

Human-wildlife interactions in western Serengeti, Tanzania

Effects of land management on migratory routes and mammal population densities

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Abstract

Rusch, G. M.¹, Stokke, S.¹, Røskoft, E.^{1,2} Mwakalebe, G.³, Wiik, H.⁴, Arnemo, J. M.⁵ & Lyamuya, R.³ 2005. Human-wildlife interactions in western Serengeti, Tanzania. Effects of land management on migratory routes and mammal population densities. NINA rapport 85. 47 pp.

The Serengeti-Mara ecosystem constitutes one of the last great migratory systems in Africa and supports the highest concentrations of large predators in the world. The health of the ecosystem, as judged by fundamental processes has been regarded as good, however, the prospects for the future maintenance of its integrity need to consider the enormous expansion of human activities in the region as well as the current global notion that protected areas cannot be managed in isolation from the local claims of poverty alleviation and rural development. Consequently, a better understanding of the interactions between land management and wildlife biodiversity is critical to face current challenges of protected area management. In this study, we focused on three issues aiming to gain knowledge on land management – wildlife interactions. First, we documented the distribution patterns of all larger mammal species along ground transects stretching from the protected area into the open land (in our case, the communal land in the non-protected area) on a monthly basis and during a period of 3 years. Second, we assessed the patterns of migratory behaviour of Serengeti wildebeest (*Connochaetes taurinus*) using modern telemetry, which yielded the most complete and accurate data set to date. Thirdly, we established the distribution and quality of forage in terms of the biomass of herbaceous vegetation in three land-management areas and assessed consumption during the migration period to link forage availability to the use of the area by herbivores.

Our results on wildebeest movements agree generally with earlier notions that the migration in Serengeti occurs mostly within the protected area. However, the transect records showed that large herds of wildebeests use non-protected areas while migrating north which reveals that there are at present important areas of the ecosystem, as defined by the migrants that are not protected. Our data also indicate important differences in the northward migration route compared to the one described earlier in the late seventies, when the migration made an extensive use of the western corridor area. In contrast, our data suggest a more eastern route, following a narrow fringe along the borderline between the national park and the game reserve areas.

Both the wildebeest distribution maps and the daily movement distances indicate that in the dry season, the wildebeest made a more concentrated use of the range compared to the rain season period. This pattern can be attributed to relatively higher forage availability (higher standing biomass) in the dry season range compared to that in the plains in the rain season. Other possible causes can be the availability of fewer water sources in this season that force the animals to concentrate the use in their vicinity or the impact of agricultural activities that have greatly expanded in the Mara area in the last decades.

The transect data reveal differences in density distributions between the protected and non-protected areas. Common large herbivores (i. e. impala (*Aepyceros melampus*), Thomson's gazelle (*Gazella thomsoni*), Burchell's zebra (*Equus burchelli*), Grant's gazelle (*Gazella granti*), topi (*Damaliscus korrigum*), giraffe (*Giraffa camelopardalis*) and warthog (*Phacochoerus aethiopicus*) had significantly lower densities along the transects stretching through the open land and the game reserve areas compared with the areas within the National Park. The open land is characterised by some vegetation types typically influenced by human activities (scrub, scrub grassland and vegetation dominated by weeds) that were absent both in the game reserve and the national park areas. But there were differences between the Game Reserve and the National Park as well. The game reserve area had a prevalence of more open types (grassland and wooded grassland), which may be a result of a more intense disturbance regime. The forage availability data were also indicative of a general higher disturbance pressure (grazing, fire and cultivation combined) in the Game Reserve compared with the National Park,

as for example, the lower standing biomass which can be attributed to a higher frequency of fires.

Fire was widespread in the study area at the time of the onset of the northern migration. Twenty eight per cent of the sites were burnt and the majority of them was located along the borderline between the Game Reserve and the National Park (24 and 18 burnt plots respectively). No burning was recorded in the open land. At this time, burnt sites not only had a significantly reduced amount of total standing biomass (10% of non-burnt sites) but of green biomass as well. Consequently, if the area affected by fire is large, the 'early burning' practice will result in a substantial reduction of the forage available during migration and in the dry season. A more careful consideration of the timing of the burning and of the frequency of fires appears to be necessary when planning future management practices and regulations since food availability during the dry season is critical to the wildebeest.

The open land had high total standing biomass and green biomass, as well as a higher proportion of sites with no evident signs of grazing both before and after the northern migration passed the area. These results are in agreement with the GPS-tracking and transect data that indicate a low use of the area by migratory wildebeest and other wildlife. It is also in agreement with the findings of the socio-economic studies that show that the use of the area by livestock is also limited at the moment. The results indicate that biomass parameters are not good predictors of regional herbivore forage choice in anthropogenic habitats.

The differences in standing biomass and biomass compartments between the game reserve and the national park are more surprising since there were no *a priori* indications of differences in forage availability and quality between the areas. The lower amount of standing biomass in non-burnt sites together with a lower proportion of stem biomass and a higher proportion of green leaves in the Game reserve can probably be attributed to the incidence of higher intensity of fires and grazing. The game reserve area also had a higher predominance of open vegetation types which is also in agreement with higher disturbance. The practice of burning seems to be common in the game reserve areas and the consumption data indicated a very intensive use of some areas.

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Sammendrag

Rusch, G. M.¹, Stokke, S.¹, Røskoft, E.^{1,2} Mwakalebe, G.³, Wiik, H.⁴ & Arnemo, J. M.⁵, Lya-muya, R.³ 2005. Human-wildlife interactions in western Serengeti, Tanzania. Effects of land management on migratory routes and mammal population densities. NINA report 85. 47 pp.

Serengeti-Maraøkosystemet omfatter et av de siste store migrasjonssystemer i Afrika og har verdens største tetthet av store predatorer. Helsetilstanden til økosystemet sett ut i fra fundamentale prosesser har blitt karakterisert som god. Men for å vedlikeholde systemets integritet i framtiden må det tas hensyn til den enorme befolkningsekspansjonen i randområdene, og den eksisterende globale holdningen at beskyttede områder vanskelig kan forvaltes uten å tilgode-se de lokale krav om velstandsøkning og utvikling. For å møte de utfordringene som arealforvaltningen står ovenfor, er det nødvendig med økt kunnskap om interaksjonen i grensen mellom arealforvaltning og biodiversitetsspørsmål. I dette studiet fokuserer vi på tre temaer som søker å høyne vår forståelse av interaksjonene mellom arealforvaltning og de organismene som blir involvert i prosessene. Først dokumenterte vi, på en månedlig basis over tre år, utbredelsesmønsteret til alle større pattedyr langs bakketransekter som krysset vernede og uvernede områder. For det andre fastslo vi migrasjonsmønsteret til gnu- (*Connochaetes taurinus*) populasjonen i Serengeti, ved hjelp av moderne GPS-teknologi, og oppnådde derved den hittil mest komplette databasen for denne migrasjonen. For de tredje estimerte vi fordelingen og kvaliteten av beitegrunnlaget i tre arealforvaltede områder og vurderte beitetrykket under migrasjonen for å knytte fortilgjengeligheten til herbivorenes bruk av området.

Våre resultater vedrørende gnuens bevegelser er i overensstemmelse med tidligere funn som sier at migrasjonen stort sett foregår i beskyttede områder. Men data fra transektobservasjonene viste at store gnuflokker kom innom uvernede områder under den nordlige migrasjonen. Dette viser at gnuflokkene utnytter store arealer som for tiden ikke er underlagt vernebestemmelser. I forhold til eksisterende oppfatning viser våre data at gnuflokkene utnytter den vestlige korridoren i langt mindre grad enn tidligere. Våre data tilsier at gnuflokkene følger en forholdsvis smal korridor mellom nasjonalparken og omkringliggende viltreservatområder.

Våre utbredelseskart og mål på daglig bevegelse indikerer at dyra hadde en mer konsentrert arealbruk i tørketiden sammenlignet med regntiden. Vi mener dette kan relateres til mer tilgjengelig beitemasse (større andel stående biomasse) i de nordlige områdene sammenlignet med sletteområdene i regntiden. Andre mulige årsaker kan være få tilgjengelige vannkilder i denne årstiden slik at dyrene tvinges til å bruke snevre områder som i stadig økende grad trues av jordbruksinteresser i Mara området i de siste tiårene.

Transektdataene tyder på at det er ulike dyretettheter i vernede og uvernede områder. Vanlige store herbivorer (for eksempel impala (*Aepyceros melampus*), Thomsons gasell (*Gazella thomsoni*), sebra (*Equus burchelli*), Grants gasell (*Gazella granti*), topi (*Damaliscus korrigum*), giraff (*Giraffa camelopardalis*) og vortesvin (*Phacochoerus aethiopicus*) hadde lavere tettheter i områder utenom nasjonalparken og andre vernede områder. De åpne landområdene er karakterisert av noen typisk kulturpregede vegetasjonstyper (buskvekstområder, gressmark med busker og ruderalplanter) som var fraværende både i viltreservatet og nasjonalparken. Men det var også forskjeller mellom viltreservatet og nasjonalparken. Viltreservatområdet var gjennomgående preget av en mer åpen vegetasjonstype (gressmark og skogbevokst gressmark), noe som kan indikere en forhistorie preget av frekvente inngrep. Tilgjengeligheten av beite tydet også på en forhistorie preget av inngrep (beiting, brann i relasjon til kultivering) i viltreservatet i forhold til i nasjonalparken, som for eksempel mindre stående biomasse – noe som indikerer høyere frekvens av brann.

Brannflater var vanlige i studieområdet når den nordlige migrasjonen tok til. Tjueåtte prosent av plottene var brent og majoriteten av dem lå langs grensen mellom viltreservatet og nasjonalparken (henholdsvis 24 og 18 brente plott). I det åpne landområdet ble ingen brann påvist.

Brente områder hadde på denne tiden en signifikant reduksjon både av total stående biomasse (10 % av ikkebrente plot) og av grønn biomasse. Dersom det berørte området er stort, vil den etablerte "tidlig brenning"-praksisen resultere i en betydelig reduksjon av beitetilgjengeligheten under migrasjonen og i tørketiden dersom det berørte området er stort. Førtilgjengeligheten for gnuflokkene i tørketiden synes å være svært avgjørende for migrasjonen. En kritisk vurdering av tidspunktet og omfanget av brenningen bør derfor nøye vurderes når framtidige planer for forvaltningspraksis og reguleringer fastsettes.

Det åpne landområdet hadde en stor andel stående biomasse inklusiv grønn biomasse samt en høyere andel av prøveflater uten tegn til beiting både før og etter at den nordlige migrasjonen hadde passert området. Dette stemmer godt med GPS- og transektdataene som indikerer at gnu og andre ville dyr utnytter området lite. Det er også god overensstemmelse med de sosioøkonomiske studiene som indikerer at husdyr for tiden heller ikke bruker området i større utstrekning. Resultatene indikerer at biomasseparametre ikke er spesielt gode indikatorer på beitedyrenes regionale forvalg i områder med målbar menneskelig påvirkning.

Forskjellen i biomasse og biomassekomposisjon mellom viltreservatområdene og nasjonalparken er noe overraskende fordi det var ingen *a priori* indikasjon på forskjeller i førtilgjengelighet og kvalitet mellom områdene. Mindre andelen av stående biomasse i ikkebrente områder sammen med lavere andel stammebiomasse og høyere andel av grønne blad i viltreservatet kan muligens tilskrives en høyere frekvens av brann og beitetrykk. I tillegg hadde viltreservatet en høyere predominans av åpne vegetasjonstyper som også er i overensstemmelse med større grad av forstyrrelser. Brenning synes å være vanlig praksis i viltreservatet, og beitedataene indikerte en høy grad av påvirkning i visse områder.

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Acronyms

| | |
|--------|---|
| BHWI | <i>Biodiversity and the human-wildlife interface in western Serengeti Project</i> |
| GGR | Grumeti Game Reserve |
| IGR | Ikorongo Game Reserve |
| IOA | Ikoma Open Area |
| IRA | Institute of Resource Assessment, University of Dar es Salaam |
| LWMA | Loliondo Wildlife Management Area |
| MGR | Maswa Game Reserve |
| MMNR | Masai Mara National Reserve, Kenya |
| MNRT | Ministry of Natural Resources and Tourism, Tanzania |
| NCA | Ngorongoro Conservation Area |
| NFR | Research Council of Norway |
| NINA | Norwegian Institute for Nature Research |
| Norad | Norwegian Agency for Development Cooperation |
| SENAPA | Serengeti National Park |
| SUA | Sokoine University of Agriculture (Tanzania) |
| SWRC | Serengeti Wildlife Research Centre (TAWIRI) |
| TANAPA | Tanzania National Parks |
| TAWIRI | Tanzania Wildlife Research Institute |

Abbreviations

| | |
|-----|---|
| GR | Game reserve area |
| GPS | Geographic positioning system |
| NP | National Park |
| OL | Open land (land outside the protected area) |
| SNP | Serengeti National Park |
| UTM | Universal Transverse Mercator projection |

Foreword

This report forms part of a series of publications that present the results from the *Biodiversity and the human-wildlife interface in western Serengeti* (BHWI) a cross-disciplinary research project aiming to reveal some critical issues about the interactions between humans and wildlife in the border area between the Serengeti National Park, the associated game reserve areas, and the neighbouring settlements in western Serengeti. The project has had two major components dealing with social and economic issues on one hand, and on ecological questions of antropogenic impacts on the other. The core data sets and main discipline-specific results of the social and economic parts of the project dealing with the cultural and economic importance of wildlife for the communities that live in the areas neighbouring with the protected area have been reported earlier in Kaltenborn et al. (2003), Holmern et al. (2004) and in other related publications that are presented in the project reference list in this report. This report addresses the questions of the impacts of land use and land management on wildlife diversity and migratory behaviour with a focus on the indirect impacts of human activities on the characteristics of the vegetation and on the availability of forage.

The project has been conducted in partnership with the Tanzania Wildlife Research Institute (TAWIRI), with core funding from the *Biological Diversity: Dynamics, Threats and Management* programme of the Research Council of Norway and with matching funds from the *Management of Natural Resources Programme*- Norad under the Ministry of Natural Resources and Tourism, Tanzania (MNRT).

The authors are grateful to NFR and MNRT for their support and also wish to thank TAWIRI's staff at the Serengeti Wildlife Research Center (SWRC), Tanzania National Parks (TANAPA), the community at Robanda and all our colleagues and friends in Tanzania and in Norway that have assisted the project in innumerable ways, including patient and tenacious support during the field work. Our special gratitude to the technical and administrative staff at TAWIRI: Janeth. Abbu, Habiba Hassan, Robert Fyumagwa, Jane Kabondo, Joshua Kabondo, Herry Lema, Alphayo Londare, Jimmy Makuru, Onesmo Mwakabejela, Wilfred Marealle, Richard Ndaskoi and Kitoi Sarakikya. Torgeir Nygård at NINA, Shombe Hassan and Vedasto Ndibalema at SUA and Tomas Holmern and Trine Setsaas at NTNU participated in the collection of GPS-collars and in the transect studies. We are also grateful to our colleagues at the University of Dar es Salaam, Prof. Feetham Banyikwa, Prof. Rhamadani Senzota, Dr. Fatina Mturi and Dr. Herbert Lyaruu for valuable discussions when identifying the priorities of the study, relevant for Tanzania and for their collaboration in the sampling set up of the vegetation study. Marc Daverdin established the database for the animal census data at the SWRC. Hassan Nkya and Samuel Bakari were directors of the SWRC and Julius Keyyu the project manager of BHWI during the course of the project. We thank them for their assistance with logistics and many practicalities.

