



SPATIAL DISTRIBUTION OF WILDEBEEST IN SERENGETI NATIONAL PARK, TANZANIA

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ABSTRACT

Serengeti wildebeest *Connochaetes taurinus* often come in contact with human activities which together with population growth, climate change and poverty tend to regulate wildebeest population. Since wildebeest distribution in relation to natural and man made changes is poorly understood, I examined ten GPS collared wildebeest from 2002 to 2004 to test for the spatial differences in distribution and movement rates. A pair-wise comparison of different habitats computed using log-ratio of compositional analysis among GPS collared wildebeests indicated that open grassland, open woodland and wooded grassland were used significantly more frequently than other vegetation types. Habitat uses changed with seasons reflecting opportunistic feeding due to resources variability. Despite the relative potential of green grass and surface water migrating wildebeest avoided the western corridor during the migration. The pattern of space use was better explained by the movements which seemed to have increased even in the most frequently used habitats reflecting resource competition amongst wildebeest. Differences in daily movement rate between wildebeest sexes were better explained by the interaction between sexes and period of the day. Females appeared to be less active at night compared to males, especially during calving period (wet season), a strategy probably to minimize predation on less mobile neonates. Long-term data set from large sample sizes of wildebeest with detailed daily location GPS fixes is needed to enhance future management practices. Managers would benefit more from

the study that compares foraging movements between resident and migratory sub-populations in the habitats which serves also as migratory corridors.

Key words: migration, movement, Serengeti, wildebeest, vegetation, human exploitation.

INTRODUCTION

A central focus in animal ecology is to consider the association of an animal with its environments, particularly the varieties of habitats it occupies or prefers. The means in which ungulates respond to environmental heterogeneity impinges on their movement patterns in many ways (Etzenhouser *et al.* 1998; Johnson *et al.* 1992). The movements between habitat patches in most environments are mainly constrained by resources and landscape heterogeneity together with terrain features. For example, Serengeti wildebeest function best in environments with variable resource availability particular suitable niches at different times of the year. They move between habitat patches in response to changes in climate associated with fluctuations in resource availability (Boone *et al.* 2006; Mduma *et al.* 1999, Wilmshurst *et al.* 1999). Notwithstanding uneven distribution of rainfall associated with climate change, specific nutrients in foliage (Murray 1995; McNaughton 1990; Kleuren 1975), predation pressure (Fryxell & Sinclair 1988), fire (S.N.Hassan pers. comm.) and habitat suitability have great



influence on spatial distribution and movements between habitat patches (Andersen 1991). Above all, foraging economics during movements and changed seasons play an important role in habitat choice between habitat patches (Bergman et al. 2001, Wilmshurst et al. 2000; Poldosky and Price 1990).

In order to conserve migratory mammals in Serengeti, it is essential to know what resource categories influence spatial choices and correlate the choice with distribution patterns of the vegetation characteristics in the geographical region. Telemetry study in Serengeti (Thirgood et al. 2004) including simulation models (Boone et al. 2006; Musiega et al. 2004) suggest a close link between wildebeest movement and new forage growth linked to rainfall. Observation also affirms that both vegetation and landscape heterogeneity are key players determining wildebeest movement.

Previous study on collared wildebeest in Serengeti National Park (Boone et al. 2006; Thirgood et al., 2004; English 1976) suggests that there is limited use of areas outside core protected zones. Wildebeest mobility and residence time in these areas have increased in the presence of drought during north migration (Thirgood et al. 2004; Hilborn et al. 1994). In view of these findings my telemetry study examined the distribution and abundance of wildebeest in Serengeti National Park and its adjacent protected areas using detailed GPS collared data to relate the spatial distribution of wildebeest with available vegetation/land-cover maps in order to answer the following questions; i) is the spatial distribution of wildebeest related to habitat use? ii) if so, is the use significantly different among the GPS collared individuals by relating to the habitat available? iii) What factors significantly influence the rate of movement amongst wildebeest individuals?

