

The demographics and use of space of the black rhino population of the Sweetwaters Game Reserve, an enclosed reserve in Kenya



Felix Patton¹
Martin Jones¹

¹Division of Biology, Chemistry and Health Science
Manchester Metropolitan University, Manchester, M1 5GD, UK

felixp@africaonline.co.ke

Abstract

Photo-identification was used to confirm the black rhino (*Diceros bicornis*) population of Sweetwaters Game Reserve, Kenya. Despite being an enclosed area, from the photographs taken of individuals, the rhino population at the end of May 2005 was found to be 43 and not 40 as had been previously recorded. Three rhinos were photographed which had not been previously identified as different but which had been confused with other individuals. By analysing GPS location fixes collected on foot by rhino patrols and from additional vehicle patrols, the space covered by each of the 43 rhinos, their spatial relationship with each other, and the natural relocation of individuals from one area to another in the Reserve over a four year period was noted. Adult females, in groups of two to four, were found to use similar areas while adult males seemed largely to be territorial. On becoming independent of their mothers, most young (juvenile or sub-adult) rhinos stayed in their natal area but formed an association with another independent young rhino for around three years. Prior to having their first calf, females appear to move away from the area they had been regularly using although this may only be to a short distance to an area adjacent to it. Immature males aged around 8 to 10 years are likely to move the longest distances in search of an area safe from territorial males.

Additional key words: dispersion, dispersal, home range, territory, territorial, natal range

Introduction

The Black Rhino Conservation Strategy and Management Plan, instituted by the Kenya Wildlife Service in 1993, contained policies to guide management for five years until the end of 1998. While the protection of black rhino populations was largely achieved through this management plan, the anticipated growth in their numbers was achieved to a lesser extent. This is because the remaining rhino populations were not, to a large extent, managed for maximum sustained growth through the application of active biological management principles (KWS 2003).

The guiding policy in biological management is that emphasis should be

placed on the biological management of each sub-population, and the meta-population as a whole, with the aim of understanding the factors which affect breeding performance and the taking of appropriate corrective measures when necessary. Biological management is defined (KWS 2003) as the management of rhino populations (primarily through adjusting rhino stocking densities, but also managing the densities of other browsers and habitat management) to maintain rapid, healthy population growth, and to minimise inbreeding and loss of genetic diversity (KWS 2003). Rhino removal and introduction decisions (to alter age and sex structure) are based mainly on a population's breeding performance, social behaviour, genetic relationships, the rhino density relative to an area's habitat carrying capacity, and vegetation conditions. Without accurate monitoring data – including ensuring the accurate identification of individuals in a population and correcting any inaccuracies so that the population demography on which decisions are made is correctly recorded - the informed biological management decisions cannot be made and progress towards meeting the population increase goal cannot be properly assessed. The monitoring of populations should be undertaken using recognised, individual identification techniques (KWS 2003).

Use of space

The distribution of animals in space at one moment in time, designated by Brown and Orians (1970) as dispersion, is the direct response of individuals to features of the environment and to the presence or absence of other individuals of the species. Black rhinos are a distant species where agonistic behaviour typically occurs when two or more conspecific individuals approach each other closer than a certain threshold distance

which has been termed individual distance. Social groups may show a phenomenon similar to individual distance where several individuals may live in home ranges which overlap greatly but normally remain separated by a certain distance and do not mix. However, individuals may form associations for a number of reasons including group defence against predators, group defence of a feeding area, the ability to exploit a resource not readily captured by solitary individuals and the ability to profit from the foraging success of other individuals by observing where they find food (Brown and Orians 1970).

Dispersal was defined by Howard (1960) as the movement of an animal from its natal range to where it will potentially breed. The impetus for dispersal is low in a low density population (relative to carrying capacity) because adequate resources are available within the natal range but once the population density reaches a certain point it becomes advantageous to leave the natal range in search of new habitat. Stenseth (1983) proposed the term non-adaptive dispersal where animals are forced from natal or established home ranges by social factors inherent in high density populations, for example dispersal of young males prevents excessive inbreeding and reduces competition for resources among family members. Therefore dispersal can occur at any density depending on the circumstances.