Trondheim, September 26th 2005

Graciela M. Rusch

1 Introduction

Wildlife resources in Tanzania constitute a unique natural heritage and a resource with a great national and global importance. In recognizing this valuable resource, the Tanzanian government has set aside about a quarter of its land as wildlife conservation areas. Currently, protected areas are not relicts of biological diversity that are exploited by tourism alone. Often, protected areas constitute a reservoir for local settlements that harvest wildlife, in many instances, illegally (Arcese et al. 1995, Holmern 2000). The coexistence of highly diverse and rich protected areas together with crowded settlements near their borders is a source of stress. Although there is a general agreement that local communities should benefit from wildlife and biodiversity (Sibanda and Omwega 1996), there is much less consensus on the ways to achieve this goal (Prins 1992, Lélé and Norgaard 1996, Arcese and Sinclair 1995). The current and global notion of ecosystem management, which incorporates the concept of multiple use management, requires sufficient knowledge about the processes underlying wildlife populations trends and the maintenance of biodiversity, and a sound evaluation of the short and long-term impact of human intervention on wildlife and biodiversity (Noss 1997, Barrett and Arcese 1995).

The Serengeti-Mara ecosystem constitutes one of the last great migratory systems in Africa (Prins 1992) and supports the largest herds of migratory ungulates and the highest concentrations of large predators in the world (Sinclair 1995). The annual movement of wildebeest (*Connochaetes taurinus*) nomadic herds (*sensu* (McNaughton 1979a) constitutes the system's most ecologically significant feature (McNaughton 1985). The ecosystem spans more than 25,000 km² of north-west Tanzania and south-west Kenya (Fig. 1) and at a regional scale, the migratory herds define the spatial limits of the ecosystem (Maddock 1979) and are a major shaping force of its structure and function (McNaughton 1979a, 1983, 1985). The Serengeti wildebeest graze on the open grasslands in southeast Serengeti during the wet season (November - May) and migrate to northern Serengeti where they spend the dry season (June - October) (Maddock 1979). Central to the migratory system is that forage accumulates in ranges (e.g. Western corridor, Northern Extension) that herbivores occupy during 'bottleneck' seasons when low or no forage production occurs (Frank et al. 1998).

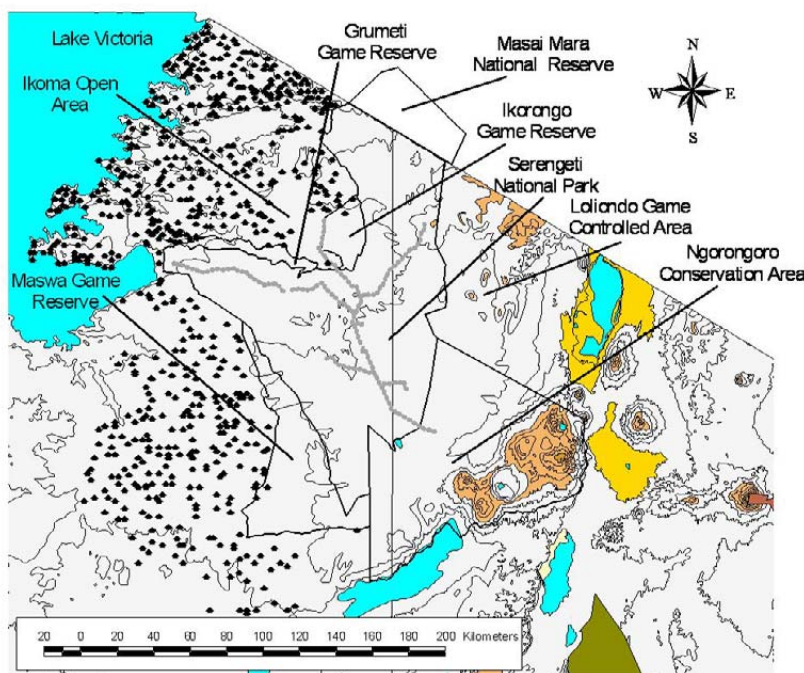


Fig. 1. The study area with protected and open areas. Settlements are indicated as black triangles and transects in the animal counts study indicated as grey dots. Source: Tanzania National Grid of Topographic Series (1:200 000). IRA.

The health of the Serengeti ecosystem, as judged by fundamental processes (i. e. interactions between vegetation, herbivores and predators) is currently good (McNaughton & Banyikwa 1999), even though our knowledge about some important processes (e.g. infectious diseases and their links between wildlife and humans and/or livestock) is at the moment poor. Wildebeest population size has been maintained around 1.3 million between 1970 and 2000 with yearly fluctuations that are related to the mean rainfall in the dry season (Serneels & Lambin 2001) and current levels of legal and illegal harvest have been regarded as not threatening (Mduma et al. 1999). Most of the habitats used by the Serengeti migration are currently under protection, but migration also takes place through areas under various degrees of human pressure (Frank et al. 1998; Serneels & Lambin 2001). The maintenance of the integrity of the migratory system is crucial for keeping high wildlife biomass, population numbers and species diversity, and consequently also the resource base for consumptive and non-consumptive use. Also, because the Serengeti constitutes one of the few remaining natural grazing systems globally, and due to the evolutionary bounds between grazing tolerant flora and large ungulates, the system constitutes a 'genetic storehouse' of plant genotypes that confer resistance to intensive grazing in the semiarid tropics (McNaughton 1979b).



Fig 2: *Wildebeest herd in western Serengeti during the northern migration period. Photo G. M. Rusch*

The prospects for the future maintenance of the integrity of the Serengeti system, however, need to consider the enormous expansion of human activities in the region as well as the current global notion that protected areas cannot be managed in isolation from the local claims of poverty alleviation and rural development. Particularly in the areas west of Serengeti in Tanzania, population has almost tripled during the period 1967-2002 (Kilahama 2003). Encroachment in the area bordering protected areas and uncontrolled land- and resource use expansion can lead to unsustainable use, through the reduction of wildlife ranges, augmented human-wildlife conflicts, and in extreme cases result in loss of species and ecological integrity (Homewood et al. 2001) (Fig. 3). The impacts of land-use on animal distributions have been attributed to the disruption of historical migration routes by fences and roads (Wheelwright 1996) but also to changes related to forage availability through competition with livestock (Prins 1992, Bergström & Skarpe 1999), indiscriminate burning of the vegetation (Prins 1992), and overgrazing leading to range degradation and vegetation change (Rusch & Oesterheld 1997, Wheelwright 1996).



Fig. 4: *Wildebeest grazing on fallow crop-land in the open land area, Robanda Village in western Serengeti. Photo G. M. Rusch.*

A wealth of research has been conducted on the Serengeti ecosystem in the past 40 years, with a primary focus on threatened animal species and on the role of herbivores on ecosystem function (summary papers in Sinclair & Norton-Griffiths 1979 and Sinclair & Arcese 1995). The impacts of human encroachment have been modelled (Campbell and Hofer 1995) but there is still an important knowledge gap about the patterns that characterise the interactions between land management practices in the protected area and the open land in terms of the ecological effects of land-use on wildlife biodiversity and behaviour. We consider it all-important to contribute to a better understanding of these relationships in the face of the imminent challenge of establishing adequate management systems that reconcile biodiversity and ecosystem conservation goals with poverty alleviation and economic development in rural areas adjacent to the protected area. The knowledge about wildlife habitats and food resources under different land-uses linked to the spatio-temporal distribution of wildlife populations is critical for the development of sustainable management practices both in economic and ecological terms.

Our main question dealt, consequently, with the understanding of the effects of land management on wildlife biodiversity and migratory behaviour. More specifically, we first focus on the migratory behaviour of Serengeti wildebeest by documenting daily movements during a 2-years period. Secondly, we document the occurrence of all larger mammal species along transects within and outside the protected area to assess the distribution patterns of mammal diversity. Thirdly, we assessed the distribution and quality of forage in natural and man-influenced ('anthropogenic') vegetation to gain a better understanding of the patterns of wildlife distribution in relation to land-management. We assessed forage availability and consumption patterns in areas with a high interaction between wildlife and humans, particularly during the northern migration. The amount and quality of the forage is a major driver of herbivore foraging behaviour (Frank et al. 1998 and Wilmshurst et al. 1999) and much understanding of migration patterns can be gained in establishing the variables that influence herbivore distribution patterns (Wilmshurst et al. 1999). We discuss thereafter the effects of human activities (cultivation, grazing by domestic herbivores, fire spread) on forage availability as a central issue affecting the migratory system.

2 Data sets and methods

Migration routes in the Serengeti were identified in the 1970's (Maddock 1979) and radio-tracking and aerial habitat surveys from this same period have been related to broad-scale vegetation utilisation patterns during migration (Wilmshurst et al. 1999). Building on previous knowledge, our aim was to make a detailed and accurate description of the current spatial utilization by wildebeest throughout the migratory cycle and including the entire migration area used, both in protected and non-protected areas. We therefore assessed the distribution of

wildlife through two complementary data sets that provide, to our knowledge, the most comprehensive description of large mammal distribution and of wildebeest nomadic patterns hitherto produced. We analyse the relative use of areas with different degrees of protection, the monthly shifts in area use, and in daily movement distances and speed. We compare the nomadic behaviour of males and females and assessed differences in timing between sexes at the onset of migration and in the distance covered daily along the year. The habitat and forage availability data are primarily based on biomass data of herbaceous vegetation across vegetation physiognomic types and along land-use gradients in areas used by migratory herds during the migration and where the contact with human presence and activities is high. Forage data under different land-management systems and availability for migration are also novel for the system.

2.1 GPS-collaring and re-sampling

During this study we obtained data from a total of ten GPS-collars distributed over two migratory cycles from April 2002 until the end of May 2004. Ten wildebeest, 5 females and 5 males, were fitted with GPS collars on April 4 to 16th in 2002 in the Ndutu area south of Naabi gate in SNP. The animals were stalked with a car and the darting gun (Daninject) was operated from inside the vehicle to avoid unnecessary disturbance. When the animal was down and calm the remaining team arrived in a trailing car to assist with the mounting of the collars. Drugs used for immobilisation of wildebeest included combinations of etorphine (9 mg/ml, M99) + medetomidine (10 mg/ml, Zalopine) or etorphine + medetomidine + ketamine (100 mg/ml, Ketalar) (Fig 4).



Fig 4. Immobilised wildebeest when fitting a GPS collar. Photo: M. Daverdin.

Televilt of Sweden delivered the GPS-Simplex collars including VHF beacons for manual tracking and pre-programmed (one-year) drop-off units. The system also includes a radio-link (VHF) for remote downloading of positions to a RX-900 receiver. We used the SPM Simplex project manager software to set up a scheduled program for the GPS-units. The collars were programmed to record their positions every third hour until the drop-off function was triggered on March 30th 2003. Remote downloading was programmed to occur once a month, but the topography, remoteness and climatic conditions of the area made this approach very difficult. Therefore we relied on recovering the collars after one year of service when the drop-off units had been triggered.

From March 31 to late April 2003, a crew of three people searched for the collars from an aircraft (Cessna) equipped with two h-2 antennas that was fixed to the supporting rods beneath the wings. One observer operated an ATS-R2000 receiver that continuously scanned for all the frequencies that were transmitted by the dropped GPS-collars. Another observer used a GPS unit to record the positions of located collars. A team of five people with two vehicles used conventional VHF receivers and GPS equipment to retrieve the collars on the ground. The SPM Simplex project manager was used to transfer the data from the collars to a laptop.

In total seven collars (five males and two females) were successfully retrieved, whereas two other collars were localised but never collected due to heavy rainfall in inaccessible areas during April and early May 2003. One of the collars was delivered at the Serengeti Regional Conservation Project (SRCP) in Fort Ikoma in December 2002. This animal (a male) had most likely been illegally killed when it migrated northwards. The data recorded by the GPS data-logger was, however, intact (Table 1). Two of the remaining collars, belonging to two males had records until December 2002 and mid-January 2003 only (Table 1). Altogether seven collars registered the position during the migration northwards, and six collars recorded data while the wildebeest migrated southwards (Table 1).

Table 1: Overview of the individually coloured wildebeests, their sex, functioning time for the collars and number of fixes obtained. Animals marked with [□] represent the last sampled migration and had one fix per hour.

| Wildebeest ID number | Sex | Function time | Number of fixes |
|-------------------------|--------|---------------------------------|-----------------|
| 1 (killed) | Male | 4 April – 4 August 2002 | 891 |
| 2 | Male | 4 April – 26 December 2002 | 2108 |
| 3 | Male | 16 April 2002 – 16 January 2003 | 2160 |
| 4 | Male | 4 April 2002 – 30 March 2003 | 2824 |
| 5 | Female | 16 April 2002 – 30 March 2003 | 2864 |
| 6 | Female | 16 April 2002 – 30 March 2003 | 2873 |
| 7 | Male | 4 April 2002 – 30 March 2003 | 2901 |
| 8 [□] | Female | 5 May 2003 – 5 May 2004 | 8704 |
| 9 [□] | Male | 7 May 2003 – 7 July 2003 | 1417 |
| 10 [□] | Male | 5 May 2003 – 25 January 2004 | 6066 |
| Total | | | 32808 |

After retrieval, the seven collars were refurbished and remounted on different animals (two females and five males) following the before mentioned procedures. However, this time the GPS-

units were programmed to record their position every hour instead of every third hour as the year before. Five animals (three males and two females) were collared between 5th and 7th of May 2003 in the Ndutu area, whereas two males were marked in the western corridor on the 11th of October. After one year of service we managed to retrieve only three of these collars during the roundup in May 2004. Unfortunately none of the collars from the Western corridor were retrieved during October 2004. Only one of the retrieved collars had managed to log fixes throughout the whole sampling period. The remaining two collars had stored fixes covering 16% and 75% respectively of the intended sampling period (Table 1). The accuracy of the fixes is estimated to average ± 8.5 meters. This is based on control records from five collars kept at a fixed position during more than seven days.

2.2 Transect records

We applied the line transect distance sampling method (Buckland et al. 2001) to estimate population densities of all larger mammals at the size of a bushduiker and larger (i.e. > ca. 10 kg). The sampling included also, two conspicuous land-bird species, ostrich and helmeted guinea-fowl. Active line transects were favoured over passive point transects. This is because line transects are a technique that has been in use longer, it is better developed and also better suited for mobile species and species that are unlikely to be detected unless they are flushed or disturbed (Buckland et al. 2001).



Fig. 5. Mammal records on transect study, Lobo transect. Photo: G. M. Rusch.

The method is based on records of the distance from the line to each object detected when the observer travels along the line. The occurrence of animals was observed by two observers covering a sector of 180 degrees to the right and left sides of the transect, respectively (Fig. 5). When animals were spotted a rangefinder was used to determine distance and angle to the transect. We computed perpendicular distances based on the following records: 1) measurements of the distances from the observer to single animals or to the centre of animal clusters and 2) corresponding measurements of the angles between the transect line and the lines between the observer and detected objects. This basic information was used with the Distance software (Buckland et al. 2001) to fit detection functions that determined the density of animal species per main transect. One great advantage of this approach is that we need draw no distinction, within reasonable limits, between habitats with good or poor visibility. The fitted detection function reflects both the decrease in detectability with distance and the lower proportion of animals that are potentially detectable (Buckland et al. 2001). It is sufficient to assume that all objects close to the line are seen. Assumptions of the line transect survey in the distance sampling method in order of importance are:

1. Objects on the transect line are always detected (i.e. the detection probability on the transect line is 1.)
2. Objects are detected at their initial location prior to any movement in response to the observer and no animals are counted twice due to influence by the observers.
3. Distances and angles are measured accurately and objects are correctly counted in their proper distance category.
4. Sightings are independent events, i.e. flushing of one animal does not cause another to flush.

Multi-species comparisons hinge on the assumption that all species have equal detection probability, which is unlikely. In theory this is not a concern, but it addresses some practical problems. However, these difficulties can largely be mitigated if we for each species fulfil the following demands: 1) adequate sample size, 2) a detection function exhibiting a distinct shoulder and 3) all individuals on the line are detected (Buckland et al. 2001).