MATERIALS AND METHODS

Study Area

The Serengeti Ecosystem (SE) is comprised of nearly 25,000 km² on the boarder between Tanzania and Kenya. The system has a conservation core zone consisting of Serengeti National Park (SNP) and Masai Mara National Reserve (MMNR) in Tanzania and Kenya respectively. The SNP is shielded by Maswa Game Reserve (MGR), Grumeti Game Reserve (GGR) and Ikorongo Game Reserve (IGR) to the south and north-west and Ngorongoro Conservation Area (NCA) to the south-east (Fig. 1). Grassland forms the most extensive land cover, reaching to less than 75% in areas of extensive woodland (Campbell & Hofer 1995). Open grassland dominates in the southeast whereas woodland dominates the western and northern parts (Senzota, 1982). Apart from dry season rainfall, the density of migratory wildebeest in the open woodland and wooded grassland habitats, north and outside the Serengeti plains, is influenced by the level of human disturbance (Campbell & Hofer 1995). Since wildebeest is food regulated (Mduma et al. 1999), short term habitat alteration from bushfire; agro-pastoral and poaching activities (Kideghesho et al. 2005; Sinclair & Arcese 1995) may largely constrain resources available for the migrating wildebeest.

GPS Collaring

Sixteen adult wildebeest, ten (six males and four females) and six (four males and two female) were fitted with GPS collars in Ndotu area, South of Naabi gate in Serengeti National Park on April 27, 2002 and May 5, 2003 respectively. These animals were stalked with a car and darted to the rump region with a combination of etorfin and medetomidin from inside the vehicle. The GPS collar was fitted when the wildebeest was down and calm and the anaesthesia was



reversed using diprenorphine. Collared wildebeests were closely monitored for one hour to ensure that there are no undesirable effects during and after handling process. Televit of Sweden delivered the GPS-Simplex collars with their assembly.

All GPS-collars fitted in 2002 were set to record their positions every third hour and those fitted in 2003 took positions every one hour. Remote downloading using SPM Simplex project manager software was programmed to occur once every month but the topography, remoteness and climatic conditions of the area made this approach very difficult. Collars were recovered after one year of service when the drop-off unit had been triggered.

Available habitat, habitat use and compositional analysis

We used minimum convex polygon (MCP) from pooled GPS coordinates in collared wildebeest for spatial analyses. The vegetation composition from this home-range was based on the Serengeti ecosystem vegetation map of 1994 (supplied by IRA-University of Dar Es Salaam). Accordingly, habitat use was found by acquiring the vegetation type at each GPS location, based on the same vegetation map as mentioned above. The compositional analysis method (Aebischer *et al.* 1993) was used to calculate the proportions of different vegetation types within the estimated available area specified by the frequency of wildebeest observations. In the calculation, it was first assumed that the proportion of habitat used is the same as the proportion of habitat available. Secondly, that each individual collared wildebeest was independent of the other, hence there was no dependence for relocations. Thus, in order to test for overall spatial selection, we used the differences in log-ratios (d_i) and tested whether the vector of mean values of d (d_1, d_2, \dots, d_6) was significantly different from a zero vector, using Wilk's lambda test. Habitat types whose use observations were proportionally low were

pooled together and a zero data was replaced by an arbitrary small positive number when calculating d_i values, in case of zero record for the i_{th} value. In addition, a one sample t-test was used to compare the mean of d_i value to zero and subsequently a paired t-test for pairs of sample means.

Since the data was divided into groups of categorical variables i.e. sex, year, seasons and period of the day, a generalised linear model was performed to test the effect of interacting variables in habitat selection. An individual GPS collared wildebeests whose fixes in year days covered less than 50% were omitted to avoid bias from fewer observations in habitat use. Available data reflect time from April 2002 through March 2004 whereas seasons considered the annual movements and habitat use in distinct periods covering January - May, June - July and August - December for wet, early dry and late dry range respectively.