Home Range and Territory

Home range is the area over which an animal normally travels in pursuit of its routine activities (Jewell 1966). The size and shape of home ranges and hence the form of spatial relationships within a community is often a starting point for the analysis of a social system. Home range estimation is usually based on sighting data but sightings are a fragmentary glimpse of usage and it

is important to know the relationship between the real use of space by the individual and these glimpses.

Home ranges may overlap or there may be no or minimal overlap due typically to behaviour. In most cases this behaviour can be classified as territoriality which is different to exclusive occupancy (Brown and Orians 1970). Maher & Lott (1995) found that the most common definition of territoriality is a fixed, exclusive and defended area where the defence can be aggressive – attacking, chasing - or passive – scent marking, where such acts keep a rival out.

Researchers report a divergence of opinion as to whether black rhinos are territorial or not which may be explained by Estes (1999) who writes that black rhinos are solitary and territorial in some areas, semi-social and non-territorial in others. His “guess” for this was that black rhinos’ sociable tendencies were a response to crowding and open habitat. “Territorial” behaviour is of relevance to rhino population management because it sets a limit to the number of competing rhino (mainly males) that can co-exist in a given reserve (Adcock 2001). When these numbers are exceeded, rhino social pressures escalate (mainly among males but possibly also among females), leading to fighting, injuries and rhino deaths.

Methods and Materials

The 93 sq km fully enclosed Sweetwaters Game Reserve is situated on the Laikipia plateau in central Kenya. Identification photographs were obtained for all the Reserves black rhinos and each individual identified by the experienced rhino patrols. Histories of the rhinos including their date of birth were obtained from records. From this the population demography for the Sweetwaters rhinos was determined.

Between the beginning of June 2001 and the end of May 2005, the locations

of rhino sightings were collected by the daily rhino foot patrols using hand held GPS (Garmin 12) units. Rhinos were located by four rhino monitoring teams who patrol the game reserve daily. From 2003, the observations were supplemented by driven patrols.

For the purpose of reporting the data collected, the reserve was sectorised into 4 – West, North, Centre and South – see figure 1. The West sector was separated by the north/south running Ewaso Nyiro river while the other sectors approximately corresponded to the areas dominated by each of the three mature males.

Location fixes were mapped for each individual in Excel using a simple X,Y graph with the Y axis representing Northings and the X axis Eastings. An outline of the reserve was created from location fixes of each point where there was a change in the direction of the fence. Use of space areas for the study period were constructed by hand (Macdonald et al 1980) by joining up the outer points of the sighting data to form a convex polygon but with lone fixes over 1km from the nearest fix discounted as probable excursions. In order to monitor non-seasonal changes in the area/sector used by an individual, use of space areas were mapped for each 25 location fixes (based on Tatman et al 2000 for home range). Where a significant change in area occurred which was seen to be stable over a period of six months, for example a movement from one sector to another, the polygon was drawn up to the last location in the former area despite it being less than 25 fixes and a new polygon was started for the new area. Movements of rhinos from dependent to independent status was mapped, as above, by comparing the location fixes of the individual when it was with its mother, to when it had left.

Results

Table 1 shows the population demographics of the Sweetwaters rhinos. When compared to the information compiled by the Reserve, there was found to be one rhino (Mystery), a young female, which had not been previously identified as different. After further discussion, photography and assessment, a further two new rhinos (both called Nameless), a female with male dependent juvenile, were also identified.

The rhino population in Sweetwaters is not evenly distributed but in each sector there is a combination of males, females, sub-adults and calves. It can be seen from table 2 that the North sector represents 37% of the reserve space but is only inhabited by 19% of the population while a near similar proportion of the rhinos inhabit the centre section but utilizing only 18 % of the space of the reserve.

A Chi square goodness of fit test

comparing the actual distribution of rhinos in each sector of the reserve with that expected based on the proportion of the area of the reserve in each sector showed that the difference between the observed and expected distribution could easily have been due to chance ($\chi^2 = 2.58, P = 0.462$).

