; mean $= 14.7 \pm 2.1$ h/male). Marking behaviours consisted of a scattering of dung with vigorous kicks of the rear legs both before and after defecation, and spray-urination during which 2–5 pulses of urine were sprayed backwards, often after scraping the rear legs along the ground or over vegetation. Males expressing these behaviours consistently were classified as 'territorial males'. Territorial males always were observed to defecate and urinate in these characteristic manners at a mean rate of 3.0 ± 1.19 acts/active h. Non-territorial males urinated in a stream like females, and did not scatter their dung. We observed four non-territorial young adults (ages 6–10 years) begin to exhibit marking behaviours, but these behaviours were performed sporadically and less vigorously.

The structure of the male territories in the fenced Whovi Game Park shifted after one territorial male (M-07) was killed in a fight with a neighbouring territory holder. Prior to the shift, only three males had established territories ranging in size from 1462 ha to 5041 ha (Table 1). One additional male (M-25) began to express marking
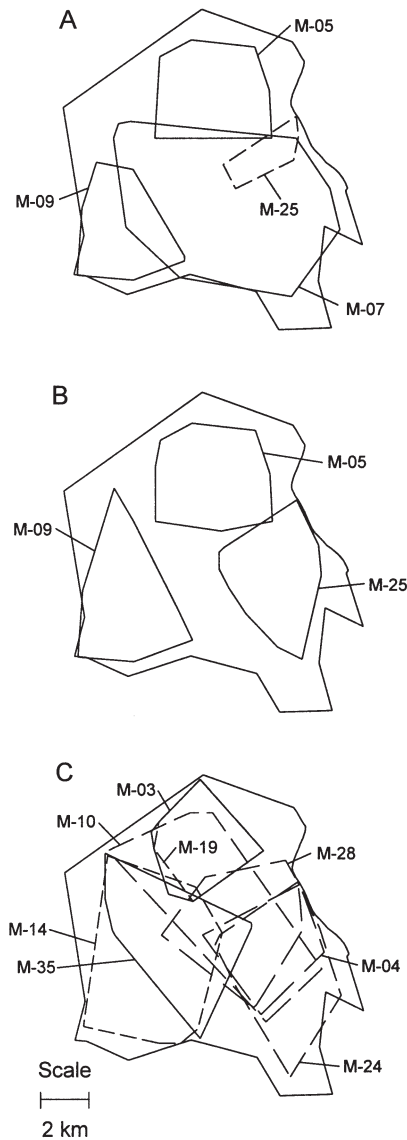
Fig. 1. (A) Male territories in the fenced Whovi Game Park estimated using the 100% minimum convex polygon method prior to a shift in territory structure that occurred after the death of M-07; (B) male territories after the shift (M-25 began expressing scent-marking behaviours $\approx$ 2 months prior to the territory shift, but did not consistently delineate a range with scent marking until after the death of M-07); and (C) home ranges of non-territorial males in the Whovi Game Park estimated using the 100% minimum convex polygon method.

behaviours on the edges of two established territories about 2 months prior to the shift, but restricted his movements to a relatively small area (Fig. 1a). Following the death of M-07, territory expansion occurred, in which two neighbouring males incorporated portions of the vacant area into their existing territories (Fig. 1b). We observed a sharp increase in the rates of marking behaviour during territory expansion; males increasing the sizes of their territories exhibited a 5-fold rise in

Table 2. Home range sizes of non-territorial adult males and adult females in the Whovi Game Park (high-density), and of adult females in the Hazelside Area (low-density) calculated using the 95% adaptive kernel (ADK) and 100% minimum convex polygon (MCP) methods. Range estimates are in hectares, and sample sizes equal the number of locations per individual.

	ID	*n*	95% ADK	100% MCP
Whovi Game Park	M-03	31	1548	1323
non-territorial adult males	M-04	37	1838	1406
	M-10	43	3397	3361
	M-14	48	3239	3219
	M-19	28	1621	1224
	M-24	54	2550	2210
	M-28	44	2478	2145
	M-35	47	2288	2316
Whovi Game Park	F-01	45	3191	2119
adult females	F-06	20	1729	796
	F-08	50	1506	789
	F-11	20	1874	914
	F-12	16	2069	774
	F-13	41	2184	1430
	F-15	33	2642	1579
	F-16	49	749	546
	F-18	24	2453	826
	F-21	20	1874	513
	F-22	44	2076	914
	F-23	15	1379	1216
	F-26	40	593	357
	F-27	26	2882	2007
	F-33	24	1318	1314
Hazelside Area adult females	F-29	38	6896	3980
	F-30	39	5812	3166
	F-32	30	4961	3711

rates of scent-marking (M-09: 0.36–1.98 acts/active h; and M-25: 1.32–6.42 acts/active h). We did not observe a similar increase in marking behaviour by the territorial male that did not expand his boundaries (M-05: 3.24–2.40 acts/active h).

