Ranging behaviour and habitat usage in black rhinoceros, *Diceros bicornis*, in a Kenyan sanctuary

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Abstract

Home range area and habitat utilization by translocated black rhinoceros *Diceros bicornis* were studied at Sweetwaters Rhino Sanctuary in the Laikipia district of Kenya. Home ranges were estimated from sightings and tracking data; home range area was very variable between individuals (range 2.25–14.39 km^2, minimum convex polygons), and was independent of age or sex. Groups of rhinoceros shared common home ranges, with little or no overlap between groups; each group consisted of one adult male, one or more adult females and their calves, and sometimes immature animals. Rhinoceros utilize a variety of habitats, but within these show positive selection for certain habitats. Home ranges generally included more *Euclea* bush, and less grassland and *Acacia* bush than expected. Rhinoceros make use of regular resting places, or bedding sites, generally situated in bushland in secluded areas, often in dense thickets. Rhinoceros defaecate at dung piles or middens. Middens are located throughout the range not just on the boundaries; the highest density of middens was found in riverine woodland, and the lowest density in grassland and *Acacia* bush.

Key words: Diceros, habitat, home range, Kenya, behaviour

Résumé

On a étudié la surface de l'habitat et l'utilisation du territoire des rinocéros noirs *Diceros bicornis* qui ont été déplacés vers le Sanctuaire des Rhinos de Sweetwaters, dans le District de Laikipia, au Kenya. On a évalué la surface des territoires par des observations directes et des traces. Cette surface était très variable selon les individus (entre 2,25 et 14,39 km^2, polygones convexes minimum) et ne dépendait pas de l'âge ni du sexe. Des groupes de rhinocéros partageaient des territoires communs, avec un recouvrement faible ou nul entre les groupes. Chaque groupe se composait d'un mâle adulte, une ou plusieurs femelles adultes avec leurs petits et parfois des animaux subadultes. Les rhinocéros fréquentent toute une variété d'habitats mais marquent cependant une préférence pour certains d'entre eux. Les territoires renfermaient généralement plus de buissons d'*Euclea* et moins de prairies ou de buissons d'*Acacia* que prévu. Les rhinocéros utilisent régulièrement des sites de repos, situés généralement dans des endroits buissonneux retirés, souvent dans des taillis denses. Les rhinocéros défèquent à des endroits fixes. Ces endroits sont répartis sur tout le territoire, pas seulement sur les bords; on en a trouvé les plus fortes densités dans les forêts ripariennes, et les plus faibles densités dans les prairies et les buissons d'*Acacia*.

Introduction

Most research into black rhinoceros (*Diceros bicornis* L.) population biology and ecology was conducted when large numbers of free-ranging rhinoceros still existed (e.g. Goddard, 1966, 1967, 1970; Schenkel & Schenkel-Hulliger, 1969). Relatively little research has been carried out on small populations of rhinoceros confined to limited areas. The optimum habitat appears to be thick scrub and bushland, often with some woodland, which supports the highest densities (1.4 rhinoceros/km^2, Goddard, 1970; 1.6 rhinoceros/km^2, Conway & Goodman, 1989) and the smallest home range size, as little as 2.6 km^2 (Goddard, 1967). Open grassland appears the least favourable habitat, supporting densities as low as 0.04 rhinoceros/km^2

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(Goddard, 1970) and home ranges up to 100 km^2 (Frame, 1980), the latter being larger than some of the fenced rhinoceros sanctuaries (Anon., 1993). The most important habitat features affecting area appear to be availability of water, food and cover, and absence of human disturbance (Goddard, 1967; Mukinya, 1973; Frame, 1980; Conway & Goodman, 1989; Berger & Cunningham, 1995).

Black rhinoceros are generally thought to be solitary, with the only strong social bond being between a cow and her youngest calf (Schenkel & Schenkel-Hulliger, 1969; Goddard, 1966; Mukinya, 1973; Frame, 1980; Hitchins & Anderson, 1983). In addition bulls are known to have a consort relationship with oestrous cows (Schenkel & Schenkel-Hulliger, 1969), and subadults and young adults frequently form loose associations with older individuals of either sex (Klingel & Klingel, 1966; Goddard, 1967; Schenkel & Schenkel-Hulliger, 1969).

