Ranging patterns in white rhinoceros, *Ceratotherium simum simum*: implications for mating strategies

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How animals use space has important consequences for feeding ecology, social organization, mating strategies and conservation management. In white rhinoceros, female home ranges are much larger than male territories, suggesting that movement patterns are influenced by factors other than resource distribution. In this study we placed radiotransmitters on 15 female white rhinoceros, recording 1758 locations and collecting behavioural data during 1671 observation sessions, making this the largest data set of its kind in this species. We investigated how habitat variables and male territories influenced female movement and reproductive behaviour. Female home ranges were approximately 20 km^2 and core areas were 5 km^2, with male territories roughly the same size as female core areas. Female range size did not vary with season, but the pattern of space use did vary. Females used grassland habitat preferentially, utilizing these areas significantly more than expected based on availability. Findings relevant to the mating strategy include: (1) the amount of grassland in a male's territory predicted female use of the territory; (2) the time that a female spent in a male's territory was a significant predictor of reproductive activity with the male, indicating that females probably mate with the most familiar male; and (3) the temporal pattern of female space use suggests that females did not increase mate sampling behaviour nor did they become more choosy about which males they visited when reproductively active. These findings suggest that males may maximize reproductive success by defending areas containing more grassland habitat.

Most if not all mammals develop a home range, which may be defined as nonrandom use of space that brings the animal back to the same areas repeatedly. A primary benefit is that the animal becomes familiar with the distribution of resources through space and time, increasing its ability to exploit these resources efficiently. Home range size, however, is constrained by increased travel costs and lack of familiarity with environmental features. The distribution of resources also influences the costs and benefits of social living and thereby governs social organization. Moreover, resource availability may change from season to season or

year to year, prompting animals to shift their home range, make seasonal excursions or migrations, or alter patterns of social organization (Lott 1991). Conflict over access to resources limiting an individual's ability to reproduce can affect the sexes differently, and the interplay between resource availability and social processes in determining mating systems has received much attention in the literature (Shuster & Wade 2003).

In white rhinoceros, females are distributed widely across the landscape and, owing to lengthy inter-calf intervals, only enter a receptive period approximately every 3 years (Owen-Smith 1988). By comparison, males defend mutually exclusive territories (although they do allow subordinate males access) that are much smaller than females' ranges. Territories appear to be constrained by fierce male–male competition (Owen-Smith 1975, 1988) and they expand only when released from social influences in low-density populations (Rachlow et al. 1999).

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Female home ranges are also constricted at higher densities (Rachlow et al. 1999), suggesting that females move over larger areas than needed strictly to acquire resources for feeding. Given that larger home ranges may result in increased social and travel costs, females may roam over larger areas to expose themselves to multiple males for mate selection opportunities. Owen-Smith (1975, 1988) proposed that females may select a male for mating simply by entering his territory during her fertile period.

We investigated female ranging patterns to determine how they relate to mating strategies in this species. We posed the following questions. (1) Do females use male territories nonrandomly and, if so, are their preferences related to habitat variables in the male's territory? (2) If females distribute their time unequally among male territories, does the time spent in a particular male's territory predict the probability of mating with the territory occupant? (3) Do females change their ranging patterns when reproductively active in a way that indicates increased mate sampling (visiting more male territories) or mate choice (confining their movements to fewer preferred males' territories)? Observations of these aspects of female spatial ecology can provide valuable insight into reproductive strategies used by white rhinoceros.

Our study was also intended to inform conservation management. The restriction of many species, particularly large mammals, almost exclusively to protected areas has been instrumental in ensuring their survival. In southern Africa many species are managed in fenced game reserves for protection from poaching and to minimize conflicts with neighbouring human communities. Because this management strategy hinders natural dispersal, metapopulation management has become the cornerstone of rhinoceros conservation action in southern Africa (Emslie & Brooks 1999; Linklater 2003). Managers need to determine an acceptable level of off-take from populations that are performing well to be translocated to establish or augment populations elsewhere. Knowledge of home range size, overlap, seasonal movement patterns, and other aspects of spatial ecology are necessary for effective reserve design, for example, to estimate the needed area to contain a target number of individuals or home ranges. Knowledge of home range ecology figures prominently in the conservation of many species (e.g. Price et al. 1994; Wong et al. 2004).

