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Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania

Thesis for the degree philosophiae doctor

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PREFACE

The study presented in this thesis is the result of collaborative efforts between the Norwegian Institute for Nature Research (NINA) and the Sokoine University of Agriculture (SUA) with the inestimable funding from the Norwegian Programme for Development, Research and Education (NUFU). Professor Eivin Røskaft then Director of NINA, and Professor Romanus Ishengoma, Dean of the Faculty of Forestry and Nature Conservation SUA initiated a platform for smooth collaborative arrangements which gave me an opportunity to study the ranging patterns and population structure of wildebeest *Connochaetes taurinus* in the Serengeti National Park. Indeed, my ambitious objectives made the focus of the study difficult to achieve given the size of the Serengeti ecosystem and conflicting interests in the wildebeest from various researchers. Accordingly, as time went by, some of the objectives were changed to become more focused and I should sincerely thank my supervisors, Professor Eivin Røskaft, Professor Johan du Toit, Dr. Sigbjørn Stokke and Dr. Simon Mduma, for their proper guidance and support. Professor Eivin Røskaft gave up much of his precious time for discussion, sometimes without appointment.

Many people and institutions assisted me in various ways before and during data collection, analysis and write-up while in Serengeti and Trondheim. I have also benefited from using some of the data from others, with few restrictions. The funding and efforts they spent in data collection deserve my sincere gratitude. Very many thanks to my employer, the Sokoine University of Agriculture, for granting permission to further my studies and my host, the Department of Biology at the Norwegian University of Science and Technology (NTNU), for creating a positive working environment. I have also had the opportunity to work with Mr. Kai Collins and Mr. Craig Tumbling at the University of Pretoria, South Africa, who assisted me tirelessly with the basics of GIS (ArcView and ArcGIS) and vortex modelling, as well as literature. Miss Rosena Kibasa at Serengeti

GIS Centre, Mr. Gabriel Maliti at Conservation Information Monitoring (CIMU) and Dr. Ivar Herfindal at NTNU gave me much help with the GIS (ArcView and ArcGIS) software applications, and Dr. Børge Moe assisted me in the analyses using S-PLUS. I am so grateful to Dr. Charles Mlingwa (former Director General of TAWIRI) and the Serengeti TAWIRI staff for hosting me during the entire period of data collection. I am greatly indebted to the Serengeti National Park authority and its staff for field assistance, likewise the staff of Maswa Game Reserve, Ikorongo-Grumeti Game Reserve, Frankfurt Zoological Society and Serengeti GIS Centre who made themselves available for regular consultations.

I am also grateful to my beloved wife, Edina Kokusima, who willingly accepted and endured my long absences. My children, Laura, Linda, Lisa and Victor, were very composed and sympathetic whenever I called them. I also enjoyed the support of my parents, sisters and brothers through their prayers. Last, but not least, I would like to thank my colleagues and fellow students for sharing ideas and jokes. All of this would have been impossible without the blessing the Almighty God gave me.

Tusen takk!

Thanks! Ahsante!

Trondheim, 2007

Vedasto Gabriel Ndibalema

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LIST OF PAPERS

This thesis is based on the following papers, which will be referred to by their Roman numerals:

I. **Ndibalema V. G.** (Submitted manuscript). A comparative review of sex ratio, birth periods and calf survival among Serengeti wildebeest sub-populations

II. **Ndibalema V. G.,** Stokke, S., Røskaft, E. (Submitted manuscript). Variation in adult wildebeest body condition in the Serengeti National Park, Tanzania

III. **Ndibalema V. G.,** Mduma, S., Stokke, S., Røskaft, E. (Submitted manuscript). The relationship between road dust and ungulate density in Serengeti National Park, Tanzania

IV. **Ndibalema V. G.,** Stokke, S., Rusch, G., Røskaft, E. (Submitted manuscript). Habitat use of migrating wildebeest in Serengeti National Park, Tanzania

SUMMARY

This thesis investigates the demographic variation, distribution and wildebeest habitat use in the Serengeti National Park (SNP) and its adjacent protected areas in northern Tanzania. Specifically, the study i) examines whether life history strategies displayed by wildebeest sub-populations could cause variations in sex ratio and calf survival, ii) tests whether the orientation of wildebeest to spatial variations in food resources may have a considerable consequence on their body conditions when sub-populations and group sexes are compared, iii) investigates to what extent dust raised by moving vehicles affects the density and foraging distribution of grazers along the roads, iv) recommends management options suitable for conservation planning of migrating wildebeest.

The sex ratio in the resident sub-population was significantly more female biased than that in the migratory sub-population throughout the study period. Higher birth rates with a more synchronous birth season were more evident in the migratory than the resident sub-population, although in both cases they coincided with seasonal rainfall. Furthermore, a higher annual mean calf survival rate [estimate (0.49)] was recorded in the migratory sub-population than among the residents (0.31). The proportionately higher calf mortality in the resident sub-population can probably be attributed to predation resulting from asynchronous birth. Predator swamping from synchronous birth in the migrants appeared to be more important for the calf than yearling survivals, which was much lower (0.44) than in the resident (0.90) populations. Since birth seasonality in resident (December-January) and migratory (February-March) sub-populations appeared to be distinct, their different life forms strategies may have demographic consequences worsened by environmental and human factors.

Demographic variations between sub-populations were associated with nutritional differences among wildebeest individuals grouped into sexes and seasons. The residents were on the whole

nutritionally better-off than the migrants, perhaps due to a better nutritional environment relative to the energetic costs of migrating. Equally, the timing of reproductive investment strategically differed between the sexes due to their life history traits. Nutritional costs associated with pregnancy, lactation and parental care constrained the body condition of females (through reproduction and survival) in the event of serious food shortage, in contrast to males who thrived comparatively better, even in relatively poor environments. Northward migration, motivated by food abundance, correlated with a south-north rainfall gradient as claimed by previous migration hypotheses.

Grazing along roadsides correlated negatively with the density of dust, which increased progressively with traffic volume and speed as seasons advanced. More dust gathered in the grass on the west than on the east side of the road, basically due to wind effects. Dust deposition was comparatively higher on the short grasses than the long grasses during the dry and late-dry seasons than during the wet season when paired distances (≤ 300m) were compared. However, most grazers fed further out on the west side due to higher dust densities on roadside swards than on the east side. This trend supported the ‘dust aversion hypothesis’, which states that grasses which trap a higher level of dust density are avoided as ungulates tend to feed further away from roads than expected from a random distribution. The test predictions from responsive behaviours of most grazers due to the ‘road disturbance’ and ‘road attraction’ hypotheses were not supported.

Notwithstanding a heterogeneous distribution of resources in the Serengeti ecosystem, habitat use at the ecosystem scale indicates regular selection for open grassland compared to other vegetation types, probably due to availability rather than actual preference. The use of open grassland appeared to be strongest in the Serengeti National Park (SNP), probably due to the level of protection coupled with productivity and nutritional suitability. Open woodland, bush with emergent trees and wooded grassland only served as important habitats during the critical period of food shortage. Resource selection in these habitat patches was largely dictated by grass greenness, the period of the day and the speed of wildebeest movement, which was sex related.

Thus, when managing wildebeest populations, effort should be made to control the effects of anthropogenic activities on the landscape and the wildebeest through habitat changes and demographic variations, respectively. In conjunction with the ongoing natural and man-made changes, wildebeest population viability models need to be in place so that managers can predict the future of the Serengeti wildebeest and their migration.

INTRODUCTION

Predicting the source of variations in the size of populations and identifying factors causing fluctuations in species abundance are basic questions, both in theoretical and applied ecology (Begon *et al*. 1987). Population fluctuations have been explained better by the relative importance of density-dependent (Elton 1949; Nicholson 1933, 1958) and density-independent processes (Andrewartha & Birch 1954; Haldane 1953); nevertheless, density-dependent theory has been central to the dynamics of most animal populations. In their studies, Andrewartha & Birch (1954) focused on population limitations, whereas Nicholson (1958) dwelt on population regulation. Limitation is the process that sets an equilibrium point and is caused by all forms of mortality and loss in reproduction, whereas regulation is the tendency of the population to return, due to density-dependent factors, to the equilibrium level when disturbed from it (Daufresne & Renault 2006; Sinclair & Perch 1996). Therefore, against this backdrop, environmental constraints and regulatory processes are likely to cause population oscillations, limit resources and alter the density of populations by increasing mortality and/or dispersal, reducing reproduction, or both.

The population dynamics of ungulates are determined by a combination of stochastic and density-dependent factors (Sæther et al. 2002; Coulson et al. 2001). Fluctuating climatic conditions tend to affect the population dynamics of various arrays of animal species (Hone & Clutton-Brock 2007; Sæther *et al.* 2004; Stenseth *et al.* 2002; Post & Stenseth 1999). Stochastic processes through environmental factors impede the reproductive output of ungulate populations through delayed maturity, reduced pregnancy rates and calf survival (Herfindal *et al.* 2006; Gaillard *et al.* 1998; Clutton-Brock *et al.* 1988; Schaffer 1974). For example, great variations in climate and food availability between seasons in temperate and arctic regions affect ungulate populations so that they scarcely meet their nutritional requirements in winter because of low-quality forage (Herfindal *et al.*

Banyikwa 1995; McNaughton 1990). Short grasslands have substantially higher concentrations of minerals in the wet-season range of migratory wildebeest than other Serengeti grasslands (McNaughton & Banyikwa 1995; McNaughton 1989). The body condition of wildebeest therefore improves where the best foraging niche (i.e. quality and quantity) is accessed and deteriorates in poor niches (Mduma *et al.* 1999; Sinclair & Arcese 1995). Moreover, feeding strategies may differ among wildebeest individuals, and apparent differences exist due to behavioural adaptation of sub-groups and sex-specific nutritional requirements coupled with body-size related forage selection.

The current study therefore provided an opportunity to examine the differences in sex ratios and annual calf and yearling survival between the two Serengeti wildebeest sub-populations. Previous studies (Mduma *et al*. 1999; Mduma 1996; Hilborn & Sinclair 1979; Estes 1976; Sinclair 1977b; Watson 1969; Anderson & Talbot 1965), through simple population counts, dwelt on population dynamics and did not compare demographic variations between ‘migratory’ and ‘resident’ sub-populations. Life history strategies displayed between wildebeest sub-populations are also assumed to cause differences in body condition during different seasons due to changes in food quality and abundance. Predictions derived from deviations in the body condition, along with food regulation hypotheses, were previously tested using analyses of bone-marrow fat (Mduma *et al*. 1999; Mduma 1996; Sinclair & Arcese 1995). These predictions, however, were based on wildebeest predation and did not focus on visually observable variations in physical condition between sexes and sub-populations in distinct reproductive periods. The body condition was therefore compared to test the effect of spatial variation in wildebeest resource use and nutrition.

Furthermore, tracking of food compels ungulates to randomly use road verges. However, it is hypothesised that most grazers avoid roads due to densities of dust and/or disturbance from vehicles, whereas locally enhanced runoff from rainfall combined with soil disturbance provides green grass near roads which attracts ungulates to feed along the verges. Therefore, it was predicted that road dust and/or traffic disturbance from the 'dust aversion' and 'road disturbance' hypotheses in the SNP would cause ungulates to feed further from roads than expected from a random distribution. Alternatively, it was predicted that road attractants in the SNP would elicit a responsive behaviour among ungulates towards roads. All the predictions were tested together with resource use by surrogate species to explore the likely effects of natural and anthropogenic causes on the wildebeest population between habitat patches at the ecosystem scale. Finally, a recent study on wildebeest movements (Thirgood *et al*. 2004) indicated patterns of residence time and timing of migration in the Serengeti ecosystem, but the conclusions were supported by relatively little detailed information. In the present study, patterns of wildebeest movement, including habitat use, are estimated on a finer scale and tested for differences in movement and patterns of use in habitat patches among individual, collared wildebeest.

This thesis investigates the factors behind the observed variations in demographic patterns between the Serengeti wildebeest sub-populations. Mortality agents other than food are predicted to affect the sex ratio, birth rate and its synchrony because of life-history events. I address age-specific mortality through the calf-survival rate and adult mortality from sex ratio differences as a reflection of wildebeest regulation from density-dependent and/or density-independent mechanisms (Paper I). Nutritional differences and the demographic consequences of feeding strategies displayed between the two sub-populations and sexes are also compared (Paper II).

The study used the feeding response from surrogate species to test whether the density and distribution of wildebeest are ecologically affected by the influence of motor traffic on roadside forage resources to raise the awareness of ecologists and managers to the potential threat of roads and associated tourist facilities (Paper III). Since optimal foraging models assume that animals use ‘rules of thumb’ to decide where to forage (Musiega & Kazaidi 2004; Bailey *et al.* 1996), wildebeests would use ‘spatial memory’ to improve foraging efficiency by orienting themselves to nutrient-rich sites more frequently than to nutrient poor-sites. Finally, the study examined how biotic and abiotic components of the Serengeti ecosystem affect the distribution and grazing patterns of wildebeest. Telemetry data were analysed to investigate, among other things, the spatial influence of humans on wildebeest movements (Paper IV), as human activities interfere with animal distribution patterns or pre-empt access to critical habits (Kideghesho *et al.* 2005; Williamsom *et al.* 1988; Coughenour & Singer 1991; Corfield 1973).

In conclusion, the study looks into the interactive effect of biotic and abiotic factors to consider management options appropriate for conserving Serengeti wildebeest sub-populations and migration.

AIMS OF THE THESIS

The main aim of this thesis is to assess the effects of ecological gradients and anthropogenic activities on wildebeest in the Serengeti ecosystem in order to enhance management practices. The 40 years’ records of Serengeti history confirm wildebeest to be the most studied animal, with much emphasis on population structure and dynamics (see Boone *et al.* 2006; Musiega & Kazaidi 2004; Thirgood *et al.* 2004; Mduma *et al.* 1999; Mduma 1996; Campbell & Borner 1995; Sinclair 1995; Dublin *et al.* 1990; Sinclair 1985; Sinclair & Norton-Griffiths 1982; Norton-Griffith 1973; Watson 1967). Therefore, the thesis focuses on strategic differences between the two Serengeti sub-populations in utilising environmental gradients with the aim to address the following questions:

1. Can different life history strategies among Serengeti wildebeests account for the variations in population structure between the resident and migratory sub-populations? (Papers I & II)
2. Does the spatial variation in environmental conditions and resources have an effect on body condition between sub-populations and group sexes of wildebeest? (Paper II)
3. To what extent can the density and distribution of grazers be affected by distance from a road with variable densities of dust produced by motor traffic? (Paper III)
4. What conservation strategy would be suitable to protect migrating wildebeest if the habitats are utilised selectively? (Paper IV)

STUDY AREA

The Serengeti-Mara ecosystem (as described in papers I, II and IV) (Fig. 4) is defined as the total range of the migratory population of wildebeest, zebra (*Equus burchelli*), Thompson's gazelle (*Gazella thompson*) and elands (*Taurotragus oryx*) (Pennycuick 1975). The system stretches over northern Tanzania and southern Kenya (34° to 36° E, 1°15' to 3°30' S) covering nearly 25,000 km^2 (Sinclair 1979a). Tanzania is bound by pastoral-agricultural communities in the west, whereas the forested Loita hills in Kenya mark the north-eastern edge (Fig. 4). The margin of the Serengeti plains delimits the southern extension and the Ngorongoro crater highland and Gregory rift escarpment merged by the Loita hills, extend south to Tanzania to form the eastern boundary. The system has a conservation core zone consisting of the SNP, which is continuous with the Masai-Mara National Reserve in Kenya, the Ngorongoro Conservation Area (NCA), the Loliondo Game Controlled Area, and the Maswa, Grumeti and Ikorongo game reserves in Tanzania.

(Estes 1991), feed in the morning and afternoon, and are known to eat tree leaves when grass is not available (Kingdon 1989). Unlike most African mammals, wildebeest practise birth synchrony, most of the young being born during a few weeks (Estes 1966, 1976).

Five ‘subspecies’ of blue wildebeest have been described in Africa, based on morphological criteria. Two of these occur in east Africa, with *C. t. albojubatus* - the palest - being found to the east and *C. t. mearnsi* - the darkest – to the west of the Eastern Rift Valley in Kenya and Tanzania, respectively. Three other subspecies, *C. t. johnstoni*, *C. t. cooksoni* and *C. t. taurinus*, are found in southern Tanzania, Zambia’s Luangwa Valley and southern Africa, respectively (Estes 1991). Large herds numbering thousands are observed on the Tanzania Serengeti equatorial plain where the study was based. Smaller herds of about thirty are found in northern Botswana, Zimbabwe (Unwin 2003) and the South African locations of Waterberg, the Krüger National Park and Mala Mala (Hogan *et al.* 2006).

Over one million wildebeests in Serengeti are sustained by a migratory system which provides seasonal grazing; a strategy to avoid competition with other ungulates for part of the year (Fryxell & Sinclair 1988; Maddock 1979). Details of the natural history and ranging pattern of Serengeti wildebeest are available elsewhere (Estes 1966; 1976; 1991; Kingdon 1982; Leuthold 1977; Sinclair 1977a; 1977b; Talbot and Talbolt 1963; Watson 1967). While the status of the species is considered secure as a whole, there is concern for its viability as its habitat range is being slowly marginalised by hunting, cattle ranching and habitat intrusion stemming from overpopulation by humans (Hogan *et al.* 2006; Campbell & Hofer 1995).

RESULTS AND DISCUSSION

Question 1: Can different life history strategies among Serengeti wildebeest account for variations in population structure between resident and migratory sub-populations? (Paper I)

Sampled wildebeest indicated a considerable variation in the relative percentages of individual females and calves between the resident and migratory sub-populations. The percentage of male individuals was also more pronounced in migrants, but overall the male-female sex ratio indicated a strong female-biased resident sub-population compared to the migratory one in all study years. These differences in sex ratios may suggest selective mortality in the sedentary population and not in mobile aggregated male individuals. Two assumptions based on previous models could explain the biased sex ratio, i) recruitment of initially skewed sexes at birth (Trivers & Willard 1973), ii) higher male mortality (Fischer & Linsernmair 2002; Holland *et al*., 2002; Fowler & Smith 1981; Leuthold 1977; Caughley 1976; Estes 1974). Both assumptions reflect a scenario typical for both Serengeti wildebeest sub-populations, but residents appeared to be more vulnerable to predation and/or illegal hunting (Holmern *et al*. 2006; Ottichilo *et al.* 2001; Hofer *et al.* 1993; Georgiadis 1988) than migrants by virtue of their relative densities. Generally, the sex ratio is considered to be equal or slightly in favour of males at birth, but it changes slowly until males separate from females owing to increased male mortality due to higher exposure to mortality agents (Sinclair & Arcese 1995).

The two sub-populations also indicated clear differences in birth seasonality, suggesting an early birth in residents (December-February) and a late birth in migrants (February-April) with consequent peak fluctuations. The timing of labour appeared to be greatly dependent on the influence of the seasonal rainfall on food resources coupled with the condition of wildebeest sexes predetermined by life history events. Births in the migratory sub-population were highly synchronised with a higher proportional mean annual calf survival rate of 0.49 compared to 0.31 in the residents; and since peak seasons closely matched with rainfall, variability appeared to be controlled by seasonal rainfall. The observed differences in birth peaks among migrants in the two breeding seasons were perhaps typical responses to climatic variations (Estes 1976; Watson 1969; Talbot & Talbot 1963). Rainfall, by improving forage quality, was the main factor behind such variations, as the timing of birth positively correlated with the seasonal variability in rainfall. Higher mean calf survival in the migrants confirmed previous observations that calf mortalities are not regulated by natural predation, but are instead density dependent (Mduma *et al*. 1999; Mduma 1996; Talbot & Talbot 1963), including separation of calves from their mothers when large aggregations are disturbed. Accordingly, the accelerated removal of dominant males in the resident sub-population, through natural and/or human predation, might have allowed partially incompetent males to take part in the breeding process, the consequence of which is the reduced birth rate for residents compared to a closely balanced sex ratio in the migratory sub-population.