Daily wildebeest movement

The rate of movement in different habitats was obtained by calculating the mean lengths of line paths from daily fixes of all GPS wildebeest covered in each habitat for the entire study period. The movements between line paths for daily fixes recorded after one and three hours were standardised in km per hour and later averaged across days. In order to capture the differences in movements as a function of period of the day, daily fixes were split into day and night. All wildebeest fixes retrieved from 7:00 to 18:59 and from 19:00 to 6:59 hours covered day and night sections of 24 hours respectively. Movement data were tested for normality and later \log_{10} transformed where graphs were non-normal. A mixed linear model was developed to test the effect of interacting factors and the model that best explain the rate of movement. Wildebeest individuals were entered in the model as a random factor whereas study years, seasons, period of the day, habitat types and



protected areas as fixed factors. The parameter estimates of wildebeest movement were independently tested to determine if the variations from the intercept significantly differed in factor combinations using S-Plus v7.0 (Insightful Corp.). Other statistics were done in SPSS inc. (2006) and are 2-tailed with 0.05 significance level.

RESULTS

Movement patterns in 2002 -2004

A total of 14,996 and 13,166 positions (fixes) were recorded in 2003 and 2004 respectively. Eight collars (six males and two females) were retrieved in 2003 and the remaining two were localized but never collected due to difficult terrain associated with the wet season (April-May). Only two collars (one male and one female) were retrieved in 2004 and the remaining four were never localized. There was a higher proportional use of areas under core protection than areas with lower

protection status, Serengeti National Park (SNP) being predominantly used than other protected areas (Table 1). Frequencies of wildebeest uses in different protected areas during the study period were significantly different ($\chi^2=901$, DF=5, P<0.001). The general pattern of movements indicated an even distribution of collared wildebeest in the south-east of the SNP and NCA short grass plains toward Maswa Game Reserve (MGR) during wet season (Fig. 2b). At the onset of the dry season the movement headed north of SNP through the west (Fig. 2c). The open land and the protected areas outside SNP appeared to be avoided as wildebeest moved west and north-west of the park toward Masai Mara National Reserve (MMNR) in Kenya (Fig. 2c). A substantial amount of time was spent within the habitats of Tanzania-Kenya boarder of the ecosystem and later collared wildebeests moved back to SNP spreading throughout the centre, south-east and part of NCA during late dry season (Fig. 2d).

Table 1: Wildebeest fixes from ten collars (7 males and 3 females) recorded during the year 2003 and 2004 migration in Serengeti averaged to obtain mean percent observed frequency locations of daily use. Wildebeest fixes in 2002 and 2003 were recorded after every 3 and 1 hour respectively.

Year	Mean wildebeest fixes in different protected areas							Total year days	Day	(% year)
	Beest	SNP	NCA	IG	GR	MGR	LGR			
2003	3222*	1783	480	23	11	97	-	306	85.0	
	3152**	1516	740	-	-	6	106	304	84.0	
	3202*	1521	451	-	-	63	64	285	79.0	
	3212*	1577	446	119	-	8	-	279	77.5	
	3162**	1004	711	3	-	401	3	271	75.3	
	3242*	1644	189	32	-	-	10	241	67.0	
	3232*	488	318	77	-	-	-	177	49.2	
2004		10,300	3,598	251	11	619	205			
	4162**	6701	1204	17	-	256	-	368	100	
	4222*	3215	-	-	-	68	-	167	45.6	
	4202*	999	419	-	-	-	-	63	17.0	
		10,915	1,983	17	-	324	-			
Mean percent observ. freq.		74.6	19.6	0.9	0.07	3.3	1.4			

*male; **female

SNP=Serengeti National Park, NCA=Ngorongoro Conservation Area Authority, MGR=Maswa Game Reserve, IGR=Ikorongo Game Reserve, LGCA=Loliondo Game Controlled Area.



Table 2: Vegetation description used in the study (After Pratt & Gwynne 1966).