METHODS

Study Site and Animals

We studied spatial patterns of white rhinoceros in the iMfolozi section of Hluhluwe-iMfolozi Game Reserve (HiP), KwaZulu-Natal, South Africa (28°S, 31°E). HiP is a 965-km² fenced reserve categorized predominantly as savannah habitat. This reserve is considered prime white rhinoceros habitat, and management of the area requires removal of surplus individuals every year. The majority of rainfall in the area occurs in the summer months between October and March. Fifteen adult (>5 years) female rhinoceros were fitted with radiotransmitters following methods described by Shrader & Beauchamp (2001).

During a 3-year period, we followed these females regularly to assess their reproductive state through behavioural observations. Females were observed for approximately 2 h during 1671 observation sessions, making this study the most intensive one reported for this species to date, especially for females (cf. Owen-Smith 1975). Typical observation periods were during early morning and late afternoon peak activity hours (Owen-Smith 1973). We collected positional data using a GPS at the beginning of each observation period. To avoid problems with autocorrelation (Swihart & Slade 1985), one point per day was generally used; however, in some cases, a maximum of two locations per day were used if they were taken at least 8 h apart. We collected a total of 1758 location points for these 15 females during all times of year.

Males were not radiotagged, so data on males was collected opportunistically through sightings of individuals in the field. All males included in the study were individually recognizable by ear-notches, ear tears and horn patterns. Males were identified as territorial if they were observed to urine spray, a behaviour in white rhinoceros that is exclusive to territorial holders (Owen-Smith 1971, 1975).

Habitat Classifications

Vegetation was classified into seven habitat types based on structural differences in canopy cover (woody plants > 4 m) and underbrush (woody plants < 4 m). Open grassland habitat was defined by an absence of canopy cover and underbrush. Thicket vegetation types had minimal canopy (0–25%) with varying degrees of underbrush thickness (open thicket: 0–50%, medium dense thicket: 51–75%, dense thicket: 76–100%). Woodland habitat varied in underbrush thickness, with classifications based on the percentage of canopy thickness (open woodland: 26–50%, medium dense woodland: 51–75%, dense woodland: 76–100%). These habitat delineations were based on previous work conducted in HiP on African buffalo, *Syncerus caffer* (Dora 2004; Jolles 2004). Dora (2004) used a maximum likelihood approach to transform satellite imagery into habitat classifications based on Landsat ETM bands (see Dora 2004, for a detailed description of map generation). The accuracy of the map was verified using field data and corresponded to the classifications that were generated 83% of the time.

Delineating Female Movement Patterns

We used two approaches to examine general movement patterns within our study area. We analysed female habitat usage using a minimum convex polygon (MCP) approach (Mohr 1947). While other home range estimates exclude areas that are avoided or underutilized, MCP includes these areas. Although this approach often overestimates home range size calculations, MCP allowed us to explore why individuals settle in particular areas and avoid others, as opposed to addressing questions of differential use within an established home range. Although we did not use MCP as our primary home range size estimate,

we present these estimates because they have the advantage of being comparable to other studies because of their widespread usage (Harris et al. 1990).

We also used utilization distribution methods to consider the amount of use in various portions of the utilized area. To obtain estimates of home range size and to investigate movement patterns within an individual's settlement area relative to season, we used a fixed kernel estimator with least-square cross validation of the smoothing parameter (Worton 1989). We report 50% contours to describe core usage by individuals. Defining home range usage can be relatively subjective (White & Garrott 1990). We defined the extent of a home range by consecutively incorporating 5% contours to the core area. Based on this method, we chose to delineate home ranges with 90% contours because, on average, inclusion of 95% contours nearly doubled estimated home range size compared to the 90% contour, thus clearly including large areas that were rarely used by rhinos. All range analyses were calculated using Home Range extension to Arcview (Rodgers & Carr 2001).

Defining Male Territories

Our location sample size for individually recognizable males varied greatly and in general was too small to warrant use of a home range estimator (range 10–71). Although MCP methods can estimate area usage with small sample sizes, the area of overlap would be greatly exaggerated by this approach owing to natural nonlinearity in male territory delineation. Therefore, to accurately depict biologically meaningful territory boundaries, we performed a Neighbourhood analysis using ArcMap. Basically, this approach involves overlaying a grid on the study area. Each cell is then classified as belonging to the male whose data points 'occupied' the majority of the cell. Cells that could not be attributed to a particular male were classified as unknown. By definition, this approach produces mutually exclusive male territories (validly reflecting the norm of this species: see Owen-Smith 1975). While these methods provide unbiased estimates of male territory boundaries adequate to determine how female ranges are influenced by males and their territories, these estimates are not precise measures of male territory size.