Our transects were organised as a grid of systematically spaced lines that were superimposed on the existing road-system in the study area (Fig. 1). Transects were largely restricted to Serengeti National Park (SNP) and small fractions of Ngorongoro Conservation Area (NCA), Grumeti Game Reserve and Ikorongo Game Reserve (IGR). Other more loosely protected areas used by mammal populations in the area but not surveyed by transects are: Grumeti Game Reserve (GGR), Loliondo Game Controlled Area, Maswa Game Reserve (MGR) and Masai Mara National Reserve MMNR (Fig. 1). Each transect had a total length of 1 km and transects were spaced with intervals of 2 km. All transects were permanently "marked" by recording the GPS-positions at their start and end points. Altogether 195 transects were recorded (Table 2). Transects in succession (a run) located in a certain geographical region were given a common name associating them with the region. Although 30 different runs located in different regions were established, we only apply information from the main and largest transect runs in the present study (Table 2). The smaller transect runs were established to be used mainly as control transects and will be incorporated in more thorough analyses to be done later. The main transect runs used in the present analyses are as follows (Fig 1, Table 2):

Fort Ikoma transects – starting from the central area going northwards into the Ikoma open area and following the western borderline of IGR. Partly covering anthropologically affected areas outside SNP.

Grumeti transects – parting westwards from Fort Ikoma Transects and into GGR. These transects are the only ones that are located completely outside SNP and is thus less protected.

Northern transects – starting from the central area going north-east-wards up to the Lobo area, covering woodland as well as small stretches with plains.

Plains transects – starting from Seronera and going south eastwards into NCA and ending at Olduvai Gorge. These transects thus covers some stretches covered with shrubs and trees and are not composed of open grassland only.

Sopa transects – parting west wards from the Plains transects and ending at Sopa Lodge. Covering open grassland and some shrub and wooded savannah areas.

Western corridor transects – starting at Serena and going west wards and ends close to the SNP border at Lake Victoria. Consists of a mosaic of open areas and shrub and woodlands.

Most habitat types within the park were covered by these transects. However, it is important to point out that all transects constitute a mosaic of different habitats. We started the transect study in 2001 and all transects have since then been repeatedly driven as frequent as circumstances allowed to detect and estimate (as far as possible) the densities of larger diurnal mammals in the study area. In table 3 is an annual overview of the total effort invested into each main transect.

The occurrence of animals was observed from a pickup that travelled along the transects at a speed of 15-20 km/hr with two observers standing at the backside, each covering a sector of 180 degrees to the right and left sides of the transect, respectively (Fig. 5). In addition, the

driver observed animals on the road. When animals were spotted, the vehicle immediately halted and the observers recorded the UTM-position of the car, and the measurements needed to enable the use of the DISTANCE software (mentioned above). A rangefinder covering the range 10 to 1000 meters with an integrated electronic compass was used to determine distances and angles. By using these measurements we can, as an extra bonus, compute exact positions (UTM) for the sites where animals were spotted. After the locations of the animals were recorded, the observers could approach animal groups if necessary to improve the counting accuracy of cluster sizes.

Table 2. Overview of all established transect runs in the study area. Only the larger main transect runs marked with an asterisk were applied in this report. The other transects will be useful in later analyses as control transects for the density analyses.

| Transect name | Nr of sub-transects |
|------------------------|---------------------|
| Airstrip | 2 |
| Bologonja | 2 |
| Eastern Transects * | 6 |
| Fort Ikoma Nyakit | 2 |
| Fort Ikoma Nyamum | 2 |
| Fort Ikoma Nyasir | 2 |
| Fort-Ikoma Transects * | 24 |
| Grumeti Transects * | 19 |
| Handajega | 2 |
| Hippo pool | 2 |
| Loliondo road | 2 |
| Migration Camp | 2 |
| Moru Kopjes | 2 |
| Musabi Plains | 2 |
| Naab-Gol | 2 |
| Naironya spring | 2 |
| Ndassiat hills | 2 |
| Ndutu Lodge | 4 |
| Northern transects * | 20 |
| Nyakitono | 2 |
| Plain Sand hole | 2 |
| Plain transects * | 28 |
| Pofu Special Camp | 2 |
| RG South | 2 |
| Robanda Disp | 2 |
| Robanda water pump | 2 |
| Rongai Plain | 2 |
| Serena Lodge | 2 |
| Sopa Transects * | 10 |
| Western Transects * | 40 |
| Total | 195 |

Table 3. The table shows the number of visits to each main transect run and the corresponding length (in km.) driven per year from 2001 up to and including 2004.

| Year | Transects name | Visits | Kms driven |
|------|-------------------------------|------------|-------------|
| 2001 | Eastern Transects | 7 | 42 |
| 2001 | Fort-Ikoma Trans | 7 | 168 |
| 2001 | Northern Transects | 7 | 140 |
| 2001 | Plains Transects | 7 | 196 |
| 2001 | Sopa Transects | 7 | 70 |
| 2001 | Western Transects | 8 | 320 |
| 2002 | Eastern Transects | 2 | 12 |
| 2002 | Fort-Ikoma Trans | 2 | 48 |
| 2002 | Northern Transects | 2 | 40 |
| 2002 | Plains Transects | 2 | 56 |
| 2002 | Sopa Transects | 3 | 30 |
| 2002 | Western Transects | 2 | 80 |
| 2003 | Eastern Transects | 5 | 30 |
| 2003 | Fort-Ikoma Trans | 5 | 120 |
| 2003 | Grumeti Transects | 5 | 100 |
| 2003 | Northern Transects | 5 | 100 |
| 2003 | Plains Transects | 5 | 140 |
| 2003 | Sopa Transects | 5 | 50 |
| 2003 | Western Transects | 5 | 200 |
| 2004 | Eastern Transects | 11 | 66 |
| 2004 | Fort-Ikoma Trans | 11 | 264 |
| 2004 | Grumeti Transects | 11 | 220 |
| 2004 | Northern Transects | 11 | 220 |
| 2004 | Plains Transects | 11 | 308 |
| 2004 | Sopa Transects | 11 | 110 |
| 2004 | Western Transects | 11 | 440 |
| | Total visits/km driven | 184 | 3570 |

2.3 Forage availability and vegetation utilisation by migration

Sampling was designed to establish the availability and consumption of forage in an area critical in terms of the interaction between the protected area with the neighbouring open land in western Serengeti. Samples were collected before (June/July) and after (October) the period when the major migration passed the area.

Biomass assessment comprised the herbaceous vegetation (grasslands and field layer of woodlands) since it constitutes the main forage for migratory ungulates in Serengeti. Samples were collected at 60 sampling sites across a 5 x 50 km grid stretching from the open land in the area of the village of Robanda, into the National Park (green box in Figure 7). At a first stage, protected areas borders were ground-truthed, geo-referenced with a GPS and located on a topographical – vegetation map (Tanzania National Grid of Topographic Series (1:200 000). Thereafter, three management areas were identified (national park, game reserve and open land) and the sampling grid covering the three areas was established in a systematic manner. The sites were layed out starting in the open land area about 5 km West of the game reserve border, at 1 km intervals by pre-programming waypoints in a GPS which were later localised using the GPS 'go to waypoint' function.

At each site a 30 x 30 plot was delimited, where the pre-programmed coordinates were the NW corner. The sites were described in terms of the vegetation type (physiognomy and dominant species) (Table 3). The sampling period coincided with that when intentional burning ('early burning') is practiced.

Site biomass (standing biomass and litter) was sampled by clipping 3 random 25 x 25 cm sub-samples within the 30 x 30 m plot (Fig. 6). The samples were labelled and kept in plastic bags until processing (sorting) in the lab. Prior to the biomass collection, we assessed sub-plot sward height by averaging the height measured at 4 points and we assessed grazing intensity according to the classes indicated in Table 3. High and very high categories were lumped in some of the analysis to attain statistical power. Traces of fire were recorded at the site and at 25 x 25 cm plot level (burnt and non-burnt).



Fig. 6. Biomass sampling.
Photo G. M. Rusch

In the laboratory, the samples were processed within 72 hours. They were sorted into biomass compartments: i) green leaves of grasses, ii) green stems of grasses, iii) green biomass of

forbs, iv) total standing dead biomass and v) total litter (Table 3). The sorted samples were kept in paper bags, air dried and weighted. The amount of standing biomass was used as an estimate of forage availability and the amounts of the different green compartments (total green biomass, proportion of grass green leaves) as estimates of forage quality.

Table 3: Contrast variables and factors included in the study for biomass assessments

| Variable | Classes/compartments |
|------------------------------|--|
| Vegetation physiognomic type | Woodland, wooded grassland, scrub, scrub-grassland, ruderal vegetation, riverine vegetation, open woodland, grassland |
| Management area | NP= Serengeti National Park GR= Ikorongo Game Reserve OA= Open land in the area of Robanda |
| Biomass compartments | Green leaves of grasses |
| | Green stems of grasses |
| | Green biomass of forbs |
| | Total standing biomass |
| | Total litter |
| | Total green biomass |
| | Green biomass/total biomass ratio |
| Fire | Burnt / non burnt |
| Grazing intensity | <i>Low</i> : no bites / no evident signs of defoliation <i>Moderate</i> : < 50 % of shoots with bite signs <i>High</i> : > 50 % of shoots with bite signs <i>Very high</i> : > 50 % of shoots with bite signs and substantial reduction of estimated average canopy height. |

2.4 Data analyses

Animal census data storage and manipulation was performed in Visual FoxPro 8.0. All observations of wildebeest herds from the transect driving were used to calculate UTM-co-ordinates for the centre of clusters by using trigonometric functions in Visual FoxPro, and imported into the Geographic Information System software package ArcView (version 3.3) where the positions were superimposed on a map of the area. Circles of variable diameters were used to illustrate different sizes of the herds. We grouped the records from January/February and September/October to highlight the periods when the migrants are concentrated in Masai Mara in north and on the Plains in south.

We conducted a spatial analysis by projecting GPS-fixes for the ten wildebeest into UTM co-ordinates in SPM Simplex project manager (version 1.2.0) and then imported to ArcView (3.3) and superimposed on a map of the area to enable spatial analyses. We used the same partitioning of the year as for the transect data to show the individual and aggregated movements for the ten collared wildebeests.

We applied animal movement analysis to calculate the distance between successive moves of the animals. The outcome was used in Visual FoxPro to calculate average travelling speed per day on an annual basis as well as daily movement per month. However, these movements will not necessarily describe the actual travelling speed during migration. In order to sort migratory movement from those when the animals were roaming in south and north, we visually inspected the fixes for each of the animals in ArcView to identify “migratory” patterns. We defined a migratory pattern as being a clear directional movement towards the Mara or the Plains area. We determined the onset and termination of the migration by contrasting directional movements with roving movements within a restricted area that are characteristic when the animals

are roaming in south- and northern Serengeti. By using this approach we were able to determine a time and date for the onset and termination of the migration in both directions and the travelling speeds for the animals could be calculated. We used ANOVA tests in the SPSS (version 11.5) statistical package to determine differences in travelling speed among the collared wildebeests.

The software DISTANCE (Laake et al. 1994) 3.5 Release 6 was used to estimate population densities for the 7 most frequently encountered species in each main transect run, therefore yielding overall species yearly densities and an estimation of the wildebeest seasonal movements between major areas within and outside the protected area. Thus the scale of this analysis was for the entire area and not broken down to the habitat level, since the aim of the analyses in this report was to assess general patterns of animal distributions and movements between different areas by pooling monthly records to assess average densities per year. The lack of independence of repeated records on the same transects was considered in the analyses.

Right truncations at certain distances were performed for each species to remove observations at great distances, because they provide little information on density and are difficult to model (Buckland et al. 2001). The records that were excluded depended on the visual inspection of the detection curves for outliers and the distance corresponding to a recommended truncation value of 0.15 of the detection function (Buckland et al. 2001). The DISTANCE software estimates the detection probability as a function of distance by fitting up to six probability functions to the data (Buckland et al. 2001). The estimators used most frequently were those recommended by Buckland et al. (2001), i.e. half-normal and uniform with cosine or simple polynomial expansions. Each model was checked for presence of a shoulder and fit near 0 to evaluate if they met the recommended criterion by Buckland et al. (2001). The estimator used to compute density estimates was chosen based on the least Akaike's Information Criterion (AIC) and Chi-squared goodness-of-fit tests. Differences regarding density for each species per region and year were determined by applying the "stratification by region" option to extract the appropriate 95% confidence intervals that can be used to discriminate among groups.

Data manipulation of the biomass data set was done in Microsoft Excel. Statistical analyses and graphs were produced with the software package SPSS for Windows. We used the Univariate Analyses of Variance procedure for numerical variables and Likelihood Ratio Chi Square tests in the Crosstabs procedure for categorical variables (grazing intensity). Maps were produced with the GIS software ArcView (version 3.3).

3 Results

3.1 Migration and seasonal distribution of wildebeest

3.1.1 Spatial and temporal use of the area

The total number of fixes registered for the ten collared wildebeest was 32808 (Table 1), 60 % of the positions that potentially could to be sampled during the period. The area within which the positions for all fixes from the two migratory cycles were recorded are exhibited in Fig. 7. The GPS data set reveals that migratory wildebeest rarely moved outside the protected areas and only 5 % of their annual time was spent in the open land (Table 4). The Serengeti National Park is apparently the most important area for the migrants as 56 % of their annual cycle was spent there. The Ngorongoro Conservation Area was used in 19 % of the time, whereas Masai-Mara National Reserve (in Kenya) was used in 14 % of the annual cycle. The remaining protected areas were used in 6 % of their annual cycle. Apparently the sexes did not exhibit a synchronous use of the areas, as males and females spent unequal time in the different regions ($\chi^2 = 307$, $df = 7$, $p < 0.001$; Table 4). There were also important individual differences between animals. For example, the proportion of the time spent in the SNP by the individuals

for whom records for the entire migratory period were available, ranged between 35 % and 78 %. There were also animals that spent a considerable time (up to 16 %) in non-protected areas.

Based on the 2003 data set, which encompasses the largest set of complete migrations, we found no statistical differences among sexes regarding the onset and the end of the migratory behaviour (Watson-Williams test: $F = 0.58$, $P = 0.49$ and $F = 0.88$, $P = 0.43$), although, it must be noted that sample sizes were small. None of the animals appeared to be temporally or spatially synchronised during migratory movements, suggesting that none of the marked animals migrated together. A comparison of the positions of individual animals at the onset of the northward migration revealed that the two closest and farthest apart animals were 13.8 km and 126.2 km, respectively. Also, because of the gregarious behaviour of wildebeest during migration, the positions recorded by the ten GPS units represent the movements of a large number of animals migrating together.

The recorded migratory pattern (see Fig. 7) reveal a limited use of the Western Corridor both in the northern and southern routes. None of the animals moved very far west into the Western Corridor close to Lake Victoria. The northward migration largely occurred within the SNP borders. Three males and one female occasionally spilled over into the Grumeti Game Reserve (GGR), Ikoma Open Area (IOA) or Ikorongo Game Reserve (IGR). The southward migration was also largely restricted within the SNP as only two males used areas beyond the National Park border, one went into IGR and the other barely visited Loliondo Wildlife Management Area (LWMA). The movement pattern exhibited by the animals in the following migratory cycle was essentially the same.

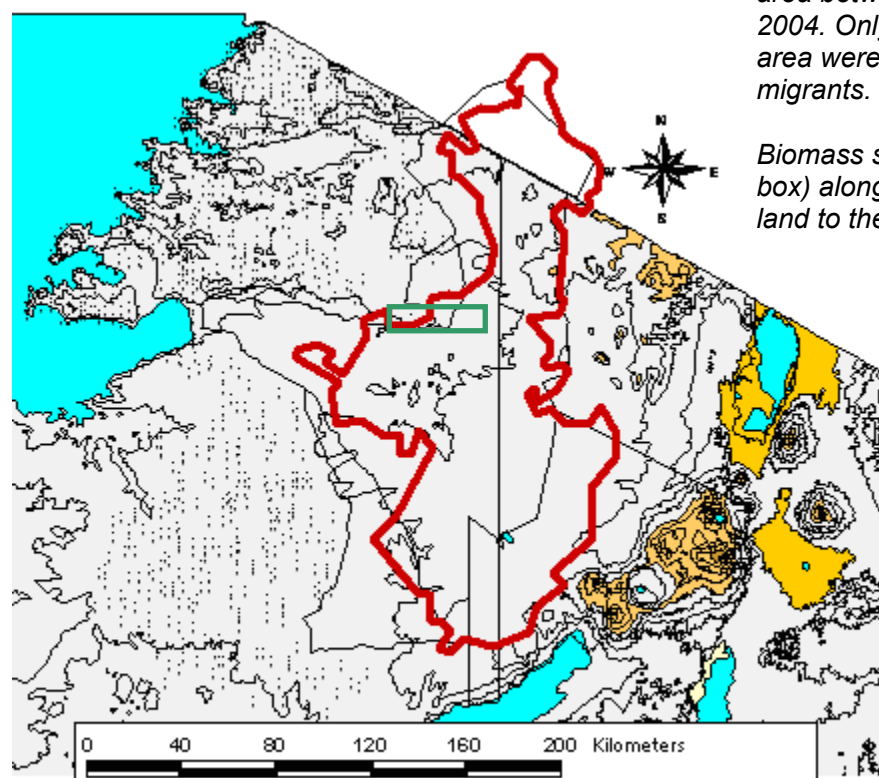


Fig. 7. The area within the red outline includes the 32 808 fixes that were collected from the ten collared wildebeests in the Serengeti-Mara area between March 2002 and May 2004. Only small sections within this area were never used by the tagged migrants.