Vegetation	Description
Open grassland (OG)	Land dominated by grasses and occasionally other herbs, sometimes with widely scattered or grouped tree and shrubs (<2% canopy cover)
Bshed grassland (BG)	Grassland with scattered or groped shrubs (<20% cover) subjected to periodic burning
Open woddland (OW)	A stand of trees (up to 18m high) with an open but not thickly interlaced canopy with shrubs interspersed (<20% canopy cover)
Open bushland (OB)	An assemblage of woody plants, mostly of open shrubby habit having a shrub canopy of <6m high and canopy cover of <20%
Wooded grassland (WG)	Grassland with scattered or conspicuous grouped trees, but having canopy cover of <20% and often subjected to periodic burning
Bushland with emergent Trees (BET)	An assemblage of woddy plants, mostly of shrubby habit with a shrub canopy of <6m in high and occasional emergent <i>Acacia spp.</i>
Bare soil (BS)	Land (e.g. rock, saline, and desert) naturally devoid of vascular plants
Grassland with scattered cropland (GSC)	Land dominated by grasses and occasionally other herbs sometimes with widely scattered cropland
Inland water and swamp (IWS)	Permanent standing water and associated plant communities (e.g. reeds, sedges, rushes, trees or shrubs and aquatic species)
Woodland with scattered cropland (WSC)	A stand of trees (<18m high) with an open thickly interlaced canopy. Scattered crop and grasses dominate ground cover

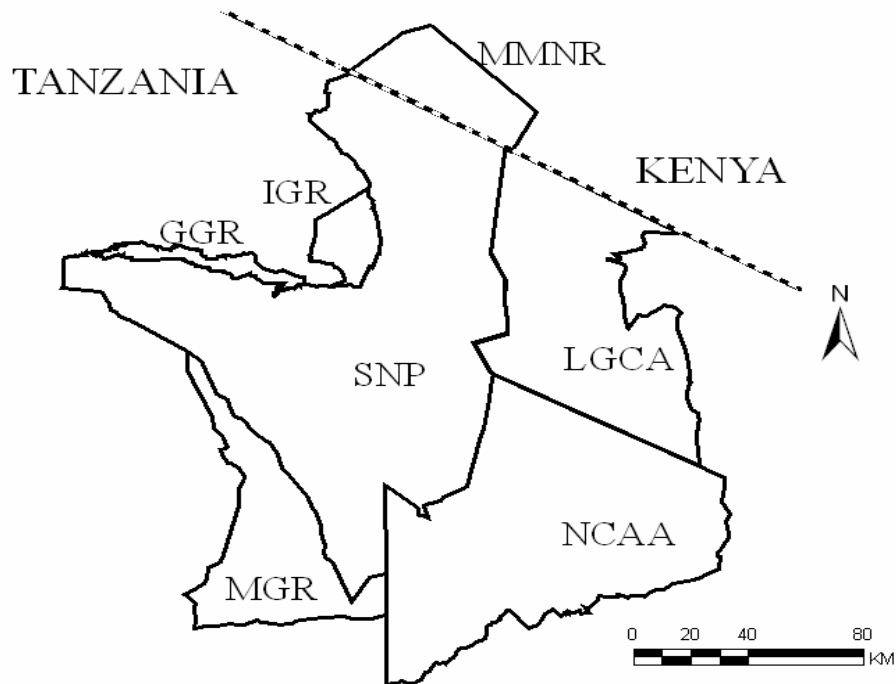


Figure 1: Map of the Serengeti Ecosystem indicating the location of protected categories. SNP=Serengeti National Park, NCAA=Ngorongoro Conservation Area Authority, MGR=Maswa Game Reserve, GGR=Grumeti Game Reserve, IGR=Ikorongo Game Reserve, LGCA=Loliondo Game Controlled Area. SNP and NCA are core protected areas whereas, MGR, IGR,GGR and LGCA are partial protected areas

