Home Range and Movement Behaviour of the African savanna Elephant (*Loxodonta africana africana L.*) in the Nimule National Park Landscape

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ABSTRACT

Savanna elephants require large areas to meet their spatio-temporal needs. Yet, current conservation strategies in South Sudan focus on securing numbers and habitats within protected areas. Using a GPS collar, the home ranges and movement behaviour of an adult male elephant were determined in Nimule National Park using the Fixed Kernel method and its speed of movement analyzed using the Spatial Analyst extension in Arch GIS. The bull's home range was 167.3 km² with over 74% of the range occurring outside the park. Though 53% of the locations were recorded inside the park, the bull's core area under protection covered just 17.01 km². The elephant's wet and dry season home ranges were not significantly different, spatially explicit and were not influenced by rainfall. It moved at speeds ranging from 0.2 - 2.1 km h⁻¹ with the highest monthly average speed of 0.4 km h⁻¹ attained at the onset of the rainy season in March and April. The bull moved faster during the dry season $(0.313 \pm 0.213 \text{ km hr}^{-1})$ than the wet season $(0.304 \pm 0.271 \text{ km hr}^{-1})$. Movements in the different land use types were significantly different with the bull moving faster in the non-protected areas at 0.363 ± 0.243 km h⁻¹. Streaking behaviour was rare with 98.2% of the bulls' movement pattern associated with foraging and shifting between foraging sites. Presence of a large proportion of the elephant's range outside the park and the low movement speed in the landscape suggested that fragmentation of the landscape was not a hindrance to elephant movement if they are actively protected by the Uganda Wildlife Authority. A transboundary landscape management strategy could improve the viability of the population in the landscape.

Keywords: Home Range, Speed, Elephant, Conservation, Nimule National Park, Landscape.

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INTRODUCTION

African savanna elephants have characteristics that influence their method of management. To maintain viable populations, elephants require large areas to meet their spatiotemporal needs for water, food and land (Armbruster and Lande 1999; Leggett 2006; Harris *et al.*, 2008; Owen-Smith *et al.*, 2010). Knowledge of factors that determine movements and habitat selection enhance our understanding of how factors such as habitat fragmentation, human presence, seasonality and climate change may influence elephant home range and movement behaviour (Douglas-Hamilton *et al.*, 2005; Harris *et al.*, 2008; Graham *et al.*, 2009; Ngene *et al.*, 2009; Grenados *et al.*, 2012). Other studies showed that the spatial and temporal distribution of resources across landscapes created heterogeneity that dictated the movement of animals based on their biological needs in space and time (Mitchell & Powel 2004; Young *et al.*, 2009; Owen-Smith *et al.*, 2010). While our understanding of elephant movement and home range behaviour has improved, the conservation of the species requires site specific collation of information to inform management decisions. In South Sudan, despite the reportedly large population of elephant and range in the 1970s and 1980s (Said *et al.*, 1995; Blanc *et al.*, 2007), knowledge of the ecology of the species in the network of protected areas is limited.

One of the protected areas in which South Sudan's elephants live is Nimule National Park (NNP). Though the park is one of the oldest in the country, very little information is available to managers and decision makers at all levels on the park's elephant. Available information on the species is

fragmented, inaccessible and not suitable for integration into decision-making, planning and management of the population in the landscape. Like many elephant populations in Africa, the NNP elephant population lives in a small island of suitable habitat surrounded by a sea of agricultural and human settlements (Blanc *et al.* 2007; Stephenson and Ntiamoa-Baidu, 2010). In such insular habitats, it is reported that about 80% of elephant range lies in the unprotected human dominated landscape (Douglas-Hamilton *et al.*, 2005). This occurrence has been linked to increased competition for natural habitats and conflicts between elephants and humans (Graham *et al.*, 2010; Grenados *et al.*, 2012). With the reported increase in human population and associated development activities in the landscape (William *et al.*, 2002), conflicts are inevitable. Unfortunately, developing an effective conservation strategy for the landscape is difficult because there is no information on movement and home range behavior for the population. Yet elephants are known to travel beyond the park's boundaries where their activities conflict with human activities and interests. Being a mega species in the landscape, the Nimule elephant population has potential for use as a target species for conservation strategies such as the "landscape species approach" (Stephenson *et al.*, 2010). Therefore, to serve that purpose, this study on the spatio-temporal home ranges and movement behaviours was undertaken.