Question 2: Does the spatial variation in environmental conditions and resources have an effect on body conditions between sub-populations and group sexes of wildebeest? (Paper II)

General observations of the body condition indicated a healthy Serengeti wildebeest population where 79% of the individuals were in good body condition, 19% in moderate and 2% in poor body condition. However, differences in the body condition were evident between sub-populations and sexes. When data were pooled, the resident sub-population and female individuals were in better condition. Seasonal changes correlated with differences in body condition within and between sub-populations and sexes during pre- and post-reproductive periods. Residents were, on average, nutritionally in better condition than migrants because they subsist optimally on abundant food.

This observation supports the ‘predation hypothesis’, in that migratory wildebeest should be in a worse body condition than residents due to the energetic costs of migrating.

Predictions from the ‘nutrition hypothesis’, that the migrants should be in better condition than the residents since the energetic benefits of better food should more than compensate for the costs of migrating, were not supported. This could be attributed to the assumed body condition weakening from the cost of migration rather than from absolute food abundance. As predicted, the northward migration was associated with the improved condition of migrant individuals, which nevertheless did not compare favourably to residents because of the assumed predation-sensitive food foraging. Predation-sensitive foraging influences such behaviour as vigilance (Peacor *et al*. 2002); patch use, diet and habitat selection, including the sexual activities of individual animals (Nelson *et al*. 2004; Kie 1999; Sinclair & Arcese 1995).

In addition, resident males were in better condition during post-rut than pre-rut compared to migrants, whereas migratory males were in better condition during rut and their condition dropped abruptly during the post-rut period. These differences were perhaps attributed to chance. But males usually accumulate fat reserves after rut for the next breeding cycle; nevertheless, the timing between the two sub-populations appeared to differ significantly, probably due to variations in social and reproductive phenology. Although the two sub-populations revealed the benefits of improved nutrition during rut, the condition of migratory males dropped considerably after rut, with a quick recovery thereafter. The behavioural mechanisms for locating high-quality food in specific habitats with different mortality risks probably have selective advantages to migrants (Kinnison *et al*. 2001). As the sex ratio among the migratory and resident sub-populations varied disproportionately (Paper I), it seemed profitable for migratory males to search for higher energy food for competitive mating during the dormant period (Forsyth *et al*. 2005; Sinclair & Fryxell 1985).

Basically, resource competition among migratory males during and after rut could be more severe than would be expected among residents, because there were relatively fewer males amongst residents. Moreover, resident males optimise energy from easily accessible resources in close habitats, which imposes less physiological stress to adversely constrain body conditions in post- rather than pre-rut periods. The condition of females varied throughout the periods, but was generally better during the post-birth stage in both the resident and migratory sub-populations. The drop in condition in migrant females toward the dry period was probably attributable to nutritional stress associated with predation-sensitive foraging (Sinclair & Arcese 1995). Generally, however, females were more affected by variations in the environment than males, perhaps due to a higher demand for energy linked to pregnancy, lactation and parental care.

Question 3: To what extent can grazer density and distribution be affected by distance from the road with variable densities of dust produced by motor traffic? (Paper III)

The increasing number of tourist vehicles was associated with the increased density of dust along Serengeti roads. The effects of wind speed and direction, vehicle intensity and speed were additive during the dry season. The density of dust decreased with distances from the road up to 300 m and indicated a strong correlation with traffic volume at the closest distance of 100 m. Minor seasonal variations in the density of dust was evident at 200 m, and increased significantly more on the west side than the east side of a road due to the effect of the westerly wind blowing at an average speed of 13.2 km hr^{-1}.

The distribution and relative density of grazers determined by distance sampling revealed road aversion behaviour on the west side where foliage was heavily dust contaminated compared to the east side. Nevertheless, it was hard to link a road aversion response with vehicle disturbances (i.e. noise and/or road kills) because the test predictions for these hypotheses were not supported. Moreover, the frequencies of observations averaged during the study period at the closest perpendicular distances would have been practically equal on either side of the road for the vehicle disturbance and road attraction hypotheses to be supported, given the random nature of resource distribution. Belsky (1985) suggested that very little impact of road traffic on the vegetation distribution was required to significantly alter the foraging patterns of sampled grazers.

Usually, foliage contaminated with a fairly high level of dust contains teeth abrasive silica (Williams & Kay 2001; McNaughton *et al.* 1985). Only the Thompson's Gazelle seemed to show a preference for moist *Digitaria macroblephara* grasses on roadsides which apparently had an increased level of dust density during the dry season. The reason for this was not obvious, but it was perhaps a response to immediate metabolic demands for moist grass (Wilmshurst *et al.* 1999). Although the relationship between the foraging distribution of grazers and road ecology is complex, our findings have fundamental ecological implications in that there is a more than 30% annual increase in vehicle numbers, and their speed, in addition to producing more road dust, has signalled an important ecological variant to herbivore distribution and grazing pattern along the SNP roadsides. Based on extrapolated figures, our conservative estimate speculates that over 700 km^2 of SNP roadside vegetation are contaminated by dust which accumulates annually through vehicular movements associated also with road kills.

Question 4: What conservation strategy would be suitable to protect migration if wildebeest habitat use is constrained by human activities? (Paper IV)

Movements of wildebeest were strongly correlated with the highly variable habitat conditions during the study period. Habitat use indicated regular selection for open grassland compared to other habitats, although, at the ecosystem scale, wildebeest appeared to be influenced by food availability rather than actual habitat preference. The use of open grassland appeared to be strongest in the Serengeti National Park (SNP), doubtless due to the level of protection and nutritional suitability (McNaughton 1990; Murray 1995; Banyikwa 1976). Since open short grasslands are greatly more productive during the wet season than other seasons (Wilmshurst *et al*. 1999; Murray 1995; McNaughton 1990; McNaughton & Banyikwa 1995), there is a great need for high-quality food in productive areas which serve as mating and calving grounds (Mduma 1996; Estes 1969).

Habitats the western Serengeti seem to have been only slightly used in the early dry period when collared wildebeest were apparently moving quickly northwards. During this period, open woodland, bush with emergent trees and wooded grassland appeared to be important habitats overall. Strong selection for open woodland compared to wooded grassland, and for wooded grassland relative to bush with emergent trees, could be linked to changed weather, period of the day and sexes. This suggests that wildebeest may feed opportunistically when food resources are scarce, and indicate selection only when food is abundant. The availability of green grass and the presence of surface water apparently strongly correlated with wildebeest movements, even though selection for inland water and permanent swamps/marsh was not apparent. Perhaps open woodland and wooded grassland were selected most in the western corridor during the transition period due to the presence of rivers, rather than the dominance and composition of green grasses.

Our findings and previous studies (Thirgood *et al*. 2004; Talbot & Talbot 1963) indicate that wildebeest movements are being increasingly concentrated in core protected areas, probably more so today than past studies indicate (Fig. 3). The increased rate of daily wildebeest speed in open grassland, bush with emergent trees, bush grassland, open bush and open woodland may be associated with effective avoidance of, or flight response from, environments where they risked predation (Caro 2005; Fryxell & Sinclair 1988) as these habitats are adjacent to the western corridor where human activities are intensive. Given the level of sensitivity toward predation, on average, females moved faster than males in these habitats.

MANAGEMENT AND CONSERVATION IMPLICATIONS

The thesis reveals that the observed demographic variations in the studied sub-populations stem from ecological and anthropogenic actions. For instance, cultivation and settlement outside the park boundaries have blocked elephant *Loxodonta africana* movements and changed their distribution. The combination of elephants, uncontrolled fires and subsequent browsing and stunting of re-growth by giraffes has caused a decline in woodlands and a drop in rainfall (Fig. 5). Since the quality and quantity of forage resources at the ecosystem scale depend on the amount of rainfall, the biotic components of the system may be severely affected. All told, if the ecological effects of large herbivores are combined with human population growth west of the park, which has expanded rapidly over the past 40 years and brought an increase in wildlife and livestock populations, wildebeest can be affected because they are density dependent.

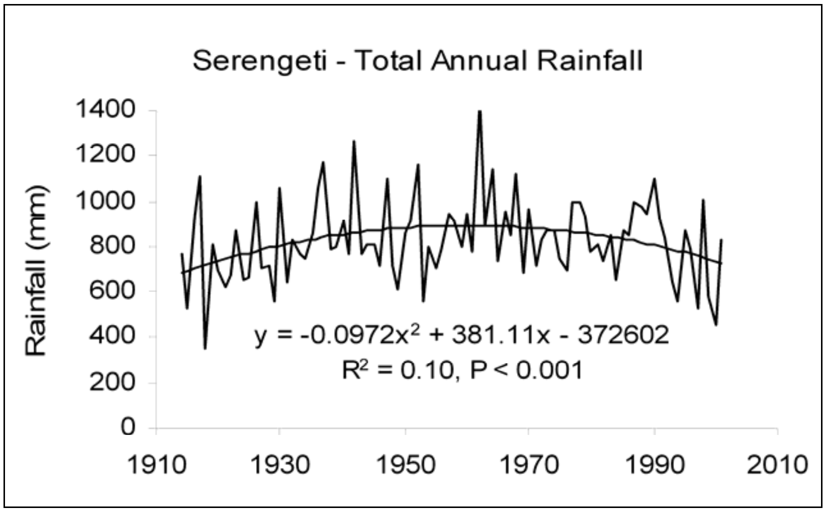

Figure 5. Total Serengeti annual rainfall (after Coughenour 2005)

Likewise, the demand for land appears to be increasingly higher in the western part of Serengeti since wildlife resources are depleted elsewhere. As a consequence, 1) grazing land is becoming scarce as pasture land is converted into cropland, 2) local people are vulnerable to external development and large-scale agricultural schemes which do not benefit local communities. Agricultural encroachments have appeared on park boundaries and former subsistence poaching is slowly becoming large scale and commercial, with an estimated 40,000 - 200,000 animals being killed annually (Mduma 1996; Campbell & Hofer 1995), 3) the need for wild meat has also been exacerbated by the relatively low contribution from tourism to the local economy (Leader-Williams *et al.* 1996). Trends from a previous telemetry study (Thirgood *et al*. 2004; including this one) have indicated a potential human threat to significantly confining wildebeest ranges within core protected areas; yet, the ecological effects of roads seem to be additive.

Perhaps long-term conservation plans involving local communities (e.g. Wildlife Management Areas – WMA), which have been introduced in western Serengeti, should be enhanced. Managers should also intervene when conservation objectives are being compromised by financial gains. For instance, the increased vehicular traffic on Serengeti roads not only disrupts animal behaviour, but also impinges on the foliage quality, and kills many animals. The imposed and suggested restrictions on speed (e.g. speed bumps) and types of vehicle, especially heavy-duty vehicles, in the SNP will just be a good starting point.

FUTURE CHALLENGES

Several studies (including this one) have pinpointed potential threats from natural and man-made changes to the Serengeti ecosystem and wildebeest in particular. Since natural changes occur over a long period of time, management should keep abreast of predictable population and ecosystem changes by undertaking long-term studies to permit interpretations of possibly unpredictable consequences. Many of the observed demographic variations in the wildebeest sub-populations, together with resource selection at a spatial scale, could be associated with complex interactions of natural changes in the Serengeti environment through environmental events as well as ecological succession**.** For instance, rainfall through food supply is the main driver of the ecosystem and varies greatly from year to year, with a tendency to fail after every 10-year cycle.

Non-natural changes may result from tourism, habitat encroachment (e.g. large- and small-scale farming), excessive hunting, fire and disease transfer from humans to wildlife. When these changes are detected, comparison should be made inside and outside the protected areas. For instance, an introduction of alien species into Serengeti through tourism may have profound ecological dimensions including changes in the vegetation structure and species composition. Most of the exotic grass species adapt quickly, thereby ravaging forage plants preferred by ungulates and consequently impinging on the quality of grasses, hence reshaping the patterns of migration owing to poor historical knowledge. Moreover, the ecosystem has lost over 18% of its rangeland to cultivation between 1975 and 1996 around Kenya’s Masai-Mara National Reserve (Homewood et al. 2001; Homewood et al. 2002) and the western and north-western dispersal areas are still being transformed from pastoral grazing land to arable land and human settlement (Sinclair 1995; Sinclair & Arcese 1995). Managers should therefore strive to mitigate non-natural changes within protected areas by controlling tourism and preventing illegal extraction of resources. If the newly introduced community-run wildlife management areas (WMA) become operational, an additional buffer zone around the western Serengeti will reduce encroachment and probably widen the seasonal migratory range. In addition, the WMA approaches will instil conservation awareness and make local communities feel that they are custodians of wildlife resources, while benefiting directly through sustainable utilisation.

Since managing migratory movements entails managing the Serengeti ecosystem, conservation of large species such as wildebeest can be challenging because they require sizeable protected areas. So far, the existing management challenges clearly show that the park is still extremely important as far as conservation migration is concerned, but it alone cannot protect wildebeest. Overall, however, long-term data are needed to develop a complex spatial model to explain the interactive effects of catastrophic events (i.e. drought) and man-made changes for the viability of wildebeest. The fact that the population is not threatened from extinction should not preclude viability analyses, as wildebeest can be vulnerable to catastrophic events, as well as regulatory phenomena which are density dependent.

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A comparative review of sex ratio, birth periods and calf survival among Serengeti wildebeest sub-populations, Tanzania

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A comparative review of sex ratio, birth periods and calf survival among Serengeti wildebeest sub-populations

Abstract

Although mode of life and environmental conditions can predict the composition of relative age and sex structure in most savannah ungulate populations; no comparable demographic studies have previously been reported in Serengeti wildebeest (*Connochaetes taurinus*) sub-populations, Tanzania. Here, I report estimated annual sex ratio, calf survival rate and birth seasonality between resident and migratory sub-populations to test the variation in demographic rates and patterns. Results indicate that the sex ratio was significantly more female biased in the resident and slightly balanced in the migratory sub-population. Migrants had a higher birth rate with a more synchronous birth season than the resident sub-population. Apparently, birth seasonality in the migratory sub-population coincided with seasonal variability of rainfall and birth synchrony was more variable in the migrants than in the resident sub-population. The migratory sub-population had a higher annual proportional mean calf survival estimate (0.49) than the residents (0.31) probably due to higher calf predation mortality in the western corridor. Nevertheless, the proportion of yearling survival rate was much lower (0.44) in migrants compared to residents (0.90). Our results indicate that different life history strategies in the two sub-populations have demographic and conservation consequences engrossed in ecological, environmental and human factors.

Key words: birth synchrony; calf mortality; *Connochates taurinus;* migratory wildebeest; population structure; resident wildebeest

Introduction

The explanation for variation in sex ratios at birth is ingrained on relative profitability of raising sons and daughters between individual parents (Trivers & Willard, 1973). Regardless of the mechanisms based on sex determination, males and females are produced in approximately equal numbers in most species (Edward, 1998; Seger & Stubblefield, 2002). Sex ratio patterns after birth, however, are likely to change if the population is strongly subjected to density dependent factors (Kruuk *et al.,* 1999) and/ or environmental variations (Kruuk *et al.,* 1999; Van Shaik & Hrdy, 1991) apart from predation (Kruuk, 1972; Milner-Gulland *et al.,* 2003; Owen-Smith & Mason, 2005).

In most adult ungulate populations, sex ratios tend to be female biased exhibiting attributes typical for polygynous mating systems due to higher male mortality (Fischer & Linsernmair, 2002; Holland *et al.*, 2002). Thus, male capacity to inseminate a female is only limited when the adult sex ratio is severely skewed (Ginsberg & Milner-Gulland, 1994; Milner-Gulland *et al.,* 2003; Mysterud *et al.*, 2002) especially for species with narrow birth peaks, resulting into extended mating during the peak mating season (Laurian *et al.,* 2000; White *et al.,* 2001); the consequences of which may result in decreased fertility rate.

Detailed reviews of birth seasonality by Sinclair *et al*., (2000) indicate that there is a diverse array in the patterns of birth among tropical ungulates. Generally, however, birth seasonality seems to be well adjusted so that birth peaks coincide with abundant food supply in both temperate (Linell & Andersen, 1998; Post *et al.,* 2003; Rutberg, 1987) and tropical ungulates (Estes, 1976; Mduma *et al.,* 1999; Sinclair *et al.,* 2000). Apart from food supply, the phenology and birth synchrony in most seasonal gregarious breeders are adaptively coordinated to minimize predation risk on newborns (Estes 1976; Estes & Estes, 1979; Sinclair *et al*., 2000).

Therefore, in order to truly understand the dynamics of large-mammal populations, a measure of age and sex structure is required in addition to simple population counts. Demographic data from annual censuses coupled with an assessment of the wildebeest population structure (Estes, 1976; Hilborn & Sinclair, 1979; Mduma, 1996; Mduma *et al*., 1999; Sinclair, 1977; Watson, 1969) enable sex ratios and annual survival rates to be determined. Apparently, none of the previous studies in Serengeti compared the demographic variations between 'migratory' and 'resident' sub-populations. The migratory sub-population is comprised of aggregated wildebeest with no lasting association between adult sexes; where males establish temporary territories when the aggregation is stationary, or, on the move toward north. These animals largely tend to seek short green grass over a large area. Resident sub-population includes all individuals in discrete small groups of regularly associated females which seem to have short distance migration towards the lake during the dry season and back to Kirawira-Nyasirori when it is wet but exclusively found within Kirawira, Ndabaka, and Dutwa plains the whole year round (Sinclair, 1972). These groups have largely restricted movements to the open short grass plains of the western corridor.

This study aimed at recording the sexes, age composition and birth distributions of the two Serengeti sub-populations to test i) if the demographic patterns differ between them, ii) if their differences can be linked to their ecology and mode of life, iii) if the existing hypothesis that 'seasonal breeding coincides with food supply' can be explained by seasonal variability of rainfall (Sinclair *et al.,* 2000) in the two sub-populations.

The sex ratios for all wildebeest sub-populations were predicted to be equal throughout the study period (P1). Variation in demographic patterns through predation and life-history events, apart from food resources, were predicted to affect birth rate and synchrony among the resident than migratory sub-population (P2). This prediction however, dilutes the relative importance of general adaptation hypotheses first that, seasonal breeding is a response to seasonal variability in resource and weather (Schaller, 1967) and the second that birth synchrony reduces predation on newborns (Estes, 1976; Estes & Estes, 1979). The latter agree with the strategy displayed among individual migrants. Since rainfall vary spatially, the peak breeding season in migrants may vary between years and hence predicted easily by peak rainfall (P3).

Materials and Methods

Study area

Field work was conducted in Serengeti National Park (SNP) from September 2003 to June 2005. The Serengeti-Mara Ecosystem (Fig. 1) includes SNP, Maswa, Ikorongo and Grumeti Game Reserve and parts of Ngorongoro Conservation Area (NCA) and Masai-Mara National Reserve to the north (in Kenya). It cover some 25,000 km^2 and is defined by nomadic movements of wildebeest. The wet season has short-rains recorded from November to December and the long rains from March to May (Norton-Griffiths *et al.,* 1975). There is an annual rainfall gradient from south-east (500mm) to north-west (1100mm). Soils have been described elsewhere (Anderson *et al.,* 2004; Anderson & Talbot, 1965). The plains cover about 6,500 km^2 in south-east of SNP and Ngorongoro Conservation Area (NCA) and support large herds of migratory wildebeest during their calving in the long wet season. The wildebeest seasonal movements in relation to resources in the west, north to Masai-Mara and back to the short-grass plain are described elsewhere (Anderson *et al.,* 2004; Hilborn & Sinclair, 1979; Maddock, 1979; Sinclair & Arcese, 1995;Thirgood *et al.,* 2004).

Sampling and data collection

Age and sex counts

Considering the size of SNP which is periodically criss-crossed by wildebeest, we divided the area into four distinct sampling zones (i.e. west, south-east, central and north). Demographic data were determined from ‘haphazardly’ recorded age and sexes at different locations depending on animal sightability twice every month, from October 2003 through June 2005, except July to September 2004. Resident sub-population was sampled from the western zone and migrants all over sampling zones.