The names, sex and age groupings of the rhinos in each sector are shown in table 3 while Figures 2, 3 and 4 show the use of space by each of the rhinos in the reserve in the form of convex polygons drawn from the location fixes. Table 3 shows that in each of the sectors there are two to four breeding females with calves, single or pairs of sub-adults and a single breeding male except in the West sector where there are three males.

Figure 1:
The four sectors of Sweetwaters Game Reserve.

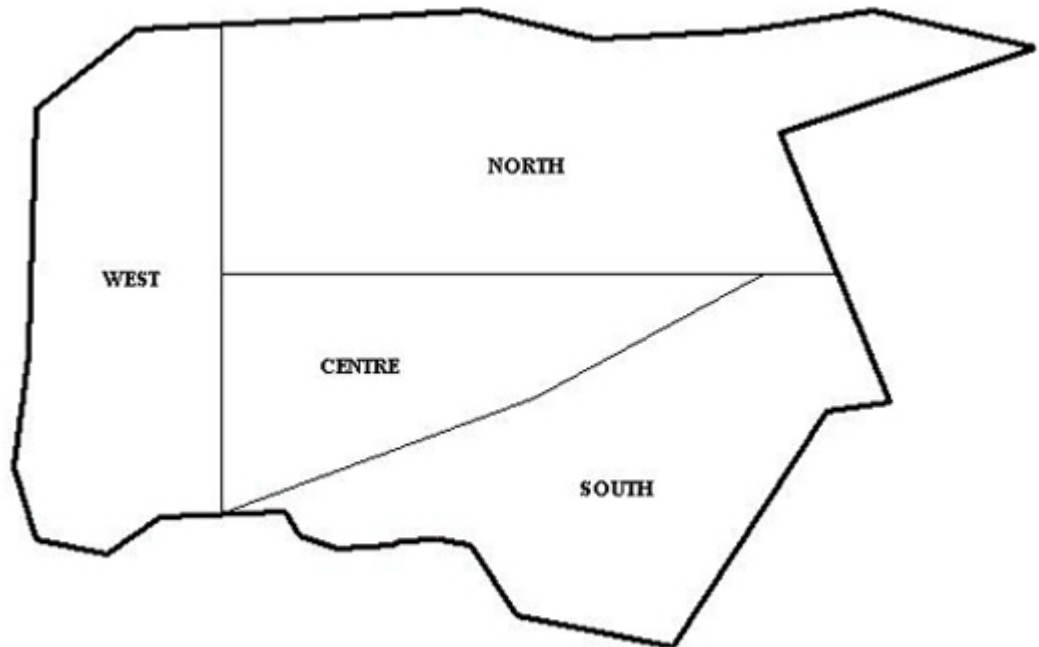


Table 1:

The Population Demographics of the Black Rhinos at Sweetwaters Game Reserve at the end of May 2005.

Adults				Dependent Sub-Adults	
Males	Females	Males	Females	Males	Females
Otoro	Kilo	Safari	Latili	Nameless	
Job	Saba	Uhuru	Manchester		Batian
Rodney	Carol	Maendeleo	Solo		
Jupiter	Shemsha	Sheria			
Kurkura	Tulivu	Juba			
Loita	Tamu	Benja			
Baraka	Mkora				
Hifadhi	Waya				
				Dependent Calves	
Tulia	Ishirini	Males	Females	Males	Females
Jama	Roberto		Cathy	Mkora calf	Berkley
			Jasho	Tulivu calf	Kilo calf
	Mystery		Lemoile	Tamu calf	Waya calf?

Adults are rhinos over 7 years of age, sub-adults are rhinos between 3.5 and 7 years of age, juveniles and calves are rhinos under 3.5 years of age. 'Independent' means no longer bonded to their mother and 'dependent' means bonded with their mother.

Females

Had Chema not been poached (an unnatural death) in October 2004, the spread of females across the four sectors would have been between 2 and 3.5 per sector, with 11 of the females being accompanied by calves or dependents.

with minimal overlap of the space used. In the West sector there were three mature males. Otoro and Jupiter shared the same area. Job occupied a small space in the south of the sector, away from the area normally covered by Otoro and Jupiter.