This study therefore, reported on the movement and home range behavior of a satellite-tagged male elephant in the Nimule National Park landscape. It ascertained whether the collared bull displayed a notable preference for specific land use types in the landscape in terms of rate of occupancy and assessed whether land use preferences were reflected by variation in the bull's daily, monthly, seasonal and annual home ranges and movement characteristics as measured by the size of home ranges and speed of displacement. The findings were interpreted based on foraging theory and risk aversion hypothesis (Graham *et al.*, 2009). Such information is essential for the development of effective conservation and management strategies when landscape management scenarios are envisaged for the park as possible solutions to range limitation for the species and its sustainable management.

MATERIALS AND METHODS

Study area

The study area, located at the Uganda-South Sudan boarder, covers the 410 km 2 Nimule National Park (31° 48′ – 32° 2′ E and 3° 19′ – 3° 35′ N) and the surrounding communal lands to the east, north and south of the park (Fig. 1).

Topographically, rugged hills and water courses interspersed within the landscape form the natural boundaries of the park whose elevation ranges from 500-1200 metres above sea level. The White Nile and its opposite flowing tributaries, Anyama and Kayo respectively, mark the eastern, southern and northern boundaries of the park. Along the western boundary of the park run the Illungu hills that cut off the park from Uganda. The African savanna elephant is the major biodiversity component of the landscape that survived three wars. It is known to expand its foraging to areas outside the park's boundary in Adjumani District in Uganda and Magwi County in South Sudan. An aerial survey of the park reported a total count of 69 elephants in 2008 living in four herds, one of which is a bachelor herd of 10 individuals (Fay *et al.*, 2008).

Data collection and Analysis

In April 2010, one adult male elephant belonging to a bachelor herd of 10 individuals that split and regrouped from time to time in what is termed as fission-fusion (Archie *et al.*, 2006) was collared by the Uganda Wildlife Authority and code named U21. The collaring followed standard procedures of Douglas-Hamilton (1998). The collar was initially set to download six GPS fixes per day but was reprogrammed in May 2010 to download fixes every eight hours. Location data on the elephant for a-15-month period, from April 28th 2010 to July 8th 2011, was sourced from Uganda Wildlife Authority (UWA) in Adjumani for this study. The excel spreadsheets location data were transformed into GIS format in ArcGIS 9.2 software (Environmental Systems Research Institute, 2007) and analyzed using Spatial Analyst and Tracking Analyst extensions.

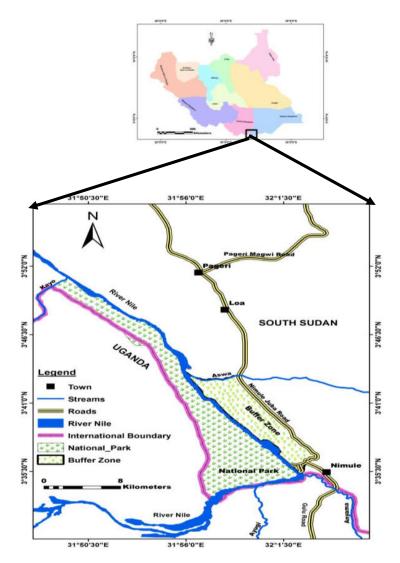


Figure 1. Map of Nimule National Park showing location of the study area.