While inside an open vehicle, any spotted wildebeest group was approached carefully ($\leq$15 km hr^{-1}) at a distance to avoid disturbance and thereafter a group of 30- individuals (i.e. sampling unit) were counted while simultaneously recording sex and age classes. The sex and age for each individual was determined using diagnostic features developed by Watson, (1967) basing on the genitalia and horn-shape/size. Sex counts were restricted on sub-adult and adult individuals only. Wildebeest individuals in a single file were recorded very closely at regular interval of sections of 30- individuals until the last section was recorded in the entire herd. Sightings and recording of extremely large non-moving herds were made by establishing temporary transects bisecting the herds and slowly driving through while simultaneously recording sections of 30- individuals in every sub-transect of 100 m on either sides of vehicle. A 200 m non-transect was added at the end of each transect to avoid double counting. The area, location name, date, time, GPS position, herd type, sex and body condition scores were recorded on data sheets with the aid of a binocular and tape recorder and later entered into a computer.

Sex ratio, calving periods and calf survival

Monthly records of males, females and calves from each section of the sub-populations were pooled into pre-natal (October-December), natal (January-March) and post-natal (April-June) periods. Variations in adult sex ratio both for migratory and resident groups were determined from recorded numbers of adult males divided by adult females in each case. Records of sex ratio were averaged from daily counts across months and years. Chi-square tests were performed for successive years as independent sample units to test for significance differences in the count of sex structures between sub-populations.

Calving periods were denoted by the recorded numbers of calves together with their mothers. Since wildebeest produce one offspring per season, changes in the proportions of calves to adult females after the calving season were used as an index of relative calf survival (Mason, 1990). The age distributions of newborn calves were obtained from the ratios of recorded number of newborn calves per adult females in a group of 30- individuals. These ratios indicate the mean monthly newborn calves to mature females and were used as index of calving periods between sub-populations; this procedure was important to overcome bias from unequal samples of wildebeest counted on each month. Mature females in this case refer to all adult females including about 20% sub-adult females known to have started breeding (Mduma, 1996). A similar change of ratio in successive months was used as an index of the annual mean calf survival rate. The yearling survival rate was also estimated based on monthly changes of recorded yearlings to adults, since they are always seen associated with both adult sexes.

Rainfall data for the entire study period was obtained from SNP (ecology unit) and analyses were based mostly on the frequently inspected rain gauges grouped according to the established sectors. Mean monthly rainfall records (in millimetres) in the western corridor was assumed to reflect available rainfall to the residents whereas the combined monthly rainfall records from other sectors invariably controlled migratory herd’s movements in quest for water and forage resources.

The monthly mean calves per mature females ratio recorded at the natal and pre-natal periods reflect calf survival rate during the wet and dry seasons respectively. Calf survival rate was calculated as percentage of proportions of calves per breeding females, recorded as yearlings in the next breeding season (Equation 1). Yearling survival rate was estimated from the proportion of recorded sub-adults per adult ratios, survived from yearlings at year (t - 1) and (t). In this case yearlings were considered as calves that survived year (t) to year (t+1) and the sub-adult stage, which usually last for three years, was maintained by yearlings that survived from year (t - 1), t_1 and (t+1). Since the adult component of the population was also affected by mortality factors, I used 99.5% annual monthly mean survival rate previously estimated by Mduma, (1996) in the estimates. I assumed a constant calf survival rate in order to calculate the proportion of calves which survived as yearlings per month in the following equation:

$$\left(\frac{\left(Y_{t+1}\right).\left[0.995(Q+\delta)_{t+1}+0.2(SQ_{t+1})\right]^{-1}}{C_t\left[Q_t+0.2(SQ_t)\right]^{-1}}\right)100\!\!\diagup_{12} \text{..............................equation 1}$$

Where, t = year_t and t+1= year_{t+1}

C = calves,

Y= yearlings,

S= sub-adults

Q = females and δ= males.

The yearling mortality (recorded in 2005) was estimated using equation 2 below. Since the sub-adult stage lasts for three years, its proportion was divided by three and the estimated annual survival rate was based on the mean ratio of the subsequent recorded calves as yearlings and sub-adults during January and March birth peaks for residents and migratory respectively. Year 2003 was assumed to have the same birth patterns as subsequent years. For all estimates a constant adult mortality rate was assumed with regular female birth rates. The annual mean yearling mortality rate was thus given by the following equation;

$$\left(\frac{\left(\boldsymbol{S}_{t+2}\right)^{-1}.3\left[0.995(Q+\delta)_{t+2}\right]^{-1}}{Y_{t+1}\left[0.995\left(Q+\delta\right)_{t+1}\right]^{-1}}\right)100\!\!\diagup_{12} \text{..equation 2}$$

Results

Individual age and sexes

The 18-month period of data collection resulted into a total count of 103,500 individual wildebeest from 3,450 30-individual group samples (ca. 9% of Serengeti population). The data comprised 65,359 (63.1%) adults, 14,916 (14.4%) sub-adults, 6,420 (6.2%) yearlings, and 16,805 (16.2%) calves. Adult proportions including both populations by percentages were 41.1% and 25.6% females and males respectively (See Table 1 for the values). The estimated sex- and age-ratios from all samples had a considerably higher proportion of adult females and more pronounced calves in the resident than migratory sub-population (Table 1). Resident groups were recognized by the distinctive size of calves compared to the migratory groups especially when the two sub-populations mix together during transition season (early dry).

Adult sex ratio

The mean male per female monthly sex ratios for residents and migratory sub-populations were generally significantly different within the resident (χ^2=45.8, df=2, p=0.000) and migratory (χ^2=240, df=2, p=0.000) sub-populations in all study years (Table 2). All over, the pooled sex ratio for all study years significantly differed between the resident (estimate 0.26) and migratory (0.91) sub-populations ($p < 0.001$; Table 2). Sex ratios were generally female biased in the resident than migratory sub-population (Table 2). An independent test for the monthly male-female counts indicates significant differences between the two sub-populations, except for January and November 2004 months (Table 2). A multivariate analysis indicate that variations in adult sex ratio was best explained by the interaction between sub-populations and study years (GLM, F=8.67, df=1, P = 0.003).

Distribution of births and calf survival rate

The average numbers of calves available per adult females in each calving season (Table 3), indicate that the calving period in the resident sub-population started in December through May, whereas in migrants started in late February through April. Residents maintained the calving peak at late January in all study years. Despite the pronounced birth peaks, birth seasons in the migrants unusually fluctuated between February and April in year 2004 and 2005 respectively (Table 3).

Rainfall on the central and south-east sectors is known to be very erratic (Norton-Griffith *et al.*, 1975; Wolanski & Gereta 2001) and the year 2004 had early rains compared to recorded late rains in 2005 (Fig. 2). These trends in rainfall greatly affected the patterns of births, as the records in 2004 indicate that nearly 50% of the calves were dropped in less than two weeks. Nevertheless, births in migrants were highly synchronous and indicated higher production potential compared to the resident sub-population in both years (Fig. 2). A partial correlation analysis also indicates a significant positive correlation between current-season rainfall and calving controlling for sub-populations (r^2=0.179, df=344, p = 0.001).

The estimated mean annual calf survival rate (Equation 1) was $31.5 \pm 4.7\%$ and $49 \pm 3.4\%$ for resident and migratory sub-populations respectively. When an equal birth rate between year 2003 and 2004 was assumed, the mean annual yearling survival estimate (Equation 2) was $90.7 \pm 2.3\%$ and $44.3 \pm 3.8\%$ for residents and migratory sub-populations respectively. These results suggest a higher calf mortality rate in the resident sub-population followed by a steady yearling survival rate. The calf mortality in migrants was considered to be normal despite of low yearling survival rate. These rates however, underestimate calves born outside the birth peaks, as accurate estimates for Serengeti populations suggests that nearly 80% of the young are born within three weeks in a normal season (Estes, 1976; Watson, 1969; Estes, 1966). The independence test for group differences was also highly significant when the birth distributions were compared both in 2004 (Mann-Whitney U-test, Z=-4.104, P < 0.001) and 2005 (Z=-9.758, P < 0.001).

Discussion

The observed demographic patterns clearly indicate variations between the migratory and residents sub-populations, signifying that these two sub-populations perform differently and their life history strategies have different survival costs and benefits. Sex ratio differences indicate that selective mortality factors in adult individuals manifested better in the sedentary than in the mobile aggregated males. Arguably one may assert a biased sex ratio from recruitment of initially skewed sexes at birth as Trivers & Willard, (1973) models suggests; but a higher male mortality in the western corridor could probably be linked to the predation and/or illegal hunting (Georgiadis, 1988; Hofer *et al.,* 1993; Holmern *et al*., 2006; Ottichilo *et al.,* 2001) which invariably alter sex ratios. Despite inadequate demographic data on the resident sub-population, it is generally established that bovid sex ratios are equal or slightly in favour of males at birth. However, the sex ratio change slowly until males significantly separate from females owing to increased male mortality due to higher encounter to mortality factors (Sinclair & Arcese, 1995).

Although it may prove difficult to vividly explain the underlying factors behind sex ratio variation in the two sub-populations from simple population counts, female skewed sex ratio in the west could be attributed to illegal wild meat hunting other than natural predation due to i) inadequate evidence for wildebeest mortality from carcass counts (own unpublished data) in the west compared to other locations, ii) few groups of lions (*Panthera leo*) and hyenas

(*Crocuta crocuta*) recorded in the west during the non-migration phase; more over, their densities are considered to be low there (Campbell & Hofer, 1995), iii) frequent harassment of predators by illegal hunters (Holmern *et al*., 2006.; Loibooki *et al.*, 2002). Notwithstanding occasional observations, natural predators like hyenas (Hofer *et al.*, 1993) and lions (Patterson *et al.*, 2004) can change the demographic patterns contrary to the prediction (PI).

Over 55% of the cross-section of illegal hunters (n=107) arrested in the western corridor practiced hunting when migrants were out of range (own unpublished data). This trend suggests that hunters optimize their kills on resident males as previous study indicates (Holmern *et al*., 2006) probably due to their territorial behaviour. Since higher male mortality is a well-established phenomenon in most polygynous mating system (Fischer & Linsernmair, 2002; Hofer *et al.*, 1993; Holmern *et al.*, 2006; Watson, 1967), the lone territorial bulls sighted in the west all-the-year-round would potentially be vulnerable to human and natural predation.

Migratory males could potentially be vulnerable along western corridor during north and south migration as reflected by January and November 2004 sex ratio data, but the harvest rate is small relative to the population size (Mduma *et al.*, 1999). Similarly, the observed monthly drop in migratory males could be attributed to sampling bias due to the size of the park and nature of group composition together with the distribution especially during south bound migration. While a female-biased sex ratio ensures males to maximize reproduction and help maintain a polygynous mating system, severely skewed sex ratios can reduce fertility rates and hence production (Bergerud, 1974; Ginsberg & Milner-Gulland, 1994; Milner-Gulland, 2003; Mysterud *et al.*, 2002). Although the Serengeti populations are no where close to this threat, in the long run the population may severely be affected.

The consequences of a female skewed sex ratio can be related to the less synchronised births as records of the many out of season calves in the resident sub-population suggests (Fig. 2) supporting prediction (P2). Observed differences in birth peaks in the two breeding seasons among the migratory herds were perhaps typical responses to climatic variations (Estes, 1976; Talbot & Talbot, 1963; Watson, 1969). Rainfall through improved forage quality was probably the main factor behind such variations as the timing of birth positively correlated to seasonal variability in rainfall. On the other hand, accelerated removal of dominant males through natural and human predation in the resident sub-population, might have allowed partially incompetent males to take part in the breeding process. The consequence is lowered birth rates among resident sub-populations compared to the migrants.

It is a well established knowledge that male wildebeest regularly succeed in fertilizing 80% of the females in a 3-week mating peak in Serengeti (Estes, 1976; Estes & Estes, 1979). This adaptive synchronised breeding (Lent, 1974; Watson, 1967) which tightly correlated to seasonal rainfall was clearly demonstrated in the migratory sub-population, despite unusual change in rain season from February to April between the years 2004 and 2005. Thus, variability in migrants birth peaks supported the prediction (P3).

The higher proportional mean annual calf survival rate of 0.49 in migrants compared to 0.31 recorded in the residents suggest that survival among migrants depends upon the dry season food availability (Hilborn & Sinclair, 1979; Mduma, 1996; Mduma *et al.,* 1999). The relatively higher mean calf survival in the migratory sub-population supported previous observations (Mduma, 1996; Mduma *et al.*, 1999; Talbot & Talbot, 1963) that calf mortalities are not regulated by natural predation but are rather density dependent. Other mortality factors include separation of calves from their mothers when disturbed in large aggregations.

Drinking water (Gereta & Wolanski, 1998) and quality forage for lactating mothers are also important since under-nourished calves are randomly selected by other mortality agents such as diseases and predation. In bad rainfall years, annual proportional mean calf survival rates were estimated as low as 0.21 in 1966 (Watson, 1967) and about 0.40 between 1992-1994 (Mduma, 1996). Since the proportional annual mean calf survival for residents was low (0.31), predation mortality on calves might have accounted for more than half of the crop by the end of the first year. Nevertheless, what maintain the resident sub-population is still unclear given the observed high calf mortality.

Conclusion

Different life strategies may subject wildebeest sub-populations to different vulnerabilities leading to various demographic consequences that act strongly on isolated individuals or individuals living in groups. Contrary to prediction (P1), the differences in sex and age structures between the two sub-populations clearly indicate that the female biased resident sub-population is more vulnerable to predation or illegal hunting than to environmental perturbations. Consistent to prediction (P2), it is persuasive to believe that birth is more synchronised in migrants than resident sub-population as a result of demographic variation. Apparently, birth rate and synchrony coincides with seasonal rainfall whereby seasonal breeding and calf survival rate in migrants seems to be highly regulated by rainfall hence support prediction (P3).

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Table 1. Number of individuals and groups of Serengeti wildebeests separated into sex and age groups during the study period 2003-2005.

Population	Adult♂	Adult♀	Sub-adult♂	Sub-adult♀	Yearling	Calf
Residents N(ind.)	4,565	17 970	2,522	2,662	2,562	8,151
N(group)	1,281	1,281	1,281	1,281	1,281	1,281
% (ind.)	**11.9**	**46.7**	**6.5**	**6.9**	**6.6**	**21.2**
Migratory N(ind.)	20 555	22 269	5,757	3,975	3,858	8,659
N(group)	2,169	2,169	2,169	2,169	2,169	2,169
Percent	**31.6**	**34.2**	**8.8**	**6.1**	**5.9**	**13.3**

Table 2. Test for the differences between sex ratios recorded between resident and migratory adult wildebeest. The overall monthly mean sex ratio for all combined years is indicated at the bottom of the table.

Resident			Migratory		χ^2 - test
Year/Month	N males /N females	Ratio	N males /N females	Ratio	
2003 October	112/497	0.23	849/730	1.16	0.000
November	285/673	0.42	1,139/1,060	1.07	0.000
December	420/1,508	0.28	1,196/1,705	0.7	0.000
2004 January	442/1,536	0.29	92/261	0.35	0.126
February	146/857	0.17	925/793	1.17	0.000
March	50/324	0.15	1,344/288	4.67	0.000
April	83/686	0.12	1,541/1,232	1.25	0.000
June	305/1,608	0.19	918/2,605	0.35	0.000
October	265/1,364	0.19	1,814/1,405	1.29	0.000
November	307/701	0.44	2,202/4,545	0.48	0.168
2005 January	597/2,092	0.29	2,140/1,175	1.82	0.000
February	244/803	0.30	2,426/2,278	1.06	0.000
March	141/534	0.26	644/769	0.84	0.000
April	592/2,151	0.28	796/729	1.09	0.000
May	163/831	0.2	362/573	0.64	0.000
June	161/527	0.31	311/384	0.81	0.000
All years	4,313/16 692	0.26	18,701/20 532	0.91	0.000

Table 3. Newborn calves/adult females mean monthly ratio in Serengeti National Park. Highlighted are the recorded mean ratio peak months in both populations

Year	**Month**	**Resident**			**Migratory**		
		Mean	N	S.D.	Mean	N	S.D.
2003	December	0.27	98	0.26			
2004	January	0.51	103	0.19			
	February	0.44	64	0.18	0.79	31	2.1
	March	0.27	21	0.36	0.52	27	0.28
	April	0.13	49	0.11	0.37	112	0.23
	June	0.12	119	0.09	0.16	12	0.20
	November	0.05	62	0.01			
2005	January	0.62	189	0.29			
	February	0.61	63	0.30	0.46	114	0.27
	March	0.43	44	0.20	0.57	90	0.35
	April	0.33	164	0.25	0.86	83	1.34
	May	0.17	54	0.14	0.53	47	0.24
	June	0.12	41	0.06	0.48	32	0.22

Note: The data for migratory females in December 2003, January 2004 and 2005 are missing because they did not have calves at that time.

Figure Legend

Fig. 1. Serengeti ecosystem indicating wildebeest sampled areas between 2003 and 2005. Filled gray triangles indicate residents and open circles indicate migratory herds. The distinction between resident and migratory herds in the western corridors where there is a mix during transition range is explained in the methodology. Sampling zones includes West (W), Central (C), South-east (S) and North (N).

Fig. 2. Monthly mean newborn calf per adult female (Fig.2 A) as influenced by seasonal rainfall (Fig. 2 B). Open and filled squares indicate resident and migratory sub-populations.

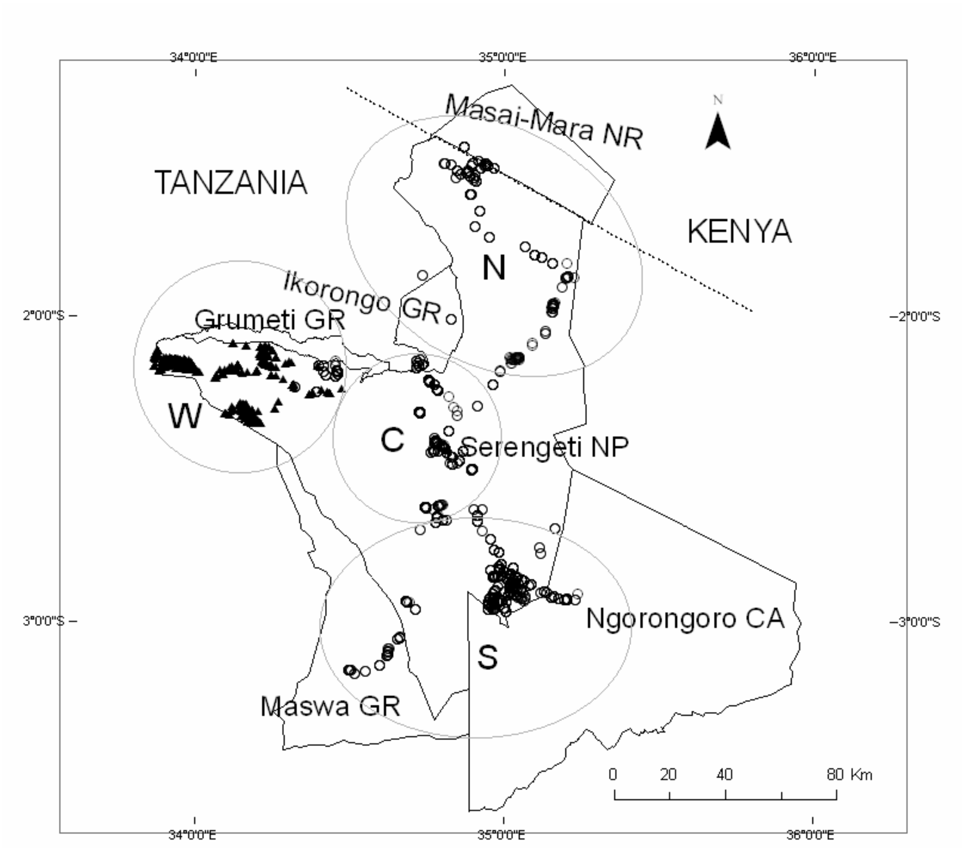
34°0'0"E
35°0'0"E
36°0'0"E
2°0'0"S
3°0'0"S
Masai-Mara NR
TANZANIA
KENYA
N
Ikorongo GR
Grumeti GR
W
C
Serengeti NP
Ngorongoro CA
S
Maswa GR
0
20
40
80 Km

Fig. 1.