Calves

During the study period there were 13 calves born – 3 in the West, 2 in the North, 3 in the Centre and 5 in the South. Two of the adult breeding females in the North did not have new calves but maintained a dependent association with their juvenile offspring aged 5 years 4 months old and the other 3 year 10 months respectively.

Sub-Adults

Three sub-adult males were located in the West sector. Baraka, remained in a small area at the south of the area used by the adult male Jupiter. Jama only latterly moved to the West sector and more data are needed to record where he has settled. Tulia maintained a very small space in the north of the area originally sharing it with Waya (as a sub-adult pair) and the old male Job. While they have moved, Tulia has remained.

Males

In each of the North, Centre and South sectors there was a single mature male

Safari was the only sub-adult male in the Centre sector and had been tol-

Table 2:
Proportion of Reserve area by sector with proportion of rhino population in each sector.

SECTOR	% of Reserve	% of Rhinos
WEST	22	31
NORTH	37	19
CENTRE	18	21
SOUTH	23	29

Table 3:

The distribution of the Sweetwaters rhino population in each sector at the end of the study period, end May 2005.

Sector	Males	Females	Calves and Dependents	Sub Adult Males	Females	Pairs
WEST	Otoro	Tulivu	yes	Tulia	none	Uhuru & Cathy
	Jupiter	Waya	yes	Baraka		
	Job	Mystery		Jama		
NORTH	Kurkura	Saba	Millenium	Juba	none	none
		Shemsha	Batian			
		Mkora	yes			
		Carol 25%	Berkely 25%			
CENTRE	Rodney	Carol 50%	Berkely 50%	Safari	Roberto	none
		Nameless	yes			
		Kilo 25%	yes 25%			
		Chema	yes			
SOUTH	Loita	Kilo 75%	yes 75%	Hifadhi	Jasho	Solo & Sheria & Latilli
		Carol 25%	Berkely 25%			
		Tamu	yes		Lemoile	
		Ischerine	Benja			

Notes: Chema poached in late 2004 but estimated to have remained with new calf in the same area; calves denoted as "yes" have not been named; sub-adults include immature adults; some rhinos range between sectors and this is denoted by a % estimated from location fixes.