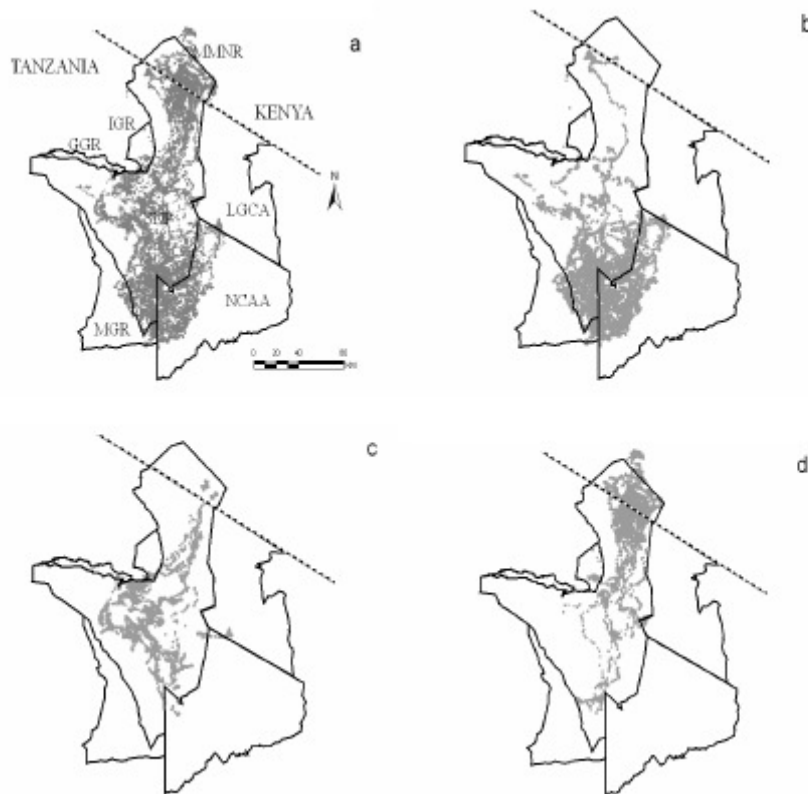


Figure 2: Movements of combined individual collared migratory wildebeest in the Serengeti ecosystem during 2002 – 2003. Fig. 1a) indicate broad distribution of wildebeest by GPS position fixes during the study years. Seasonal movements are predicted by wet and dry seasons i.e. wet season range (January-May), early dry season (June-July) and late dry season (August-December) for Fig. 2b, c and d, respectively.

Habitat use

Spatial distribution of GPS collared wildebeest was recorded in a range of habitats (Table 2) in decreasing order of importance: open grassland (OG), bushed grassland (BG), bushland with emergent trees (BET), wooded grassland (WG), open woodland (OW), open bushland (OB), bare soil (BS), dense bushland (DB), grassland with scattered cropland (GSC), inland water and permanent swamp/marsh (IW) and woodland with scattered cropland (WSC). Pairwise comparison of different habitat combination indicated a significantly higher selection for open grassland compared to open woodland and bush land with emergent

trees, when their mean differences were compared across the ten collared wildebeest (Table 3). Open woodland was selected more frequently compared to wooded grassland whereas wooded grassland was selected more frequent compared to bush land with emergent trees. Although, there was a clear difference between frequencies of habitat use dominated by open grassland, open woodland was an important habitat during the wet season whereas bushed and wooded grasslands were selected more frequently than other habitats in the late dry season (Fig. 3).



Table 3: Means, standard deviation (SD) and t-test results for compositional analyses of habitat types and habitat pairwise comparisons (one sample and paired t-tests with nine df)

Comparison	Differences (di)	Mean	SD	P value
OG/OT	d1	0.787	1.17	0.063
BG/OT	d2	0.340	2.86	0.716 NS
OW/OT	d3	-0.416	2.02	0.532 NS
WG/OT	d4	0.173	1.92	0.378 NS
BET/OT	d6	-0.796	1.47	0.121 NS
OG versus BG	d1-d2	0.447	1.91	0.479 NS
OG versus OW	d1-d3	1.202	1.48	0.030
OG versus OB	d1 - d4	0.614	1.01	0.087 NS
OG versus WG	d1 - d5	0.351	0.74	0.166 NS
OG versus BET	d1 - d6	1.583	1.28	0.004
BG versus OW	D2 - d3	0.756	2.43	0.352 NS
BG versus OB	D2 - d5	0.167	1.83	0.779 NS
BG versus WG	D2 - d5	0.095	1.87	0.876 NS
BG versus BET	D2 - d6	1.136	1.99	0.105 NS
OW versus OB	D3 - d4	-0.589	0.99	0.093 NS
OW versus WG	D3 - d5	-0.851	1.01	0.026
OW versus BET	D3 - d6	0.380	1.91	0.546 NS
OB versus WG	D4 - d5	-0.263	0.83	0.345 NS
OB versus BET	D4 - d6	0.969	1.84	0.130 NS
WG versus BET	D5 - d5	1.232	1.35	0.018