Data Analysis and Hypotheses

To evaluate possible female habitat preferences, we compared expected values for habitat use (based on the proportion of overlap between each female's MCP range and each habitat type) with the number of times that each female was found within each habitat (i.e. the observed value). We used these data to calculate ratios of observed/ expected values necessary for G test statistics. When expected values were <5, we combined habitat types into an 'Other' category for analysis. Observed zero values were changed to 0.01 to allow for analysis (see Aebischer et al. 1993). Data were adjusted for small sample sizes following recommendations by Sokal & Rohlf (1995). Observed/expected ratios were additionally used as

selectivity indexes in which a ratio of >1 indicated that a female used the habitat more than expected given random use (preferred habitat) and a value <1 indicated that a female used the habitat less than expected given random use (nonpreferred habitat).

To compare preferential use of habitats during the seasons, we calculated observed values in the wet (October–March) and dry (April–September) seasons separately. Additionally, we investigated differences in seasonal usage of home ranges during the wet and dry season months using a multiresponse permutation procedure (MRPP) (White & Garrott 1990) using Blossom software (Cade & Richards 2005). Only females with at least 40 sample points per season were used in this analysis. We use a paired t test to compare overall home range size differences between the two seasons and between estimates using kernel and MCP estimators.

We used a separate analysis to determine more directly whether females become more selective when they are cycling (i.e. during a period that they would be locating and assessing potential mates) than when they are not cycling. That is, do they change preferential use of various males' territories when they are reproductively active? Females were determined to be cycling if they were displaying behavioural signs of oestrous (see Patton et al. 1999; Swaisgood et al. 2006). First, we calculated territory selectivity ratios for each female in each territory when she was cycling and when she was not cycling by comparing the observed/expected values of territory use described above. We then calculated a general index of selectivity by subtracting the lowest ratio from the highest ratio. We restricted this analysis to the five male territories most often visited by the female. This selectivity index, then, is a measure of how choosy a female was with regard to male territories. A high value indicates that the female showed strong preferences for some male territories at the expense of utilizing other male territories. A strong preference could indicate attraction to resources on the territory or, alternatively, may indicate active preferences for particular males. However, a change of female use of male territories from inactive to active reproductive periods would strongly suggest that female spatial movement is part of a mating strategy. From this hypothesis, we generated the following three predictions.

(1) If the selectivity index increases during active reproductive periods, the female is becoming choosier about where she spends her time, suggesting strong preference for some male territories over others.

(2) If the selectivity index decreases, the female is becoming less choosy about where she spends her time, suggesting that she may be 'sampling' and assessing a greater number of males and/or their territories.

(3) If there is no change in the selectivity index, the female's preference for certain male territories does not change when she becomes reproductively active, indicating either that she has no preference or that her preference was established previously during the nonreproductive periods.

This analysis, then, does not measure mate choice for particular males or their territories, but rather measures whether females become more choosy about the males

with whom they interact when they are reproductively active.

The above methods only relate to use of space and do not consider actual interactions between males and females. We used our data on male–female consorts to further evaluate the relationship between space use and mating strategies. A female and male were determined to be consorting if they displayed behavioural signs of courtship, including chin resting, mounting and mating. We used a logistic regression to determine whether the degree of male territory overlap with the female range or the percentage of time that the female spent in the male's territory predicted the likelihood of a female consorting with a male. The unit of analysis was a male–female dyad. Data were included for all females for which we obtained any consortship observations, indicating that they were reproductively active during the study.