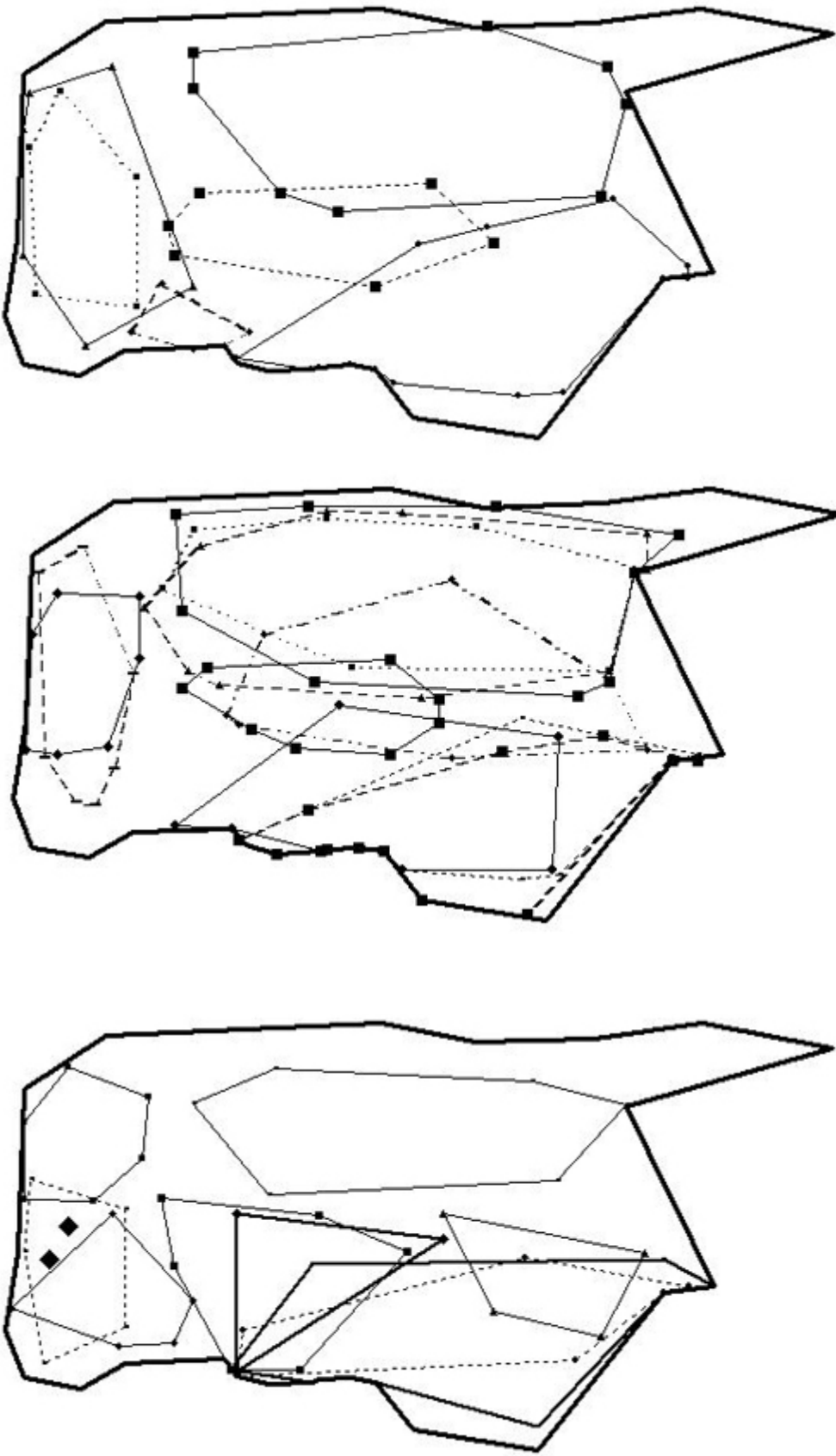


Figure 2-4:
 The use of space by adult male (top), adult female (middle), and immature/sub-adult rhinos (bottom) at Sweetwaters Game Reserve.

Table 4:
The age at independence and area inhabited of rhinos at Sweetwaters Game Reserve.

Males	Age in days	Area	Females	Age in days	Area
Baraka	1467	N	Ischerine	1004	A*
Hifadhi **	1219	N	Roberto **	1206	N
Tulia	1103	A	Latilli	992	N*
Jama **	1399	N	Solo	782	N
Safari	880	N	Cathy	798	N
Sheria	1004	A*	Jasho	941	N
Maendeleo	1052	N	Manchester	1125	N
Uhuru	863	N	Lemoile	981	N
Juba	944	N			
Benja	1050	N			
MEAN	1098			979	
	n = 10			n = 8	

N = remained in natal area; A = moved from natal area

* Ischerine moved from her natal area and paired with Safari; Sheria M moved to an area adjacent to his natal area and paired with Latilli who remained in her natal area but favoured the east part.

**While some individuals stayed in their natal area immediately after becoming independent, they moved out of the area later - Hifadhi moved when 5years 2 months, Roberto at 6 years 6 months and Jama at 6 years.

erated by the territorial male Rodney. Hifadhi moved latterly into the north east of the South sector but whether the territorial male Loita would tolerate its presence was not clear.

Sub-Adults also form pairs. There were no sub-adult pairs in the North sector as single sub-adults moved to other sectors and none in the Centre sector. In the West sector, the two successive calves of Tulivu, Uhuru (m) and Cathy (f) formed a pair as soon as the younger, Cathy, became independent. In the South sector there were two male/female pairs Maendeleo/Solo and Sheria/Latilli.