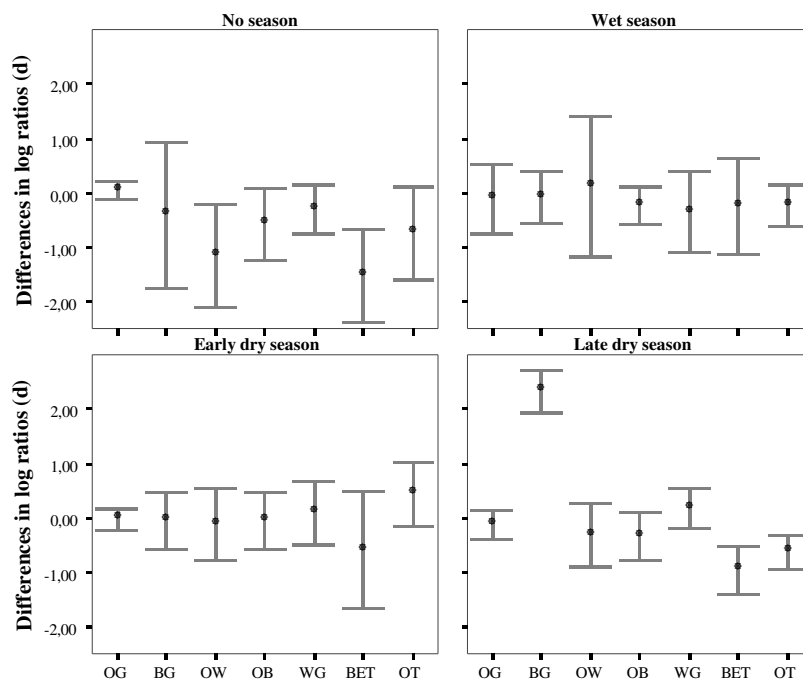


Figure 3: Mean log ratios (available/used habitat) and Error bars indicating 95.0% Confidence Interval of mean presenting the differences in habitat use. Higher preference for any given habitat is indicated by positive values. No seasons means all seasons together



The Multivariate Analysis (Wilk's Lambda tests) indicated significant habitat selection reflected by the interaction between period of the day (day and night) and seasons [General Linear Model (GLM), $F=10.8$, $DF=3$, $P<0.001$] and the season and habitats GLM, $F=6.26$, $DF=18$, $P<0.001$]. Other interactions (i.e. period of the day*sex; period of the day*habitat; period of the day*season*sex; period of the day*season*habitat; period of the day*sex*habitats; season*sex; season*sex*habitat) were not significant.

Rate of movement in different habitats

Daily mean rate of movement averaged from wildebeest fixes in all study years was 4.9 (± 1.2 km, $N=26,290$). The lowest and highest movement rates were 0.04 to 63 and 0.8 to 32.6 km for year 2003 and 2004 respectively. The movement rate between

period of the day, seasons, vegetation types and protected areas was significantly different (Table 4). Daily mean rates between wildebeest sexes was better explained by the interaction between sex and period of the day. Males appeared to be more active at night compared to females, and night movement rate was reduced by almost 50% in both sexes (Table 4). Although females covered significantly longer distances (4.9 ± 1.2 km day⁻¹) than males (3.4 ± 1.2 km day⁻¹) during the day than night time (Table 5), they were relatively slower during the wet season (4.9 ± 1.2 km) compared to the early dry (5.9 ± 1.0 km) and late dry season (6.2 ± 1.0 km) (Table 5). Individual collared wildebeest appeared to move faster in GGR and SNP (6.1 ± 1.6 km and 4.9 ± 1.2 km day⁻¹ respectively) and were relatively slower both in MGR and LGR (3.6 ± 1.1 km day⁻¹).