Biomass sampling grid (within green box) along a gradient from open land to the protected area.

| Area | Males | Female- | All |
|-----------------|-------|---------|------|
| Grumeti G. R. | 0.2 | | 0.1 |
| Ikorongo G. R. | 0.4 | 0.1 | 0.2 |
| Loliondo G. C. | 1.2 | 1.1 | 1.2 |
| Masai Mara N. | 18.5 | 11.0 | 14.0 |
| Maswa G. R. | 2.8 | 5.7 | 4.5 |
| Ngorongoro C. | 16.1 | 21.4 | 19.3 |
| Serengeti N. P. | 57.2 | 55.2 | 56.0 |
| Unprotected | 3.7 | 6.0 | 4.7 |

Table 4. Percentage of fixes per region for: (1) males and females as two groups and (2) all animals as one group.

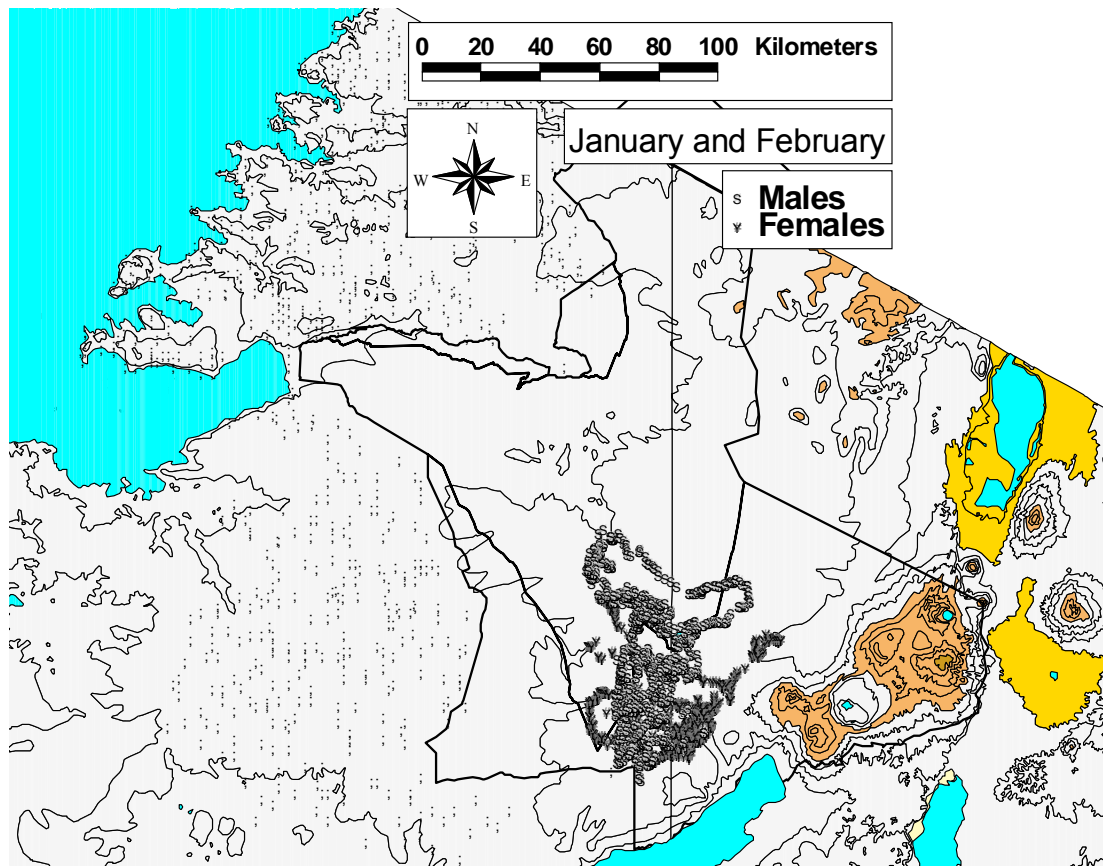


Figure 8. Propagation of the aggregated migratory pattern for the collared wildebeests as detected in the Serengeti-Mara area. The figure exhibits the concentration of wildebeest in the south in January and February.

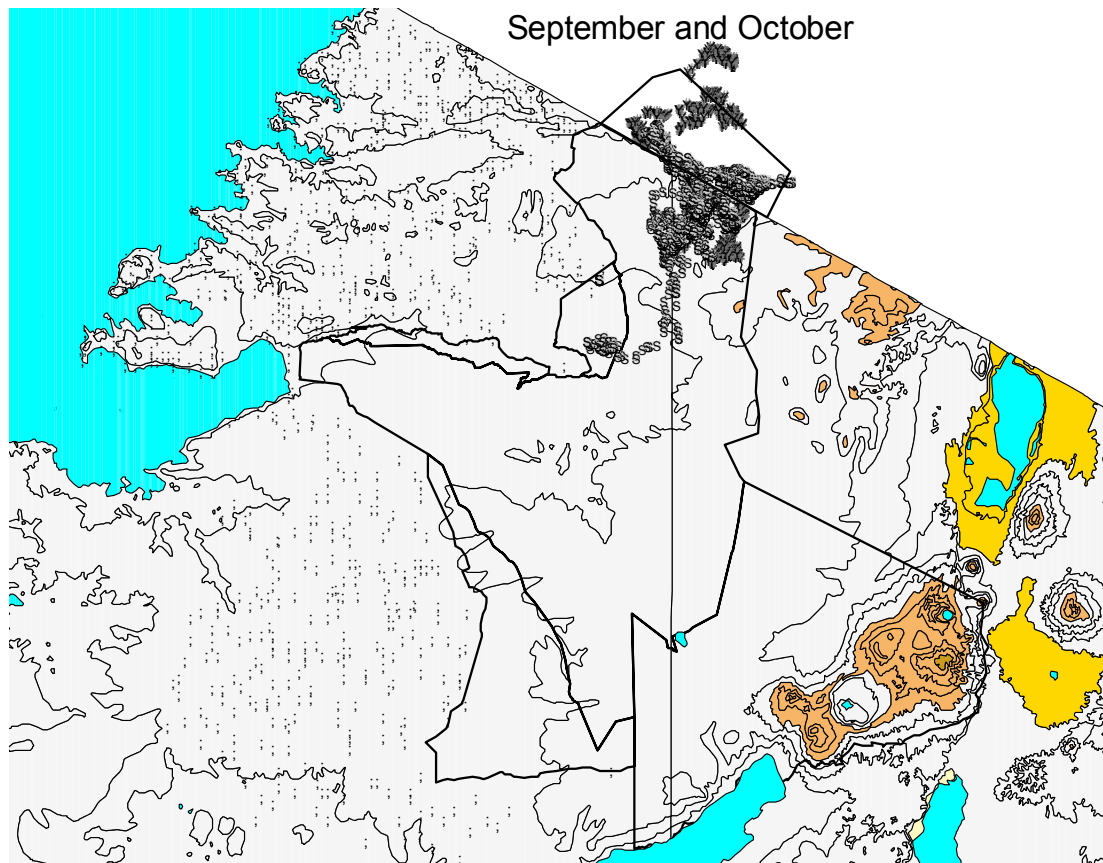


Figure 9. Propagation of the aggregated migratory pattern for the collared wildebeests as detected in the Serengeti-Mara area. The figure exhibits the concentration of wildebeest a somewhat looser aggregation of the population during September and October in the north, compared to the wet season range.

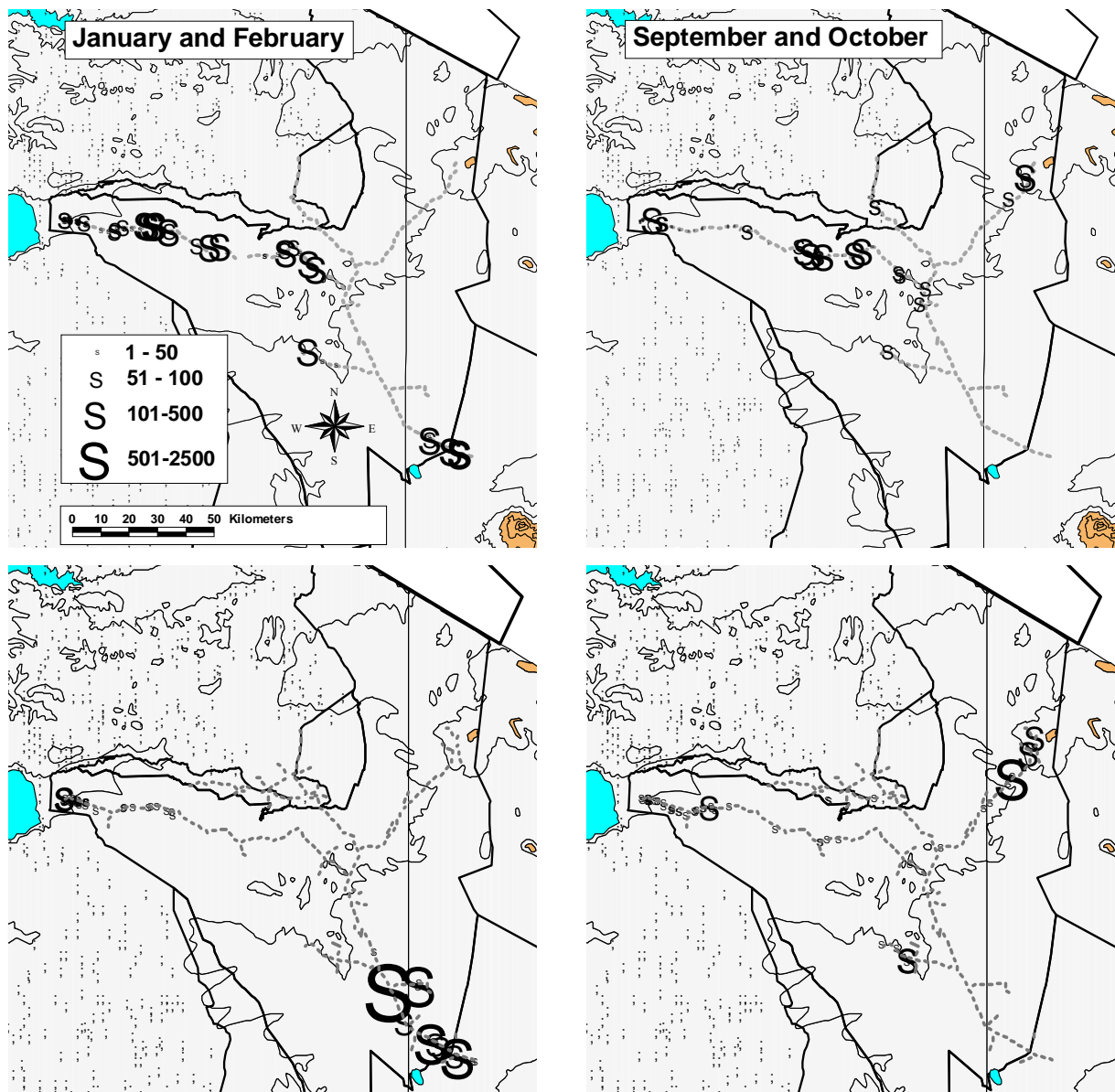


Figure 10. Wildebeest observations from the transect study in the Serengeti area corresponding to the time intervals of the first recorded migratory cycle (the two upper graphs) and the second (the two lower graphs). The partitioning of the year is the same as in fig. 9. Variable herd sizes are illustrated with increasing circle diameters for progressively larger herds. Transects are shown for clarity.

Fig. 8 and 9 illustrate the aggregated migratory pattern of the seven wildebeests recorded during the first migratory cycle. The figure exhibits the extremes of the migratory cycle. In January and February the animals were concentrated in the southern plains in SNP, the south-western part of Ngorongoro Conservation Area (NCA) and in the eastern part of Maswa Game Reserve (MGR). In September and October the wildebeest were highly aggregated in the northern part of SNP and in the MMNR. Apparently the animals were much more concentrated spatially in the dry season range in MMNR than when in the southern plains. The intermediate movements can be interpreted from figure 8. From March and onwards the wildebeest spread out considerably making use of a larger area towards the north and thus sweeping across all of the southern plains. First they moved north-west alongside MGR towards the entrance of the

Western Corridor, thereafter they moved north-eastwards up to LWMA. Thereafter they moved north-west to the entrance of Western corridor and carried on northwards largely inside the northern part of SNP. The migration towards the Mara area appears to have used a relatively narrow fringe of the area in the SNP bordering with the GGR, the IGR and the IOA.

The observations from the transect study are largely consistent with the migratory pattern of the collared wildebeests. The main difference is that wildebeests were observed all year round in the Western Corridor close to Lake Victoria, even in January and February when the GPS data indicate the clearest concentration of the collared wildebeest in the southern plains (Fig. 10). Large herds were also seen in the corridor and in the Ikoma Open Area during the northward migration and also some scattered small herds were observed in the central area of SNP when the migrants were concentrated in the northern range (Fig. 10).

3.1.2 Ranging capacity

The results in this section apply only to data from the first (2003) recorded migratory cycle (the most complete data set) unless otherwise stated. When pooling all data over the year, males and females moved on average similar daily distances ($F = 0.01$, $df = 1$, $p = 0.92$; Fig. 11). The average distance was $6.7 (\pm 0.3)$ km per day, whereas the average distance for the last recorded migration cycle was 8.3 ± 0.5 km per day, suggesting extended movements compared to the first cycle (however the last figure is only based on one complete migration). The wildebeest moved significantly shorter distances in the dry-season compared to the wet-season range. Both sexes covered approximately twice as long daily distances when moving towards Masai-Mara National Reserve or the south-eastern plains than when roaming in these areas ($F = 61.38$, $df = 3$, $p < 0.001$; Fig. 14) but we found no differences between sexes in the distances travelled per day neither when migrating or while in north and south ranges ($F = 1.93$, $df = 3$, $p = 0.12$; Fig. 12). It is important to observe that these calculated distances based on adjacent fixes will always be less than the real length of the path followed by an animal between the same points, because animals do not follow the straight lines we use to calculate movement paths.

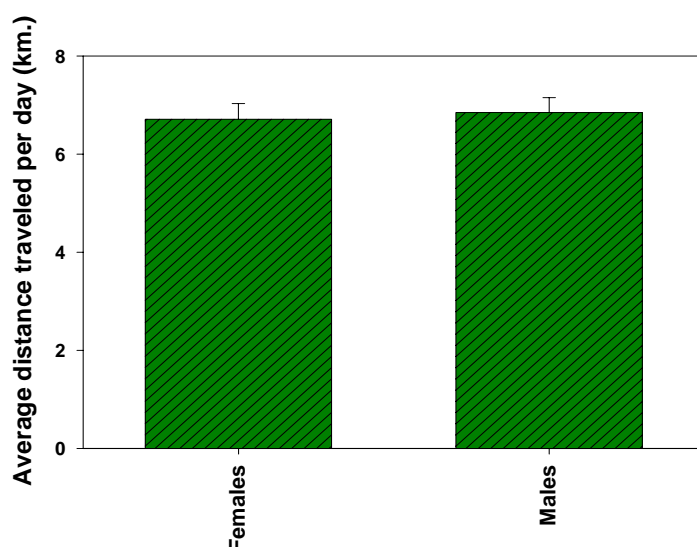


Figure 11. Grouped average movement per day throughout the year for all male and female wildebeests in the Serengeti-Mara area. Values are shown as the mean with 95% confidence interval.