The black rhinoceros is now endangered wherever it occurs in Africa; Kenya has the only substantial breeding populations of the East African subspecies *D. b. michaeli*, estimated at over 400 animals in 1993 (Anon., 1993). The majority of these animals are now in protected sanctuaries, which are generally fenced, can be closely monitored and effectively guarded. The sanctuary policy, combined with intensive antipoaching efforts, appears effective, with the longest established sanctuaries showing a population increase of about 10% per year (Anon., 1993). The long-term management plan for black rhinoceros incorporates restocking historical ranges with surplus animals from the protected sanctuaries as populations increase (Anon., 1993). In this paper we describe the home range size and habitat utilization of translocated black rhinoceros in a fenced sanctuary, and use the position and overlap of home ranges to show some aspects of their social behaviour.

Methods

Study area

Sweetwaters Rhinoceros Sanctuary is located in the Laikipia District of Kenya, between 0°00′N and 0°05′N, and between 36°53′E and 37°00′E. The terrain is gently undulating, between 1770 m and 1820 m altitude. Rainfall averages 800 mm per year, concentrated into two rainy seasons, March to May and October to December (Anon., 1993). The 93 km^2 sanctuary is enclosed by an electrified fence, and is considered to be prime rhinoceros habitat, capable of supporting a high-density, high-productivity rhinoceros population, of great importance to the overall rhinoceros recovery plan in Kenya (R. A. Brett, unpublished report; Anon., 1993).

Black rhinoceros were first introduced into the sanctuary in 1989. By July 1995 the total population was nineteen wild rhinoceros. Rhinoceros were assigned to three age classes, similar to those used by Goddard (1967). Adults are full sized animals, immatures are less than full sized but independent of their mothers, and calves are still dependent on their mothers. During the study period the population comprised four adult males, four adult females with dependent calves, three adult females without calves, three immature males and one immature female.

Data collection

Data were collected between July and September 1995, and 165 h of observations were recorded. Census walks were conducted in all areas of the reserve, attempting to cover all areas equally. Rhinoceros and their signs were located with the help of the rangers employed to locate and guard the rhinoceros. Signs included footprints (spoor), dung middens and bedding sites (rhinoceros frequently use the same place to rest, and through regular use these become bare of vegetation and clearly visible). The rangers know all the animals and are adept at identifying footprints, by their distinguishing characteristics and size. Spoor was only used when identity could be confirmed (e.g. by following tracks until a rhinoceros was located). Rangers frequently find rhinoceros at bedding sites, or pick up spoor by bedding sites or middens, so can be certain which animals use which sites. The position of all sign and sightings of rhinoceros was recorded using a GPS Compass (Model XL1000, Silva (UK) Ltd, Egham, Surrey).

Additional data were collated from reports of identifiable rhinoceros sightings made by reserve staff over 20 months between December 1994 and July 1995, and between October 1995 and September 1996. These sightings were plotted on a map of the reserve, and were analysed separately to determine whether home ranges were maintained over a long period.

We made detailed measurements of a number of bedding sites and middens, measuring the largest and smallest diameter and recorded details of the surrounding vegetation. Efforts were made to sample bedding sites and middens in all the main habitat types and in all areas used by rhinoceros. The position of middens within the home range was analysed to determine if they are located nearer range boundaries than other types of location, as would be the case if middens are used as boundary markers. The arithmetic mean centre of all location fixes was calculated for each rhinoceros, and from this point the distance to each location. Distances to different sign types for each rhinoceros were then compared using ANOVA.

Home ranges

We calculated home ranges as minimum convex polygons (Mohr, 1947; Southwood, 1966), and harmonic mean 95% isopleth (Dixon & Chapman, 1980), using all signs (sightings, spoor, middens and bedding sites).