Territorial males used ranges that were essentially exclusive of those of other territorial males. Mean overlap among territorial males in the Whovi Game Park ($n = 3$) was 9.4 $\pm$ 3.7% of an individual's territory before the shift in territory structure, and 0.1 $\pm$ 0.1% after the restructuring (Fig. 1a,b). In contrast, non-territorial adult males ($n = 8$) used similar sized ranges (Table 2) that overlapped widely. Mean overlap among non-territorial males was 26.8 $\pm$ 2.6% (Fig. 1c). Range overlap among non-territorial adult males was significantly greater than that observed among territorial males either before (Mann–Whitney $U = 23.0$; $P = 0.025$) or after (Mann–Whitney $U = 24.0$; $P = 0.014$) the shift in territory arrangement.

Overlap between territorial and non-territorial males also was extensive (mean = 29.2 $\pm$ 1.8% and 24.4 $\pm$ 1.9% before and after the shift, respectively). However, we did not observe cohabitation of one territory by a dominant 'alpha' male and a subordinate 'beta' male as observed in other populations (Owen-Smith, 1971, 1988). We did note a tendency for pairs of non-territorial males to form associations that persisted for several months.
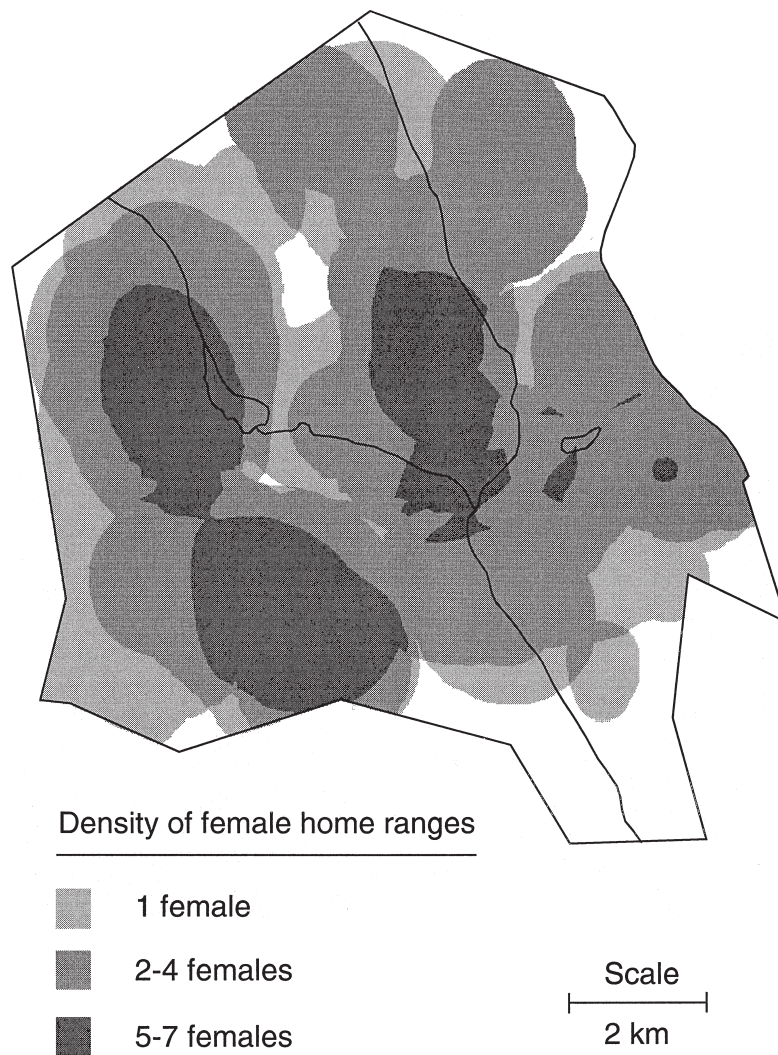
Fig. 2. Home range overlap among adult females in the Whovi Game Park. Home ranges were calculated using the 95% adaptive kernel method. Mean overlap among females was 40% ($\pm$ 15.7) of an individual's home range.