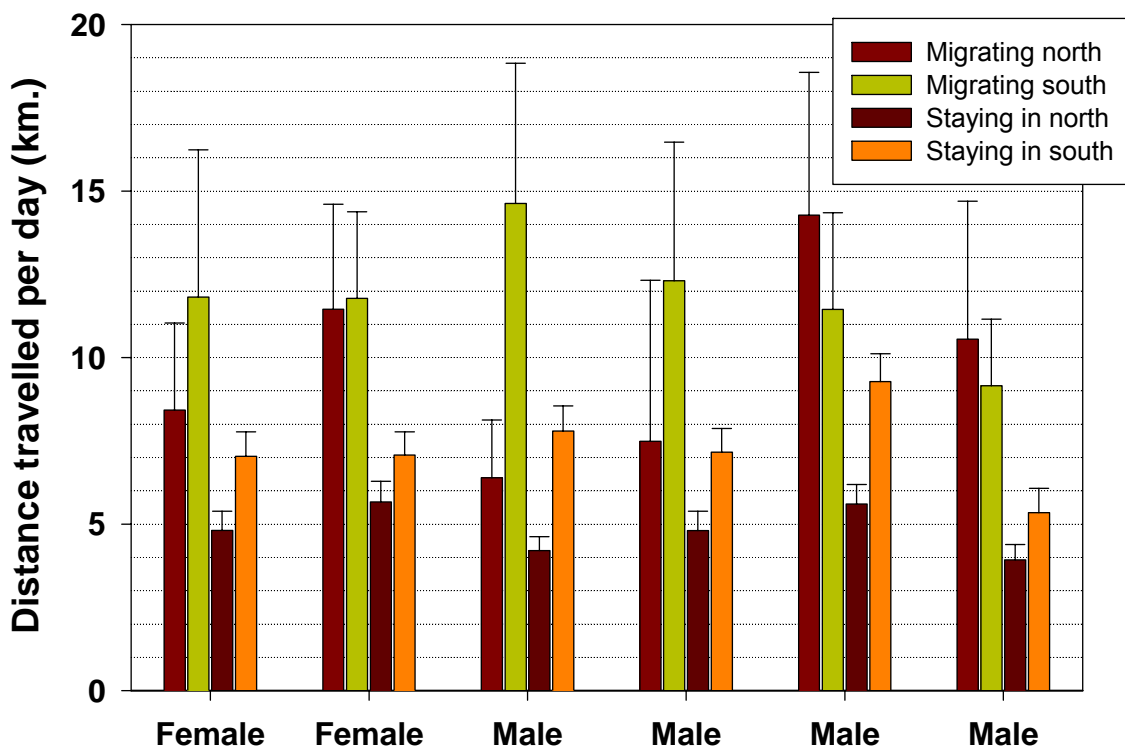


Figure 12. Daily movements for two females and four males during migration, and when roaming in north and south. Values are shown as the mean with 95% confidence interval.

3.2 Density and distribution of larger mammals

During the survey period we observed a total of 53 species. This means that a new species was “detected” every 63.8 km. on average (Table 6, Appendix I). Some species were encountered more frequently than others, meaning with an ‘encounter’ the observation of either solitary individuals or a cluster of individuals. Table 7 shows the frequency of encounters for all species that were observed during the study. Thomson’s gazelle (*Gazella thomsoni*), Impala (*Aepyceros melampus*), Burchell’s zebra (*Equus burchelli*) and wildebeest were clearly the most frequent species to be seen in the study area, whereas 11 species were seen only once.

The cumulative density of the 7 most common species varied clearly among the regions ($\chi^2 = 128.9$, $df = 30$, $p < 0.001$). Highest cumulative density was recorded for The Sopa area that supported a density of 129.4 ind./km² (Table 8, Appendix II). Thereafter followed the Plains, Western- and Northern regions holding 114.6, 61.3 and 48.7 ind./km² respectively (Table 8, Appendix II). These figures contrast the cumulative densities for the more unprotected areas, Fort Ikoma- and Grumeti regions, supporting comparatively modest densities of 28.7 and 23.7 ind./km² respectively. If we grade the cumulative densities per species for all regions it turns out that 3 species were more frequent overall than the others. Thomson, zebra and impala occurred at cumulative densities of 177.6, 103.0 and 84.8 ind./km² respectively (Table 8, Appendix II). Thus, the migratory species Thomson’s gazelle and zebra, appeared to be most fre-

quent in the study area when taking all regions into account. The remaining 4 species: Grant's gazelle, giraffe, topi and warthog are all residents and were much less frequent in the area, having cumulative densities of 18.1, 12.8, 7.0 and 3.1 ind/km² respectively (Table 8, Appendix II).

Table 7. The number of encounters per species during the study period.

| Species | Scientific name | Number of encounters |
|----------------------|---------------------------------------|----------------------|
| Thomson's gazelle | <i>Gazella thomsonii</i> | 2410 |
| Impala | <i>Aepyceros melampus</i> | 1502 |
| Burchell's zebra | <i>Equus burchelli</i> | 1241 |
| Blue wildebeest | <i>Connochaetes taurinus</i> | 1016 |
| Grant's gazelle | <i>Gazella granti</i> | 829 |
| Topi | <i>Damaliscus korrigum</i> | 636 |
| Giraffe | <i>Giraffa camelopardalis</i> | 633 |
| Warthog | <i>Phacochoerus aethiopicus</i> | 485 |
| Baboon olive | <i>Papio cynocephalus anubis</i> | 362 |
| African buffalo | <i>Syncerus caffer</i> | 235 |
| Coke's hartebeest | <i>Alcelaphus buselaphus</i> | 204 |
| African ostrich | <i>Struthio camelus</i> | 192 |
| Helmeted guineafowl | <i>Numida meleagris</i> | 188 |
| Vervet monkey | <i>Cercopithecus aethiops</i> | 133 |
| Spotted Hyena | <i>Crocuta crocuta</i> | 107 |
| Defassa waterbuck | <i>Kobus ellipsiprymnus</i> | 89 |
| Domestic Cow | <i>Bos taurus</i> | 82 |
| Kirk's Dikdik | <i>Madoqua kirkii</i> | 79 |
| African elephant | <i>Loxodonta africana</i> | 73 |
| Hippopotamus | <i>Hippopotamus amphibius</i> | 72 |
| Domestic goat | <i>Capra hircus</i> | 53 |
| Bohor reedbuck | <i>Redunca redunca</i> | 48 |
| Black backed jackal | <i>Canis mesomelas</i> | 41 |
| Lion | <i>Panthera leo</i> | 30 |
| Eland | <i>Tragelaphus oryx</i> | 24 |
| Banded mongoose | <i>Mungos mungo</i> | 24 |
| Domestic sheep | <i>Ovis aries</i> | 16 |
| Bushbuck | <i>Tragelaphus scriptus</i> | 15 |
| Bat-eared fox | <i>Otocyon megalotis</i> | 10 |
| Crocodile | <i>Crocodylus niloticus niloticus</i> | 9 |
| Dwarf mongoose | <i>Helogale parvula</i> | 7 |
| Klipspringer | <i>Oreotragus oreotragus</i> | 6 |
| Cheetah | <i>Acinonyx jubatus</i> | 6 |
| Rock hyrax | <i>Procavia johnstoni</i> | 5 |
| Domestic cat | <i>Felis domesticus</i> | 4 |
| Domestic dog | <i>Canis familiaris</i> | 4 |
| Slender mongoose | <i>Herpestes sanguineus</i> | 3 |
| Golden jackal | <i>Canis aureus</i> | 3 |
| Common duiker | <i>Sylvicapra grimmia</i> | 3 |
| Genet | <i>Genetta species</i> | 2 |
| Serval | <i>Felis serval</i> | 2 |
| African honey badger | <i>Mellivora capensis</i> | 2 |

| | | |
|-------------------------|------------------------------|---|
| Leopard | <i>Panthera pardus</i> | 1 |
| Gerenuk | <i>Litocranius walleri</i> | 1 |
| Rabbit spp | <i>Oryctolagus spp</i> | 1 |
| Bush hyrax | <i>Heterohyrax brucei</i> | 1 |
| Hare spp. | <i>Lepus spp.</i> | 1 |
| African Wildcat | <i>Felis libyca</i> | 1 |
| Oribi | <i>Ourebia ourebia</i> | 1 |
| Steenbok | <i>Raphicerus campestris</i> | 1 |
| Bushpig | <i>Potamochoerus porcus</i> | 1 |
| Spring hare | <i>Pedetes capensis</i> | 1 |
| Black and white colobus | <i>Colobus abyssinicus</i> | 1 |

When we consider intraregional population density variation per year for the species, it turns out that migratory species exhibited significant population density variation. Population densities for zebra varied among years in 4 regions (Northern, Plains, Sopa and Western) out of 6, whereas thomson showed variation in 2 out of the 6 regions (Table 8, Appendix II). Only two of the resident species showed similar variation among years in population density, and this variation was less pronounced than for the migrants. Both giraffe and warthog had a significant variation among years in the Western region (Table 8, Appendix II).

An intraspecies comparison among regions showed that impala had lower densities in Grumeti than in all the other regions (Table 8, Appendix II). Thomson's and Grant's gazelles had higher densities in Sopa- and Plains regions than in the others, whereas giraffe had highest densities in the Western region and tended to be high in the Northern region as well. The remaining species were apparently rather stable in density among regions (Table 8, Appendix II).

3.3 The effect of land-management on forage quality and availability

3.3.1 Land management and forage availability

The three management areas, i. e. Serengeti National Park, Ikorongo Game Reserve and the neighbouring open land in the vicinity of the Village of Robanda, differed in terms of the dominant vegetation types (Fig. 13). The game reserve area had comparatively more open vegetation with the dominance of grasslands and wooded grasslands. The national park area had comparatively less area of these types and more sites with wooded vegetation (wooded grassland and open woodland). The open land had a similar area of grassland and wooded grassland with the addition of typically anthropogenic vegetation as scrub, scrub-grassland and ruderal vegetation (i. e. vegetation in very disturbed habitats with dominance of weed species). These differences need to be taken into consideration when interpreting biomass availability data.

The three management areas differed significantly in the amount of forage available prior to the wildebeest migration in the area. Total standing biomass of herbaceous vegetation was lowest in the game reserve area, with nearly 50% of the standing biomass of the OL (Fig.14). There is however a considerable variation in standing biomass among sites within each management area, indicative of a patchy distribution of growth conditions (soils and rainfall) and/or grazing by non-migrants.

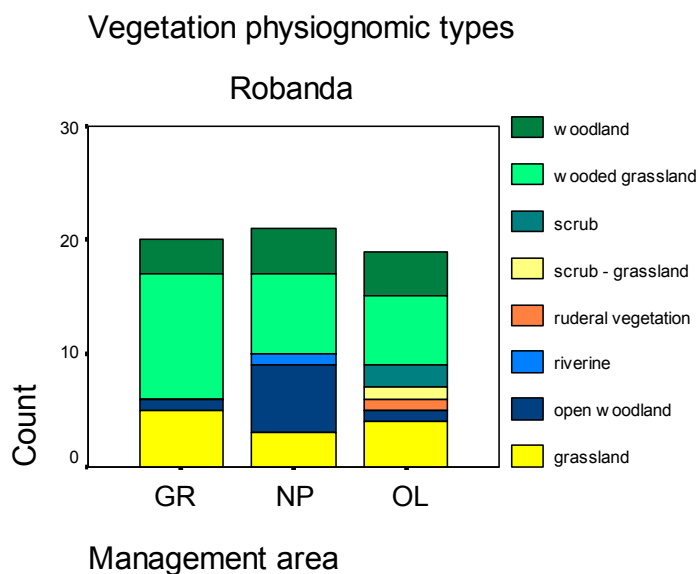


Fig 13: Vegetation types in the sampling grid across land management areas: the Serengeti National Park (NP), the Ikorongo Game Reserve (GR), and in the open land in the area of Robanda (OL)

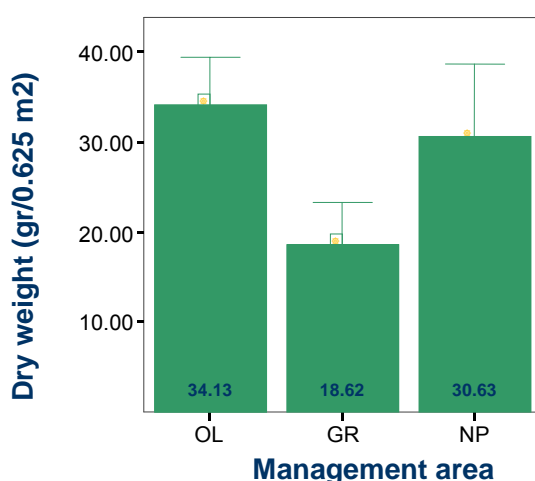


Fig. 14 Average above ground total standing biomass in July 2001 in three management areas in Western Seregenti : Open land (OL), Ikorongo Game reserve (GR) and Serengeti National Park (NP).

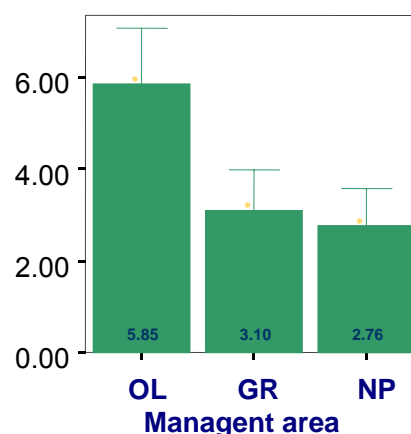


Fig. 15 Average grass green leaves biomass (air dry weight) in July 2001 in three management areas in Western Seregenti : Open land (OL), Ikorongo Game reserve (GR) and Serengeti National Park (NP). Means and SE.

The areas differed also in the composition of the different biomass compartments. There was in average nearly twice as much green leaf biomass in the OL compared both to the GR and NP areas (Fig. 15) but NP sites had the highest biomass of grass green stems (Fig. 16). The concentration of green forage, the amount of green biomass per unit of canopy height was significantly higher in the open land (Fig. 17). In average, green biomass was approximately 40 % more spread through the canopy in the NP compared to the OL sites. These differences in the amount and distribution of biomass compartments indicate that land-management practices affect the amount and the total and relative amounts of biomass for migratory herds moving

northward. The differences were not only evident between the open land and the protected area, but also between the national park and the game reserve.

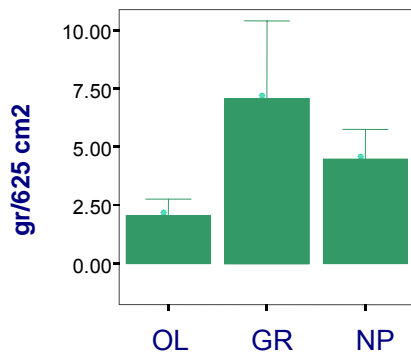


Fig. 16 Average grass stem biomass (air dry weight) in July 2001 in three management areas in Western Seregenti: Open land (OL), Ikorongo Game reserve (GR) and Serengeti National Park (NP). Means and SE.

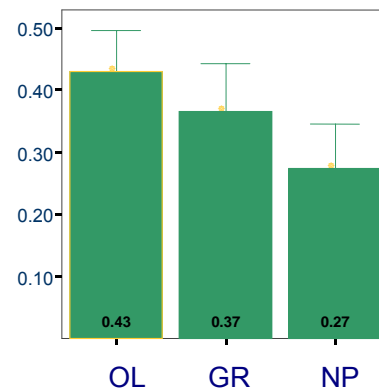


Fig. 17 Biomass concentration (average standing biomass / sward height) in July 2001 in three management areas in Western Seregenti: Open land (OL), Ikorongo Game reserve (GR) and Serengeti National Park (NP). Means and SE.