Table 4: Summary of a mixed linear model analysing the log₁₀transformed wildebeest movement rate as a function of year, season, time of the day, sex, vegetation type and protected areas (fixed factors). Wildebeest was entered as a 'random factor' to control for repeated measures of movement for the same collared wildebeest. Wildebeest movement was log transformed to get better normal distribution

Final model	numDF	denDF	F	P	
Intercept		1	26290	179.54	<0.0001
Period of the day	1	26290	831.93		<0.0001
Sex	1	8		0.89	0.3720
Season	2	26290		8.01	0.0003
Vegetation	9	26290		14.02	<0.0001
Protected aareas	5	26290		4.71	0.0003
Period of day x sex	1	26290		161.20	<0.0001
Rejected terms	Seasons x sex	2	26288	1.02	0.3588



Table 5: Summary of the test effect of interactive parameters in the final model independently explaining estimates of wildebeest movement rates in \log_{10} (km day⁻¹) changed to km day⁻¹.

Parameter	Estiamtes (SE)	df	t-value	p-value
Intercept	4.90 (1.15)	26290	11.81	<0.0001
Night	-2.29(1.03)	26290	-28.948	<0.0001
Male	-.154(1.18)	8	-2.619	0.0387
Early dry season	1.05(1.03)	26290	1.786	0.0740
Late dry season	1.13(1.02)	26290	4.453	<0.0001
BG	-1.11(1.03)	26290	-3.425	0.0006
OW	-1.07(1.04)	26290	-1.585	0.1128
OB	1.01(1.04)	26290	0.173	0.8620
WG	-1.25(1.04)	26290	-5.421	<0.00001
BET	-1.21(1.03)	26290	-4.874	<0.0001
BS	-1.27(1.08)	26290	-2.932	0.0034
GSC	-2.56(1.16)	26290	-6.084	<0.0001
IWS	2.17(1.61)	26290	1.624	0.1043
WSC	1.10(1.82)	26290	0.160	0.8727
Ngorongoro	-1.03(1.02)	26290	-0.989	0.3224
Ikorongo	-1.16(1.11)	26290	-1.388	0.1651
Grumeti	1.16(1.61)	26290	0.303	0.7611
Maswa	-1.26(1.04)	26290	-3.922	0.0001
Loliondo	-1.35(1.12)	26290	-2.474	0.9133
Rejected Terms				
Early dry season x male	-1.05(1.05)	26288	-0.890	0.373
Late dry sason x male	1.04	26288	0.812	0.417
Rejected Terms				
Early dry season × male	-1.05(1.05)	26288	-0.890	0.373
Late dry season × male	1.04(1.05)	26288	0.812	0.417

DISCUSSION

This study indicates that natural factors and anthropogenic activities linked with poverty from increased human population may potentially deter spatial use of wildebeest in reserves with lower protection status adjacent to core protection areas. In this study, Grumeti Game Reserve appeared to be avoided whereas in agreement with a previous study, the Ikorongo Game Reserve was partially used (Thirgood et al. 2004). Indeed, threats (particularly poaching) to wildebeest outside the core protected areas are linked with annual wildebeest migration (Holmern et al. 2007; Thigood et al. 2004; Homewood et al. 2001, Serneels & Lambin 2001b.). Moreover, in connection with documented threats, complex

interactions linking protected areas network of Serengeti ecosystem have been associated with increased human population (Kideghesho et al. 2005). Increased illegal hunting from densely populated areas in western Serengeti together with natural predation is likely to disrupt wildebeest movement and ranging patterns, when trying to balance physiological needs and safety.

Although the pattern of space use could be described by the rate of wildebeest movement the data should be treated cautiously due to the differences in data interpretation which arise when comparing GPS collared individuals with varying time intervals between fixes (Ferguson et al. 1998). Ignoring possible differences due to



time interval between years, the study indicates that there were consistent preference for open grassland compared to other habitats in the SNP (Table 1) probably due to the level of protection and nutritional suitability of the south-east plains grasslands (Murray 1995; McNaughton 1990). Generally, open short grasslands are considered to be extremely productive areas in Serengeti primarily during the wet season (Wilmschurst *et al.* 1999; Banyikwa 1995; McNaughton & Murray 1995; McNaughton 1990). Despite of elevated requirements for high-quality food in open grassland areas, the estimated rate of wildebeest movement was comparatively higher probably due to strong competition for quality resources. Other factors being equal, higher movement rate between habitat patches would reflect little use possibly due to either intra- and inter specific competition or disturbance from predators and human activities or both. Alternatively, the amount of plant biomass available per unit area is important for forage intake rates (Distel *et al.* 2005) as lower sward bulk density in high-quality short grasslands could result in higher movement rates.