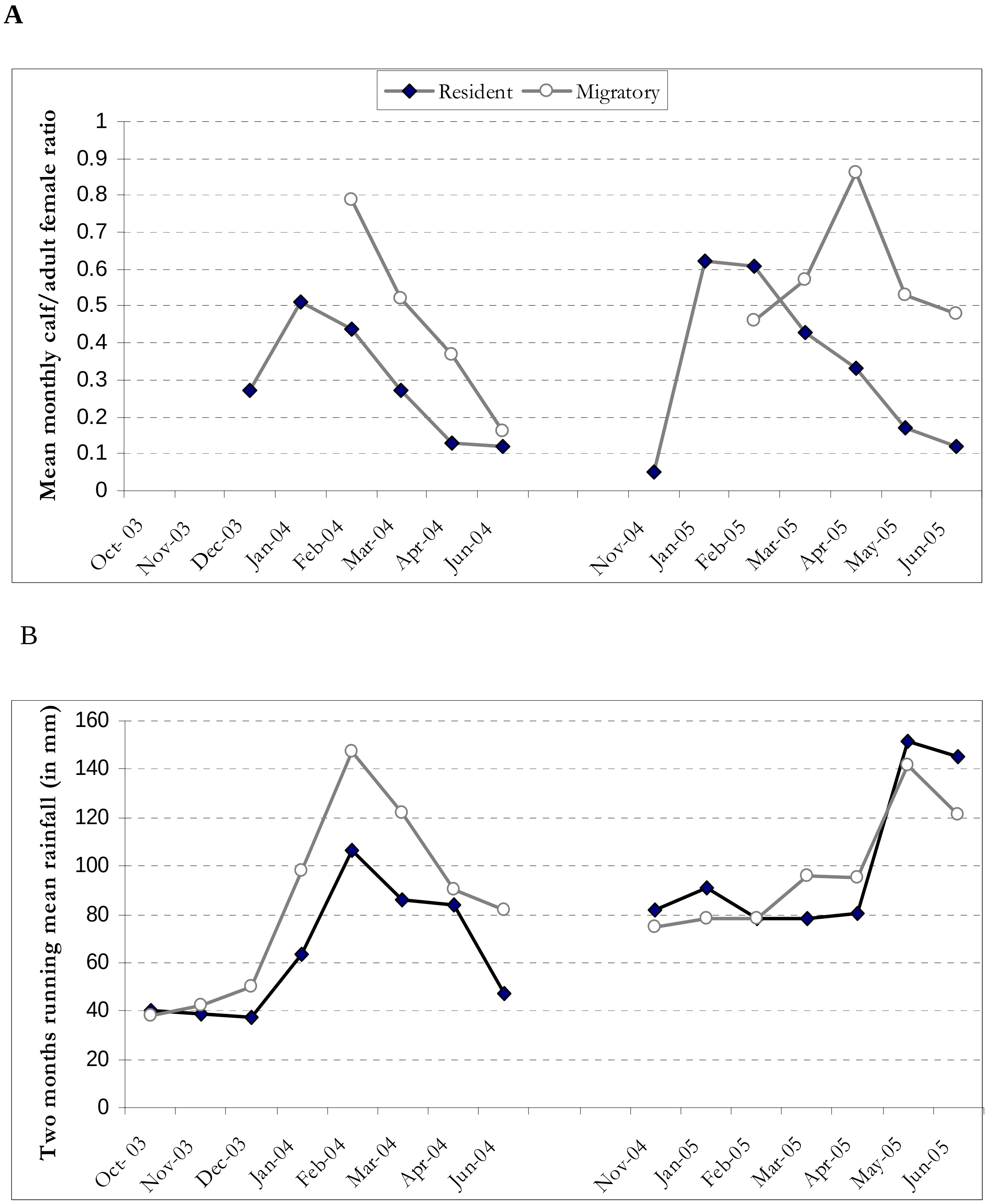
A
Resident
Migratory
Mean monthly calf/adult female ratio
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Oct- 03
Nov-03
Dec-03
Jan-04
Feb-04
Mar-04
Apr-04
Jun-04
Nov-04
Jan-05
Feb-05
Mar-05
Apr-05
May-05
Jun-05
B
Two months running mean rainfall (in mm)
160
140
120
100
80
60
40
20
0
Oct- 03
Nov-03
Dec-03
Jan-04
Feb-04
Mar-04
Apr-04
Jun-04
Nov-04
Jan-05
Feb-05
Mar-05
Apr-05
May-05
Jun-05

Fig. 2.

Running Title: Body conditions of adult wildebeest

Variation in adult wildebeest body condition in the Serengeti National Park, Tanzania

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Variation in adult wildebeest body condition in the Serengeti National Park, Tanzania

ABSTRACT

In this study, body conditions were scored to examine the nutritional differences between the wildebeest (*Connochaetes taurinus*) sub-populations. Variations in body conditions were reviewed basing on three factors (i.e. food abundance, predation disturbance) reflected in the existing Serengeti migration hypotheses. Predictions from these hypotheses were tested by examining body condition differences from October 2003 through June 2005. Results indicate that body conditions differed significantly within and between sub-populations, when sexes were compared in different reproductive periods. All-over, residents were nutritionally in better body condition than migratory individuals supporting predictions derived from the 'predation risk hypothesis'. Body conditions among migrants correlated with food in a south-north rainfall gradient; nevertheless, the test prediction derived from the 'nutrition hypothesis' during the dry season food migration was not supported. Whereas, the energetic benefits of better food in migrants, north of Serengeti, compensated only for the costs of migrating, residents invariably optimized time and energy efficiently to improve their nutritional security. Additionally, the timing of reproductive investment differed between sexes and was dependent on the life history strategies. Male individuals thrived relatively in better conditions signifying that nutritional costs affects survival and reproduction of females in the event of serious food shortage than males.

Key words: body condition; migration; nutrition; predation; Serengeti wildebeest.

INTRODUCTION

Generally, regular periodic movements in large numbers usually to and from a place of origin, producing lifetime tracks, are vital to the dynamics of wildlife populations (Bian 2000). Ungulates choose migration in response to changes in climate and fluctuations in resources. They are however constrained by the amount of food across habitat patches not available year round which otherwise would be utilized to maximize energy intake and minimize competition (Bergman *et al*. 2001; Etzenhouser *et al*. 1998; Fritz & De Garine-Wichatisky 1996), humans threats (Berger 2004) and predation (Fryxell & Sinclair 1988).

In temperate and arctic regions, ungulates hardly meet their nutritional requirements during winter because of low-quality forage hence winter nutrition is dependent on autolysis (Ball *et al.* 2001; Mautz 1978; Packer *et al*. 1999). Likewise, the quality of forage in tropical grazing systems decline progressively with advancing dry season resulting into reduced nutritional security rendering most ungulates to predation and disease (Anderson & Talbot 1965; Ogutu & Owen-Smith 2003). This means that migration behaviour forces ungulates to move between habitat patches to track abundant food supply and enhance access to patches with nutritious food despite the predation risk. Predation risk is a key determinant of lifetime reproductive success of large ungulate herbivores (Kjellander *et al*. 2004), and hence ungulate life history (Geist 2002). At a spatial scale, the most basic anti-predator strategy is to avoid areas with high predator density (Caro 2005); one of the key benefits of long-distance migration in ungulates (Bergerund *et al.* 1984; Fryxell *et al.* 1988; Hebblewhite & Merrill 2007).

Migratory movements are sometimes dictated by sex specific nutritional requirements and/or body-size related forage selection. Where the nutritional requirements are governed by the body size, males are likely to suffer nutritional deficiency more than females particularly in poor seasons. This is because of territorial defence, reproduction and maintenance (Ralls 1977; Toigo & Gaillard 2003) since males are substantially larger than females. Overall however, females endure nutritional costs to escalated maternal investment which frequently increases with gestation and lactation (Clutton-Brock *et al.* 1983; Robbins 1983 cited in Forsyth *et al.* 2005).

The migration phenomenon in Serengeti, Tanzania, is generally linked to seasonal shifts in habitat use by huge numbers of ‘migratory’ wildebeest *Connochaetus taurinus* between their wet season range on the open-grass lands and wooded grasslands in higher-rainfall areas during the dry-season range (Maddock 1979, Wolanski *et al.* 1999). A small group of ‘resident’ wildebeests occur in the western Serengeti corridor restricted within Kirawira, Ndabaka and Dutwa plains the whole year-round. Nevertheless, there is a certain amount of overlap between the ranges of these sub-populations during the transition period (Pennycuick 1975, Watson 1967).

Migratory movements are dictated by forage availability during the dry season (Mduma *et al.* 1999; McNaughton 1988; Sinclair & Arcese 1995a) together with essential nutrients (Kleuren 1975; Murray 1995, McNaughton 1990); although rainfall and salinity predict the timing (Wolanski & Gereta 2001; Wolanski *et al.* 1999). Despite the controversy over underlying causes of migration in Serengeti, the existing hypotheses have linked migration with, i) fluctuations in food supply as a result of a rainfall gradient (Andere 1981; Maddock 1979; Owen-Smith & Ogutu 2003), ii) predation risk from lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* (Hanby *et al.* 1995; Hofer & East 1993) and, iii) search for water quality (Wollanski & Gereta 2001).

In this paper therefore, we analysed and compared body condition scores between resident and migratory wildebeest in order to test predictions based on two existing migration hypotheses in the Serengeti Ecosystem. Previous studies have tested predictions derived from deviations in body condition along with the 'nutrition hypothesis' using analyses of bone-marrow fat (Sinclair & Arcese 1995a; Mduma 1996; Mduma *et al*. 1999). The authors, however, did not focus on variation in visual physical conditions in the contrasting reproductive periods between and within sexes and sub-populations. Thus, according to the 'nutrition hypothesis' if the north migration provides the nutritional benefits then the migrants should generally be in better condition than the residents since the energetic benefits of better food should more than compensate for the costs of migrating (P1). Alternatively, if migration is driven by predation (the 'predation risk' hypothesis) the migratory wildebeest should be in worse body condition than the residents due to the energetic costs of migrating (P2). Males and females were tested in response to rut and birth seasons respectively (see Table 1).

METHODS AND MATERIALS

Study Area Description

Field work was conducted in Serengeti National Park (SNP) Tanzania from September 2003 through June 2005. The Serengeti-Mara Ecosystem, defined by the annual wildebeest migration, includes SNP, Maswa Game Reserve (MGR), Ikorongo Game Reserve (IGR), Grumeti Game Reserve (GGR), part of Loliondo Game Controlled Area (LGCA) and Ngorongoro Conservation Area (NCA) on the Tanzanian side and Masai-Mara National Reserve (MMNR) in northern Kenya, covers some 25,000 km^2 (Fig. 1). The system is characterised by wet and dry seasons driven by the intercontinental convergence zone where short-rains start from November to December and the long rains from March through May (Norton-Griffiths *et al.* 1975; Williams *et al*. 1998). There is an annual rainfall gradient from south-east (500 mm) to north-west (1100 mm). Temperature is moderate with a mean of 22°C and a daily maximum of about 30°C and minimum of 15°C. Soils have been described elsewhere (Anderson & Talbot 1965; Anderson, McNaughton & Ritchie 2004). Migratory wildebeest here refers to wildebeest herds which move to the north of Serengeti ecosystem towards Masai-Mara during the dry season and return south on the Serengeti plains during the wet season. Resident wildebeest on the other hand are those confined to the west of SNP throughout the year.

Data Collection

Body condition scoring

Although it has been difficult to assess the nutritional status of wild gregarious ungulates in the field, body condition score has largely been useful (Riney 1960). Generally, body condition reflects the amount of energy stores such as fat or protein reserves (Green 2001). Most frequently however, live mass, health, competitive ability (muscles) and nutrition status are used as proxies for body condition and have always been related to ecological fitness (Berry & Louw 1982; Milner *et al*. 2003; Riney 1960). Body conditions were ‘haphazardly’ scored every two weeks from various locations depending on sightability by following the herds’ movements all over Serengeti from September 2003 to June 2005, except July to September 2004. Generally, most observations were frequently made along the roads. Resident sub-populations were sampled from the western Serengeti corridor (west zone) and migrants all over Serengeti areas (all sampling zones). Group size, structure and composition were carefully used to separate the two sub-populations in the eastern part particularly during mixing. Once spotted a large group, the vehicle approached it cautiously (<15 km/hr) to minimise disturbance and thereafter 30 adult individuals (i.e. sampling unit) were counted and their sexes determined.

A criteria developed by Watson (1967) was used to estimate the age and sex (sexually mature are about 3 years and older). Individuals were grouped according to three visual ranking criteria (i.e. good, medium and poor condition) using visible skeletal details around hindquarter by eye (Berry & Louw 1982). Good condition imply round body with well rounded hindquarters (ribs are not visible) and the general appearance in relation to the coat sheen is excellent, ii) medium condition is denoted by angular hindquarter in appearance and well defined ribs, whereas, iii) poor condition is reflected by prominent pelvic bones and protruding ribs with deprived general appearance, posture and coat condition.

Observations were made closer to the group where large herds were encountered and condition of each adult sex within a section of 30 animals was recorded accordingly up to the last individual in the section. The number of sections in each herd was determined by the herd size and behaviour. Sighting of large stationary groups involved the use of non-permanent transects by driving through the herds while simultaneously counting and recording conditions of adult sexes in every section of 30 individuals on either side of the vehicle at every 100 m distance within a transect**.** A 200 m non-transect was added at the end of each 100 m transect to avoid double recording. The area, location name, date, time, GPS position, herd type, sex and body condition scores were recorded on data sheets (with the aid of a binocular and tape recorder) and later entered into a computer. The search was purely haphazard and was only dictated by availability and distribution of the wildebeest throughout the entire study area (Fig. 1) though most observations were made along the roads.

Differences in male and female’s body conditions at pre- and post reproductive periods (explained in Table 1) were tested using Chi-square tests. Two months data from each reproductive stage was compared to test for the variation in conditions between populations and sexes. Other periods (Table 1) were also compared to track variations in body conditions due to the lifestyle and feeding strategies. All data during the study period were pooled together because the annual differences between the sub-populations were not detected.

Rainfall and body condition

In order to test if body conditions reflect resource availability as driven by rainfall, a partial correlation analysis was performed to compare the conditional classes across groups. Rainfall data were obtained from SNP (Ecology Unit) and analyses were mostly based on regularly inspected monthly storage rain gauges. Monthly records were computed as millimetre (mm) of rain per month from 96 different stations. Stations were grouped in four major zones representing major habitats for wildebeest movements in SNP. Monthly rainfall records for each zone were averaged and the frequently visited areas were combined to establish correlation between body condition and rainfall. But, since rainfall do not directly impinges on grass productivity and hence body condition, a two-month running mean of rainfall was used in the analyses to indicate the likelihood of changes in grass biomass as a reflection of subsequent changes in wildebeest body conditions. This was very crucial since the observed changes in wildebeest body condition do not reflect existing resource conditions, but rather the impact of changes in resources that was available a month or two ago.

RESULTS

General body condition between wildebeest sexes and groups

A total of 3,450 groups (each consisting of 30 individuals) were sampled from September 2003 through June 2005. Adult wildebeest contributed 65,359 individuals or 63%. Of these, males and females proportions were 25,119 (38.4%) and 40,240 (61.6%) respectively. In total, adult individuals from migratory and resident population were 42,824 (66%) and 22,535 (34%) respectively. All over, a small number of wildebeest (< 2.4% of observations) were in poor condition. Those in medium condition comprised of 18.9% whereas majority of observations (78.7%) were in good condition. The proportions of the three different condition group differed significantly between sexes (χ^2= 407, df=2, p < 0.001) in favour of males that was recorded in better condition. Furthermore, when data between sub-populations were compared body conditions of residents appeared to be better than migratory individuals (Table 2).

Variation in body conditions during reproductive phases

The body conditions of migratory males were slightly better during the rut and dropped sharply during the post-rut period. On contrary, resident males were observed in worse body conditions during the rut, but improved significantly during the post and pre-rut periods (Table 2). The difference between the two sub-populations indicates that the body conditions in males were more distinct during pre- and post-rut periods (Table 2). Female conditions differed significantly between residents and migratory sub-populations throughout the different reproductive stages (Table 2). In both sub-populations, female conditions improved toward birth and post birth periods. During pre-birth (dry season) period the body condition of migrants was relatively poor (Table 2). Generally, resident females were recorded in better condition than migratory females in all periods (Table 2).

Resident males were in better condition during post-rut than during pre-rut period (Table 2, $\chi^2 = 9.61$, df = 2, P = 0.008) while the opposite was found for migratory males (Table 2, $\chi^2 = 270$, df = 2, P < 0.001). On the other hand, female wildebeest in both populations were recorded in better conditions during the post-birth than the during pre-birth period (Table 2, residents. $\chi^2 = 489$, df = 2, P < 0.001, migratory; $\chi^2 = 229$, df = 2, P < 0.001).

The correlation between rainfall and body condition rating controlling for months and group sexes was statistically significantly stronger in the migratory ($-0.089< r < 0.295$, $p < 0.01$) than in the resident population ($-0.069 < r < 0.055$, $p < 0.05$).

DISCUSSION

Migration has long been hypothesized to reduce predation risk for many ungulates although there have been few direct empirical tests to ascertain the costs associated with migration. Our study provided conflicting support for the hypothesis that migration reduced predation risk for wildebeest, because migrant and resident wildebeest exploited trade-offs between natural and human predation differently across the Serengeti ecosystem. Predictions derived from the migration hypotheses through comparing body condition data strongly supported the ‘predation risk’ hypothesis (P2), in that, resident were nutritionally better-off than migratory wildebeest probably due to energetic costs of migrating in a predation risk environment. Although the ‘nutrition hypothesis’ has commonly dominated the theory behind Serengeti migration (Mduma *et al*. 1999), the benefits derived by migrating northward for better food appeared only to compensate for the costs of migrating, thus we were unable to support prediction (P1). This means that predation risk avoidance constrained foraging strategies during the trade-off situation when food was a limiting factor.

The predation risk hypothesis asserts that predators limit populations such that as food supply decreases animals increase their predation risk through increased search for food. The search for food in habitats that are not readily available the whole year round was expected to increase energetic cost (Anderson *et al*. 2004; Fryxell *et al*. 1988; McNaughton 1990; Sinclair & Arcese 1995b) and stress to constrain migrating individuals (Table 2). For instance, the body condition of females in both sub-populations dropped during pre- birth indicating that females were probably nutritionally stressed due to escalated maternal nutritional demand associated with pregnancy. Thus, predation behaviour strongly affects migrants through body condition weakening by virtue of their movement probably more than actual off-take. Also, body condition results indicated that north migration was associated with improved body conditions of migrants which even so could not significantly be compared to residents perhaps due to the imposed predation-sensitive food stress. Predation sensitive foraging influences behaviours including vigilance; patch use, diet and habitat selection, including sexual activities of individual animals (Sinclair & Arcese 1995a; Peacor 2002; Nelson, Mathew & Rosenheim 2004; Kie 1999).

The observed differences among sexes in different breeding seasons could be attributed to life history strategies. Males appeared to have gradually accumulated more fat reserves after rut for the next breeding cycle; nevertheless the timing between the two populations was different probably due to differences in social and reproductive phenology. Although the two populations showed the benefits of improved nutrition in the wet seasons (realised during rut), the drop of condition in migratory males after rut was heightened with a surprisingly quick recovery. The behavioural mechanisms for locating high quality food to specific habitats with different mortality risks have probably selective advantages to migrants (Kinnison *et al*. 2001). Frequently, experienced males trade-off food intake against predation risk (Sinclair 1995b;

Hofer *et al.* 1993) in suitable grazing areas which not only provide nutritional security to repel and/or evade predators, but also assure body maintenance and genetic fitness (Ralls 1977; Toigo & Gaillard 2003).