RESULTS

Female Home Range Size and Seasonal Use

Using a 90% kernel home range estimator, mean $\pm$ SE female home range size was $19.74 \pm 2.9 \ \text{km}^2$ (Table 1). Core area usage within these home ranges was approximately one-fourth of the total calculated range ($5.17 \pm 1.24 \ \text{km}^2$, range $0.72-18.01 \ \text{km}^2$). MCP estimates of home range size were significantly more than 90% kernel estimates (paired t test: $t_{14} = 3.21$, $P = 0.006$), as expected, based on methodological differences (see Methods). Neither female home range size (paired t test: $t_8 = 0.65$, $P = 0.54$) nor core usage ($t_8 = 0.60$, $P = 0.56$) differed between the wet and dry seasons. Mean $\pm$ SE percentage of overlap between the areas covered in wet and dry seasons within yearly home ranges were high ($86.9 \pm 16.3\%$, range $60-100\%$); however, area of overlap does not allow evaluation of differential usage of areas within a home range (White & Garrott 1990). MRPP revealed that five of the nine females for which wet and

dry season comparisons were possible significantly changed usage within their home ranges during the wet and dry season, with another four females altering their ranges, albeit nonsignificantly (Table 1).

Male Territories

Our analysis of recognizable male location data resulted in the identification of 17 mutually exclusive territories; however, sufficient data existed for 13 of these bulls to accurately reflect the majority of their range. The mean $\pm$ SE territory size for these 13 bulls was $4.79 \pm 0.49 \ \text{km}^2$ (range $2.62-8.95 \ \text{km}^2$). Although our estimate for male territory size is larger than the $1-2 \ \text{km}^2$ average found by Owen-Smith (1988) in the same reserve, the density of the population studied by Owen-Smith was nearly double what it was during our study. Moreover, results from other more sparsely populated reserves yield larger estimates for male territory size (Rachlow et al. 1999: 15–20 km^2; Kretzschmar 2002: 60–116 km^2). Thus, even with the different methods for calculating territory size used in our study, it appears that our estimate is a reasonable approximation. After we delineated territories using the Neighbourhood function, we cross-referenced all male GPS points to determine the accuracy of our territory demarcations with a mean $\pm$ SE success rate of $89.3 \pm 3.9\%$.

Preferential Use of Habitat and Male Territories by Females

Females' ranges were largely composed of three main habitat types, with open woodland habitat accounting for the majority of the area, followed by grassland and dense thicket habitat classifications (Table 2, Fig. 1). Although male territories were much smaller, habitat composition was similar to that of females but more variable. The majority of females showed preferential use of habitat within their yearly range, and when grassland was sufficiently

Table 1. Estimates of home range size and seasonal variation in home range use for female white rhinoceros

Female	N	MCP	Kernel	Wet (N)	Dry (N)	P*
N05	53	6.52	6.95	—	—	
N25	128	41.88	19.86	—	—	
N35	52	29.81	12.50	—	—	
N37	95	38.29	14.39	15.63 (52)	13.71 (43)	0.08
N40	97	22.35	13.65	13.42 (52)	10.99 (45)	0.08
N55	127	28.68	17.13	17.00 (61)	16.23 (66)	>0.10
N58	119	19.63	13.74	11.40 (46)	17.14 (73)	0.04
N59	64	15.00	14.08	—	—	
N60	137	22.15	19.41	—	—	
N61	175	12.55	7.00	6.73 (102)	6.72 (73)	0.09
N62	167	66.80	46.05	58.47 (102)	33.52 (65)	0.01
N63	100	38.31	34.18	18.34 (59)	35.05 (41)	<0.001
N64	174	44.59	33.61	26.91 (88)	31.40 (86)	<0.001
N77	73	32.96	16.41	—	—	
N78	205	26.11	9.89	6.14 (118)	9.21 (87)	<0.001

Sample size and home range estimates (km^2) for females are given using both minimum convex polygon (MCP) and fixed kernel estimators. Kernel home range size for both wet and dry seasons are shown. Home range size did not differ significantly between seasons (see Results).
*Multiresponse permutation procedure (MRPP) was used to determine whether patterns of usage differed between wet and dry seasons.