To show the intensity of spatial use, a utilization distribution (UD) technique (Harris *et al.*, 1990) was used to estimate and map elephant home range in the landscape. The Fixed Kernel (FK) was chosen over the Adaptive Kernel (AD) method because it has proven to be less biased and has a better surface fit (Seaman *et al.*, 1999). It was also reported to be more reliable for estimating the outer contours and centres of activity in home ranges (Kernohan *et al.*, 2001). Kernel estimates of home range were based on the 95% and 50% isopleths and defined as "95% kernel" and "50% kernel" respectively. The 95% kernel was used to represent the elephant's general home range size and the 50% kernel represented the area more frequently used by the elephant known in the literature as the core area (Douglas-Hamilton *et al.*, 2005). All home range estimates were calculated using the Hawths extension in ArcGIS 9.2. The programme was allowed to automatically select the appropriate smoothing parameters.

To assess movement behaviour, the landscape was categorized into protected (park and buffer zone) and non-protected (Adjumani District) data sets. Seasons were also categorized into dry (November – March) and wet (April – October) data sets. For every 24 hours, location data were categorized into day and night data sets after filtering out overlapping location intervals. As an index of movement, the speed, based on the linear distance between locations and time spent to cover those distances were calculated using the Spatial Analyst Distance to Point extension in Arc GIS 9.2 software (ESRI, 2007).

The location data sets were filtered for erroneous fixes through visual inspection. Since tracking data are known to exhibit homogeneity of variances and are generally not normally distributed, the

data sets were log-transformed to ensure heterogeneity of variances and normal distribution in the sets. The log-transformed data sets were then analyzed by parametric t-tests for independence and comparison between groups. Where normality and heterogeneity of variances could not be achieved through log-transformation, a Mann-Whitney U test and Wilcoxon-signed test were used to compare values between two groups and conditions respectively. The observed proportional use of the different land use categories was compared against expected proportional use using Chi squared goodness of fit test (X^2) . All claims of significance were based on a 95% confidence level.

RESULTS

A total of 1234 fixes were recorded for the collared bull elephant between April 2010 and July 2011 (Table 1). Though over half of the elephant's overall locations occurred inside the park (55.3%), occupancy of the land use types as represented by the number of days spent in each type, did not differ significantly (Wald $X^2 = 1.643$; df = 1; P = 0.200) and was not influenced by seasonal differences in occupancy (Wald $X^2 = 0.040$; df = 1; P = 0.842). Overall, the elephant showed nomadic movement between the park and the non-protected component of the landscape, with a majority of the transboundary movements occurring in the wet season and exclusively at night. Based on the 100% minimum convex polyon (MCP) method, the elephant's home range size was estimated to be 334.5 km² with a larger part of the range occurring outside the park (Figure. 2). Estimates of home range based on the FK fitted tightly with the location data. Based on the FK, elephant used an area that covered 167.3 km² on both sides of the border with the most used part of the range covering just 35.9 km². Much of the elephant's range (125.07 km²) occurred outside the park in Adjumani District. Within the park, the bull's home range fitted tightly to both sides of the Nile River covering 42.22 km² with the most used core area covering just 17.19 km². The bull's monthly area of occupancy averaged 94.35±8.74 km² with the core area averaging 22.32±8.47 km² (Table 1). The bull's dry season (Figure. 3) and wet season (Figure.4) core area (F=2.645, df=1, p=0.135) and home ranges (F=3.482, df=1, p=0.091) were not significantly different and overlapped for most of the tracking period. Although the bull's home ranges increased with increasing rainfall (Fig. 5), the correlation was not significant (r = 0.291; p = 0.359).

Table 1. Monthly movement pattern of a collared elephant in Nimule National Park landscape.

Month	Number	Number/ Border	Mean Speed	Distance/Day	Total Distance
	of Fixes	Crossing	$(kmhr^{-1}) \pm SD$	(km)	(km)
January	89	0	0.278±0.203	6.6	201.9
February	82	4	0.296 ± 0.200	7.1	194.8
March	91	4	0.382 ± 0.262	9.2	278.3
April	91	3	0.466±0.286	11.2	341.2
May	99	0	0.212±0.162	5.3	163.8
June	85	0	0.196±0.197	4.7	134.6
July	84	3	0.306±0.250	7.1	214.5
August	83	2	0.360 ± 0.250	8.4	147.2
September	83	2	0.307±0.345	7.3	206.3
October	83	4	0.286±0.267	6.9	189.6
November	63	0	0.260 ± 0.147	6.2	144.7
December	87	1	0.324 ± 0.203	7.5	234.8