Recent findings (Ndibalema in prep.) of male to female sex ratio of 1:1 and 0.3:1 for migratory and resident population respectively, indicate that a higher rate of energy intake among migratory males is probably crucial for competition (and hence mating) during the dormant period (Forsyth *et al*. 2005; Sinclair & Fryxell 1985). Males opportunistically elevate their energy intake during the non-reproductive period by accumulating fat reserves prior to the mating period so as to maximize their reproductive success (Estes 1966; Forsyth *et al*. 2005). Therefore, resource competition among migratory males during rut could be more severe than would be expected since in nature strong males compete favourably. Apart from being territorial throughout the year, resident males optimize their energy from easily accessible resources in habitats which compel minimum energy hence least competition during rut.

Resident females were nutritionally better-off than migratory females probably due to optimal environments, despite of limited foraging options in the western corridor which is potentially predation risky (Georgiadis 1988; Hofer *et al*. 1993). The condition of both populations appeared to drop during the pre-birth period and improved substantially during the post-birth period in favour of residents, most likely due to timing of reproductive events (Table 2). Resident females normally give birth from December to February (Ndibalema pers. observ.) which coincides with Lake Victoria shore rainfall which is important during lactation. Migratory females give birth one month later and were seen wandering between Seronera and Maswa plains probably because they were food constrained. Considering pronounced north-south SNP rainfall gradient (Owen-Smith & Ogutu 2003; Wollanski & Gereta 2001), resident females might optimize time and energy more quickly to recover from nutritional stress compared to migrants. Moreover, females require quality food to support pregnancy followed by lactation (Forsyth *et al*. 2005; Sand 1998; Sinclair, Mduma & Arcese 2000; Sinclair & Arcese 1995a). The combined effects with energy expenditure associated with migratory movements in subsequent short dry spell might have significantly lowered the body conditions of migratory females.

Altogether, females appeared to be nutritionally more stressed than males because of parental care and a long gestation period (see also Table 2). An obvious decline in condition at pre-birth (during gestation) compared to post-birth period (during lactation) could have resulted from diverted stored energy to the developing foetus (Oftedal 1985 cited in Forsyth *et al*. 2005) as most females are food limited during this period (Mduma *et al*. 1999). Also pregnant wildebeest are constrained by nutrients, mainly calcium (Kleuren 1975), magnesium, sodium and phosphorus (Murray 1995; McNaughton 1988; McNaughton & Banyikwa 1995) which spur long-distance movements for quality pastures; even though the cost of pregnancy is assumed to be small compared to that of lactation (Clutton-Brock *et al*. 1983; Oftedal 1985 cited in Sand 1998). The peak in condition for all females at the post-birth period (Table 2) presumably coincided with abundant food resource in the wet season.

A stronger relationship between rainfall and body condition that was revealed in migrants suggest that annual differences in the pattern of wildebeest movements in relation to resources can be linked to Serengeti rainfall (Maddock 1979; Pennycuick 1975; Sinclair 1995a; Wollanski *et al*. 1999). Rainfall not only improves forage quality, but also provides surface water important for drinking which spatially regulates wildebeest movements (Thirgood *et al*. 2004; Wolanski & Gereta 2001).

CONCLUSION

This study indicates that wildebeest populations in Serengeti were at no stage under serious nutritive stress (< 2.4% of observations in poor condition). Food together with predation appeared to constrain wildebeest movement as reflected by body condition assessment. However, food is a key component of north migration and the relative profitability between the sub-populations is determined by the nutrition environment. Predation risk foraging coupled with energetic costs of migrating in a rather competitive environment constrained the condition of migrants in favour of resident individuals. Nutritional variation within and between sexes in different periods was explained better by comparative advantages associated with life history strategies and timing of weather between sub-populations. Moreover, body condition assessment indicated that females would be most disadvantaged compared to males due to escalated nutritional demands associated with gestation and lactation. The measurements of body condition can be used by the park managers to quickly evaluate wildebeest nutritional status in different sub-populations through simple visual assessment in order to underscore habitat conditions.

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Table 1. Periods selected to test the differences in body conditions due to the timing of events between wildebeest sub-populations and sexes in Serengeti Ecosystem.

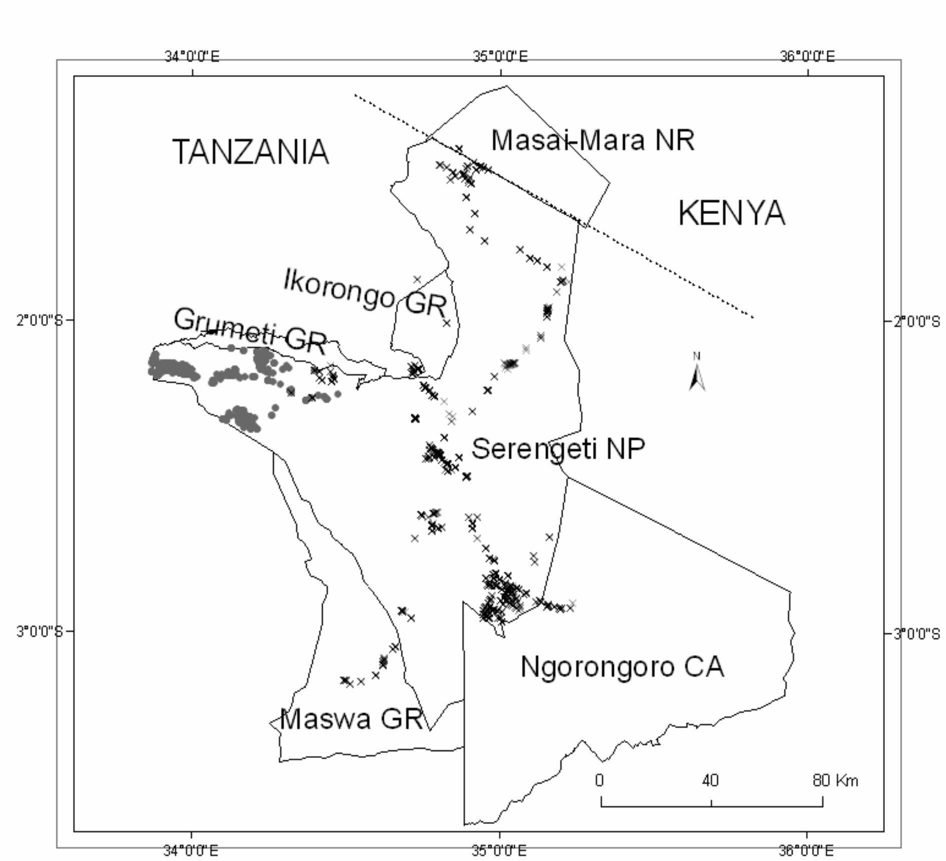
Sex/ pop.	**Pre-rut/birth**	**Rut /birth**	**Post-rut /birth**	**Between rut/birth**
Males				
Resident	Feb. – March	April – May	June – July	August – January
Migratory	April – May	June – July	Aug. – October	Nov. – March
Females				
Residents	Oct. – November	Dec. – February	March – April	June – September
Migratory	Dec. – January	Feb. – April	May – June	July – November

Table 2. Number of male and female wildebeest of Serengeti sub-populations in good (G), medium (M) and poor (P) body condition tested in seasons. Statistical differences are tested by Chi-square test and the percentages of individual counts (N) in each condition category are given in brackets (See table 1 for definition of breeding seasons).

Males					
Residents	Pre-rut N (Percent)	Rut N (Percent)	Post-rut N (Percent)	In-between N (Percent)	Combined N (Percent)
G	560 (90.8)	795 (88.2)	462 (95.4)	2112 (82.4)	3929 (86.1)
M	55 (8.9)	100 (11.1)	22 (4.5)	397 (15.5)	574 (12.6)
P	2 (0.3)	6 (0.6)	0 (0.0)	54 (2.1)	62 (1.3)
Migratory					
G	2594 (86.7)	1326 (87.9)	465 (52.0)	12451 (82.2)	16836 (81.9)
M	388 (12.9)	173 (11.5)	382 (42.7)	2452 (16.2)	3395 (16.5)
P	25 (0.8)	9 (0.6)	47 (5.3)	243 (1.6)	324 (1.6)
χ^2	9.62	0.119	270	5.98	457
df	2	2	2	2	2
p	0.008	0.942	0.000	0.137	0.000

Females					
Residents	Pre-birth N (Percent)	Birth N (Percent)	Post-birth N (Percent)	In-between N (Percent)	Combined N (Percent)
G	1814 (64.1)	6564 (81.1)	3325 (85.2)	2827 (89.9)	14530 (80.8)
M	813 (28.7)	1385 (17.1)	561 (14.4)	317 (10.1)	3076 (17.1)
P	203 (7.2)	143 (1.8)	16 (0.4)	2 (0.1)	364 (2.0)
Migratory					
G	5708 (68.1)	5192 (77.9)	3026 (80.5)	2232 (64.4)	16158 (72.5)
M	2254 (26.9)	1333 (20.0)	687 (18.3)	1048 (30.2)	5322 (23.9)
P	417 (4.9)	140 (2.1)	47 (1.2)	185 (5.3)	789 (3.5)
χ^2	26.1	23.4	39.4	627	389
df	2	2	2	2	2
p	0.000	0.000	0.000	0.000	0.000

Fig. 1. Serengeti-ecosystem map indicating wildebeest sampled areas. Sampled migratory individuals are represented by a cross whereas residents are represented by black circles.



1.0 Title: Relationship between road dust and ungulate density in Serengeti National Park, Tanzania

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2.0 ABSTRACT

Responses of grazers to roads were recorded through dust measurements on grass and distance sampling of ungulates in Serengeti National Park (SNP), Tanzania. Data were collected on the east and west side of the Ngorongoro-Seronera main gravel road to test if vehicle traffic and dust were important factors determining distribution patterns amongst grazers. Results indicate that dust increased progressively with traffic speed and volume as seasons advanced. More dust was intercepted by the grass on the west than the east side of the road mainly due to westerly wind. Dust deposition measured as density was higher on the short grasses than the long grasses during the dry and late-dry seasons than during the wet season, when paired perpendicular distances up to 300m were compared. Mean number of sighted grazers species indicated that most fed further from the west side of the road than the east perhaps to minimize higher density of dust commonly spread on foliage up to 200 m from the road. Despite that most grazers avoided road side grass shoulders, supporting the ‘dust aversion hypothesis’, the test predictions from the ‘road disturbance’ and the ‘road attraction’ hypotheses did not support the responsive behaviours of grazers toward roads.

Key words: distance sampling, dust pollution, ecology, grazing, road, vehicle traffic

3.0 INTRODUCTION

The effects of roads and associated vehicular traffic on the environment, animal populations and behaviour near roadsides are immense (Cuperus *et al*. 1996; Forman *et al*. 2003; Lonsdale & Lane, 1994; Reijnen & Foppen, 1991; Spellerberg, 1998). Roadside resources may attract many mammals which end up as victims of road accidents and poisoned from grasses fed on the road shoulders contaminated by lead and other heavy metals used as additives in gasoline (Smith 1971) and de-icing agents in temperate countries (Hofstra & Hall, 1971; Davison, 1971).

Unpaved roads are particularly important sources of dust pollution which not only cause gaseous phototoxic pollutants (Farmer, 1991) but also failure in photosynthesis, respiration and plant transpiration (Thompson *et al*. 1984). Grazers too, suffer from excessive tooth wear from dust contaminated forage (Williams & Kay, 2001; McNaughton *et al*. 1985). Deposition rate of dust from the road to grass is nevertheless dependent on wind speed and direction, leaf area index, moisture, particulate size and traffic intensity. The size of dust declines with the distance from road and diameter of the particulates from motor vehicles range from 0.01 to 5000µm (Ninomiya *et al*. 1971).

Most tourist activities inside African national parks and reserves are associated with increasing number of traffic volumes (Freitag-Ronaldson & Foxcroft, 2003), whose effects on wildlife, have rarely been documented. Studies have focused on altered animal behaviour (Reijnen, 1995; Wasser *et al*. 1997), movements (Dyer *et al*. 2002; Kerley *et al*. 2002; Reijnen & Foppen, 1995) and mortality along roadsides (Pienaar, 1968; Walker & Everett, 1987) at an individual, species and population level. However, at the ecosystem and landscape level, roads influence abundance, distribution, mortality and colonization rate (Tshiguvho, 2000 cited in Freitag-Ronaldson & Foxcroft, 2003).

In order to test the underlying influence of roads to animals, we conducted a study in Serengeti National Park (SNP), Tanzania. SNP represents an extant member of a prominent grazing ecosystem in the world (Fryxell & Sinclair, 1988) whose resources attract huge numbers of tourists. However, tourism have had environmental problems linked to motor traffic and/or frequent road repair processes (Belsky, 1985). The aim of this study was to record the effects of road dust and traffic on ungulate distribution and foraging responses along the Seronera - Ngorongoro main road with the following specific objectives; 1) to test if there is any variation in the dust intercepted by the grasses and its overall effect to ungulate distributions on the road sides; 2) to test whether motor traffic produced dust and/or disturbance elicit any response to grazers distribution while feeding along the road; 3) to test for seasonal variation in the dust with consequent effects on grazers foraging distribution.

We hypothesized that, H1: Dust on grass causes ungulates to feed further from roads than expected from a random distribution (dust aversion hypothesis). H2: Vehicle traffic disturbs animals and force them to move away from roads (road disturbance hypothesis). H3: Locally enhanced runoff of rainfall combined with soil disturbance provides green grass near roads, which attracts ungulates to feed along the road verges (road attraction hypothesis).

The ‘dust aversion hypothesis’ (H1) predicts more sighting frequency of ungulate species away from grasses exposed in extreme dust than on the grass that intercept less dust i.e. more sightings on the sides of the road with less dust (P1). The ‘road disturbance hypothesis’ predicts more sightings away from the road due to the traffic disturbance other than dust, i.e.

there should be no difference in grazers distributions on the road sides (P2). The ‘road attraction hypothesis’ predicts that grazers’ trade-off food with dust and/or vehicle traffic disturbance during the period when food is limiting than when it is plenty (P3). The study was confounded by several ecological limitations and had the following assumptions; i) forage quality was similar across the study area, ii) rainfall was uniformly distributed over the entire study area, iii) road soil properties were the same all along and bigger vehicles had more road impact than small vehicles, iv) grazers had the same foraging strategy, and were observed while feeding.

4.0 MATERIALS AND METHODS

4.1 Study Area Description

Field work was conducted in the central SNP (Fig. 1) from October 2003 to June 2005. SNP is composed of 13,000 km^2 of grassland, open savannah and sparse woodlands that lie in altitudes between 1,350 and 1,800 m. The park has the characteristic wet and dry seasons driven by the intercontinental convergence zone: the short rains start from November to December and the long rains from March to May (Williams *et al*. 1998). Rainfall increases from 500 mm annually in the south-east where the soil is composed of highly saline volcanic ash, to 1,100 mm in the north-west, where the soil is derived from granitic substrate (Jager, 1982). Vegetation composition and community structures are largely governed by rainfall (Williams *et al*. 1998; McNaughton, 1985). Short grass communities occur in the arid south east, where mid-grass savannah occurs in the centre of the park where data was collected (Fig. 1).

Common grazers on the plains include wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), Thomson's gazelle (*Gazella thomsoni*), Grant gazelle (*Gazella granti*), topi (*Damaliscus lunatus*), buffalo (*Syncerus caffer*) and warthog *(Phacochoerus aethiopicus*). Intense grazing on the short grass plains during the rainy season maintain the height of the herbaceous vegetation below 5 cm south of Naabi gate (Fig. 1A) while mild grazing in the mid and tall-grass savannas, north of Naabi gate during dry season (Fig. 1B) allow the vegetation to grow between 0.5 m to 2.0 m in height. The park vegetation is frequently subjected to natural disturbances, fires, erosion and termites (Belsky, 1985).

4.2 Sampling design

4.2.1 Road dust and traffic intensity

Samples of grasses for dust were clipped from 96 sites positioned perpendicular east and west of the road on 12 dust transects, six from both south and north of Naabi gate on Serengeti short grass plains (Figure 1). The road dust transects were superimposed on existing road count transects in order to record the effect of grazers distribution as influenced by roads. These transects were spaced after every 5 km each with four paired sites at 100 m, 200 m, 300 m and 1000 m perpendicular to the road. Grasses were clipped to determine the deposition rate of dust and the direction and sequence for clipping was pre-determined each time a station was sampled. A handful of grass tufts devoid of forbs or shrubs were clipped carefully and systematically from all sites in order to standardize the handling procedure in the laboratory. About 80 gm of grass sample was clipped once above ground level at each location using a heavy-duty scissor.

Clipped grass was scrupulously put in labelled plastic bags, tightened and subsequently packed serially in boxes before were taken to the laboratory for dust extraction and measurements. These boxes were properly covered using a plastic paper during transportation to prevent additional dust from the surroundings. Later, each sample was washed thoroughly well in a 2.0 l water jar, semi-filled with 1.0 l of distilled water before was emptied in corresponding labelled filter paper (0.001 mm fisher-brand) affixed to a 0.5 l funnel. Washed grasses together with dust filters were put into well-labelled paper bags and air dried for 12 hours prior to oven drying at 60°C for 24 hours. Oven-dried grass and filter papers were measured instantly by a sensitive scale (Mettler PM100) calibrated to three decimals. Net grass weight and dust were obtained by subtracting average weight of repeated measured empty filters and polythene papers from gross weights of respective grass samples. Furthermore, the measurement from each sample was recorded on the data sheet for further analyses. We used gram dust per gram grass as a currency to describe the density of dust.

4.2.2 Sampling of vehicle and wind speed

Motor traffic records were obtained from SNP at Naabi gate each day. This involved monthly recording of incoming and outgoing vehicles at Naabi gate (Fig. 1) from October 2003 to June 2005. The speed of vehicles was also monitored using hand-held speed gun (Laser detection device) provided by SNP. A vantage point was located and a speed gun was systematically pointed straight to any selected approaching vehicle in order to read its speed. A systematic random sampling was adopted by recording the speed of every third vehicle within three peak intervals i.e. 7:00-9:00 a.m., 12:00-2:00 p.m., and 5:00-7:00 p.m. once every week. The speed was averaged first within each day and then across months in all study years.

The wind speed and direction were recorded randomly alongside transects by raising an anemometer 5 m above the ground where the initial and last readings were noted each time of recording. The records were later converted to km hr^{-1}. The speed was calculated from a continuous 15 minutes of wind observations and later a fraction of that speed (15/60) was adjusted to one hour. Sampling sites were visited according to an established sampling schedule. This involved subsequent alternation between sampling of the long and the short grass transects to minimize systematic sampling errors.

4.2.3 Sampling of animals

Distance sampling method was used to read data from animal counts on transects randomly superimposed to the existing road-system in the study area. Each transect had a total length of 1km spaced by 2 km intervals with marked GPS-positions at the beginning and end points of transect. All sampling were conducted inside a pick-up that moved along transects at slow speed (< 20 km hr^{-1}) with two observers standing at the backside, each covering a sector of 180^o. When an animal was spotted, the vehicle immediately halted and observers recorded the

UTM-position of the car followed by distance to the animals by the use of a range finder. If the object was a cluster of animals, the distance was defined to represent the line from the observers to the middle of the observed animal group. The maximum operational distance for the range finder was 1000 m. The angle to the animals as well as to the road was also determined in order to estimate the exact position of the animals and calculate their perpendicular distance from the road. The frequency of animal sightings in every transect count were used in the analysis to get the total number and mean sighting frequency. The analyses were limited to small groups, of less than 50 individual from each species of animal sampled, as the accuracy of mid-point of big groups is distorted by distribution of animals sighted through a range finder.

The following factors other than road dust, were important source of errors during the sampling process although did not radically change our results, i) soil disturbance from animals, ii) rain wash/splashing on grass, iii) grass characteristics (i.e. tall/short, moist/dry, smooth/hairy), iv) wind speed and direction.