Table 2. Percentage of habitat composition in territories and home ranges of male and female white rhinoceros, respectively

	Male (N=13)		Female (N=15)	
Habitat type	% Territory	Range	% Home range	Range
Dense thicket	11.72±2.61	3.80−38.00	10.78±2.48	6.85−17.34
Dense woodland	0.58±0.47	0.00−6.140	0.37±0.40	0.00−1.57
Grassland	13.82±2.91	1.00−35.70	12.05±4.24	5.47−23.54
Medium thicket	2.55±1.76	0.00−23.30	3.40±1.67	0.51−6.98
Medium woodland	6.54±1.60	1.00−18.70	7.64±3.26	1.41−13.00
Open thicket	1.02±0.51	0.00−6.20	0.75±0.65	0.00−2.35
Open woodland	62.21±3.46	32.60−76.90	63.52±3.82	52.72−70.69
Unclassified	0.76±0.28	0.10−3.80	0.59±0.32	0.27−1.58
Water	0.82±0.52	0.00−5.30	0.91±1.29	0.00−4.57

Mean values ± SE are presented.

available to allow for separate analysis, all females disproportionately utilized this habitat (Table 3). Although female preference for grassland habitat was largely independent of season, females appeared to be somewhat less selective during the dry season, which may account for the seasonal differences reported above.

We found that each female's MCP home range overlapped with a mean ± SE of 7.13 ± 0.83 male territories (range 4−15), although females were not observed in all these territories (5.6 ± 0.58; range 3−11). Females did not distribute themselves randomly among territories within their range; rather, all females showed preferential use of particular territories when compared with predictions of random use based on female−male range overlap (Table 4). Almost all females favoured territories in which the expected value of the territory was highest. Thus, females showed preferential use of male territories whose ranges overlapped more with the female range. In three cases (females N37, N55 and N63), the female spent
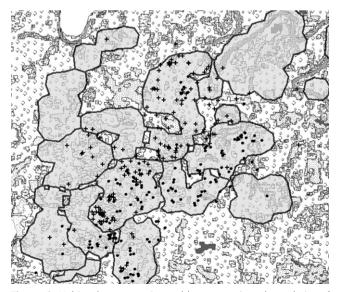

Figure 1. Habitat heterogeneity and known territory boundaries of male white rhinoceros within the study site. Two examples of female movement patterns are shown.

disproportionately more time in undefined areas where the territorial male or boundaries were unknown (Table 4).

Since grassland habitat appeared to be consistently preferred by females, we used a Spearman rank correlation to determine whether the amount of grassland in a male's territory predicted female use of the territory. The total amount of grassland habitat in each male's territory was correlated with the sum of all females' G test log-likelihood values for each male. Female preferential use of territories correlated significantly with total grassland area in male territories ($r_S = 0.63$, $N = 13$, $P = 0.03$).

Results from logistic regression ($N = 61$) indicated that the percentage of time that a female spent in a particular male's territory predicted the likelihood of consorting with that male ($\chi^2 = 7.93$, $P = 0.005$), but the percentage of female range overlap with male territories did not ($\chi^2 = 0.08$, $P = 0.78$). These results indicate that females are most likely to mate with males on whose territories they spend the most time.

The mean ± SE number of male territories that females visited did not differ when females were cycling ($4.9 ± 1.0$) and not cycling ($5.3 ± 1.2$; paired t test: $t_7 = 0.68$, $P = 0.52$). The selectivity index analysis also failed to provide support for the hypothesis that females change their ranging pattern with regard to male territories when they are reproductively active. For the top five preferred male territories, females' preference among them did not change between noncycling ($2.5 ± 0.4$) and cycling ($3.3 ± 0.8$) periods (paired t test: $t_7 = 0.90$, $P = 0.40$).

DISCUSSION

Home Range Ecology and Conservation Implications

Our findings are consistent with those of previous studies (Owen-Smith 1975; Pienaar et al. 1993; Rachlow et al. 1999) showing that female home ranges are large and overlap substantively with the ranges of other males and females, and that males are more territorial, confining their ranges to smaller areas where they exclude other dominant males. Female home range and male territory size estimates reported here are larger than those found