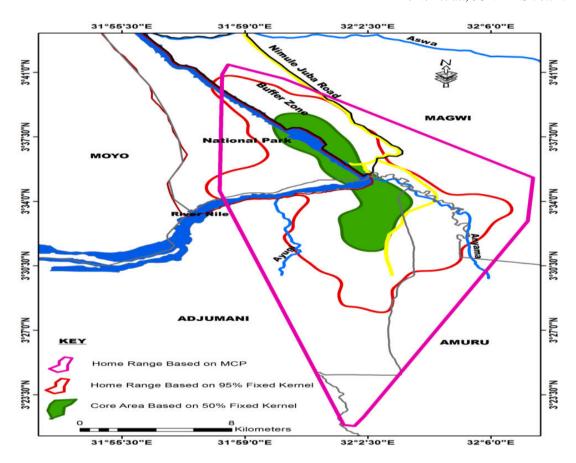


Figure 2. Home ranges of a bachelor herd based on Minimum Convex Polygon, 95% Fixed Kernel and 50% Fixed Kernel in the Nimule National Park landscape.

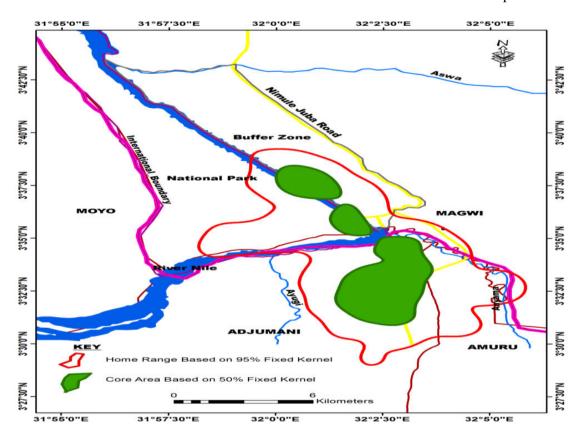


Figure 3. Dry season home range sizes of a bachelor herd in Nimule National Park landscape

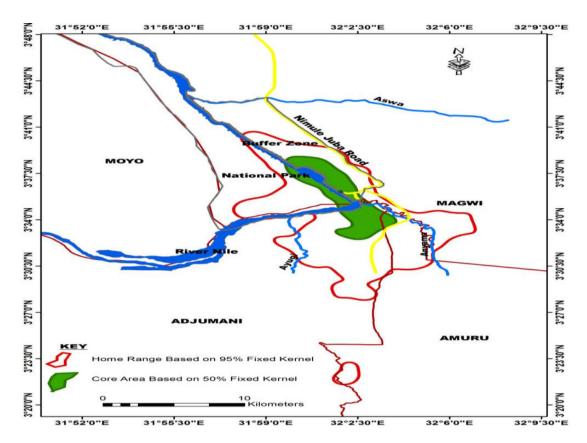


Figure 4. Wet season home range sizes of a bachelor herd in Nimule National Park landscape

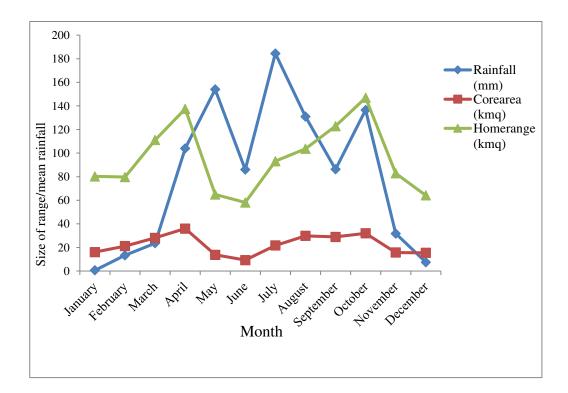


Figure 5. Monthly space use by a collared elephant in relation to rainfall in Nimule National Park landscape.