3.3.2 The use of the area by grazers

For the entire sampling area, more than 50% of the plots showed no signs of grazing before the migration passed the area, but there were however, some differences between management areas in terms of grazing pressure. The OL and NP areas had least signs of grazing in June, where 90 and 80 % of the plots, respectively showed no evident signs of grazing. In contrast, only about 50 % of the GR plots had been heavily grazed at this time (Fig. 18).

Overall, the protected area (national park and game reserve together), was highly used by grazers during the northward migration, but there was also an important proportion of plots that were only moderately grazed or not grazed at all (Fig. 19) The GR and NP areas were used relatively equally. In both cases, approximately 30 % of the plots were grazed heavily or very heavily and 40 % showed no evident signs of grazing. In contrast, grazing pressure in the open land was low, i. e. the majority (>60%) of the OL plots showed no signs of grazing, and very few were grazed heavily.

Regardless of the management type, the degree of forage utilization during the period of northward migration was inversely related to plot standing biomass. Plots with no signs of grazing after the herds passed the area were those with highest standing biomass before the migration. Non-grazed plots in October had had, in June, more than twice the standing biomass of moderately and heavily grazed plots and more than 80 % of the biomass of very heavily grazed plots. However, this relationship was a function of the site vegetation type. In grasslands, very heavily grazed sites were those that had highest standing biomass in June, but the opposite trend was observed in woodlands (Fig 20a and 20b). In contrast to the total amount of biomass available, we did not find a clear relationship between consumption and the amount of green biomass among plots with different grazing intensity. In grasslands, there were no sig-

nificant differences and in woodlands, there was a tendency of plots with highest green biomass of being least grazed (Fig 21 a & b).

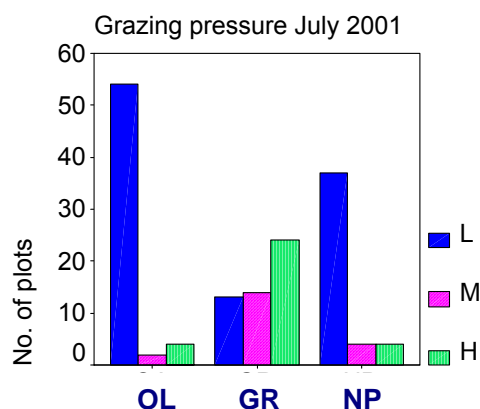


Fig. 18 Grazing pressure in July 2001 in three management areas in Western Serengeti : Open land (OL), Ikorongo Game reserve (GR) and Serengeti National Park (NP). L:: No evident signs of grazing, M: < 50 % shoots bitten off, H: > 50 % shoots bitten off. $P= 0.001$.

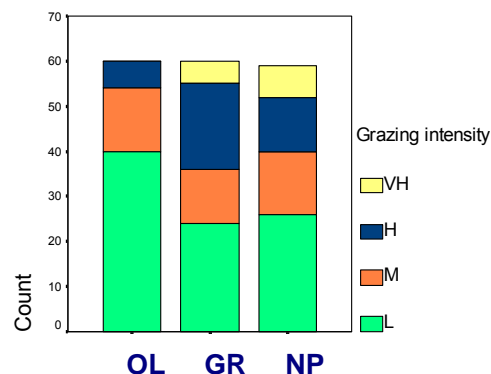
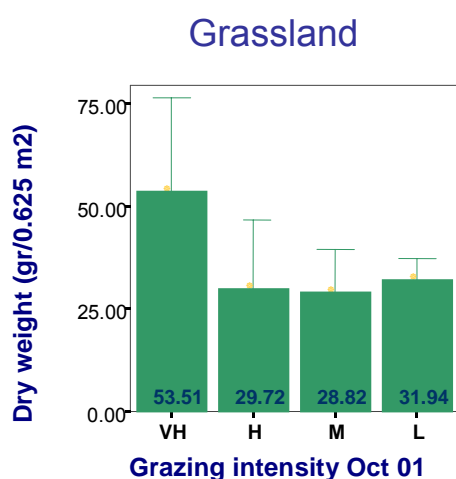
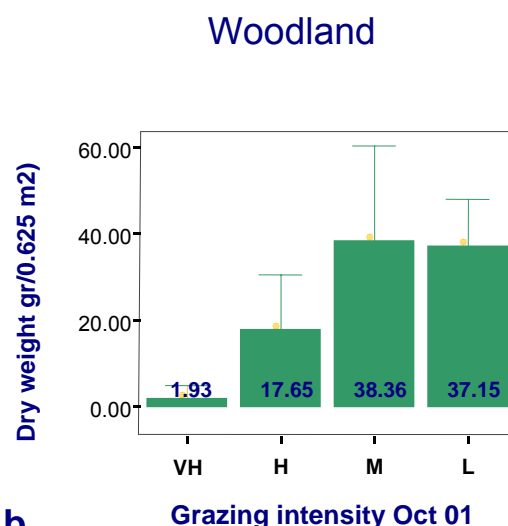


Fig. 19 Grazing pressure in October 2001 in three management areas in Western Serengeti : Open land (OL), Ikorongo Game reserve (GR) and Serengeti National Park (NP). L:: No evident signs of grazing, M: < 50 % shoots bitten off, H: > 50 % shoots bitten off, VH: > 50 % shoots bitten off and substantial reduction of estimated average sward height. $P= 0.001$.



a



b

Fig. 20 Average total standing biomass in July 2001 and grazing intensity categories in October 2001. L:: No evident signs of grazing, M: < 50 % shoots bitten off, H: > 50 % shoots bitten off, VH: > 50 % shoots bitten off and substantial reduction of estimated average sward height. a: grassland and b: woodland

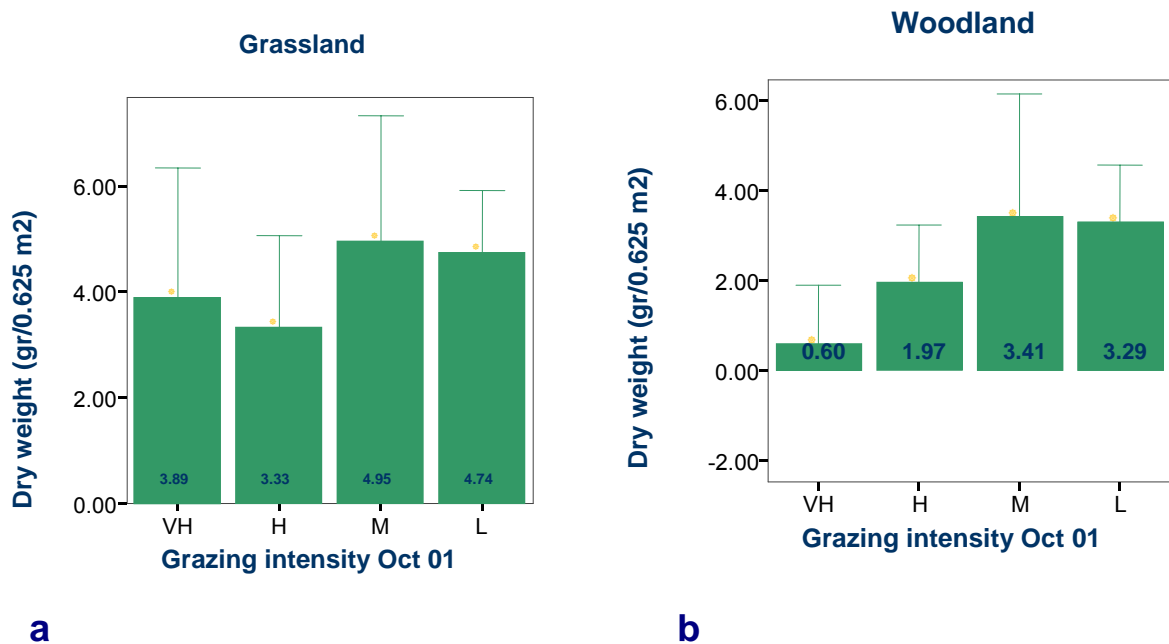


Fig. 21 Average green biomass in July 2001 and grazing intensity categories in October 2001. L:: No evident signs of grazing, M: < 50 % shoots bitten off, H: > 50 % shoots bitten off, VH: > 50 % shoots bitten off and substantial reduction of estimated average sward height.

3.3.3 Forage availability and fire

Fire was outspread in the study area in June, and at the time of sampling large areas appeared to be newly burnt. Twenty eight per cent of the sites were burnt, being the majority of them located along the borderline between the game reserve and national park areas (24 and 18 burnt plots respectively). No burning was recorded in the OL area (Fig. 22). The differences among these contrast were highly significant (Chi square test, Likelihood ratio= 41.014, $p=0.0001$)

Fire significantly reduced both the amount of total standing biomass and of green leaves (Fig. 23). At the onset of migration, the amount of forage available in burnt sites was less than 10 % of that available in non-burnt sites. The proportion of green tissues to total standing biomass was almost equal in burnt and non-burnt sites (Fig. 24), indicating that at the time of migration, burnt areas did not differ in terms of the quality of the forage offer from non-burnt sites.

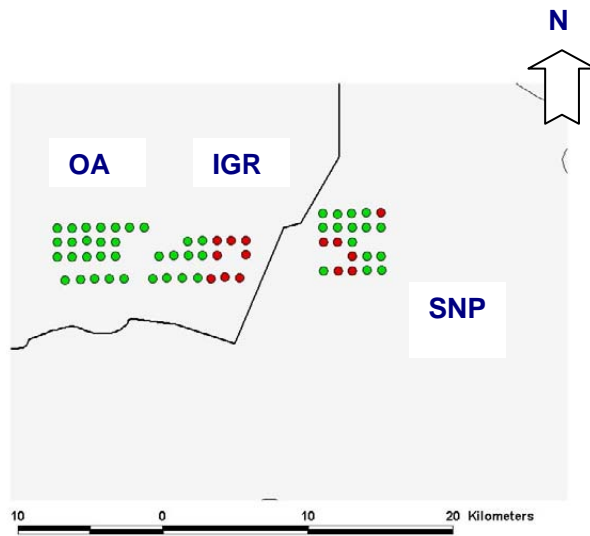


Fig. 22 Burnt (red circles) and non-burnt (green circles) sites across management areas: the Serengeti National Park (SNP), the Ikorongo Game Reserve (IGR), and in the open land in the area of Robanda (OA). Full line indicates the national park border

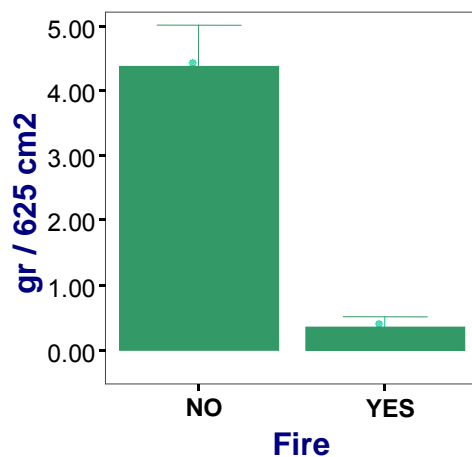


Fig. 23 Average green leaf biomass (air dry weight) in July 2001 in burnt (YES) and non-burnt (NO) in the three management areas in Western Serengeti

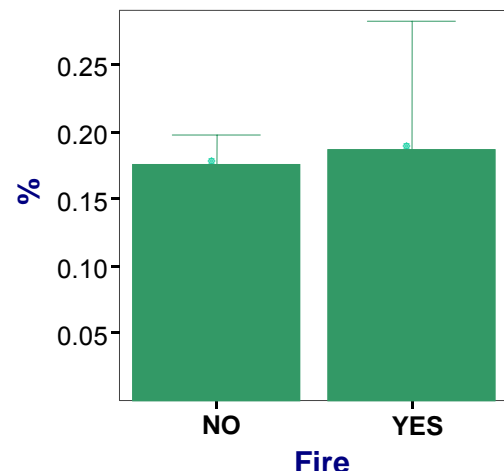


Fig. 24 Green biomass/total standing biomass ratio in July 2001 in burnt (YES) and non-burnt (NO) in the three management areas in Western Serengeti

4 Discussion and prospects

4.1 Wildebeest migration routes

Based on a large number of records of independently migrating individuals, encompassing the entire migratory cycle over 2 years and with record intervals of 3 hours, the data set in this study constitutes the most complete and detailed documentation of the Serengeti migratory

cycle at present available. Our results on wildebeest movements are generally in agreement with earlier notions that the migration in Serengeti occurs mostly within protected areas (Maddock 1979; Sinclair 1995; Thirgood et al. 2004). However, the transect study indicates that large herds of wildebeests use non-protected areas while migrating north, more specifically in the area North of Fort Ikoma, West of the game reserve area, indicating that there may be critical areas for the migration in the open land area.

On average the proportion of time spent in non-protected areas by the GPS fitted animals appears to be somewhat less than that indicated by Thirgood et al. (2004) but this difference could be attributed to sampling errors in small-sized samples, or to yearly differences in migratory patterns that can certainly be expected. In fact, it has been shown that Serengeti wildebeest change area use patterns depending on the distribution of rainfall (Maddock 1979) and Hilborn et al. (1994) have suggested that the occupation of settled areas would increase in drought years.

Our study indicates important differences in the northward migration route compared to the one described earlier by Maddock (1979) and Wilmshurst et al. (1999) where the northern migration made an extensive use of western Serengeti. In contrast, our data suggest a more eastern route, following a narrow fringe on the borderline between the National Park and the game reserve areas. This pattern is generally in agreement with the study by Thirgood and co-workers (2004).

Not surprisingly, the wildebeests moved longer daily distances during migration than when roaming in the north or in the south. When travelling southward their daily movements were about 11 kilometres reduced to about 9 km when they returned to the southern plains. Both the distribution maps and the daily movement distances indicate that in the dry season, there was a more concentrated use of the range (5 km and 7 km in dry and wet season ranges respectively). This pattern can be attributed to relatively higher forage availability (higher standing biomass) in the dry season range or due to the dependence on few water sources. However, the impact of agricultural activities are likely an important factor. In the area of the Masai-Mara National Reserve, Serneels & Lambin (2001) have documented the extent of the land conversion and habitat destruction due to large-scale farming in the past decades and have related these changes to the decline of resident wildebeest herds.

In the southern plains nutritional value of the forage is higher (Murray 1995) but standing biomass is lower, indicating that there might therefore be necessary to range wider to meet nutritional needs in these areas. The most extensive daily displacements for all marked wildebeests occurred in this area. The long movement distances are also related to the ability of grazers to track patches of above average forage quality (McNaughton 1979; McNaughton & Banyikwa 1995) that can result from the erratic distribution of showers in order to optimise energy gain (Wilmshurst et al. 1999). The extended movements from and back to the plains documented in our study coincide with earlier observations on movements during periods of temporary droughts (Maddock 1979; Wolanski et al. 1999), and are also in agreement with earlier statements about the use of forage reserves accumulated in the area during 'bottleneck' periods (Frank et al. 1988).

4.2 Density of large mammals

Compared to the density estimates derived from aerial census (Campbell and Borner 1995), our ground estimates are generally higher for species appearing in both surveys. This applies to the following species (densities given in ind/km²): impala (14.1 vs. 4.0), Grant's gazelle (3.6 vs. 1.0), giraffe (2.1 vs. 0.5) and warthog (0.5 vs. 0.3). The only exception is topi, with a density of 1.2 vs. 4.7 in Campbell and Borner (1995). The differences in density estimates can be in part attributed to the different observation technique used (ground surveys vs. air based, systematic reconnaissance flight). It is likely that the lower estimations of the air counts are because more animals are usually missed during flights as time to observe is short and shrub and trees reduce visibility. This should in particular apply to impala which is a species that utilises wood-

lands as the main habitat. However, in earlier predictions (Campbell & Hofer 1995) hunting was expected to have little influence on Grant's gazelle populations. In contrast, the comparison of ground and previous aerial census indicates that topi densities may have decreased considerably since the 1995 report. These results are also in agreement with these authors predictions about unsustainable harvest of topi.