Changes in Dispersion of Individuals

Eleven rhinos changed their ranging areas crossing between sectors to do so. Seven of the eleven were sub-adults, two were females having their first calf and two were adults - an older female

with calf and an old male. The change in ranging area involved a movement of at least 3 kilometres from the centre of one area to the centre of the new area. There are no obvious patterns to the movements and only some have clear reasons for being made. For example, the male Job moved area by some 6 kilometres after a fight with another male.

Females - Pre First Calf Movements

Over a six month period, before and just after having her first calf Juba, Mkora moved around a large area covering the south, centre and north sectors, distancing around 7 kilometres between the two furthest sightings, finally settling in an area in the North sector where she also had a second calf. Mkora is the former calf of Kilo and was probably raised in the South sector.

Isherini, when a sub-adult, associated with the sub-adult male Safari, in an area to the south and east of the South

sector adjacent to that which she probably would have been brought up in by mother Tamu. Isherini had and raised her first calf Benja in this area where she also had a second calf in June 2005.

Waya, at 10 years old, calved in March 2005. In 1999, she moved around 5 kilometres from the centre sector as a sub adult with the younger sub adult male Tulia to a small area of around 1 square kilometre in the north of the West sector where they were both likely to have had experience when being brought up. In September 2002 when 7 years, 7 months old, Waya moved around 2 kilometres to an area of around 2 square kilometres in the centre of the West sector.

Roberto occupied the same area in the North sector as her mother Saba and new calf Millennium favouring first the west part and then moving some 3 kilometres to the east part. In May 2003 when at 6½ years old, approaching breeding age, she moved some 4 kilometres to the Centre/South sector where she stayed for 2 years. Roberto then moved some 5 kilometres and across a river to the West sector in May 2005. She had not had a first calf despite being just over 8½ years old.

The sub-adult female Latilli paired with the younger sub-adult male Sheria and remained in the South sector where she was raised by Kilo. The pair split up in May 2005 with Latilli aged 6 years 2 months subsequently moving around 3 kilometres to the north east of the south sector where she was seen in the company of the immature male Hifadhi.

Females – Other Movements

Carol, with new calf Solo – her third in the reserve, traversed a wide area of over 8 kilometres between July and December 2001 covering first the Centre sector then the North sector and then the South sector. Here they settled up until April 2003 when they moved some 2 kilometres into the Centre sector

and then another kilometre to south of the North sector. Carol had her new calf Berkely in August 2003 and was raising it in the area.

Males – Movements

Job moved around 6 kilometres from a small space in the north of the West sector to a small space in the south of the West sector. The other mature males maintained their territories throughout the study period.

Immature Adult Males – Pre Maturity Movements

Immature adult males are defined here as those over 7 years who have not laid down a territory.

Baraka moved around an area in the south Centre and South sectors then moved some 2 to 3 kms in May 2003 to settle mostly in the north of the Centre sector. In September 2003 he strayed into the South sector and was involved in a fight with the male Loita. He was 8 years, 10 months old. The following June there was a more extended fight with Loita and he moved some 6 kms to a gap in the fence in the West sector and out of the reserve but was soon herded back in. He wandered around the West and deep South sectors travelling 5 km distances on occasion before settling in a small area in the south of the West sector near to human habitation.

Hifadhi moved around 2 kms from the South sector to the Centre sector in November 2001 when 5 years, 2 months old where he stayed for 18 months then moved about 2 kms to the North sector in May 2003. He remained there until April 2005, when aged 8 years, 8 months moved some 3 kms into the east of the South sector.

Jama lived in an area in the North sector moving some 3 kms in October 2003, when he was 6 years old, mainly to the Centre sector but was often found

over a wide area. In May 2005 at 7 years 7 months Jama crossed 4 kms to the West sector.

Juba remained in the North sector but was less than four years old and relatively newly independent and often seen in association with others (81% of Juba sightings) especially its mother and new calf (60% of Juba sightings).

Tulia, since moving with Waya in 1999, stayed in a very small area in the north of the West sector.

Males and Females - Dependence to Independence

Most rhinos on becoming independent remained in their natal range (the home range where they were brought up by their mother). Dependence is defined as living from birth with its mother up to Independence when the mother has a new calf or the association is broken for another reason.