To determine whether the sample sizes collected were adequate to reliably estimate home ranges we plotted the total range area as convex polygons and 95% harmonic mean isopleths against increasing sample size for the animals with the largest number of location fixes; this gave curves that reached an asymptote at between 20 and 30 fixes for both estimates. Analyses were carried out only for the twelve animals for which there were more than 25 location fixes. The four calves were never sighted away from their mothers and thus independent ranges were not calculated for these juveniles.

The software package Ranges IV for PC (Kenwood, 1990) was used to calculate home range areas; harmonic means were calculated using a 40×40 cell grid, with fixes centred in each grid cell.

To avoid bias from temporal autocorrelation of data (Swihart & Slade, 1985), when tracking a rhinoceros we recorded only the position where spoor could first be identified. Only one sighting or fresh spoor was recorded for an individual rhinoceros on any one day. When bedding sites or middens were encountered close together all were recorded, as these sites are visited repeatedly by rhinoceros, so indicate a genuine high usage of that area.

Core areas

Animals do not use their home ranges evenly – the area or areas used most intensively are generally known as the core area(s), although this is rarely defined precisely (Harris *et al.*, 1990). Cluster analysis indicated that most rhinoceros had several centres of activity. Core areas were estimated as 70% cluster polygons (Kenwood, 1990) (used as clusters show activity nucleii clearly), and the 70% isopleth of the harmonic mean range estimator. Overlap between the home range and core area estimates for all pairs of animals were also calculated.

Habitat composition of home ranges

Several habitat types were identified, based on the composition of the dominant plant species, as: (i) grassland, with less than 20% shrub cover. (ii) *Acacia* bushland: grassland with 20–90% shrub cover, dominated by whistling thorn *Acacia drepanolobium*. (iii) *Euclea* bushland: grassland with 20–90% shrub cover, dominated by mukinyei *Euclea divinorum*. (iv) Mixed bushland: grassland with 20–90% shrub cover, with no one species dominant. (v) Dense *Euclea* bushland: $>90\%$ cover, dominated by *Euclea divinorum*. (vi) Riverine woodland: dominated by Fever trees *Acacia xanthophloea*, and with an understorey dominated by *E. divinorum*. (vii) Marsh: characterized by low-growing vegetation and waterlogged soil.

All habitat data were plotted onto a 1 : 50,000 map; from this map the areas of each habitat type within the reserve and within each home range and core area were calculated.

Patterns of habitat utilization

As varying amounts of time were spent searching different habitats, an additional habitat utilization index was calculated by dividing the amount of sign found by the time spent on census walks in each habitat type. The amount of observed sign in each habitat was compared to that expected if distribution is random using χ^2.

Results

Home ranges

Minimum convex polygons and harmonic mean 95% isopleths gave similar home range sizes – average 7.65 km^2 (range 2.25–14.39 km^2) for minimum convex polygons and average 7.68 km^2 (range 2.17–

15.82 km^2) for the 95% harmonic mean isopleth (Table 1). Calculated home range areas were extremely variable between individuals. However there were no significant differences between the home ranges of males and females, or between adults and immatures, for both the minimum convex polygon and 95% isopleth areas (Mann–Whitney *U*-test, $P > 0.05$ in all cases), indicating home range size is independent of both sex and age class.

Records by reserve staff over 20 months included 480 sightings of identifiable rhinoceros, of these only fifteen (3%) were clearly outside the home ranges estimated from this study, indicating that the home ranges are stable over long periods. This study only covered the dry season, but the sightings records do not indicate any difference in ranging behaviour in the wet season.

Core areas

Core areas, calculated as 70% cluster polygons, averaged 0.55 km^2 (range 0.14–1.85 km^2), which is 7.1% (range 2.6–14.3%) of the minimum convex polygon range area; 70% cluster polygons also showed most animals to have more than one centre of activity (average 3.6, range 1–5). There was a strong negative correlation between core area size and number of nucleii (Pearson correlation coefficient $r = -0.700$, df = 10, $P < 0.01$).