5.0 RESULTS

5.1 Wind speed and direction

Over 75% of recorded winds were easterly winds blowing westwards and in very rare cases north to northwest. Winds were strong at dawn and progressively slowed down in the afternoon with monthly average speed of 16.6 (± 6.4, N=34) and 14.2 (± 6.2, N=51) km hr^{-1} respectively. The mean record of wind speed during the study period was 13.2 km hr^{-1}.

5.2 Dust from paired sites

The overall density of dust was statistically significantly higher on the west side than that of the east side of road when paired distances were compared (100 m, Z=-8.14, N=215, P<0.001; 200 m, Z=-3.01, N=201, P< 0.002; 300 m, Z=-3.56, N=197, P< 0.001) except for 1000 m (Z=-0.29, N=193, P=0.772) (Fig. 3). When the east and west side of the road was split into short and long grass corresponding to south and north side of Naabi gate respectively (Fig. 1), the difference in the density of dust was highly significant up to 300 m on the short grass and significantly different at 100 m for the long grass (Fig. 3). The density of dust varied significantly on the west side of the road even when an independent test was carried out during the wet, dry and late dry seasons. All over, the density of dust recorded beyond 100 m was not statistically significant except at 200 m during the dry season (Table 1).

5.3 Traffic volume and speed

The records for mean daily traffic volume were statistically significantly different across months in all study years (χ^2=1276.6, DF=9, P<0.001). Light duty vehicles (Land lovers/Land cruisers) represented 70% of all sampled vehicles out of which 50% and 20% were tourist and non-tourist vehicles respectively. Heavy duty vehicles (trucks and buses) represented only 30%. There was about 40% annual vehicles increase with progressive mean increase from 111, 161 to 182 vehicles day^{-1} during the wet, dry and late-dry season respectively. Overall monthly mean traffic speed in all study years was 68.2 (±4.4, N=18) km hr^{-1}. However, vehicle speed averaged within days and across months for all the study years varied significantly within months and between seasons (ANOVA, F=176, DF=9, $P<0.001$). Mean vehicle speed averaged in wet months was relatively higher 69 (±3.7, N=8) km hr^{-1} than during late 67 (± 3.8, N=7) and dry months 67 (± 0.07, N=2) km hr^{-1} respectively.

Generally, the density of dust increased with traffic volume in the dry than the wet season (Fig. 2). The average amount of dust correlated significantly with mean traffic density, both at the short ($r^2=0.234$, N=108, $P < 0.015$) and the long grass ($r^2=0.241$, N=107, $P<0.012$). There were significant differences in the density of dust between the east and west sides of the road at 100 m in all seasons. The difference in the density of dust between east and west sides at 200 m was significantly different during the dry season (Table 1). A multiple regression analysis indicated that perpendicular distance, grass height, vehicle numbers and road sides (east or west) independently explained the variation in the density of dust (Table 2). However, seasons were not important determinants of variation in the levels of dust density recorded between grass sites and heights.

5.4 Distance sampling and animal distribution along perpendicular sites

The east side, with least density of dust, recorded grazers significantly more frequently than the west side at the closest distance (i.e. 100 m) (Fig. 4A). However, the observed animal frequencies at distances beyond 100 m were not statistically significantly different (Fig. 4B-D). Despite of significant variation in the density of dust at 100 m, there was no significant difference between east and west side of the road due to seasonal variation in the observed mean frequencies of grazers. Furthermore, observed animal frequencies in the short grass plains were more variable at 100 m only during the wet season and less variable at distances beyond 100 m. The most frequently sighted grazers in decreasing order of magnitude included; Thompson’s Gazelle, Grant’s gazelle, wildebeest, warthog, topi, hartebeest (*Alcelaphus buselaphus*), ostrich (*Struthio camelus*), eland (*Taurotragus oryx*), elephant (*Loxodonta africana*) and reedbuck (*Redunca redunca*).

6.0 DISCUSSION

Our preliminary results indicate important ecological function of roads to wild ungulate species. The overall vehicle traffic effects on Serengeti roads is to repel, disturb and sometimes attract some ungulates species at different times of the year with possible ecological consequences. The prediction from ‘dust aversion hypothesis’ (P1) was supported as most grazers were seen on the east side of the road avoiding road grass shoulders on the west side probably due to dust contamination which impinge on the grass quality (Anon, 1966; Spellerberg, 1998). Neither disturbances from tourist vehicles nor attraction toward high quality herbaceous growth near roads tested by sighting frequencies of grazers near the roads (i.e. 100 m) supported prediction ‘road attraction hypothesis’ (P2) and ‘road disturbance hypothesis’ (P3). Instead, majority of the grazers appeared to be dust sensitive in their distribution with occasional sightings of indiscriminate grazing on foliage with high densities of dust.

Elevated levels of dust on the west presumably elicited herbivores aversion response towards the east side of the road as the mean sighting frequencies within 100 m of the east side suggests (Fig 4A). This indicates that the increased tendency of sighting frequencies of grazers on the east side was not attributed by chance. If the assumed motor vehicle disturbance (visual and noise/vibrations) was the case, the level of sighting frequencies would have been expected to occur at random; hence the sighting frequencies would be roughly equal on both sides of the road especially at the closest 100 m distances as the records of the paired distances beyond 100 m suggests. Previous study indicate that superficial road traffic disturbance have little effect on vegetation patterns to broadly alter the grazer’s foraging pattern (Belsky, 1985).

It is also reasonable to assume that grazers would tend to avoid excessive dust contaminated grass due to teeth abrasive silica (McNaughton *et al*. 1985; Williams & Kay, 2001). Notwithstanding occasional sightings from Thompson's Gazelle's that were seen to subsist on the roadside grasses especially *Digitaria macroblephara* (pers. obs.), deviation from this assumption can not be ruled out. Laboratory results indicate incredible levels of dust from grass samples dominated by *Digitaria macroblephara* because it is hairy and probably able to trap dust broadly.

The variations of vegetation structure and composition of grass species all over Serengeti plains during dry season might force Thompson's Gazelles to feed on moist but dust contaminated foliage hence trade-off teeth abrasion against immediate metabolic demands from moist grass (Wilmshurst *et al*. 1999). This tendency may support the predictions both from the 'road attraction hypothesis' and the 'road disturbance hypothesis'. These predictions were however not easily tested on the account of 1) traffic disturbance which impinges on responsive behaviour of grazers toward road edge resources, and 2) too few observations from some species to support the 'disturbance hypothesis'. Prediction (P3) would probably be more conclusively supported if the study was carried out at night without any traffic influence. Any road avoidance by grazers at night would definitely be linked to extreme dust pollution on grass adjacent to the road and/or predation. Potential carnivores especially lions *Panthera leo* and hyenas *Crocuta crocuta* are known to hunt actively at night (Packer, 1996; Hofer & East, 1995) and were mostly seen along the road which in this case may substitute vehicle traffic effects.

The size of vehicle, intensity and speed were probably important factors whose effects were additive during the dry season. Altogether the effect might be facilitated by easterly winds which steadily amass extra dust at the average speed of 13.2 (±6.3, N=26) km hr^{-1}. Higher traffic volumes significantly correlated with the increased amount of dust, especially in months with higher records of heavy duty vehicle indicating that the dust is spread out more with bigger vehicles particularly at a higher than at a lower vehicle speed. In view of SNP road maintenance program, scheduled during dry period when there are more visitors, roads could prompt high speed driving. As far as SNP management is concerned there is less maintenance cost (J. Hando pers. com) in dry than during the wet season. The speed limit in both NCA and SNP is set at 50 km hr^{-1}, but drivers rarely observed this speed limit, as 110 km hr^{-1} was not uncommon. Despite of heavy penalty imposed upon over-speeding, the vehicle speed averaged during the entire study period was unusually higher (i.e. 68 km hr^{-1}). The daily mean vehicle speed dropped during the time when rainfall was excessively high and only in sections where roads were in terrible shape.

7.0 CONCLUSION AND RECOMMENDATION

The relationship between road aversion behaviour by grazers and dust is complex; although our findings from major impacts of road and associated dust to the grazers can have important ecological implications. The linkages between grazing distribution pattern and dust pollution/traffic disturbance supported the dust aversion hypothesis. The test predictions for road attraction and road disturbance were not strongly supportive to confidently confirm that roads deter and/or elicit feeding response to grazers. It is therefore convincing to believe that dust (mainly from vehicles) on grass keep ungulate away from feeding closest to roads contrary to speculated random associated road events. Our observations however are not conclusive and call for additional data especially night transects for tight comparisons.

Research recommendation

i). Chemical analyses of effects of exhaust fumes on road-edge grasses and possible consequences on grazers

ii). Mineral/chemical analyses of dust to show rates and accumulation level on roadside biota and possible effects on primary production (photosynthesis)

iii). Correlated changes in plant diversity and grazers toward road habitat-edge

iv). Night distance sampling transects to track changes in distribution pattern of animals with little influence from vehicle disturbance.

Management recommendation

The speed limit set by SNP i.e. 50 km hr^{-1} should be enforced to minimize further ecological effects. So far recorded road dust linked with vehicular traffic and associated speed has signalled an important ecological variant to herbivores distribution and grazing pattern along the roadsides. In order to reduce further impacts at broader scale speed bumps should be introduced on busy roads and heavy duty carriers on transit especially lorries should be controlled by introducing a special fee.

8.0 ACKNOWLEDGMENT

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10.0 TABLES

Table 1. Differences in the density of dust (g dust/g grass) during wet and dry seasons and the mean sighting frequencies (observ.) of animals between east and west sides of the road. The mean density of dust and sightings beyond 200m are not presented here because they were not statistically significant (Mann-Whitney U-tests were used to test the differences). N= number of observations; Z= Mann-Whitney U-value

Season	Variable	E-W distance	N	Mean ±S.E.	Z	P value
Wet	Dust	E 100m	72	0.053 ± 0.005	-2.814	0.005
		W 100m	71	0.072 ± 0.006		
	Dust	E 200m	65	0.025 ± 0.002	-1.027	0.305
		W 200m	66	0.032 ± 0.004		
	Observ.	E 100m	6	6.3 ± 2.5	-0.322	0.748
		W100m	4	6.0 ± 1.2		
	Observ.	E 200m	6	4.6 ±1.2	-0.643	0.520
		W 200m	5	6.2 ± 2.0		
Dry	Dust	E 100m	60	0.082 ± 0.018	-4.750	0.000
		W100m	60	0.146 ± 0.018		
	Dust	E 200m	58	0.033 ± 0.007	-2.137	0.033
		W 200m	59	0.047 ± 0.008		
	Observ.	E 100m	9	4.2 ± 0.99	-0.216	0.829
		W100m	12	4.0 ± 0.58		
	Observ.	E 200m	10	3.6 ± 0.89	-1.632	0.103
		W 200m	12	2.1 ± 0.38		
Late-Dry	Dust	E 100m	83	0.069 ± 0.018	-4.279	0.000
		W 100m	84	0.104 ± 0.018		
	Dust	E 200m	83	0.034 ± 0.007	-1.88	0.060
		W 200m	82	0.044 ± 0.008		
	Observ.	E 100m	10	5.9 ± 1.2	-1.781	0.075
		W 100m	11	3.2 ± 0.7		
	Observ.	E 200m	9	4.4 ± 1.6	-0.833	0.405
		W 200m	10	4.9 ± 1.3		

Table 2. A multiple linear regression analysis for variables explaining the variation in the density of dust from the grass sampled along road sides in Serengeti National Park.

Independent variables	t	P
Perpendicular distance	-13.0	0.001
Short or long grass	7.59	0.001
Vehicle numbers	5.83	0.001
East or west side	4.52	0.001
Season of the year	0.21	NS

12.0 FIGURE LEGEND

Fig. 1. The Serengeti National Park (SNP) study area located between Ngorongoro (NCA) and Seronera plains marked as box A and B respectively. The land feature which divides the two sites (hereinafter referred to as short and long grass respectively) is Naabi hill Gate conspicuously divided by a continuous dotted line.

Figure 2. Monthly mean variation in the density of dust measured east and west of the road and monthly traffic volume

Figure 3. Mean (+/- SE) of dust weight east and west sides of the road in the study area. The mean dust weights for the short and the long grass are represented by filled and open squares respectively. Bars represent +/- SE of means and boxes; 3) a, b, c and d indicates 100, 200, 300 and 1000 m perpendicular distances respectively

Figure 4. Mean (+/- SE) numbers of animal groups sighted for species recorded between the established perpendicular distances east and west side of the road. Differences between east and west (Wilcoxon signed rank test: a) 100 m (Z=-2.224, P=0.026), b) 200 m (Z=-1.253, P=0.210), c) 300 m (Z=-0.204, P=0.838) and d) 1000 m (Z=-1.45, P=0.147). Bars represents +/- SE of means and the mean sighting frequencies are represented by circles and boxes 4) a, b, c and d indicates 100, 200, 300 and 1000 m perpendicular distances respectively.

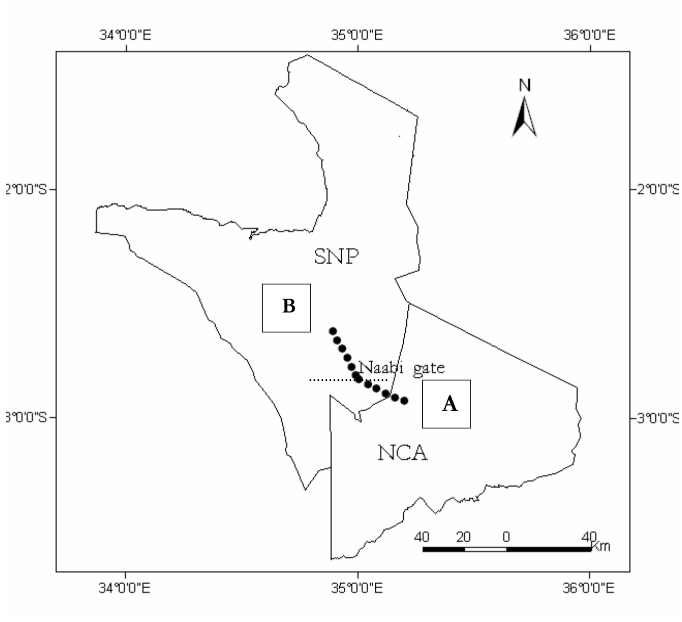

34°0'0"E
35°0'0"E
36°0'0"E
N
2°0'0"S
3°0'0"S
SNP
B
Naabi gate
A
NCA
40 20 0 40
Km

Fig. 1.

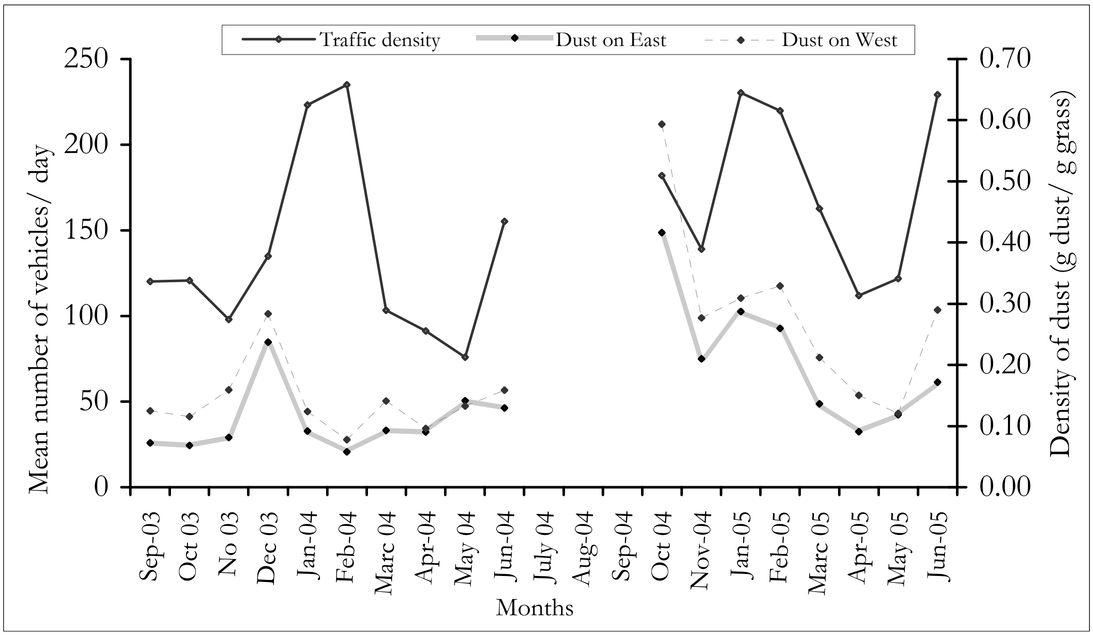

Traffic density
Dust on East
Dust on West
Mean number of vehicles/ day
250
200
150
100
50
0
Density of dust (g dust/ g grass)
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Sep-03
Oct 03
No 03
Dec 03
Jan-04
Feb-04
Marc 04
Apr-04
May 04
Jun-04
July 04
Aug-04
Sep-04
Oct 04
Nov-04
Jan-05
Feb-05
Marc 05
Apr-05
May 05
Jun-05
Months

Fig. 2.