The movement pattern of the collared male elephant as measured by its speed of movement differed significantly between the land use types with the elephant moving fastest in the non-protected areas

than in the park (Mann-Whitney U = 1.272E5; p < 0.001). On average, the elephant covered 6.4 km per day in the park compared to the non-protected area where its daily movement rate averaged 8.3 km per day (Table 2). The elephant's speed of movement differed significantly between its diurnal and nocturnal movements (Mann-Whitney U = 9.049E4; p < 0.05) with the elephant moving faster by night at an average speed of 0.32km h^{-1} than by day when its mean movement rate was 0.27 km h^{-1} . The bull's wet and dry season movement speed were also different (Mann-Whitney U = 1.131E5; p < 0.05) with the bull moving faster during the wet season than the dry season (Table 2). In this analysis, movements with speeds greater than 1.0 kmh⁻¹ were rare and when attained, such movements were associated with travel between the protected and non-protected area with the bull covering the longest distance which averaged 11.2 km in April (Table 2). Although the bull's speed of movement had no significant correlation with the monthly amount of rainfall in the landscape (r = 0.126; p = 0.697), the bull responded to increased rainfall by reducing its speed of transversing the landscape.

Table 2. Mean speed of a collared elephant in Nimule National Park landscape

Location/Time	Number	Number/Border	Mean Speed	Distance/Day	Total Distance	Difference
	of Fixes	Crossing	$(kmhr^{-1}) \pm SD$	(km)	(km)	
Protected Park	672	11	0.263±0.09	6.3	1430.0	0.001
Non-Protected*	543	12	0.362 ± 0.10	8.7	1610.3	0.001
Wet season	812	14	0.509±0.010	7.3	1993.8	0.05
Dry season	412	9	0.539±0.014	7.5	1.053.1	0.05
Day	414	3	0.263±0.096	6.4	1,221.7	0.05
Night	484	20	0.317±0.012	7.7	8,663.9	0.05

^{*} Adjumani

DISCUSSION

The size of an elephant's home range gives an indication of the availability of essential resources such as food, water and shelter (Osborn, 2004) within the limits set by human disturbance (Graham et al., 2009). Since essential resources are not uniformly distributed in the landscape, large mammals like elephants tend to seek and spend more time in areas that provide adequate daily requirements. In this study, those resources appeared not to be adequate in the park prompting the collared elephant to extend its foraging beyond the protected area boundary. The importance of areas outside protected areas to elephants has been recognized and it is believed that 80% of elephant's range occurs outside protected areas (Douglas-Hamilton et al., 2005; Blanc et al., 2007). Furthermore, the location and sizes of elephant home ranges in a landscape are known to be influenced by heterogeneity of feeding patches (Grainger et al., 2005; Murwira & Skidmore 2005; De Beer & van Aarde 2008). From the distribution of location points plotted on the map of the study area, it appeared that such heterogeneous patches are associated with the River Nile and its tributaries, Anyama and Ayugi, and mostly occur outside the park prompting periodic movement between the two land use types. In this study, 75% of the collared elephant's home range occurred outside the park where it spent 43% of the year during the tracking period (Table 1).

The home range size of the collared bull of 334.5 km² estimated using the minimum convex polygon (MCP) is misleading because the area incorporates extensive parts of Nimule town and Gordon Hill where the elephant was never located in. It is known that the MCP method tends to inflate home range sizes due to inclusion of outliers in the calculation of home ranges (Powell, 2000; Osborn, 2004). Due to its wide application in estimating home range of elephants, it is reported here for purposes of comparison with other studies. In this study, the interpretation of the collared bull's home range was based on the 95% FK, which from the plot on the map of the study, fitted the location data well (Fig 2). The bull's home range of 167.3 km² was comparable with home ranges of male elephants reported in other studies (De Villiers & Kok 1997; Douglas-Hamilton *et al.*, 2005; Shannon *et al.*, 2006). For free ranging elephants, there is compelling evidence that suggests that bulls have larger home ranges than females (De Villiers & Kok 1997; Stokke & Du Toit 2002). This has been attributed

to the fact that female herds stay close to water and move shorter distances on daily and seasonal basis because of their need for drinking water and caring for neonates (Wittemyer *et al.* 2007). Judging from the size and shape of the bull's home range it is safe to conclude that the size of range used by the bull in the landscape represented the range used by the entire population.