As can be seen in Table 4, of the 18 individuals that became independent, only 3 moved out of their natal area into a new range where they had not had previous experience. The table also summarises the age at which rhinos moved from dependent to independent which for the 18 rhinos averaged 1045 days. Modelling time to independence using the Weibull distribution showed that the 119 day difference between males and females was significant ($P = 0.031$).

Discussion

The positive outcome of identifying three new rhinos in the reserve is evidence of the importance of ensuring judges of the photographs have the ability to determine different identities from photographs (see Patton 2007) and of the need to regularly and independently verify the identity of sightings made by patrols using photographs where possible. Without the benefit of

photo-identification, most of the Reserves' previous estimations of population performance were inaccurate which might have led to incorrect management decisions being made.

Use of space

During the study period, the sighting objective of the rhino patrols at Sweetwaters was to find every rhino at least once per month and record GPS location fixes. Some rhinos were harder to find than others and some presented greater danger as they were more likely to attack humans. As such the number of location fixes obtained over the same period differs markedly between rhinos. For example in the West sector there were 213 for the male Job but only 72 for the male Jupiter. This discrepancy may have affected the ability to determine short term changes in the use of space but is unlikely to have resulted in long term/permanent events such as a change in range area being missed. Sightings were mainly recorded in the period between 8am and 12pm and never after dark. It is therefore possible that some individuals moved between sectors at night returning to their "day sector" before the patrols began. This could mean that the use of space is underestimated.

The uneven distribution of rhinos in each sector – the North sector comprises 37% of the reserve but only 19% of the population resides there with corresponding large ranging areas (and relatively poor breeding record of two of the females) – could be due to poor quality or quantity of food resource as suggested by Adcock et al. (1998) who state that the size and shape of rhino ranges is determined by the quality, quantity and distribution of food and water resources. More recent habitat evaluation further supports this (Adcock pers.comm 2006).

Adult females were found in "clus-

ters" similar to that reported by Lent and Fike (2003) and, as they found and as shown in figure 3, there was little overlap between the space used by each cluster. There was no known genetic relationship between the cluster of breeding females in any of the sectors. The only relationships apparent was between mother and calf and sometimes their former calf or calves for example, in the west sector the breeding female Tulivu shared the sector with three former calves – Tulia, Uhuru and Cathy.

Females moved away from their natal range into another sector to establish a home range in which to start breeding and raising their young usually remaining in the new home range to have subsequent calves. Similar movement was observed with a sub-adult female coming to breeding age (around 7 years old) and could be a possible sign of establishing a home range in which to have her first calf. No references could be found that identified this behaviour which could be a useful indicator of impending calving. The calves stayed with their mother becoming independent a few weeks before the mother gave birth to a new calf. In most cases newly independent juveniles/sub-adults stayed in their natal range forming a pair with another juvenile/sub-adult and remaining together for around 3+ years. At this time the males, usually around 6+ years, become solitary while the females may join up to form a new pair.

The minimal overlap of the space used by the adult males in the North, Centre and South sectors suggests they are territorial, chasing off maturing males of around 8+ years old. While the current territories were fixed for the duration of the study, they may be subject to change over a longer period. In the West sector two adult males shared the same area seemingly tolerant of each other despite both being aggressive towards human and (historically) to other rhinos. It is possible that one may not

have been breeding. A third, old, male had been attacked by one or both of them (independently) and occupied a small space close to human habitation on the periphery of the reserve indicating that it has passed breeding age as suggested by Adcock (1998). During the study period, an immature male was also in a fight and moved to a small area close to human habitation. Despite their fear of humans, the proximity of humans may act as protection to vulnerable rhinos as most rhinos avoid areas close to human activity.