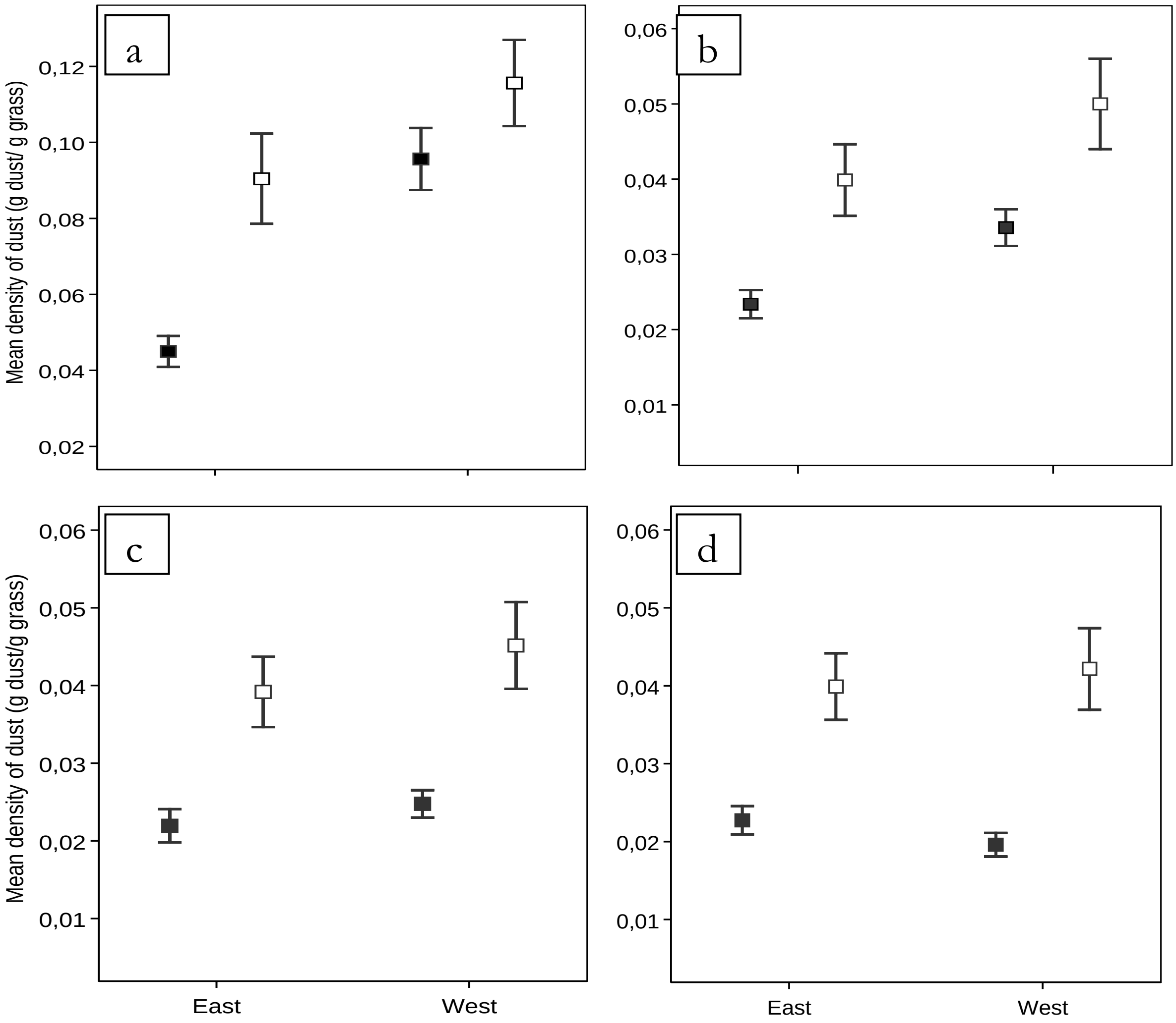
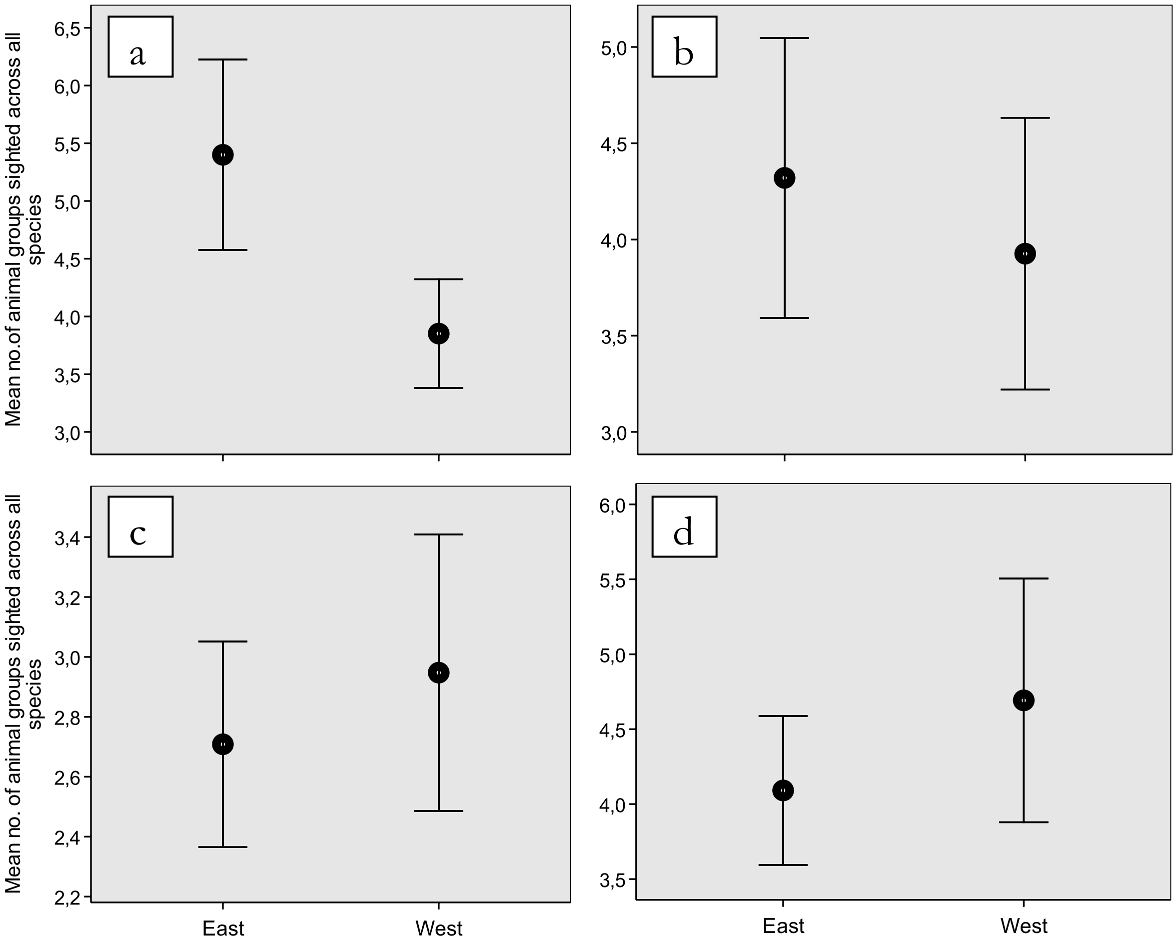

a
b
c
d
Mean density of dust (g dust/ g grass)
Mean density of dust (g dust/g grass)
0,02
0,04
0,06
0,08
0,10
0,12
0,01
0,02
0,03
0,04
0,05
0,06
East
West
East
West

Fig. 3.


a
b
c
d
Mean no.of animal groups sighted across all species
Mean no. of animal groups sighted across all species
6,5
6,0
5,5
5,0
4,5
4,0
3,5
3,0
3,4
3,2
3,0
2,8
2,6
2,4
2,2
East
West

453

454 Fig. 4.

HABITAT USE OF MIGRATING WILDEBEEST IN SERENGETI NATIONAL PARK, TANZANIA

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Word Count : Abstract =267, Full paper (excluding references) = 4,070

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ABSTRACT

Serengeti wildebeest *Connochaetes taurinus* often come in contact with human activities associated with development during their annual movements. Since the influence of these activities is poorly understood, we examined the distribution and daily wildebeest movement from ten GPS collared wildebeest from 2002 to 2004 to test for any significant difference in the habitat use. Compositional analysis and daily mean movement rate were used to asses wildebeest distribution and habitat use. A pairwise comparison of different habitats computed using log-ratio among GPS collared wildebeests indicated that open grassland, open woodland and wooded grassland were used significantly more frequently than other vegetation types. Habitat uses changed with seasons reflecting opportunistic feeding due to resources variability. Migrating wildebeest avoided the western corridor during the north migration despite the relative potential of green grass and surface water. The pattern of space use was better explained by daily wildebeest movement which seemed to have increased even in the most frequently used habitats reflecting resource competition. The difference in daily mean rate between wildebeest sexes was better explained by the interaction between sexes and period of the day. Males appeared to be more active at night compared to females. Less movement in females was recorded during the calving period (wet season), probably a strategy to minimize predation on less mobile neonates. Future monitoring of habitat use would be enhanced using a long-term data set from large sample sizes of wildebeest with detailed daily location GPS fixes. Managers would benefits more if the analyses of habitat use among wildebeest individuals compared foraging movements between resident and migratory sub-populations in habitats within the migration corridors.

Key words: available habitat, migration, movement, Serengeti, used habitat, wildebeest, vegetation.

INTRODUCTION

A central focus in animal ecology is to consider the association of an animal with its environments, particularly the varieties of habitats it occupies or prefers. Habitat preference studies correlate the use of habitats by animals against their availability (Hall et al. 1997; Manly et al. 2002; Calenge & Dufour 2006). Migrating ungulates in most grazing ecosystems e.g. northern Tanzania, have maintained diversity and abundance through selection of most suitable habitats at times extending beyond the boundaries of parks and game reserves into surrounding communal and private lands (Rodgers 2003). Habitats with food sources that vary in amount and quality both temporary and spatially are critical when migratory ungulates are making route choices (McNaughton 1988, 1990; Musiega & Kazaidi 2004). The biggest challenge in habitat selection studies is how to develop a suitable method for the analyses of selection from proposed approaches when resources are defined by several categories (Aebisher et al. 1993; Calenge & Dufour 2006; Gillies et al. 2006). Nevertheless, any study design for habitat selection fall into one of three broad methodological approaches which consider measurements of I) habitat use and availability at the population level, II) habitat used by identified animals while considering available habitat at the population level or III) both availability and use of habitat for each single animal in question.

The movements between habitat patches in most environments are constrained by resource and landscape heterogeneity together with terrain features. The means in which ungulates respond to environmental heterogeneity impinge on their movement patterns in many ways (Johnson et al. 1992; Etzenhouser et al. 1998). Wildebeest for example, function best in environments with variable resource availability particularly suitable niches at different times of the year. They move between habitat patches in response to changes in climate associated with fluctuations in resource availability (Mduma et al. 1999; Wilmshurst et al. 1999; Boone et al. 2006). Nevertheless, predation pressure (Fryxell & Sinclair 1988), uneven distribution of rainfall and surface water

(Wollanski et al. 1999; Wollanski & Gereta 2001), specific nutrients in foliage (Kleuren 1975; McNaughton 1990; Murray 1995), fire (S.N.Hassan pers. comm.) and habitat suitability have greatly influenced habitat selection and ungulate movements between habitat patches (Andersen 1991). Above all, foraging economics during movements play an important role in habitat selection (Poldolsky & Price 1990; Wilmshurst et al. 2000; Bergman et al. 2001).

Therefore, in order to conserve migration it is essential to know what resource categories influence habitat use and to correlate the distribution patterns of grazers to the vegetation characteristics in the geographical region. Recent telemetry studies in Serengeti (Thirgood et al. 2004) including simulation models (Musiega et al. 2004; Boone et al. 2006) suggest a close link between wildebeest migration routes and new forage growth as influenced by rainfall. Observation also affirms that both vegetation and landscape heterogeneity are key players determining wildebeest movement.

Studies on individual collared wildebeest (Inglish 1976; Thirgood et al., 2004; Boone et al. 2006) suggest that there is limited use of areas outside core protected zones. Wildebeest mobility and residence time in these areas have only increased in the presence of drought during north migration (Hilborn et al. 1994; Thirgood et al. 2004). In view of these findings our telemetry study examined the distribution and abundance of wildebeest in Serengeti National Park and its adjacent protected areas using detailed GPS collared data and related distribution patterns to available vegetation / land-cover maps in order to answer the following questions; i) are different habitat types used at different levels? ii) if so, is habitat use significantly different among GPS collared individuals with regard to the available habitat? iii) is the rate of movement amongst wildebeest individuals significantly influenced by habitat types, sex, season and period of the day?

MATERIALS AND METHODS

Study Area

The Serengeti Ecosystem (SE) is comprised of nearly 25,000 km^2 on the boarder between Tanzania and Kenya. The system has a conservation core zone consisting of Serengeti National Park (SNP) and Masai Mara National Reserve (MMNR) in Tanzania and Kenya respectively. The SNP is shielded by Maswa Game Reserve (MGR), Grumeti Game Reserve (GGR) and Ikorongo Game Reserve (IGR) to the south and north-west and Ngorongoro Conservation Area (NCA) to the south-east (Fig. 1). Grassland forms the most extensive land cover, reaching to less than 75% in areas of extensive woodland (Campbell & Hofer 1995). Open grassland dominates in the southeast whereas woodland dominates the western and northern parts (Senzota, 1982). Patches with over 25% woody canopy cover occur largely in the southern SNP - MGR boarder and high relief being confined to west and southwest of the Serengeti, Ngorongoro crater and Loliondo highland in the east.

Wildebeest population size has maintained around 1.3 million individuals between 1970 and 2001 with yearly fluctuations due to rainfall in the dry seasons (Serneels & Lambin 2001). Apart from dry season rainfall, the density of migratory wildebeest in the open woodland and wooded grassland habitats, north and outside the Serengeti plains, is influenced by the level of human disturbance (Campbell & Hofer 1995). Fire effects on woodland (Dublin et al. 1990, Koppel & Prins 1998) coupled with the effects of small to medium (e.g. impala *Aepyceros melampus*, wildebeest, buffalo Syncerus caffer) and large (e.g. elephants or giraffe Giraffa camelopardalis) herbivores have been instrumental in shaping the vegetation (Prins & Van der Jeugd 1993). This implies that since wildebeest is food regulated (Mduma et al. 1999), short term habitat alteration from bushfire; agro-pastoral and poaching activities (Sinclair & Arcese 1995; Kideghesho et al. 2005) may largely constrain resources available for the migrating wildebeest.

GPS Collaring

Sixteen adult wildebeest, ten (six males and four females) and six (four males and two females) were fitted with GPS collars in Ndutu area, South of Naabi gate in Serengeti National Park on April 27, 2002 and May 5, 2003 respectively. These animals were stalked with a car and darted to the rump region with a combination of etorfin (etorphine 9 mg/ml, M99) and medetomidin (medetomidine 10 mg/ml, Zalopine) from inside the vehicle. The GPS collar was fitted when the wildebeest was down and calm and the anaesthesia was reversed using diprenorphine. Wildebeests fitted with collar were closely monitored for one hour after recovery and no undesirable effects were observed during handling and monitoring process. Televit of Sweden delivered the GPS-Simplex collars with their assembly.

SPM Simplex project manager software was used to set up a scheduled program for the GPS-units. All GPS-collars fitted in 2002 were set to record their positions every third hour and those fitted in 2003 took positions every one hour. Remote downloading was programmed to occur once every month but the topography, remoteness and climatic conditions of the area made this approach very difficult. Therefore, collars were recovered after one year of service when the drop-off unit had been triggered. We managed to retrieve eight collars (six males and two females) in 2003 and the remaining two were localized but never collected due to difficult terrain associated with the wet season (April-May). Only two collars (one male and one female) were retrieved in 2004 and the remaining four were never localized. A total of 14,996 and 13,166 animal positions (fixes) were recorded in 2003 and 2004 respectively.

Available habitat, habitat use and compositional analysis

We used the minimum convex polygon (MCP) from pooled GPS coordinates from all collared wildebeest to define a home range of available habitat. The composition of available vegetation types within this home-range was based on the Serengeti ecosystem vegetation map of 1994 (supplied by IRA-University of Dar es Salaam). We assumed, we considered all wildebeest to have access to the same habitats given the migration patterns of Serengeti. Similarly, the use of habitat by the GPS-collared wildebeest was found by acquiring the vegetation type at each GPS location, based on the same vegetation map as mentioned above. Due to the lack of an updated vegetation map for MMNR (Kenya), habitat use in MMNR was not performed.

Compositional analysis (Aebischer et al. 1993) is a general approach for comparing the proportions of different types of habitat that were available and used. Resource use in this case was defined as proportions of different vegetation types within the estimated available area specified by the frequency of wildebeest observations. Based on the equations modified from Manly et al. (2002), there were ten types of available habitat units, and the proportional use of these habitats by each individual wildebeest were described by the composition H_{u1}, H_{u2}................ H_{u10}; where H_{ui} is the estimated proportion of the habitat (u) used by the individual that are of type i (Note that all proportions sum to one). Similarly, the available proportions for the same wildebeest were π_{a1}, π_{a2}................ $\pi_{a10.}$ For any component H_j of a composition, the log-ratio transformation $y_i = \log_e(H_i/ H_j)$ produces linearly independent variables with a specific choice for j. Based on this, the differences $d_i=\log_e (H_{ui}/ H_{uj}) - \log(\pi_{ai}/\pi_{aj})$ were calculated to obtain the relative use and availability of habitats i and j for all GPS collared wildebeests.

In the calculation, it was first assumed that the proportion of habitat used is the same as the proportion of habitat available. Secondly, that each individual collared wildebeest was independent of the other, hence there was no dependence for relocations. Thus, in order to test for overall habitat selection, we used the differences in log-ratios (d_i) and tested whether the vector of mean values of d ($d_{1,}$ d2........d6) was significantly different from a zero vector, using Wilk's lambda test. Habitat types whose use observations were proportionally low were pooled together and a zero data was replaced by an arbitrary small positive number when calculating d_i

values, in case of zero record for the i_{th} value. In order to test for the differences in habitat selection, a one sample t-test was used to compare the mean of d_i value to zero and subsequently a paired t-test for pairs of sample means. Since the data was divided into groups of categorical variables i.e. sex, year, seasons and period of the day, a generalised linear model was performed to test the effect of interacting variables in habitat selection. An individual GPS collared wildebeests whose fixes in year days covered less than 50% were omitted to avoid bias from fewer observations in habitat use. Available data reflect time from April 2002 through March 2004 whereas seasons considered the annual movements and habitat use in distinct periods covering January - May, June - July and August - December for wet, early dry and late dry range respectively.

Daily wildebeest movement

The rate of movement of each GPS collared wildebeest in different habitats was obtained by calculating the mean lengths of line paths from daily fixes of all wildebeest covered in each habitat for the entire study period. The movements between line paths for daily fixes recorded after one and three hours were standardised in km per hour and later averaged across days. In order to capture the differences in movements as a function of period of the day, daily fixes were split into day and night. All wildebeest fixes retrieved from 7:00 to 18:59 and from 19:00 to 6:59 hours covered day and night sections of 24 hours respectively. Movement data were tested for normality and later $\log_{10}$transformed where graphs were non-normal. A mixed linear model was developed to test the effect of interacting factors as well as the model that best explain the rate of movement. We started with the full model, including all main effects and interactions. Then we stepwise excluded non-significant terms one by one. GPS collared wildebeest individuals were entered in the model as a random factor whereas study years, seasons, period of the day, habitat types and protected areas as fixed factors. We started the full model, including all main effects and interactions. Then we stepwise excluded non-significant terms one by one. The parameter estimates of wildebeest movement were independently tested to determine if the variations from the intercept significantly differed in factor combinations using S-Plus v7.0 (Insightful Corp.). Other statistics were done in SPSS inc. (2006) and are 2-tailed with 0.05 significance level.

RESULTS

Movement patterns in 2002 -2004

Position fixes from individual collared wildebeest indicated higher proportional uses of areas under core protection than areas with lower protection status (Table 1). Serengeti National Park (SNP) was predominantly used throughout the year followed closely by Ngorongoro Conservation Area (NCA). Frequencies of wildebeest uses in different protected areas between the study years were significantly different (χ^2=901, DF=5, P<0.001). Serengeti National Park (SNP) and Ngorongoro Conservation Area (NCA) were used significantly more frequently than other protected areas in 2004 than 2003 (Table 1). All GPS collared wildebeest fixes during the study years are indicated in Fig. 2a; where seasonal uses in different habitats are indicated by a series of maps in Fig. 2.

The general pattern of movements indicated an even distribution of collared wildebeest in the south-east of the SNP and NCA short grass plains toward Maswa Game Reserve (MGR) during wet season (Fig. 2b). At the onset of the dry season the movement headed north of SNP through the west (Fig. 2c). The open land and the protected areas outside SNP appeared to be avoided as wildebeest moved west and north-west of the park toward Masai Mara National Reserve (MMNR) in Kenya (Fig. 2c). A substantial amount of time was spent within the habitats of Tanzania-Kenya boarder of the ecosystem and later collared wildebeests moved back to SNP spreading throughout the centre, south-east and part of NCA during late dry season (Fig. 2d).

Habitat use

GPS collared wildebeest were recorded during the study period in a range of habitats (Table 2) with the following decreasing order of importance: open grassland (OG), bushed grassland (BG), bushland with emergent trees (BET), wooded grassland (WG), open woodland (OW), open bushland (OB), bare soil (BS), dense bushland (DB), grassland with scattered cropland (GSC), inland water and permanent swamp/marsh (IW) and woodland with scattered cropland (WSC). The proportions of available and used habitats for individual wildebeest in each habitat are provided in Table 3. Differences in log ratios from the proportions of habitat use computed from each individual collared wildebeest are indicated in Table 4. Pairwise comparison of different habitat combination indicated a significantly higher selection for open grassland compared to open woodland and bushland with emergent trees, when their mean differences were compared across the ten collared wildebeest (Table 5). In addition, open woodland was used more frequently compared to wooded grassland whereas wooded grassland was selected more frequent compared to bush land with emergent trees (Table 5). Despite the other habitats being available in relatively higher proportions, comparisons of their mean differences from the pairs were not statistically significant (Table 5). Without considering seasonal influence on wildebeest habitat use, there was a clear difference between frequencies of habitat use dominated by open grassland (Fig. 3). Open woodland appeared to be an important habitat during the wet season whereas; bushed and wooded grasslands were selected more frequently than other habitats in the late dry season (Fig. 3).

Wilk's Lambda tests indicated significant selection when different variables interacted in a Multivariate Analysis. Habitat use was best explained by the interaction between period of the day (day and night) and seasons, [General Linear Model (GLM), F=10.8, DF=3, P<0.001) and also the season and habitats GLM, F=6.26, DF=18, P<0.001]. Other interactions (i.e. period of the day*sex; period of the day*habitat; period of the day*season*sex; period of the day*season*habitat; period of the day*sex*habitats; season*sex; season*sex*habitat) were not significant.