Core areas calculated as 70% harmonic mean isopleths were larger, averaging 2.63 km^2 (range 0.74–4.94 km^2), which is 43.4% (range 21.1–48.8%) of the harmonic mean 95% isopleth home range. As the harmonic mean method is an estimate of the probability of locating the animal in any part of its range, this can be translated as rhinoceros spending 70% of their time utilizing less than half of their range.

Seventy per cent isopleths showed a variable number of nucleii of activity (average 2.3, range 1–4), but this was not correlated with core area size (Pearson correlation coefficient $r = 0.296$, df = 10, $P > 0.10$). There was no significant difference in size of 70% isopleth core area between males and females or between adults

Table 1 Average home range and core area estimates for all rhinoceros in Sweetwaters Reserve with more than 25 location fixes during July to September 1995. Home ranges are estimated as minimum convex polygons and harmonic mean 95% isopleths. Core areas are estimated as 70% clusters and harmonic mean 70% isopleths, expressed as area and as percentage of total home range, using the previous estimates as totals. For 70% clusters the average number of cluster nucleii is also given. All areas in km^2 (±SE)

		Home ranges		Core areas				
				70% cluster		70% isopleth	% of total area	
	Number of fixes	Minimum convex polygon	Harmonic mean 95% isopleth	Area	No. nucleii	Area	70% cluster	70% isopleth
All rhino	30.8	7.65	7.68	0.55	3.8	2.63	7.1	34.7
$n = 12$	(1.4)	(1.25)	(1.27)	(0.14)	(0.4)	(0.43)	(1.2)	(2.3)
Adult males	33.0	8.19	9.05	0.38	4.5	3.03	5.5	35.0
$n = 4$	(1.7)	(2.33)	(2.68)	(0.06)	(0.3)	(0.79)	(1.0)	(4.8)
Adult females	29.3	7.36	5.29	0.44	3.8	2.24	7.1	39.9
with calves	(1.3)	(2.67)	(1.43)	(0.15)	(0.6)	(0.77)	(2.5)	(3.2)
$n = 4$								
Adult females	26.5	9.29	10.42	1.09	3.0	3.10	8.2	27.2
without calves	(2.5)	(3.63)	(4.42)	(0.76)	(2.0)	(1.84)	(5.6)	(6.1)
$n = 2$								
Immature males	33.5	5.49	6.98	0.55	3.5	2.15	8.7	31.2
$n = 2$	(7.5)	(2.72)	(2.89)	(0.39)	(0.5)	(0.85)	(2.7)	(0.7)

There are no significant differences between the home ranges of males and females, or between adults and immatures, for both the minimum convex polygon and 95% isopleth areas (Mann–Whitney *U*-test, $P > 0.05$ in all cases).

and immatures (Mann–Whitney *U*-test, $P > 0.05$ in all cases).

Home range and core area overlap

The home range data showed no overlap between adult male rhinoceros (Fig. 1). In contrast the ranges of the adult females did overlap (Fig. 2). All the rhinoceros could be divided into four groups, with extensive overlap between animals in the same group, and little or no overlap between groups. Each group consisted of three or more animals: one adult male, one or more adult females and their calves, and sometimes immatures.

The home ranges of all animals within each group overlapped with all the others, with minimal overlap between pairs of animals in different groups, Table 2. The degree of overlap between male : female pairs within the same group (mean 65.9% for minimum convex polygons, 68.8% for 95% harmonic mean isopleths) was not significantly different from the overlap between pairs of females where there was more than one female in a group (mean 39.1%, Student's *t*-test $t = 2.02$, 16 df, $P > 0.5$ for minimum convex polygons; 41.0%, $t = 1.86$, $P > 0.5$ for 95% harmonic mean isopleths).

There was no overlap of core areas between any animals in different groups, but within groups core areas of all animals overlapped to some extent, an average 17.3% overlap for 70% clusters, and 45.2% for 70% harmonic mean isopleths.