Female home ranges

Home range estimates calculated using the 95% ADK method ranged from 593 ha to 3651 ha (mean = 1901 $\pm$ 188 ha) for females in the high-density Whovi Game Park (n = 15). Females in the low-density Hazelside Area (n = 3) used significantly larger home ranges (mean = 5890 $\pm$ 560 ha) (Mann–Whitney U = 0.00; P = 0.008; Table 2).

Overlap among adult female home ranges was extensive in both the high- and low-density groups. All females in the Whovi Game Park shared portions of their ranges with $\geq$ 5 other adult females (mean = 7.4 $\pm$ 0.6 females), creating zones of high female density (Fig. 2). Mean overlap among females in the high-density group

was 40.0% ($\pm$ 15.7). Similar patterns of range overlap were observed among adult females in the Hazelside Area, even though population density was lower.

Discussion

Male territoriality

Scent-marking behaviours were useful in classifying adult males according to their patterns of space use. Territorial males scent-marked and used areas that were exclusive of other males performing these behaviours. In contrast, non-territorial males did not exhibit scent-marking behaviours and used ranges that overlapped widely with all other males. These spatial patterns are similar to those observed for white rhino males in other, larger populations (Owen-Smith, 1971; Pienaar *et al.*, 1993), with some notable differences. One primary difference was the proportion of territorial vs. non-territorial males in the population. Only one third of adult males in the fenced area of Whovi Game Park held territories, whereas up to two-thirds of adult males were territorial in other populations (Owen-Smith, 1971).

What factors have contributed to this difference in male spatial patterns? Territory size may be one. In Matobo Park, male territories were much larger than those observed in other populations. The largest territory previously reported for a white rhino male was 1390 ha (Conway & Goodman, 1989), which is smaller than the smallest territory in this study (Table 1). Matobo Park includes much rocky terrain with granite domes and kopjes, which are largely unused by white rhinos. The actual area available to grazers has been estimated to be about 50% of the total area (Grobler & Jones, 1980), and this habitat heterogeneity may influence the large territory size in Matobo Park.

A second factor that may have influenced the proportion of adult males able to establish territories in the Whovi Game Park is the presence of the fenced boundary. Owen-Smith (1982) documented that subadults of both sexes and young adult males tended to move away from areas of high density to occupy regions on the periphery of populations. In the absence of dispersal, however, the number of adult males in the Whovi Game Park has increased, and young adults cannot disperse and establish territories on the edges because of the fenced perimeter. Managers of smaller reserves should monitor territorial behaviour of adult males, and may need to regulate the sex ratio as well as the total population size within fenced areas.

A third factor potentially influencing male spatial patterns in this study is the age-structure of adult males. Several older males were removed from the Whovi Game Park in the mid-1980s when fight-related mortality increased (Rachlow, 1997). Because of these past management actions, the age structure of males was skewed towards younger animals. Territorial males tended to be older than non-territorial males in this study (Rachlow *et al.*, 1998). As male ages increase and young adult males mature, spatial patterns may shift to accommodate a larger number of smaller male territories. However, an increase in the number of territories was not observed following the death of the male holding the largest territory (Fig. 1a,b), and it is possible that the Whovi Game Park will support only a few male territories.

Although many factors likely interact to affect spatial patterns, the net result of limited dispersal, high population density, and very large male territories in the fenced Whovi Game Park was that only a few of the adult males held territories

that occupied most of the available space (Fig. 1a,b). Other males were faced with the 'choice' between challenging one of the territorial males and risking injury and potentially death, or following a non-territorial behavioural pattern. It is believed that only territorial males breed successfully (Owen-Smith, 1977, 1988), and indeed, behavioural data from this study support the hypothesis that the reproductive consequences of these two male behaviour patterns may not be equal (Rachlow *et al.*, 1998).

Female home ranges

The size of home ranges used by adult females appears to vary with population density in white rhinos. Pienaar *et al.* (1993) noted a tendency across populations of white rhinos for home ranges of females to decrease with density, however, differences in habitat could not be ruled out in that comparison. In this study, habitats were similar between the high- and low-density groups, and females in the low-density group used larger home ranges. These results suggest that females altered their spatial patterns in response to population density. Overlap among ranges of adult females was high in both groups, suggesting that shared resources or social factors also may influence spatial distributions of female white rhinos.

Acknowledgements

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