The transect data also reveal differences in density distributions between the protected and non-protected areas (Fort Ikoma and Grumeti transects). In total, common large herbivores (i. e. impala, Thomson's gazelle, Burchell's zebra, Grant's gazelle, topi, giraffe and warthog) had significantly lower densities along the transects stretching through the open land (OL) and the game reserve (GR) areas compared with the areas within the National Park (NP). These results are in agreement with the estimates of resident herbivores in the vicinity of the protected area (Campbell & Hofer 1995) and have certainly a strong component of human-interference but the immediate causes to this distribution need a closer look.

The migratory species were the most abundant species in the area, indicating that this behaviour is quite successful despite migratory species representing the bulk of the off-take, both in terms of the total carcasses and total biomass (Campbell & Hofer 1995, Holmern et al. 2004). In addition, hunting efforts are concentrated in the dry season when the northward migration passes through the area.

4.3 Habitats and the incidence of practices

The area in the vicinity of the village of Robanda (Serengeti District) including settlements, the national park and game reserve areas were identified as important to assess the impacts of human activities on habitats and forage resources since the area is critical with regard to human-wildlife interactions, particularly during the migration period. The social and socio-economic studies that have been conducted within the BHWI-project, indicate that illegal hunting is an important source of cash in this area (Johannesen 2003, Kaltenborn et al. 2004), and also that a substantial part of hunting activity is associated with the migratory route since off-take is highest when herds migrate through the area

These findings, together with the lower densities of common mammals in the non-protected transects, indicate that the direct impacts on wildlife population numbers through off-take can be large; but we also hypothesised that the indirect effects on wildlife populations could be substantial through habitat modification and changes in the availability of forage resources. These could result in shifts in the migration route since animal migratory movements are directly linked to the spatial distribution of habitats and of forage resources, since individuals utilise habitats differently and the spatial distribution of habitat types determine wildlife occurrences. The western Serengeti is an area with a mosaic of habitats and vegetation formations where woodland, bush-land and grassland intermingle but there is also a distinctive pattern along the gradient open land – National Park. The National Park area had a larger proportion of open woodlands whereas the game reserve area had generally a more open vegetation, with wooded-grasslands prevailing. Human activities in the open land created a more varied mosaic with vegetation types that included scrub, scrub grassland and ruderal vegetation all of them lacking both in the game reserve and the national park areas.

The connection of the scrub and ruderal vegetation with human activities is clear. The area immediately bordering the protected area has settlements with agricultural land and areas used for grazing by domestic animals. There is also collection of firewood and wood and plant material for constructions and other uses (Nkya 2003).

The differences between the game reserve and national park areas can be attributed both to possible differences in the physical environment, but also due the management regime that is practised. Fire is one of the main factors that determine the relative distribution of woody and herbaceous vegetation in dry savannas and burning appears to be a common practice in the area. Twenty-eight percent of the sites were newly burnt at the time of sampling and the major-

ity of them were located in the game reserve area and in the national park along the borderline between the areas. In later samplings (data not reported here) all game reserve sites were burnt in the period July-August. These results together with consultations in the area indicate that burning is an established practice in the game reserve area and that fire can be applied as often as yearly. The motivation behind the practice has not been assessed but removal of dry vegetation and promotion of grass re-growth to attract wildlife to hunting grounds, clearing for improved visibility for hunting and driving, and concentration of wildlife into non-burnt areas have been suggested in the consultations. The history of fires in the game reserves is difficult to track due to poor documentation and the often uncontrolled nature of the fires. There is however an impression, that the practice has been intensified in later years. The National Park management also applies fire as part of the practices which follow a burning scheme, but the poor fire control practices together with the results of this study indicate that the areas bordering with the game reserves may be subjected to more frequent burning than stated in the plans.

The general burning practice in the area is to apply 'early burnings', at the start of the dry season when the risk for uncontrolled spread is lower. This period generally stretches between mid-June and end of July, but fires were recorded to be set earlier (April) and also later in the season.

The records of wildebeest locations show that the 'early burning' period coincides with the time when the area is used by migratory wildebeest during the northward migration. At the same time, the biomass data show that 'early fires' substantially reduce the amount of available forage. Both total biomass and green biomass was very low in burnt sites at this time (less than 10 % of non-burnt sites) due to the short interval between the moment when the area is burnt and the use of the area by the northward migration and because rains are sporadic at this time, at the start of the dry season and limit growth. Accumulated forage in ranges that herbivores occupy during 'bottleneck' seasons when low or no forage production occurs is crucial for the migratory system (Frank et al. 1998). Consequently, if the area affected is large, the 'early burning' practice will imply a substantial reduction of the forage available for migratory herds during migration and in the dry season. A more careful consideration of the timing of the burning and of the frequency of fires appears to be necessary when planning future management practices and regulations since food availability during the dry season is critical to the wildebeest (Mduma et al. 1999, Wilmshurst et al. 1999).

4.4 Forage available for migration

On average, when burnt sites were excluded from the analyses, NP sites had higher standing biomass than GR sites prior to the migration pass through the area. Biomass in OL was marginally lower. However, forage quality in terms of the amount of green leaves of grasses was significantly higher in the OL sites. There were also other differences among areas related to the quality of forage. Both the NP and OL sites had significantly higher biomass of stems whereas biomass concentration (the amount of biomass / height unit) which is related to the forage efficiency was higher in the OL than in the NP. Also the percentage of green leaves of grasses to total standing biomass was lowest in the NP sites.

NP sites had highest standing biomass and also had a larger proportion of dead biomass and of stems. These results are indicative of a general lower disturbance pressure (grazing, fire and cultivation combined) in the NP area compared to the GR and OL.

Green biomass was high in the OL which was likely related to a low grazing pressure in the area, in agreement with the findings in the socio-economic studies that husbandry occurs in the area but only to a limited extend, and by the records of wildlife distribution indicating significantly lower densities in the transects across the OL. They are also in agreement with the estimates of forage consumption before and after the migration period. The OL has a substantially higher proportion of sites with low grazing and no sites where grazing was very high. These results are in agreement with the GPS-tracking and transect data that indicate a low use of the area by migratory wildebeest and other wildlife. It is also in agreement with the findings

of the socio-economic studies that show that the use of the area by livestock is also limited at the moment. The results are relevant to studies dealing with herbivore forage patch selection at large (regional) scale by using standing biomass predictors (e. g. Wilmshurst et al. 1999, Posse et al. 2005). Neither total standing biomass nor green biomass was a good predictor of consumption in anthropogenic habitats.

The differences between the GR and NP are more surprising since there were no *a priori* indications of differences in forage availability and quality between the areas. The lower amount of standing biomass together with a lower proportion of stem biomass and a higher proportion of green leaves in GR sites can be related to two factors that can reduce biomass accumulation. In the first place, fires seem to be more frequent in the game reserve area (see discussion in the section above). The game reserve area also had a higher predominance of open vegetation types, which is also in agreement with higher disturbance. The second can be related to intense grazing along the migratory route. The GPS records indicate that herds used a narrow fringe of the area at the western limit of the National Park bordering with the Game Reserve during the northern migration. Estimates of forage consumption after the northern migration passed the area are indicative of somewhat higher levels in the GR compared to the NP. In the game reserve, there was a tendency of a higher proportion of sites with high consumption and fewer sites with low and medium consumption compared to the NP.

The vegetation type appears to play a role in the amount herbaceous vegetation biomass that is consumed. Grazing pressure in grasslands was highest in sites with the highest standing biomass before the migration period whereas in woodlands, heavily grazed sites were those with lowest biomass prior to migration. The reasons for this pattern are not clear but it appears that migratory herds selected areas with highest standing biomass in the grasslands that are main foraging habitat. The patterns in the woodlands can be attributed to the recurrent use of some areas for protection and resting for migratory herds and other herbivores rather than the sites being used as primary foraging areas.

5 Implications for management

Although it appears that current migratory routes are more concentrated within the protected area both spatially and regarding the length of the migratory period, than described in the early 70's, the status of the ecosystem is good both in terms of maintaining large and stable migratory populations, and the migratory cycle *per se*. However, areas with settlements are poor in wildlife, both regarding resident species but also in terms of the areas used by the migrants, which appear to avoid settled areas despite that the availability of forage is not limiting. In contrast, migrants do make use of open land areas, and although not used by any of the individuals fitted with GPS collars and not being included in the ground transects, there is observational evidence of the use by migrants of the extensive, low populated area lying to the North and North-West of Fort Ikoma.

The region has had, in the past decades an enormous growth in population and expansion of settlements. From earlier studies, we know that the areas neighbouring the protected dry-season range in Kenya have had a major expansion of farming activities which have already had a tremendous impact on the local wildebeest population. In this view, and considering that the Serengeti migrants make to some extent use of non-protected areas, it appears an imminent necessity to drawing regional development plans for current open land, where land use, settlement and conservation priority areas are defined and managed accordingly in order to ensure the long-term maintenance of the ecosystem. This planning exercise is of great importance to reconcile development and conservation goals both in Tanzania and in Kenya.

The use of fire appears to be an important issue. In the game reserve areas, burning seems to be a common practice, and apparently not entirely in agreement with the practices applied in the National Park, at least in terms of the proportion of the area affected yearly. In addition, fires applied according to current prescriptions can drastically reduce the amount of forage available for migrants when they move through the area. There is a need of research on the

effects of fire regimes and to gain understanding of the motivations behind the practice in the different management zones to guide a revision of current practices including timing, frequency, extension and control measures.

The Serengeti houses a rich mammal fauna whose populations are both affected by hunting and land-management practices such as prescribed and wild fires. The largest mammal populations have been counted for over 40 years in Serengeti by aerial surveys and these long series of data obtained in a systematic way constitute an invaluable basis for research purposes and to guide management. The ground-based surveys in our study can also constitute a 'bench mark' to assess population changes in relation to environmental fluctuations and anthropogenic changes for many species that cannot be effectively recorded in aerial surveys. The data sets are complementary in the sense that the two types of surveys capture more accurately species with different characteristics in terms of body size, habitat preference and population size. Species that form large herds and use open habitats, like wildebeest, can be better assessed by aerial photography and counting since aerial surveys usually cover a larger area. However, ground data can be repeated at shorter intervals, and have therefore the potential to provide more detailed (small-scale) data on habitat associations and temporal distribution patterns, and can also be adapted to monitor impacts of regulated off-take. They can also allow reliable estimations of smaller-sized species and of those that occur in woodlands or areas where sight is limited. Despite that migratory species constitute the bulk of the current off-take, both in numbers of individuals and in the amount of meat, the comparison of our data with previous aerial data do not reveal a decline of the migratory populations. In contrast, there appears to be a declining trend in one resident population (topi). This result conforms to earlier predictions about unsustainable off-take of a number of resident species in Serengeti, including topi (Campbell & Hofer 1995). This trend is a warning that the topi population may in effect be harvested unsustainably and indicates the need for a follow up of this species in particular, but also generally of Serengeti resident populations.

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Appendix I

Table 6. Species reported from transect drives during 2001-04-22 and 2004-11-20 in alphabetical order.

| English name | Latin name |
|-------------------------|---------------------------------------|
| African buffalo | <i>Syncerus caffer</i> |
| African elephant | <i>Loxodonta africana</i> |
| African honey badger | <i>Mellivora capensis</i> |
| African ostrich | <i>Struthio camelus</i> |
| African Wildcat | <i>Felis libyca</i> |
| Baboon olive | <i>Papio cynocephalus anubis</i> |
| Banded mongoose | <i>Mungos mungo</i> |
| Bat eared fox | <i>Otocyon megalotis</i> |
| Black and white colobus | <i>Colobus abyssinicus</i> |
| Blackbacked jackal | <i>Canis mesomelas</i> |
| Blue wildebeest | <i>Connochaetes taurinus</i> |
| Bohor reedbuck | <i>Redunca redunca</i> |
| Burchell's zebra | <i>Equus burchelli</i> |
| Bush hyrax | <i>Heterohyrax brucei</i> |
| Bushbuck | <i>Tragelaphus scriptus</i> |
| Bushpig | <i>Potamochoerus porcus</i> |
| Cerval cat | <i>Felis serval</i> |
| Cheetah | <i>Acinonyx jubatus</i> |
| Coke's hartebeest | <i>Alcelaphus buselaphus</i> |
| Common duiker | <i>Sylvicapra grimmia</i> |
| Crocodile | <i>Crocodylus niloticus niloticus</i> |
| Defassa waterbuck | <i>Kobus ellipsiprymnus</i> |
| Domestic cat | <i>Felis domesticus</i> |
| Domestic cow | <i>Bos taurus</i> |
| Domestic dog | <i>Canis familiaris</i> |
| Domestic goat | <i>Capra hircus</i> |
| Domestic sheep | <i>Ovis aries</i> |
| Dwarf mongoose | <i>Helogale parvula</i> |
| Eland | <i>Tragelaphus oryx</i> |
| Genet | <i>Genetta species</i> |
| Gerenuk | <i>Litocranius walleri</i> |
| Giraffe | <i>Giraffa camelopardalis</i> |
| Golden jackal | <i>Canis aureus</i> |
| Grant's gazelle | <i>Gazella granti</i> |
| Hare spp | <i>Lepus spp</i> |
| Helmeted guineafowl | <i>Numida meleagris</i> |
| Hippopotamus | <i>Hippopotamus amphibius</i> |
| Impala | <i>Aepyceros melampus</i> |
| Kirk's dikdik | <i>Madoqua kirkii</i> |
| Klipspringer | <i>Oreotragus oreotragus</i> |
| Leopard | <i>Panthera pardus</i> |
| Lion | <i>Panthera leo</i> |
| Oribi | <i>Ourebia ourebia</i> |
| Rabbit spp | <i>Oryctolagus spp</i> |

| | |
|-------------------|---------------------------------|
| Rock hyrax | <i>Procavia johnstoni</i> |
| Slender mongoose | <i>Herpestes sanguineus</i> |
| Spotted hyena | <i>Crocuta crocuta</i> |
| Springhare | <i>Pedetes capensis</i> |
| Steenbok | <i>Raphicerus campestris</i> |
| Thomson's gazelle | <i>Gazella thomsonii</i> |
| Topi | <i>Damaliscus korrigum</i> |
| Vervet monkey | <i>Cercopithecus aethiops</i> |
| Warthog | <i>Phacochoerus aethiopicus</i> |

Appendix II

Table 8. Density estimates for the 7 most frequently encountered species in the different regions. Densities are estimated per region, species and year (2001 – 2004). A combined density estimate including all years is also showed per species and region. All estimates are given with sample size (n), lower and upper confidence intervals (LCI and UCI), percent coefficient of variation (%CV) and model (key function+series expansion). Densities are given in individuals per km².