Middens and bedding sites

Rhinoceros are known to use large dungpiles, or middens (Schenkel & Schenkel-Hulliger, 1969). Overall 88.5% ($n = 130$) of dungpiles appeared to have been used many times, with mean length of 3.62 m (range 1.0–7.8 m) and width of 1.49 m (range 0.3–4.0 m). These were designated middens. The elongated shape of many middens is due to the habit of kicking through the deposit with the hind legs, which can spread the dung greatly. A few dungpiles (11.5%) were smaller, with a mean length of 1.96 m (range 0.4–6.5 m) and width of 0.63 m (range 0.2–1.1 m), and appeared to be

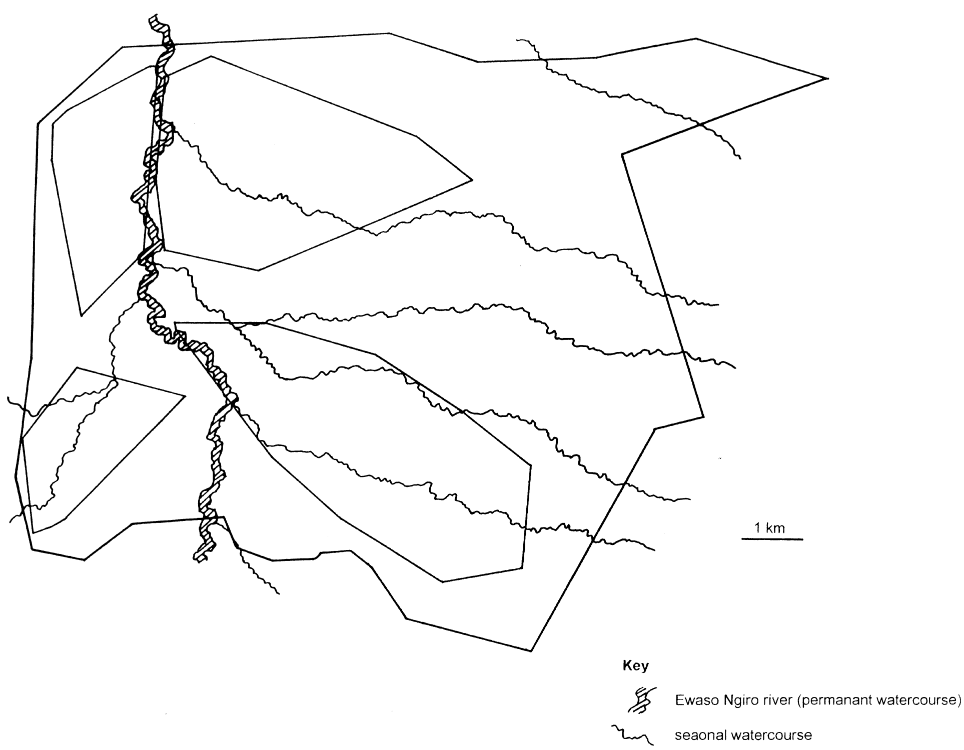

Fig 1 Home ranges of all adult male rhinoceros in Sweetwaters Reserve during July to September 1995, estimated as minimum convex polygons.