The habitats of western Serengeti were slightly used during the dry period and the collared wildebeest appeared to have been moving quickly towards the north as dry season advanced (Table 5; Fig. 2c, d). During this period open woodland, bush land with emergent trees and wooded grassland were important habitats. Preference in this regard should not be seen as a choice function along a gradient from open grassland to close woodland only. Differences in vegetation physiognomy also result from differences in the dominant woody plant species which can, in turn, reflect other environmental variability such as that caused by soil type and moisture availability. The strong selection for open woodland versus wooded grassland as well as for wooded grassland versus bush land with emergent trees could be influenced by the outcome of the interaction between sexes with

period of the day during the dry period when food resource is scarce. Moreover, casual observations indicated that availability of green grass and the presence of surface water strongly correlated with wildebeest movements. Grass quality and availability tend to limit ungulate food intake during the dormant season (Bergman *et al.* 2001; McNaughton & Georgiadis 1986). For instance, consumption of plant biomass in the north-west and western corridor of SNP shifted significantly between burnt and non-burnt patches apparently due to changes in the relative composition of the swards in terms of the amount and the quality of the forage available (S.N.Hassan pers. comm.).

Higher movement rate recorded in Grumeti Game Reserve indicated a general flight tendency in the Western Corridor due to human disturbance from large-scale farming, range competition from agropastoralists and higher poaching levels (Mduma *et al.* 1999; Arcese *et al.* 1995; Campbell & Hofer 1995). Early-dry-season (May-July) fires profusely occurring in the game reserve areas coincident with the northern migration (J. Dempewolf, unpubl. data) significantly reduced the amount of plant biomass available for migrants (Rusch *et al.* 2005). Wildebeest and other ungulate species appear to use game reserve areas less than the core protected area, even without evidence for forage resources competition with livestock (Rusch *et al.* 2005). Tourist camps and lodges strategically located on the west might have influenced the observed ranging pattern. Similarly, seasonal differences in daily movement rate could be primarily linked to differences in quality range associated with forage growth due to rainfall distribution patterns of Serengeti (Boone *et al.* 2006; Frank *et al.* 1998; Mduma *et al.* 1999; Sinclair 1995; Sinclair & Norton-Griffiths 1979).



The daily average distance across collared wildebeest (i.e. 4.9 km day^{-1}) is considerably lower from the 10 km day^{-1} reported over two decades ago (Pennycuik 1979 cited in Murray 1995). This reduction might reflect differences in sampling methods or the influence of environmental parameters on spatial variations in food resources. Differences in the rate of movement among GPS collared wildebeest during time of the day and season were another notable finding in this study.

Daily estimates of female movements were significantly lower during the calving period (wet season) compared to early dry and late dry seasons, an observation similar to seasonal movements of caribou *Rangifer tarandus* caribou (Ferguson & Elkie 2004; Bergman et al. 2000, Rettie & Messier 2001). The low rate of movement by females during the wet season could be a strategy to minimize predation on less mobile neonates, or a comparatively higher exploitation of habitats of high quality. Higher rate of movements during the dry season could be associated with effective avoidance or flight response toward predation risk-sensitive environments (Caro 2005; Fryxell & Sinclair 1988) given the level of sensitivity in females with calves. The obvious seasonal differences in the rate of movement between sexes could mainly be associated with male's territorial behaviour (Estes 1991). However, our results should be treated with caution because of small sample size (i.e. seven males and three females).

The observed differences in movement between wildebeest sexes during day and night might also reflect life history strategies engrossed in parental care and nutritional demands in females that were relatively more active during the day than night time. Male individuals were expected to be quite mobile, considering their group roles; however, physiological demands in females in search for better resources particularly water dictated by pregnancy and lactation might account for

the differences. The reduction of night movements to about 50% might be related to rumination, rest and/or sleep and to minimize encounters with predators such as lions *Panthera leo* and hyenas *Crocuta crocuta* known to maximize their hunts by night (Packer 1996; Hofer & East 1995).

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