Table 3. Preferential use of habitats by individual female white rhinoceros

Female	G_{adj}	All seasons Open woodland	Grassland	Dense thicket	G_{adj}	Wet season Open woodland	Grassland	Dense thicket	G_{adj}	Dry season Open woodland	Grassland	Dense thicket
N05	23.97**	F	—	NP	17.78**	P	—	NP				
N25	5.95	NP	NP	F	0.27	NP	—	F				
N35	28.65**	P	—	NP	21.37**	P	—	NP				
N37	5.47	F	P	NP	1.05	P	—	F	3.74	F	P	NP
N40	15.39**	NP	F	—	2.27	NP	F	—	3.79	NP	F	NP
N55	5.11	NP	NP	F	4.19	NP	P	F	1.75	NP	NP	F
N58	5.38	NP	F	NP	2.94	F	P	—	2.91	NP	F	NP
N59	11.77**	NP	F	NP								
N60	14.14**	NP	F	NP	14.13**	NP	F	NP	4.47	F	P	NP
N61	8.32	F	P	NP	4.96	F	P	NP				
N62	43.58**	NP	F	NP	25.76**	NP	F	NP	16.82**	NP	F	NP
N63	9.33	NP	P	P	9.95**	NP	—	P	0.53	P	—	NP
N64	15.44**	NP	F	NP	12.19**	NP	F	NP	7.73	P	F	NP
N77	9.50*	F	NP	NP					9.63*	F	NP	NP
N78	65.01**	NP	F	NP	44.30**	NP	F	NP	24.41**	NP	F	NP

F = favoured habitat (strongest preference); P = preferred habitat; NP = nonpreferred habitat. Habitats with expected preference values >5 are listed. *$P < 0.05$; **$P < 0.01$.

by Owen-Smith (1975) in the same reserve when rhinoceros density was greater, but smaller than those reported by others working in reserves where density was lower (Rachlow et al. 1999; Kretzschmar 2002). These differences suggest that, even for females, which tolerate range overlap with male and female conspecifics, the costs of social pressure constrains the maintenance of larger home ranges (see also Rachlow et al. 1999). However, at the higher densities that prevailed in iMfolozi three decades

Table 4. Preferential use of defined territories by individual female white rhinoceros

Female	G_{adj}	Territory
N05	14.48	**ME9**, me14
N25	188.29	**ME9**, m060, me11, mh3
N35	59.60	**ME9**, m060, me14
N37	27.06	mh13, m013b, me18, M040
N40	54.12	**MH13**, mh8, MH6, mh12, m233, me18
N55	59.26	M060, m050, me11, m013b, MH3, mh12
N58	60.58	**M013B**, m060, me18, m040, mh13
N59	24.38	**ME9**, m060, me14
N60	64.03	MH6, **M233**, MH8, mh13
N61	100.73	**ME9**, me1
N62	142.39	**M060**, MH13, m013b, mh6, me18, mh12, mh8, m050, me9
N63	92.67	me9, m060, m013b, ME1
N64	83.64	**MH13**, M013B, MH6, m060, ME18, MH8, m233, m040
N77	55.39	**M233**, mh12, mh6, MH8, mh13
N78	177.53	**MH12**, ME11, mh13, mh8, m050, m233

Preferred territories = upper case; favoured territories = upper case bold italics; nonpreferred territories = lower case. Territories are listed from most to least preferred. Only habitats with expected preference values >5 are shown. All P values < 0.001.

ago, population growth rate was higher (9.5%; Owen-Smith 1973) than the current 7.1% growth rate (unpublished HiP management reports) at approximately half the population density. Therefore, restriction of range movement at higher densities does not appear to affect the productivity of the population (although this difference in productivity may also reflect temporal differences in forage availability or quality). In addition, the much smaller and socially constrained male territories still contain adequate resources, suggesting that females range over a much larger area than required for sufficient feeding resources. A plausible explanation for large female ranges, then, is that females have the ability to interact with multiple males, which may be part of an assessment strategy to identify and evaluate potential mates (see below).

Our findings on home range ecology also have implications for conservation management. Some home range estimates for white rhinoceros, while valuable, come from newly established populations at low density (e.g. Pienaar et al. 1993), probably substantially less dense than was typical during historical times (Owen-Smith 1975). It is important, therefore, to obtain an accurate and biologically valid measure of home range size more typical for this species. This value could affect conservation actions that rely on knowledge of home range size. These include estimates of carrying capacity, population viability analysis, reserve design, and determining whether surplus animals are available for translocation or whether the receiving populations need augmentation. In terms of resource needs for feeding, white rhinoceros readily use the most common habitat, open woodland, but clearly prefer grassland. Thus, conservation actions to optimize white rhinoceros habitat should manage for grassland habitat. In addition, resources limiting population potential are often those that are seasonally less available. Our study makes inroads into understanding how female

rhinoceroses adjust their ranging patterns to deal with seasonal habitat changes.