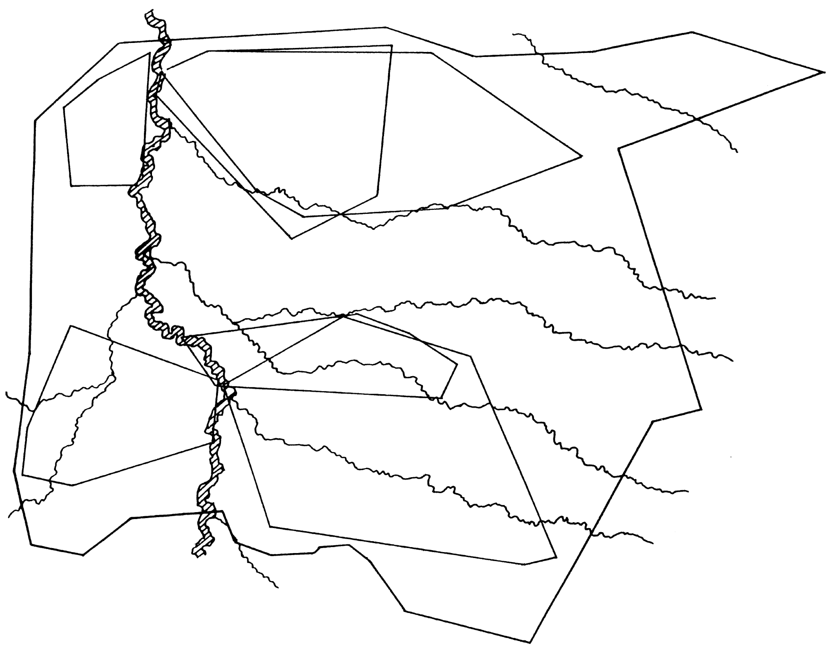

Fig 2 Home ranges of all adult female rhinoceros in Sweetwaters Reserve during July to September 1995, estimated as minimum convex polygons. Comparison with Fig. 1 indicates overlap between each adult male and one or more adult females.

the result of a single defaecation. Rhinoceros use regular paths, and 79.6% of middens were found alongside (within 5 m) such a path.

A typical bedding site is a clear space inside a dense thicket. Most are in regular use and the resting area clearly defined, these resting areas averaged 3.5 m in length (range 2.0–5.0 m, $n = 42$) and 1.9 m in width (range 1.0–3.8 m, $n = 42$). The majority (88%) were totally enclosed by tall vegetation, and in areas where dense thickets were separated by more open bushland, rhinoceros bedding sites were always found in the thickets.

Distances from the arithmetic mean centre of the home range to different types of location were compared for each rhinoceros. In nine out of twelve cases there was no significant difference between the different sign types. For the three animals (two adult males and one adult female) where there was a significant difference ($P < 0.005$), bedding sites were closest to the centre of the range, and spoor and sightings furthest away; middens being intermediate. Thus there is no evidence that middens are positioned close to the boundaries of the home range.

Habitat composition of home ranges

The total area covered by each habitat type, along with the average content of home ranges and core areas, is given in Table 3. The habitat content of the home range of each rhinoceros was significantly different from that expected if they were using each habitat in proportion to its coverage in the whole reserve (Log-likelihood chi-squared test (Sokal & Rohlf, 1981) $P < 0.02$ in all cases). Ranges in general included more *Euclea* bush than expected, and less grassland and *Acacia* bushland than expected.

Although home range areas contained less grassland than expected, the proportion of grassland in the home range (estimated by minimum convex polygon) is positively correlated with home range size ($r = 0.76$, df = 10, $P < 0.01$), this is also true for the proportion of dense *Euclea* ($r = 0.68$, df 10, $P < 0.01$). These positive correlations are also seen for the estimate of home range as 95% harmonic mean isopleths (grassland $r = 0.66$, d.f. = 10, $P < 0.01$; dense *Euclea* bushland $r = 0.67$, d.f. = 10, $P < 0.01$). Thus the smaller home ranges not only contain less grassland and dense *Euclea* bushland, they also have smaller proportions of these habitats. Hence, at least a part of the variation in home range size is accounted for by the proportions of grassland and dense *Euclea* they contain.

The habitat content of core areas also differed significantly from the surrounding home range ($P < 0.05$ for all individuals, for both 70% clusters and 70% isopleths). As for the total range, there was more *Euclea*

Table 2 Mean overlap of home range and core area, each estimated by two methods, between animals in the same group, and between animal in different groups

	Minimum convec polygon home range			Harmonic mean 95% home range			70% clusters core area	70% harmonic mean core area
	Within own group	Outside own group		Within own group	Outside own group		Within own group	Within own group
Group	Mean % overlap	Total number of ranges overlapped	Mean % overlap	Mean % overlap	Total number of ranges overlapped	Mean % overlap	Mean % overlap	Mean % overlap
South-east group	58.0	3	0.6	60.2	4	0.2	12.9	32.5
North-east group	66.1	0	0.0	73.8	9	6.1	12.6	34.3
North-west group	76.7	0	0.0	74.8	9	15.5	18.7	67.7
South-west group	73.9	1	0.3	70.0	4	0.1	25.1	46.4
Overall mean	68.7			69.7			17.3	41.0

bush and less *Acacia* bush and grassland, but there was also more mixed bush within the core area than in the surrounding home range.