Seasonality in elephant use of space was not reflected in this study. Throughout the tracking period, the bull's wet and dry season home ranges were not explicit and rainfall had no influence on the bull's pattern of space use. This finding contrasts sharply with earlier reports on African savanna elephant seasonal use of space (Thouless, 1995; Leggett, 2006). It is believed that elephants within the same locality travel long distances during the wet than the dry season because food resources are more abundant and water is more widely distributed during the wet season (Wittemyer *et al.*, 2007; Young *et al.*, 2009; Owen-Smith *et al.*, 2010). In the Nimule National Park landscape, water is available throughout the year in the River Nile and the bull appeared to be tethered to the river during the wet and dry season with no sign of variation in it's wet (Fig. 3) and dry (Figure. 4) season core areas.

Available information on elephant locomotion have previously centred on locomotion kinematics (Hutchison *et al.*, 2003; Hutchison *et al.*, 2006), the application of which in habitat studies may be limited. For instance, the idea of maximum speed may not be very useful because near maximum speeds can only be attained under experimental conditions or when an individual is disturbed or when an aggressed individual charges (Hutchinson *et al.*, 2006). Under such conditions, an elephant can reach a near maximum speed of 25 km hr⁻¹ (Hutchinson *et al.*, 2006). In this study, though the collared bull varied its speed of movement in response to the variable levels of bio-physical and anthropogenic attributes of the landscape, it could only attain a maximum speed of 2.1 km hr⁻¹ when it crossed into the Park from Uganda on September 10th 2010. With such a low maximum, the idea of maximum speed cannot be used to interpret the elephant's movement rate in response to landscape heterogeneity and anthropogenic disturbance in this study.

Therefore, to understand the elephant's use of space in the landscape, its speed of movement was interpreted in the context of foraging theory. Theories of habitat selection and optimal foraging predict that animals will select habitats that offer higher energy returns in order to enhance their fitness within a shorter space of time (Chalfoun & Martin, 2007). For elephants, it has been shown that different speeds of movement are associated with different types of behaviour and spatial distribution of hourly speed can be used as a guide for an animal's activities in the area (Douglas-Hamilton et al., 2005). Accordingly, speeds below 0.2 km hr⁻¹ are associated with foraging patch which include feeding, resting and comfort behaviour, whereas speeds greater than 0.2 km hr⁻¹ but less than 1.0 km hr⁻¹ are associated with activities within patches as well as gentle shifts between foraging patches (Hutchinson et al., 2006). Elephants traveling at speeds greater than 1.0 km hr⁻¹ usually do not forage but move between foraging patches and drinking water sources or are travelling along corridors linking foraging sites (Douglas-Hamilton et al., 2005). Based on the above segmentation of movement behaviour, 98.2% of the bull's movement pattern could be interpreted as being associated with foraging and gentle shifting between foraging patches. Slow movements associated with foraging alone were more common in the park than in the non-protected area where 67.9% of hourly speeds of movement were greater than 0.2 km hr⁻¹. For the entire tracking period, hourly movement speeds greater than 1.0 km hr⁻¹ were rare (1.8%) and were found to be associated with transboundary movements between the two land use types. Studies on elephant movement behaviour have shown that elephants have an awareness of risk associated with protected and non-protected areas and often spend more time in protected than non-protected areas (Douglas-Hamilton et al., 2005; Galanti et al., 2006; Graham et al., 2009). Nocturnal foraging and transversing the human dominated landscape at higher velocities than normal have been reported to be some of the tactics that male elephants employ (Graham et al., 2009). In this study the bull appeared to have followed these risk aversion tactics by spending a proportionally larger part of the year inside the park and showed behavioural plasticity in areas outside the park.