| Species | Transect | Year | n | Density | LCI | UCI | %CV | Combined estimate |
|-------------------|-------------|------|-----|---------|------|-------|------|---|
| Impala | Fort Ikoma | 2001 | 77 | 10.6 | 6.0 | 18.8 | 29.2 | 13.9 (10.3 – 18.8) 15.4 %CV Hazard-rate+cosine |
| | | 2002 | 40 | 22.9 | 11.3 | 46.4 | 36.5 | |
| | | 2003 | 53 | 13.4 | 7.5 | 24.1 | 29.9 | |
| | | 2004 | 163 | 14.1 | 8.8 | 22.6 | 23.8 | |
| | Grumeti | 2001 | | | | | | 2.7 (2.0 – 3.8) 15.5%CV Half-normal+cosine |
| | | 2002 | | | | | | |
| | | 2003 | 8 | 2.9 | 1.1 | 7.5 | 48.3 | |
| | | 2004 | 27 | 2.7 | 1.2 | 5.9 | 40.3 | |
| | Northern | 2001 | 69 | 13.6 | 7.3 | 25.2 | 31.5 | 20.3 (13.7 – 29.9) 13.8%CV Half-normal+cosine |
| | | 2002 | 36 | 26.5 | 11.9 | 58.8 | 41.4 | |
| | | 2003 | 64 | 23.4 | 13.8 | 39.7 | 26.8 | |
| | | 2004 | 95 | 22.1 | 12.5 | 39.2 | 29.4 | |
| | Plains | 2001 | 42 | 8.7 | 2.7 | 28.2 | 63.1 | 12.2 (5.8 – 25.4) 24.9%CV Half-normal+cosine |
| | | 2002 | 24 | 24.1 | 7.5 | 78.4 | 63.6 | |
| | | 2003 | 32 | 6.8 | 2.1 | 22.4 | 64.0 | |
| | | 2004 | 55 | 14.1 | 4.0 | 49.9 | 69.1 | |
| | Sopa | 2001 | 13 | 8.8 | 3.1 | 24.6 | 51.9 | 15.2 (7.0 – 33.2) 27.9%CV Uniform+cosine |
| | | 2002 | 9 | 5.6 | 1.4 | 22.6 | 72.9 | |
| | | 2003 | 8 | 26.1 | 6.7 | 99.3 | 69.9 | |
| | | 2004 | 25 | 18.3 | 6.3 | 53.1 | 54.1 | |
| | Western | 2001 | 168 | 18.8 | 13.4 | 26.4 | 17.2 | 20.5 (16.3 – 25.7) 9.0%CV Uniform+cosine |
| | | 2002 | 60 | 16.1 | 9.6 | 27.2 | 26.8 | |
| | | 2003 | 97 | 18.8 | 12.5 | 28.4 | 21.0 | |
| | | 2004 | 237 | 23.8 | 17.6 | 32.3 | 15.5 | |
| Thomson's gazelle | Fort Iko-ma | 2001 | 27 | 2.2 | 1.1 | 4.6 | 37.0 | 3.4 (1.5 – 7.9) 31.2%CV Negative exponetial +cosine |
| | | 2002 | 4 | - | - | - | - | |
| | | 2003 | 23 | 3.7 | 1.5 | 9.1 | 46.1 | |
| | | 2004 | 47 | 5.2 | 2.6 | 10.2 | 35.1 | |
| | Grumeti | 2001 | | | | | | 5.2 (2.3 – 11.9) 46.1%CV Half-normal+cosine |
| | | 2002 | | | | | | |
| | | 2003 | 17 | 1.6 | 0.4 | 5.9 | 72.5 | |
| | | 2004 | 84 | 6.7 | 3.5 | 12.8 | 33.1 | |
| | Northern | 2001 | 117 | 8.0 | 3.7 | 17.4 | 40.6 | 4.0 (2.3 – 7.1) 29.3%CV Half-normal+cosine |
| | | 2002 | 12 | 1.6 | 0.4 | 7.1 | 79.6 | |
| | | 2003 | 88 | 4.4 | 2.3 | 8.7 | 34.7 | |
| | | 2004 | 77 | 2.1 | 1.1 | 4.0 | 34.1 | |
| | Plains | 2001 | 258 | 40.6 | 26.1 | 63.1 | 22.4 | 71.8 (25.2 – 204.9) 34.2%CV |
| | | 2002 | 87 | 59.3 | 26.5 | 132.8 | 41.9 | |

| Species | Transect | Year | n | Density | LCI | UCI | %CV | Combined estimate |
|------------------|-------------|------|-----|---------|------|-------|------|---------------------|
| | | 2003 | 89 | 22.5 | 11.7 | 43.1 | 33.4 | Half-normal+cosine |
| | | 2004 | 379 | 123.2 | 82.7 | 183.5 | 20.1 | |
| | Sopa | 2001 | 76 | 34.4 | 24.2 | 193.1 | 50.3 | 77.4 (16.4 – 364.5) |
| | | 2002 | 0 | | | | | 52.6%CV |
| | | 2003 | 106 | 220.2 | 89.3 | 543.1 | 45.4 | Half-normal+cosine |
| | | 2004 | 89 | 41.0 | 19.2 | 87.3 | 37.8 | |
| | Western | 2001 | 174 | 13.1 | 8.2 | 20.9 | 23.9 | 15.8 (7.9 – 31.6) |
| | | 2002 | 4 | | | | | 23.0%CV |
| | | 2003 | 99 | 19.0 | 9.3 | 39.0 | 37.5 | Half-normal+cosine |
| | | 2004 | 306 | 20.8 | 14.4 | 29.9 | 18.5 | |
| Burchell's Zebra | Fort Iko-ma | 2001 | 24 | 12.5 | 5.6 | 27.9 | 41.6 | 10.2 (4.8 – 21.9) |
| | | 2002 | 0 | | | | | 26.9%CV |
| | | 2003 | 30 | 6.0 | 2.7 | 12.9 | 40.0 | Half-normal+ |
| | | 2004 | 47 | 5.9 | 5.9 | 30.0 | 42.3 | hermite polynom |
| | Grumeti | 2001 | | | | | | 10.9 (6.8 – 17.4) |
| | | 2002 | | | | | | 14.5%CV |
| | | 2003 | 48 | 9.1 | 4.5 | 18.3 | 35.4 | Half-normal+ |
| | | 2004 | 52 | 11.7 | 6.4 | 21.2 | 30.3 | hermite polynomial |
| | Northern | 2001 | 36 | 18.7 | 7.7 | 45.4 | 46.4 | 19.7 (11.5 – 33.8) |
| | | 2002 | 11 | 3.5 | 0.9 | 13.0 | 70.9 | 19.6%CV |
| | | 2003 | 52 | 25.8 | 14.5 | 46.1 | 29.7 | Half-normal+cosine |
| | | 2004 | 61 | 22.2 | 12.5 | 39.4 | 29.3 | |
| | Plains | 2001 | 24 | 5.2 | 2.0 | 13.4 | 49.6 | 17.2 (2.8 – 107.2) |
| | | 2002 | 47 | 66.5 | 25.8 | 171.1 | 50.3 | 63.5%CV |
| | | 2003 | 11 | 2.2 | 0.7 | 6.8 | 59.1 | Half-normal+cosine |
| | | 2004 | 63 | 20.2 | 9.3 | 43.8 | 40.7 | |
| | Sopa | 2001 | 25 | 43.3 | 16.2 | 115.8 | 51.7 | 28.6 (7.1 – 115.9) |
| | | 2002 | 0 | | | | | 51.9%CV |
| | | 2003 | 29 | 66.8 | 26.2 | 170.7 | 48.7 | Uniform+cosine |
| | | 2004 | 22 | 7.6 | 2.3 | 24.9 | 60.1 | |
| | Western | 2001 | 25 | 5.0 | 2.0 | 12.5 | 47.8 | 16.4 (3.1 – 87.2) |
| | | 2002 | 48 | 59.2 | 22.9 | 153.0 | 50.5 | 58.6%CV |
| | | 2003 | 12 | 4.8 | 1.3 | 17.6 | 68.4 | Hazard-rate+cosine |
| | | 2004 | 24 | 19.0 | 8.8 | 41.0 | 40.3 | |
| Grant's gazelle | Fort Iko-ma | 2001 | 5 | - | | | | 0.2 (0.09 – 0.3) |
| | | 2002 | 1 | - | | | | 20.6%CV |
| | | 2003 | 5 | - | | | | Uniform+cosine |
| | | 2004 | 4 | - | | | | |
| | Grumeti | 2001 | | | | | | - |
| | | 2002 | | | | | | |
| | | 2003 | 0 | - | | | | |
| | | 2004 | 4 | - | | | | |
| | Northern | 2001 | 19 | 0.9 | 0.4 | 2.1 | 43.5 | 1.0 (0.5 – 2.1) |
| | | 2002 | 7 | 1.4 | 0.4 | 5.3 | 67.1 | 24.0%CV |
| | | 2003 | 23 | 1.7 | 0.9 | 3.5 | 35.3 | Uniform+cosine |
| | | 2004 | 22 | 0.7 | 0.3 | 1.6 | 42.6 | |
| | Plains | 2001 | 118 | 8.8 | 5.0 | 15.8 | 29.7 | 9.9 (6.0 – 16.4) |
| | | 2002 | 50 | 10.9 | 5.2 | 22.9 | 38.6 | 22.7%CV |

| Species | Transect | Year | n | Density | LCI | UCI | %CV | Combined estimate |
|---------|-----------------|------|-----|---------|-----|------|------|--|
| | | 2003 | 83 | 15.8 | 8.2 | 30.8 | 34.3 | Hazard-rate+hermite polynomial |
| | | 2004 | 165 | 7.8 | 4.4 | 13.7 | 29.1 | |
| | Sopa | 2001 | 16 | 5.6 | 1.2 | 25.4 | 84.4 | 6.0 (2.0 – 18.4) 38.2%CV Uniform+cosine |
| | | 2002 | 2 | - | | | | |
| | | 2003 | 24 | 13.6 | 4.8 | 38.7 | 54.4 | |
| | | 2004 | 14 | 4.4 | 1.1 | 16.9 | 72.4 | |
| | Western | 2001 | 38 | 1.1 | 0.4 | 3.4 | 59.6 | 1.0 (0.4 – 2.8) 52.8%CV Hazard-rate+cosine |
| | | 2002 | 9 | 1.0 | 0.3 | 3.5 | 71.1 | |
| | | 2003 | 30 | 0.9 | 0.3 | 2.8 | 62.0 | |
| | | 2004 | 35 | 1.0 | 0.3 | 3.2 | 63.1 | |
| Topi | Fort Iko- ma | 2001 | 3 | | | | | 0.4 (0.1 – 1.3) 41.7%CV Half-normal+cosine |
| | | 2002 | 5 | | | | | |
| | | 2003 | 7 | 0.5 | 0.2 | 1.4 | 53.8 | |
| | | 2004 | 19 | 0.7 | 0.3 | 1.7 | 46.4 | |
| | Grumeti | 2001 | | | | | | 2.0 (0.4 – 4.4) 28.3%CV Half-normal+cosine |
| | | 2002 | | | | | | |
| | | 2003 | 18 | 1.3 | 0.5 | 3.0 | 43.3 | |
| | | 2004 | 24 | 2.3 | 0.6 | 9.1 | 74.3 | |
| | Northern | 2001 | 19 | 0.8 | 0.3 | 1.9 | 47.2 | 1.3 (0.4 – 4.4) 44.2%CV Hazard-rate+cosine |
| | | 2002 | 22 | 3.4 | 1.2 | 12.2 | 61.0 | |
| | | 2003 | 12 | 0.7 | 0.3 | 1.6 | 39.5 | |
| | | 2004 | 31 | 1.2 | 0.7 | 2.1 | 28.9 | |
| | Plains | 2001 | 30 | 1.5 | 0.4 | 4.9 | 64.8 | 1.3 (1.0 – 1.5) 8.7%CV Uniform+cosine |
| | | 2002 | 13 | 1.1 | 0.3 | 3.8 | 67.1 | |
| | | 2003 | 18 | 1.1 | 0.3 | 4.6 | 81.0 | |
| | | 2004 | 36 | 1.2 | 0.3 | 5.0 | 78.5 | |
| | Sopa | 2001 | 8 | 0.3 | 0.1 | 0.7 | 44.2 | 0.6 (0.3 – 1.1) 30.6%CV Half-normal+cosine |
| | | 2002 | 2 | | | | | |
| | | 2003 | 4 | | | | | |
| | | 2004 | 14 | 0.6 | 0.2 | 1.9 | 54.7 | |
| | Western | 2001 | 74 | 1.2 | 0.8 | 1.8 | 22.0 | 1.4 (1.2 – 1.7) 8.1%CV Half-normal+cosine |
| | | 2002 | 30 | 1.5 | 0.8 | 2.6 | 29.4 | |
| | | 2003 | 61 | 1.6 | 0.9 | 2.7 | 26.0 | |
| | | 2004 | 81 | 1.5 | 0.9 | 2.4 | 23.7 | |
| Giraffe | Fort Iko- ma | 2001 | 5 | - | | | | 0.2 (0.09 – 0.3) 20.6%CV Uniform+cosine |
| | | 2002 | 1 | - | | | | |
| | | 2003 | 5 | - | | | | |
| | | 2004 | 4 | - | | | | |
| | Grumeti | 2001 | | | | | | 2.7 (1.6 – 4.5) 25.8%CV Uniform+cosine |
| | | 2002 | | | | | | |
| | | 2003 | 13 | 1.1 | 0.5 | 2.5 | 42.3 | |
| | | 2004 | 32 | 3.5 | 1.9 | 6.2 | 29.5 | |
| | Northern | 2001 | 23 | 1.8 | 0.8 | 3.7 | 38.2 | 2.1 (1.3 – 3.5) 19.9%CV Half-normal+cosine |
| | | 2002 | 4 | - | | | | |
| | | 2003 | 20 | 1.9 | 1.0 | 3.6 | 32.3 | |
| | | 2004 | 47 | 2.8 | 1.7 | 4.6 | 26.0 | |
| | Plains | 2001 | 3 | - | | | | 1.6 (1.0 – 2.7) 25.8%CV |
| | | 2002 | 5 | - | | | | |

| Species | Transect | Year | n | Density | LCI | UCI | %CV | Combined estimate |
|---------|-----------------|------|-----|---------|------|------|------|--|
| | | 2003 | 13 | 1.2 | 0.5 | 3.2 | 50.3 | Uniform+cosine |
| | | 2004 | 62 | 3.2 | 1.6 | 6.5 | 35.9 | |
| | Sopa | 2001 | 27 | 1.1 | 0.4 | 2.7 | 45.1 | 1.1 (0.6 – 2.1) 28.1%CV Half-normal+cosine |
| | | 2002 | 1 | - | | | | |
| | | 2003 | 3 | - | | | | |
| | | 2004 | 15 | 1.7 | 0.5 | 5.3 | 58.8 | |
| | Western | 2001 | 39 | 2.7 | 1.6 | 4.6 | 27.5 | 5.1 (4.0 – 6.6) 12.7%CV Half-normal+cosine |
| | | 2002 | 14 | 2.7 | 1.2 | 6.1 | 43.4 | |
| | | 2003 | 52 | 4.9 | 3.1 | 7.9 | 23.6 | |
| | | 2004 | 152 | 10.2 | 7.6 | 13.6 | 14.8 | |
| Warthog | Fort Iko- ma | 2001 | 11 | 0.5 | 0.2 | 0.9 | 32.3 | 0.4 (0.2 – 0.7) 21.6%CV Uniform+simple po- lynomial |
| | | 2002 | 4 | - | | | | |
| | | 2003 | 3 | - | | | | |
| | | 2004 | 19 | 0.5 | 0.2 | 1.1 | 37.2 | |
| | Grumeti | 2001 | | | | | | 0.2 (0.1 – 0.3) 17.5%CV Uniform+cosine |
| | | 2002 | | | | | | |
| | | 2003 | 6 | 0.2 | 0.08 | 0.5 | 49.2 | |
| | | 2004 | 13 | 0.2 | 0.09 | 0.5 | 41.6 | |
| | Northern | 2001 | 13 | 0.3 | 0.08 | 1.3 | 80.6 | 0.3 (0.07 – 1.1) 73.3%CV Half-normal+cosine |
| | | 2002 | 1 | - | | | | |
| | | 2003 | 6 | 0.2 | 0.04 | 0.9 | 88.2 | |
| | | 2004 | 19 | 0.3 | 0.08 | 1.5 | 84.7 | |
| | Plains | 2001 | 22 | 0.5 | 0.2 | 1.3 | 47.4 | 0.6 (0.4 – 0.9) 44.9%CV Hazard-rate+cosine |
| | | 2002 | 5 | 0.5 | 0.2 | 1.3 | 53.7 | |
| | | 2003 | 12 | 0.5 | 0.2 | 1.4 | 56.0 | |
| | | 2004 | 30 | 0.8 | 0.3 | 2.4 | 56.9 | |
| | Sopa | 2001 | 6 | 0.2 | 0.07 | 0.5 | 48.0 | 0.5 (0.1 – 1.8) 44.9%CV Uniform+cosine |
| | | 2002 | 1 | - | | | | |
| | | 2003 | 1 | - | | | | |
| | | 2004 | 14 | 1.0 | 0.4 | 2.2 | 41.2 | |
| | Western | 2001 | 89 | 1.1 | 0.7 | 1.5 | 18.8 | 1.1 (0.7 – 1.9) 19.4%CV Hazard-rate+simple polynomial |
| | | 2002 | 19 | 0.6 | 0.3 | 1.0 | 30.3 | |
| | | 2003 | 64 | 1.8 | 1.2 | 2.8 | 22.8 | |
| | | 2004 | 87 | 1.1 | 0.8 | 1.6 | 18.6 | |

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