Habitat utilization

In total, 525 middens, 163 bedding sites and 220 spoor were found. Habitat utilization index as calculated from density of spoor, middens and bedding sites is given in Table 4. Middens were not randomly distributed between the different habitats ($\chi^2 = 128.3$, 5 df, $P < 0.001$), with fewer than expected in grassland, *Acacia* bushland and mixed bushland; and more than twice the expected number in riverine woodland. Bedding sites were not random ($\chi^2 = 66.8$, 5 df, $P < 0.001$), being concentrated in mixed bushland, where they are frequently in dense thickets; with fewer than expected in *Euclea* bushland and riverine woodland, and none at all in open grassland. Spoor were not randomly distributed ($\chi^2 = 36.7$, 5 df, $P < 0.001$), with fewer than expected in mixed bushland, and more than expected in *Euclea* bushland and riverine woodland. This shows that not only do rhino show preferences for certain habitats in locating their home ranges, but they use particular habitats in different ways. This is illustrated by the high incidence of bedding sites in mixed bush, and their low occurrence in *Acacia* bush and riverine woodland, while the latter habitat has the highest densities of middens and spoor.

Discussion

The Kenyan rhinoceros sanctuaries are managed as a metapopulation (Anon., 1993), with movement of some animals between sanctuaries as part of the genetic management plan. However almost nothing is known of their social organization and how it is affected by translocation. This study provides greater understanding of social interactions and behaviour in Kenyan Rhino sanctuaries, which is vital to aid future conservation efforts.

Home ranges

Previous studies of black rhinoceros have shown that the home range area is highly variable. In the forested parts of Ngorongoro crater Goddard (1967) found home ranges of no more than 2.6 km^2, and Conway &

Table 3 Area of each habitat type found in Sweetwaters Reserve, in km^2 and as a percentage of the whole area. The average percentage of each habitat type with the home ranges and core areas of all rhino are also given (Standard Error in brackets)

	Area		Home ranges		Core areas	
Habitat	km^2	%	Minimum convex polygon	Harmonic mean 95% isopleth	70% clusters	Harmonic mean 70% isopleth
Grassland	20.06	21	12.8 (2.6)	9.8 (1.4)	2.5 (1.3)	7.4 (3.5)
Acacia bushland	16.46	17	13.3 (1.6)	14.1 (2.4)	8.6 (3.7)	9.0 (2.6)
Mixed bushland	36.19	37	42.3 (2.5)	39.8 (3.9)	52.6 (7.0)	48.1 (5.1)
Euclea bushland	10.20	11	22.7 (3.0)	22.3 (2.9)	21.3 (7.0)	25.8 (6.5)
Dense *Euclea* bushland	10.90	11	6.5 (2.8)	7.4 (3.2)	5.3 (3.1)	5.1 (2.8)
Riverine Woodland	2.64	3	3.4 (0.8)	8.0 (2.5)	7.2 (2.4)	4.3 (1.6)
Marsh	0.24	0.2	–	–	–	–
Total	8969					

Table 4 Habitat utilization index for different types of rhinoceros sign found in different habitats, calculated as the number found divided by search time

		Categories of rhinoceros sign				
Habitat	Search time in minutes	Middens	Spoor	Bedding sites	Other*	Total
Open grass	666	0.015	0.012	0.000	0.003	0.030
Acacia bush	1085	0.026	0.016	0.013	0.005	0.062
Mixed bush	3887	0.041	0.015	0.028	0.006	0.090
Euclea bush	2351	0.066	0.034	0.009	0.004	0.113
Dense *Euclea* bush	853	0.052	0.020	0.020	0.002	0.094
Riverine Woodland	1104	0.114	0.035	0.002	0.003	0.154
Mean		0.053	0.022	0.016	0.004	0.096

* Other includes wallows and sightings. None of the different sign types was evenly distributed between habitat types (Middens $\chi^2 = 128.3$, 5 df, $P < 0.001$; Spoor $\chi^2 = 36.7$, 5 df, $P < 0.001$; Bedding sites $\chi^2 = 66.8$, 5 df, $P < 0.001$).