This study provided useful information for developing an elephant conservation strategy for the park and the non-protected elephant range in Adjumani District. Since the home ranges of the bull in the park and Adjumani were not spatially explicit and much of the movements in the landscape were associated with foraging, fragmentation may not be a hindrance in the landscape. However, the

presence of a large proportion of the elephant's range outside the Park suggested that fragmentation of the landscape was not a hindrance to elephant movement if they are actively protected by law. With rising rural population and increased fragmentation of the range due to agriculture and infrastructure development in the landscape, loss of elephant habitat outside the park will reduce the capacity of the area to sustain the elephant population. While the elephant's home ranges inside the park remains secure, their small sizes and potential reduction when the Fulla Falls hydro power dam construction gets underway limits the viability of the elephant population in the landscape. To maintain the use of the elephant's range beyond the park's boundary, some form of coexistence between elephants and people in the landscape must be established. A landscape management approach that incorporates conservation goals and human livelihood needs could ensure the long term viability of the elephant population in the landscape.

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REFERENCES

- Archie, E. A., Morrison, T. A., Foley, C. A. H., Moss, C. J. and Alberts, S. C. (2006) Dominance rank relationship amongst wild female African elephants. *Animal Behaviour*, 71: 117-127.
- **Armbruster, P. and Lande, R. (1993).** A population viability analysis for elephant: how big should reserves be? *Conservation Biology,* **7:** 602-610
- Blanc, J. J., Barnes, R. F. W., Craig, C.G., Douglas-Hamilton, I., Dublin, H. T., Hart J. A. and Thouless, C. R. (2007). *African Elephant Status Report* 2006: an update from the African Elephant Database. Occasional Paper Series of the IUCN Species Survival Commission, No. 33. Gland, Switzerland: IUCN/SSC African Elephant Specialist Group. IUCN
- **Chalfoun, A. D. and Martin, T. (2007).** Assessment of habitat preference and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology,* **44**: 383-392.
- **De Beer, Y. and van Aarde, R. J. (2008).** Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid Environments*, **72**: 2017-2025.
- **De Villiers, P. A. and Kok, O. B. (1997).** Home range, association and related aspects of elephants in the eastern Transvaal Lowveld. *African Journal of Ecology*, **35**: 221-234.
- **Douglas-Hamilton, I. (1998).** Tracking elephants using GPS technology. *Pachyderm*, **25**: 81-92.
- **Douglas-Hamilton, I., Krink, T. and Vollrath, F. (2005).** Movement and corridors of African elephants in relation to protected areas. *Naturwissenchaften*, **92**: 158-163.
- Fay, J. M., Elkan, P., Morjan, M. and Grossmann, F., (2008). Aerial Survey of wildlife, livestock and human activities in and around existing and proposed protected areas of Southern Sudan, dry season 2007. WCS report, South Sudan Programme
- Galanti, V., Preatoni, D., Martinoli, A., Wauters, L. A. and Tosi, G. (2006). Space and habitat use of the African elephant in the Tarangire-Manyara ecosystem, Tanzania: implications for conservation. *Mammalian Biology*, 71: 99-114.