Wronski (2005) studying male bushbuck (*Tragelaphus scriptus*) found that, with increasing age, sub-adult males challenge male territory holders and replace them. The maturing sub-adult males (young adults) often focused on a particular territory holder. This behaviour may have been reflected in the behaviour of two sub-adult/immature male rhinos in relation to an adult but small sized male. One moved into the territory and lost a fight when 8 years, 10 months and again some 9 months later which led him to leave suggesting it was not powerful enough to overcome the mature male. However a year later the other, at 8 years 8 months moved into the territory and was subsequently recorded by rhino patrols mating with a female (who had left her new calf alone and walked over 2 kms to mate) and also accompanying a maturing female. Although there was no observation of a fight, the older male was seen to have lost around 20% of its front horn and was sighted regularly in aggregation with two sub-adults having seemingly retreated to the periphery of his former territory. As can be seen in figure 2 there was no space available for a maturing male to establish a new territory, so the younger animal was probably forced to fight for the right to mate. Although more data are required to confirm whether the territory has been taken over, if so, it would suggest that there

may be a limit in the enclosed reserve as to the number of dominant males that can be carried. This would agree with observations made in Pilansberg National Park, South Africa, Adcock et al. (1998) and Adcock (2001).

Population management

Identification of individuals is essential for informing practical management. Following a KWS managed carrying capacity study across all reserves in Kenya, an estimate of 48 individuals was made for Sweetwaters (Okita, KWS pers. comm 2006). Biological management guidelines dictate that rhino populations should be maximised at 75% of carrying capacity (KWS 2003) giving 36 individuals. This requires a reduction of the Sweetwaters rhino population and at least 7 individuals could be translocated to other rhino areas. The understanding of movements of the rhinos at Sweetwaters gained from this study can be used to inform the selection of candidates for removal. For example, sub-adult and immature males would be expected to continue to move around the reserve and when mature enough challenge territorial males for the right to breed. Part of the existing fence is also going to be removed to extend the area available to the rhinos; some of these younger males would be expected to disperse into the new area and establish territories without the need of costly and stressful translocation.

References

- Adcock, K., Hansen, H. & Lindemann, H. 1998 Lessons from the introduced black rhino population in Pilansberg National Park. *Pachyderm* 26, 40-51
- Adcock, K. 2001 RMG Black Rhino Carrying Capacity Model version 1.0: User's Guide (Evaluation Draft) Unpublished.
- Brown, J. L. and Orians, G. H. (1970) Spacing patterns in mobile animals. *Annual Review of Ecology and Systematics*, 239-262
- Estes, R. D. (1999) *The safari companion: a guide to watching African mammals*. Vermont: Chelsea Green Publishing Company.
- Howard, W.E (1960) Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist* 63 (1) 152-161
- Jewell P. A. (1966) The concept of home range in mammals. *Symposium of the Zoological Society of London* 18, 85-109
- Kenya Wildlife Service Report (2003) Conservation and Management Strategy for the Black Rhino (*Diceros bicornis michaeli*) in Kenya (2001-2005) Revised March 2003, Kenya Wildlife Service
- Lent, P. C & Fike, B (2003) Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. *South African Journal of Wildlife Research* 33 (2): 109-118
- Macdonald, D. W., Ball, F. G. & Hough, N. G. (1980) The evaluation of home range size and configuration using radio tracking data. In: eds Amlaner, C. J. & Macdonald, D. W. *Handbook on Biotelemetry and Radio Tracking*: Pergamon Press Ltd, Oxford.
- Patton, F. J. (2007) The use of individual identification in the conservation management of black rhinoceros (*Diceros bicornis*). PhD thesis, Manchester Metropolitan University, United Kingdom. 218 p. Unpublished.
- Stenseth, N. C. (1983) Causes and consequences of dispersal in small mammals. In: eds Swingland I.R & Greenwood, P. J. *The ecology of animal movement*: Clarendon Press, Oxford 63-101
- Tatman, S.C., Stevens-Wood, B. & Smith V.B.T. (2000) Ranging behaviour and habitat usage in black rhinoceros, *Diceros bicornis*, in a Kenyan sanctuary. *African Journal of Ecology*, 38, 163-172
- Wronski, T. (2005) Home-range overlap and spatial organization as indicators for territoriality among male bushbuck (*Tragelaphus scriptus*) *Journal of Zoology* 266, 227-235