Implications of Ranging Patterns for Mating Strategies

Patterns of space use can and do provide predictive insights into social organization and mating strategies (Emlen & Oring 1977; Sandell 1989; Lott 1991). A primary prediction that has received considerable empirical support is that females should distribute themselves according to resources, whereas male space use is governed by the distribution of females. In contrast, our results indicate that female ranging patterns may be designed in part to access, and possibly assess, multiple males for mating purposes.

Females regularly entered the territories of several males, interacted with them, and ultimately mated with the most familiar males (i.e. those in whose territories the females spent the most time). However, when females range widely and are asynchronously receptive, as is the case with white rhinoceros, the economic defensibility of multiple females by males becomes increasingly difficult (Emlen & Oring 1977; Owen-Smith 1977). In accordance with the theoretical predictions of Owen-Smith (1977), white rhinoceros territoriality may more appropriately reflect a low-cost/low-benefit strategy by males whereby severe male–male competition results in spatially discrete territories. This form of male territorial defence may not serve evolutionarily to maximize male access to receptive females relative to competitors, but may instead increase the likelihood of male mating by increasing male longevity.

In the present study, female ranges overlapped with several male territories, with core areas concentrated preferentially in a subset of male territories. Females also spent significantly more time in male territories that contained more grassland habitat. A plausible explanation of apparent preferences for male territories is that females are simply drawn to the resources contained in them. Although the end result is that some male territories are preferred over others, this is best described as passive female choice (if territory use correlates with mating; see below). Alternatively, females may be drawn to these male territories because the male's ability to defend the habitat better indicates his competitive ability and, perhaps, heritable qualities that will enhance offspring fitness (i.e. the 'good genes' hypothesis; see Andersson 1994, for a discussion).

Our results on female selectivity provide additional insights into these questions. Female white rhinoceros did not appear to become more or less selective about where they spent their time when they were reproductively active. While females were typically exposed to five to seven male territories, they did not appear to increase or decrease the number of territories that they visited when they were reproductively active. Thus, females are potentially exposed to the same number of males regardless of their reproductive condition. Similarly, females showed no change in preferential use of some males' territories over others during reproductively active periods; that is, females did not become more or less choosy about which male territories they visited when they were cycling compared to when they were not cycling. Thus, white rhinoceros females do not appear to select mates via mate sampling or mate choice.

Male rhinoceros rarely encroach on each other's territories (Owen-Smith 1975; this study); thus, females remaining in a particular male's territory during their receptive period are likely to mate with that male. Indeed, our results strongly suggest that this is the case. The time that a female spent in a male's territory was a significant predictor of mating with that male, whereas the degree of range overlap with a male's territory was unrelated to reproductive behaviour. These results suggest that females are likely to mate with the most familiar males known to them. Indeed, familiarity has long been known to be a major determinant of female mate choice across a variety of mammals (Andersson 1994; Gosling & Roberts 2001).

The unequal distribution of female presence on the landscape has implications for male mating strategies. Females concentrate their activities in some habitat types (especially grassland), which are distributed unevenly on the landscape, and males defend territories that vary in the composition of preferred female habitats. This sets the stage for male–male competition for preferred female habitats, whereby some males can win more mating opportunities than others, increasing the degree of polygyny beyond the dichotomy of breeding dominant territorial males and nonbreeding subordinate males. Our results suggest that a male's mating success is positively correlated with the number of females using his territory regularly (see also Kretzschmar 2002). Because males mate with multiple females and do not defend females from other males, except on occasion when more than one male may court an oestrous female, males may be served best by maintaining territories in preferred habitat areas.

References

Aebischer, N. J., Robertson, P. A. & Kenward, R. E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, **74**, 1313–1325.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Cade, B. S. & Richards, J. D. 2005. *User Manual for Blossom Statistical Software*. Fort Collins, Colorado: U.S. Geological Survey, Fort Collins Science Center.

Dora, C. A. 2004. The influence of habitat structure and landscape heterogeneity on African buffalo (*Syncerus caffer*) group size in Hluhluwe-iMfolozi Game Reserve, South Africa. M.S. thesis, Oregon State University.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.

Emslie, R. & Brooks, M. 1999. *African Rhino Status Survey and Conservation Action Plan*. Gland, Switzerland: IUCN.

Gosling, L. M. & Roberts, S. C. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Advances in the Study of Behavior*, **30**, 169–217.