Goodman (1989) recorded a group of seven rhinoceros sharing 4.3 km^2 of moist woodland. In less favourable habitats home ranges are much larger – rhinoceros in the drier parts of the Serengeti had home ranges of 70–100 km^2 (Frame, 1980); and home ranges may be even larger in Namibia (Berger & Cunningham, 1995). However, most studies have shown home ranges intermediate to these, 2.6–58.0 km^2 at Ngorongoro Crater and 3.6–90.7 km^2 at Olduvai Gorge (both Goddard, 1967), 5.6–22.7 km^2 in the Masai Mara (Mukinya, 1973), and 15.0–54.0 km^2 in Laikipia plateau Kenya (Brett, Hodges & Wanjohi, 1989). Home range areas at Sweetwaters of 2.25–14.40 km^2 (minimum convex polygons) are smaller than many elsewhere. This may indicate the suitability of the habitat for black rhinoceros, but it is probable the rhinoceros would roam more widely if the sanctuary were not fenced.

Habitat usage

Habitat preferences are shown in two ways, the amount of sign found in the different habitats, and the habitat content of home ranges and core areas. The rhinoceros at Sweetwaters show a preference for the denser bushlands, with home ranges containing mostly mixed bush and *Euclea* bush. The highest densities of middens and spoor were in riverine woodland and *Euclea* bush, while most bedding sites were found in mixed bush and dense *Euclea* bush. The varying densities of rhinoceros sign in different habitats indicates a mosaic of habitats provide the optimum environment.

The high amount of spoor found in riverine woodland is partly due to rhino coming to drink, and may be artificially high due to the ease of finding spoor at the rivers edge. However this does not account for the high numbers of middens and absence of bedding sites from riverine woodland. There was a general avoidance of open grass or *Acacia* bush, with a very low density of rhinoceros middens and spoor, and no bedding sites found in the open. These habitats are also under-represented in the habitat content of home ranges and core areas. The preference for dense bushland has been shown in other studies – Goddard (1970) found the highest rhinoceros densities in bushland and mixed woodland habitats. Other studies have had similar results, e.g. Mukinya (1973) and Frame (1980). The selection of certain habitat types by the rhinoceros at Sweetwaters partially explains the wide variation in home range size.

Social organization

At Sweetwaters groups of rhinoceros appear to share a common home range, each group consisting of one adult male, one or more adult females and their young calves, and sometimes immature animals. The clear separation into groups seen in this study has not been reported elsewhere, and may not be apparent at higher population densities or in more nomadic populations. Previous studies have shown some overlap between male home ranges, but to a lesser extent than between females (Goddard, 1967; Conway & Goodman, 1989).

The ritualized behaviour associated with deposition of middens (Schenkel & Schenkel-Hulliger, 1969) indicates an important role in intraspecific communication. Middens are distributed over the whole home range, not just around the perimeter. For an animal with a relatively large range and limited resources for marking this may be the most effective strategy to ensure intruders encounter a marker soon after entering the range (Mills & Gorman, 1987). At Sweetwaters many middens were found close to paths, large numbers were also found close to the river, particularly near drinking places. This is consistent with middens being sited where they are most likely to be encountered by other rhinoceros, and so is further evidence of middens being used in intraspecific communication, although the function of this communication remains uncertain.

The distribution of middens and the shared home ranges found in this study indicate a more complex social behaviour than previously thought. The majority of Kenya's rhinoceros are maintained in sanctuaries, at relatively high densities. It is vital we come to a better understanding of their social behaviour if these sanctuary populations are to be managed effectively.

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