- Graham, M. D., Douglas-Hamilton, I., Adams, W. M. and Lee, P. C. (2009). The movement of African elephants in human-dominated land-use mosaic. *Animal Conservation*, 12: 445-455.
- **Grainger, M., van Aarde, R. J. and Whyte, I. J. (2005).** Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *African Journal of Ecology,* **43**: 369-375.
- Grenados, A., Weladji, R. B. and Loomis, M. R. (2012). Movement and occurrence of two elephant herds in a human-dominated landscape, the Bénoué Wildlife Conservation Area, Cameroon. *Tropical Conservation Science*, **5**: 150-162.
- Harris, S., Cresswell, W. J., Forde, P.G., Trewhella, W. J., Woollard, T. and Wray, S. (1990). Home-range analysis using radio-tracking data a review of problems and techniques particularly as applied to mammals. *Mammal Review*, **20**: 97-123.
- Harris, G. M., Russel, G. M. van Aarde, R. J. and Pimm, S.L. (2008). Rules of habitat use by elephants *Loxodonta africa* in southern Africa: insight for regional management. *Oryx*, **42**: 66-75.
- Huchinson, J. R., Famini, D., Lair, R. and Kram, R. (2003). Are fast-moving elephants really running? *Nature*, 422: 493-494.
- Huchinson, J. R., Schwerda, D., Famini, D. J., Dale, R. H. I., Fisher, M. S. and Kram, R. (2006). The locomotor kinetics of Asian and African elephant: changes with speed and size. *Journal of Experimental Biology*, **209**: 3812-3827.
- **Leggett, K.** (2006). Home range and seasonal movement of elephants in the Kunene Region, northern Namibia. *African Zoology,* 41: 17-36.
- Kernohan, B. J., Gitzen, R. A. and Millspaugh, J. J. (2001). *Analysis of animal space use and movements*. In radio tracking and animal populations. Marzluff, J.M., Millspaugh, J.J., Harvitz, P. & Handcock, M. (editors). Academic Press. San Diego, California.
- **Leggett, K.** (2006). Effect of artificial water points on the movement and behaviour of desert-dwelling elephants of north-western Namibia. *Pachyderm*, **40**: 40-51
- **Mitchell, M.S. and Powell, R. (2004).** A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modeling*, **177**: 209-232.
- Murwira, A. and Skidmore, A. K. (2005). The response of elephants to the spatial heterogeneity of vegetation in southern African agricultural landscape. *Landscape Ecology*, **20**: 217-234.
- Ngene, S. M., Skidmore, A. K., van Gils, H., Douglas-Hamilton, I. and Omondi, P. (2009). Elephant distribution around a volcanic shield dominated by a mosaic of forest and savanna (Marsabit, Kenya). *African Journal of Ecology*, 47: 234-245
- **Osborn, F.V.** (2004). The concept of home range in relation to elephants in Africa. *Pachyderm*, 37: 37-44
- Owen-Smith, N., Fryxell, J. M. and Merrill, E. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movements. *Philosophical Transactions of the Royal Society*, **365**: 2267-2278.
- **Powell, R. A. (2000).** *Animal home ranges and home range estimators*. In: L. Boitani and T.K. Fuller (eds). Research techniques in animal ecology. Columbia University Press, New York.
- Said, M. Y., Change, R. N., Craig, G. C., Thouless, C. R., Barnes, R. F. and Dublin, H. T. (1995). *African Elephant Status Report 1995*. Occasional Paper of the IUCN Species Survival Commission, No. 11. Gland, Switzerland.
- Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Burundige, G. C., Raedeke, K. J. and Gitzen, R.A. (1999). Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*, 63: 739-747.
- Shannon, G., Page, B., Slotow, R. and Duffy, K. (2006). African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology*, 41: 37-44.
- **Stephenson, P. J. and Ntiamoa-Baidu, Y. (2010).** Conservation planning for a widespread, threatened species: WWF and African elephant *Loxodonta africana*. *Oryx*, **44**: 194-204
- **Stokke, S. and du Toit J. T. (2002).** Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, **40**: 360-371.

- **Thouless, C.R.** (1995). Long distance movement of elephants in northern Kenya. *African Journal of Ecology*, 33: 321-334.
- William, J. K., Daniel, A. and Odu, J. M. (2002). The impact of conflict on the Nimule National Park: A survey on the food security situation. A report of the New Sudan Agricultural Sector supported by USAID-USDA PASA.
- Wittemyer, G., Getz, W. M., Douglas-Hamilton, I. and Vollrath, F. (2007). Social dominance, seasonal movements and spatial segregation in African elephants: a contribution to conservation behaviour. *Behavioural Ecology and Sociobiology*, **61**: 1919-1931.
- Young, K. D., Ferreira, S. M. and van Aarde, R. J. (2009). Elephant spatial use in wet and dry savannas of southern Africa. *Journal of Zoology*, 278:189-205