Harris, S., Cresswell, W. J., Firde, P. G. & Trewhella, W. J. 1990. Home-range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, **20**, 97–123.

Jolles, A. 2004. Disease ecology of tuberculosis in African buffalo. Ph.D. thesis, Princeton University.

Kretzschmar, P. 2002. Ecological, endocrinological, and ethological investigations of female mate choice in free-ranging white rhinoceros (*Ceratotherium simum simum*). Ph.D. thesis, Ernst-Moritz-Arndt-Universitat Greifswald, Berlin.

Linklater, W. L. 2003. Science and management in a conservation crisis: a case study with rhinoceros. *Conservation Biology*, **17**, 968–976.

Lott, D. 1991. *Intraspecific Variation in Social Systems of Wild Vertebrates*. Cambridge: Cambridge University Press.

Mohr, C. O. 1947. A table of equivalent populations of North American small mammals. *American Midland Naturalist*, **37**, 223–249.

Owen-Smith, R. N. 1971. Territoriality in the white rhinoceros. *Nature*, **231**, 294–296.

Owen-Smith, R. N. 1973. The behavioural ecology of the white rhinoceros. Ph.D. thesis, University of Wisconsin.

Owen-Smith, R. N. 1975. The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). *Zeitschrift für Tierpsychologie*, **38**, 337–384.

Owen-Smith, R. N. 1977. On territoriality in ungulates and an evolutionary model. *Quarterly Review of Biology*, **52**, 1–38.

Owen-Smith, R. N. 1988. *Megaherbivores: the Influence of Very Large Body Size on Ecology*. Cambridge: Cambridge University Press.

Patton, M. L., Swaisgood, R. R., Czekala, N. M., White, A. M., Fetter, G. A., Montagne, J. P., Rieches, R. G. & Lance, V. A. 1999. Reproductive cycle length and pregnancy in the southern white rhinoceros (*Ceratotherium simum simum*) as determined by fecal pregnane analysis and observations of mating behaviour. *Zoo Biology*, **18**, 111–127.

Pienaar, D. J., Bothma, J. & Theron, G. K. 1993. White rhinoceros range size in the south-western Kruger National Park. *Journal of Zoology*, **229**, 641–649.

Price, M. V., Kelly, P. A. & Goldingay, R. L. 1994. Distances moved by Stephens' kangaroo rat (*Dipodomys stephensi merriam*) and implications for conservation. *Journal of Mammalogy*, **75**, 929–939.

Rachlow, J. L., Kie, J. G. & Berger, J. 1999. Territoriality and spatial patterns of white rhinoceros in Matobo National Park, Zimbabwe. *African Journal of Ecology*, **37**, 295–304.

Rodgers, A. R. & Carr, A. P. 2001. HRE: The home range extension for Arcview. In: *Tracking Animals with GPS* (Ed. by A. Sibbald & I. J. Gordon), pp. 83–84. Aberdeen: MLuri.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. In: *Carnivore Behaviour, Ecology, and Evolution* (Ed. by J. L. Gittleman), pp. 164–182. Ithaca, New York: Cornell University Press.

Shrader, A. M. & Beauchamp, B. 2001. A new method for the implantation of radio transmitters into the horns of white and black rhinoceros. *Pachyderm*, **30**, 81–86.

Shuster, S. M. & Wade, M. J. 2003. *Mating Systems and Strategies*. Princeton, New Jersey: Princeton University Press.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*. New York: W.H. Freeman.

Swaisgood, R. R., Dickman, D. M. & White, A. M. 2006. A captive population in crisis: testing hypotheses for reproductive failure in captive-born southern white rhinoceros females. *Biological Conservation*, **129**, 168–176.

Swihart, R. K. & Slade, N. A. 1985. Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management*, **49**, 1019–1025.

White, G. C. & Garrott, R. A. 1990. *Analysis of Wildlife Radio-Tracking Data*. San Diego: Academic Press.

Wong, S. T., Servheen, C. W. & Ambu, L. 2004. Home range, movement and activity patterns, and breeding sites of Malayan sun bears *Helarctos malayanus* in the Rainforest of Borneo. *Biological Conservation*, **119**, 169–181.

Worton, B. J. 1989. Kernel methods for estimating the utilisation distribution in home-range studies. *Ecology*, **70**, 164–168.