Rate of movement in different habitats

Daily mean rate of movement averaged from wildebeest fixes for all study years was 4.9(±1.2 km, N=26,290). There was no significant difference in movement rate between the study years. The lowest and highest movement rates were 0.04 to 63 and 0.8 to 32.6 km for year 2003 and 2004 respectively. There were significantly differences in movement rate between period of the day, seasons, vegetation types and protected areas (Table 6). The difference in daily mean rate between wildebeest sexes was better explained by the interaction between sex and period of the day (Table 6). Males appeared to be more active at night compared to females, and night movement rate was reduced by almost 50% in both sexes (Table 6). On the other hand females covered significantly longer distances (6.03±1.02 km day^{-1}) than males (4.49±1.2 km day^{-1}) during the day than night time (Table 7). Despite the lack of seasonal influence on the wildebeest movement, females were relatively slower during the wet season (4.9±1.2 km) compared to the early dry (5.9±1.0 km) and late dry season (6.2±1.0 km) (Table 7). Generally, however, the daily movement rate for all collared wildebeest across habitats was highest in inland water/swamps (7.1±1.6 km) and lowest in grassland with scattered cropland (2.4±1.2 km) (Table 7). Individual collared wildebeest appeared to move faster in GGR and SNP (6.1±1.6 km and 4.9±1.2 km day^{-1} respectively) and were relatively slower both in MGR and LGR (3.6±1.1 km day^{-1}).

DISCUSSION

This study indicates that anthropogenic changes may potentially deter wildebeest from using habitats in reserves adjacent to core protection areas as habitats in SNP and NCA were used proportionally more frequently compared to those found in areas of lower protection status. For instance, Grumeti Game Reserve appeared to be completely avoided whereas in agreement with a previous study, the Ikorongo Game Reserve (Fig. 2) was partially used (Thirgood et al. 2004). Indeed, threats (particularly poaching) to wildebeest outside the core protected areas can be associated with annual wildebeest migration (Homewood et al. 2001, Serneels & Lambin 2001a, b., Thigood et al. 2004, Holmern et al. 2007). Moreover, in connection with documented threats, complex interactions linking protected areas network of Serengeti ecosystem have been associated with increased human population (Kideghesho et al. 2005). Increased illegal hunting from densely populated areas in western Serengeti together with natural predation can likely disrupt wildebeest migratory movements and ranging patterns, when balancing physiological needs and safety.

Wildebeest patterns of space use could be described by movement rates among wildebeest individuals. However, our data should be treated cautiously due to the differences in interpreting movement data that arise when comparing collared individuals with different time intervals between fixes records (Ferguson et al. 1998). Ignoring possible differences due to time interval differences between years, our study indicates that there was consistent selection for open grassland compared to other habitats. However, the use preference of open grassland was strongest in the Serengeti National Park (SNP) with more recorded fixes (Table 1) probably due to the level of protection and nutritional suitability of the south-east plains grasslands (McNaughton 1990, Murray 1995). Generally, open short grasslands are considered to be extremely productive areas in Serengeti primarily during the wet season (McNaughton 1990, McNaughton & Banyikwa 1995, Murray 1995, Wilmshurst et al. 1999).

Despite of elevated requirements for high-quality food in open grassland areas, the estimated rate of wildebeest movement was comparatively higher probably due to strong competition for quality resources. Other factors being equal, higher movement rate between habitat patches would reflect little use possibly due to either intra- and inter specific competition or disturbance from predators and human activities or both. Alternatively, the amount of plant biomass available per unit area is important for forage intake rates (Distel et al. 2005). Lower sward bulk density in high-quality short grasslands could result in higher movement rates.

The habitats of western Serengeti were slightly used during the dry period and the collared wildebeest appeared to have been moving quickly towards the north as dry season advanced (Table 7; Fig. 2c, d). During this period open woodland, bushland with emergent trees and wooded grassland were important habitats. However, preference should not be seen as a choice function along a gradient from open grassland to close woodland only. Differences in vegetation physiognomy also result from differences in the dominant woody plant species which can, in turn, reflect other environmental variability such as that caused by soil type and moisture availability. The strong selection for open woodland versus wooded grassland as well as for wooded grassland versus bushland with emergent trees could be influenced by the outcome of the interaction between sexes with period of the day during the dry period when food resource is scarce. Moreover, casual observations (Ndibalema pers. observ.) indicated that availability of green grass and the presence of surface water strongly correlated with wildebeest movements.

Grass quality and availability tend to limit ungulate food intake during the dormant season (McNaughton & Georgiadis 1986, Bergman et al. 2001). For instance, as demonstrated in a recent study (S.N.Hassan pers. comm.) consumption of plant biomass in the north-west and western corridor of SNP shifted significantly between burnt and non-burnt patches apparently due to changes in the relative composition of the swards in terms of the amount and the quality of the forage available.

Higher daily movement rate recorded in Grumeti Game Reserve indicated a general flight tendency in the Western Corridor. These could be related to human disturbance from large-scale farming, range competition from agro-pastoralists and higher poaching levels (Arcese et al. 1995, Campbell & Hofer 1995, Mduma et al. 1999). Early-dry-season (May-July) fires profusely occurring in the game reserve areas and coincident with the northern migration (J. Dempewolf, unpubl. data) significantly reduce the amount of plant biomass available for migrants (Rusch et al. 2005). Both wildebeest migrants and other wildlife species appear to use game reserve areas less than the core protected area, even with no evidence for competition for forage resources with livestock (Rusch et al. 2005). Tourist lodges and camps in the west strategically located on the wildebeest migration corridor might have also influenced the observed ranging pattern. Similarly, seasonal differences in daily movement rate could be primarily linked to differences in quality range associated with forage growth due to rainfall distribution patterns of Serengeti (Sinclair & Norton-Griffiths 1979, Pennycuick 1975, Sinclair 1995, Frank et al. 1998, Mduma et al. 1999, Boone et al. 2006).

Movement rates averaged across collared wildebeest in both study years was 4.9 km day^{-1} which differs considerably from the 10 km day^{-1} reported over two decades ago (Pennycuick 1979 cited in Murray 1995). However, this reduction in movement rate might reflect differences in sampling methods or the influence of environmental parameters on spatial variations in food resources. Differences in the rate of movement among GPS collared wildebeest during time of the day and season were another notable finding in this study.

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

The observed differences in movement between wildebeest sexes during day and night might also reflect life history strategies engrossed in parental care and nutritional demands in females that were relatively more active during the day than night time. Male individuals were expected to be quite mobile considering their group roles, but physiological demands in search for better resources associated with pregnancy and lactation in females might account for the differences (V.Ndibalema unpubl. data). In addition, the need for water resource tends to drive movements within wildebeest groups (Wolanski et al. 1999, Wolanski & Gereta 2001). The night movements were reduced to about 50% in both cases probably for rumination, rest and/or sleep and to minimize encounters with predators such as lions Panthera leo and hyenas Crocuta crocuta known to maximize their hunts by night (Hofer & East 1995, Packer 1996).

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TABLE LEGEND

Table 1. Wildebeest fixes from ten collars (7 males and 3 females) in different protected areas of Serengeti Ecosystem during the annual migration cycle of year 2003 and 2004 averaged to obtain mean percent observed frequency locations of daily use. Wildebeest fixes in 2002 and 2003 were recorded after every 3 and 1 hour respectively. SNP=Serengeti National Park, NCAA=Ngorongoro Conservation Area Authority, MGR=Maswa Game Reserve, IGR=Ikorongo Game Reserve, IGR=Ikorongo Game Reserve, LGCA=Loliondo Game Controlled Area.

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

Table 3. Differences in log-ratios calculated from data in Table 1 comparing habitat use within MCP home range to availability defined by the home ranges (See Table 2 for definitions of the habitat types).

Table 4. Used and available proportions of seven habitat types for ten radio-collared wildebeest.

Table 5. Means, standard deviation (SD) and t-test results for compositional analyses of habitat types and habitat pairwise comparisons (one sample and paired t-tests with nine df).

Table 6. Summary of a mixed linear model analysing the log$_{10}$transformed wildebeest movement rate as a function of year, season, time of the day, sex, vegetation type and protected areas (fixed factors). Wildebeest was entered as a 'random factor' to

control for repeated measures of movement for the same collared wildebeest. Wildebeest movement was log transformed to get better normal distribution.

Table 7. Summary of the test effect of interactive parameters in the final model independently explaining estimates of wildebeest movement rates in $\log_{10}$ (km day^{-1}) changed to km day^{-1}.

Table 1.

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

*male; **female

Table 2.

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

Table 3.

	OG		BG		OW		OB		WG		BET		*OT	
Beest	π[1]	H[2]	π	H	π	H	π	H	π	H	π	H	π	H
3152	0.44	0.448	0.09	0.073	0.10	0.102	0.07	0.044	0.06	0.054	0.19	0.094	0.037	0.005
3162	0.44	0.317	0.09	0.061	0.10	0.056	0.07	0.022	0.06	0.113	0.19	0.149	0.037	0.025
3202	0.44	0.50	0.09	0.078	0.10	0.017	0.07	0.068	0.06	0.036	0.19	0.025	0.037	0.016
3212	0.44	0.408	0.09	0.201	0.10	0.108	0.07	0.121	0.06	0.061	0.19	0.081	0.037	0.017
3222	0.44	0.504	0.09	0.00	0.10	0.075	0.07	0.029	0.06	0.038	0.19	0.011	0.037	0.166
3232	0.44	0.591	0.09	0.057	0.10	0.002	0.07	0.004	0.06	0.014	0.19	0.229	0.037	0.101
3242	0.44	0.468	0.09	0.191	0.10	0.071	0.07	0.093	0.06	0.054	0.19	0.005	0.037	0.003
4162	0.44	0.504	0.09	0.178	0.10	0.048	0.07	0.052	0.06	0.090	0.19	0.045	0.037	0.020
4222	0.44	0.331	0.09	0.101	0.10	0.033	0.07	0.053	0.06	0.022	0.19	0.048	0.037	0.007

[1] Available proportion of habitat

[2] Used proportion of habitat

*Pooled data from BS, GSC and IW (see table 2 for description)

Table 4.

Beest	Differences in log ratios (d)					
	OG/OT(d1)	BG/OT(d2)	OW/OT(d3)	OB/OT(d4)	WG/OT(d5)	BET/OT(d6)
3152**	1.987	1.766	1.990	1.506	1.881	1.274
3162**	0.081	0.020	-0.169	-0.747	1.042	0.166
3202*	0.947	0.681	-0.914	0.787	0.309	-1.205
3212*	0.714	1.593	0.867	1.337	0.813	-0.059
3222*	-1.348	-7.048	-1.769	-2.354	-1.942	-4.269
3232*	-0.690	-1.438	-4.782	-3.732	-2.400	-0.800
3242*	2.331	3.022	1.935	2.563	2.174	-1.238
4162**	0.765	1.315	-0.099	0.334	1.042	-0.795
4222*	1.307	1.705	0.490	1.313	0.620	0.213

*male; **female

Table 5.

Comparison	Differences (di)	Mean	SD	P value
OG/OT	d1	0.787	1.17	0.063
BG/OT	d2	0.340	2.86	0.716 NS
OW/OT	d3	-0.416	2.02	0.532 NS
OB/OT	d4	0.173	1.92	0.783 NS
WG/OT	d5	0.436	1.49	0.378 NS
BET/OT	d6	-0.796	1.47	0.121 NS
OG versus BG	d1-d2	0.447	1.91	0.479 NS
OG versus OW	d1-d3	1.202	1.48	0.030
OG versus OB	d1-d4	0.614	1.01	0.087 NS
OG versus WG	d1-d5	0.351	0.74	0.166 NS
OG versus BET	d1-d6	1.583	1.28	0.004
BG versus OW	d2-d3	0.756	2.43	0.352 NS
BG versus OB	d2-d4	0.167	1.83	0.779 NS
BG versus WG	d2-d5	0.095	1.87	0.876 NS
BG versus BET	d2-d6	1.136	1.99	0.105 NS
OW versus OB	d3-d4	-0.589	0.99	0.093 NS
OW versus WG	d3-d5	-0.851	1.01	0.026
OW versus BET	d3-d6	0.380	1.92	0.546 NS
OB versus WG	d4-d5	-0.263	0.83	0.345 NS
OB versus BET	d4-d6	0.969	1.84	0.130 NS
WG versus BET	d5-d5	1.232	1.35	0.018

Table 6.

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

Table 7.

Parameter	Estimates(SE)	DF	t-value	p-value
Intercept	4.90 (1.15)	26290	11.481	<0.0001
Night	-2.29 (1.03)	26290	-28.948	<0.0001
Male	-1.54 (1.18)	8	-2.619	0.0387
Early dry season	1.05 (1.03)	26290	1.786	0.0740
Late dry season	1.13 (1.02)	26290	4.453	<0.0001
BG	-1.11 (1.03)	26290	-3.425	0.0006
OW	-1.07 (1.04)	26290	-1.585	0.1128
OB	1.01 (1.04)	26290	0.173	0.8620
WG	-1.25 (1.04)	26290	-5.421	<0.0001
BET	-1.21 (1.03)	26290	-4.874	<0.0001
BS	-1.27 (1.08)	26290	-2.932	0.0034
GSC	-2.56 (1.16)	26290	-6.084	<0.0001
IWS	2.17 (1.61)	26290	1.624	0.1043
WSC	1.10 (1.82)	26290	0.160	0.8727
Ngorongoro	-1.03 (1.02)	26290	-0.989	0.3224
Ikorongo	-1.16 (1.11)	26290	-1.388	0.1651
Grumeti	1.16 (1.61)	26290	0.303	0.7611
Maswa	-1.26 (1.04)	26290	-3.922	0.0001
Loliondo	-1.35 (1.12)	26290	-2.474	0.0133
Rejected Terms				
Early dry season × male	-1.05 (1.05)	26288	-0.890	0.373
Late dry season × male	1.04 (1.05)	26288	0.812	0.417

FIGURE LEGEND

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

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

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

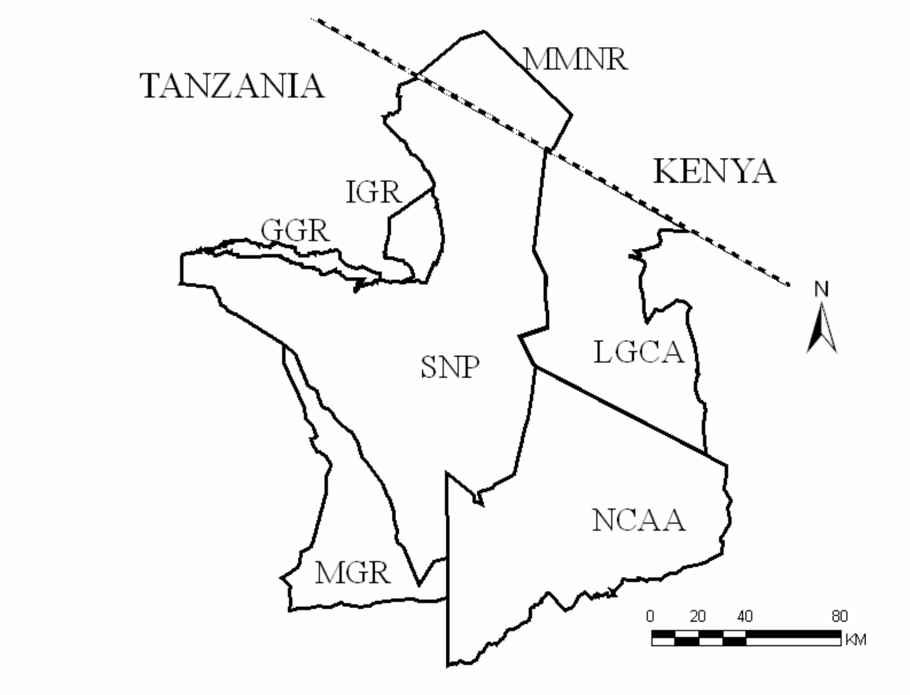

Fig. 1.

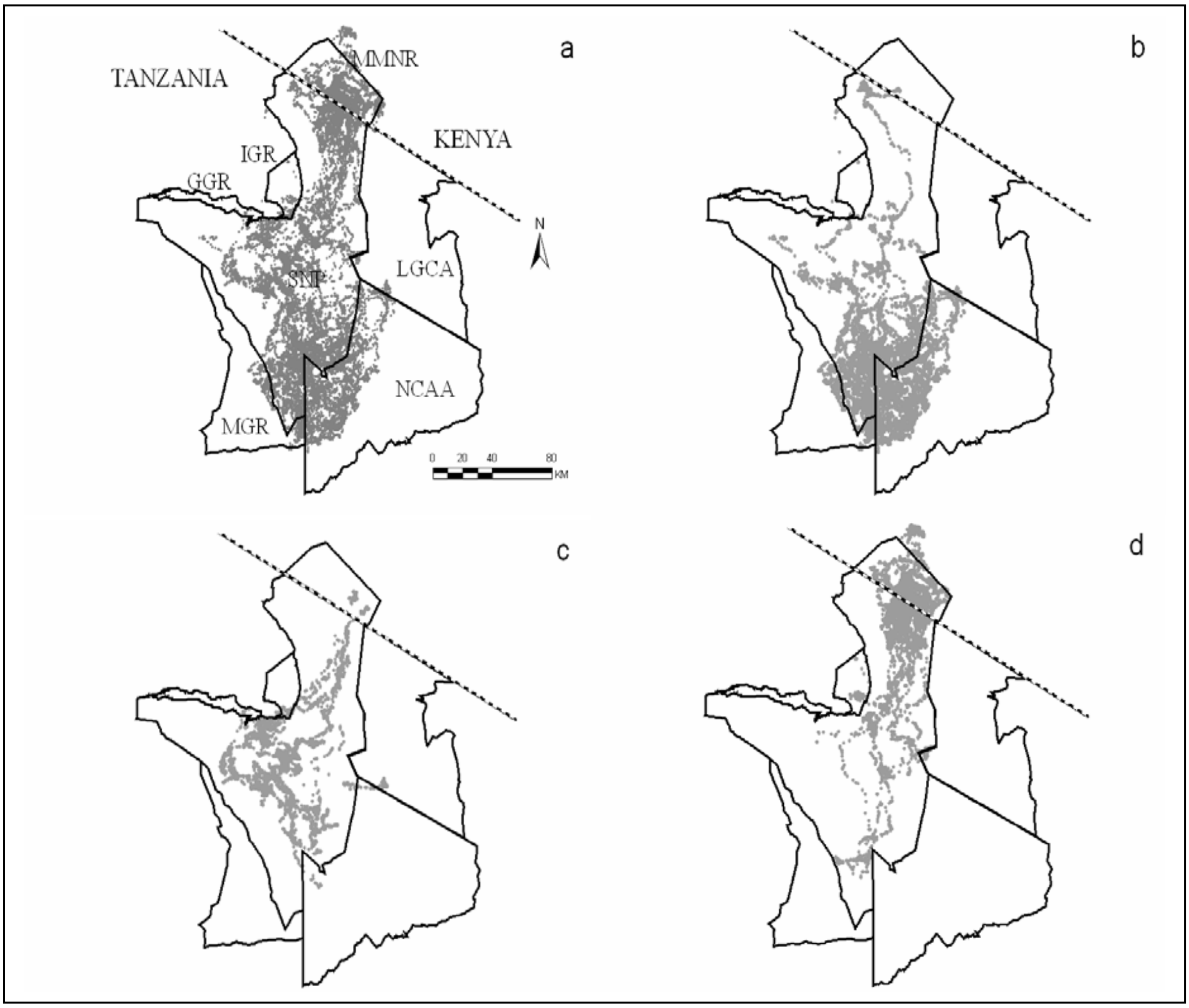
a
TANZANIA
MMNR
KENYA
IGR
GGR
SNP
LGCA
N
NCAA
MGR
0 20 40 80
KM
b
c
d

Fig. 2.

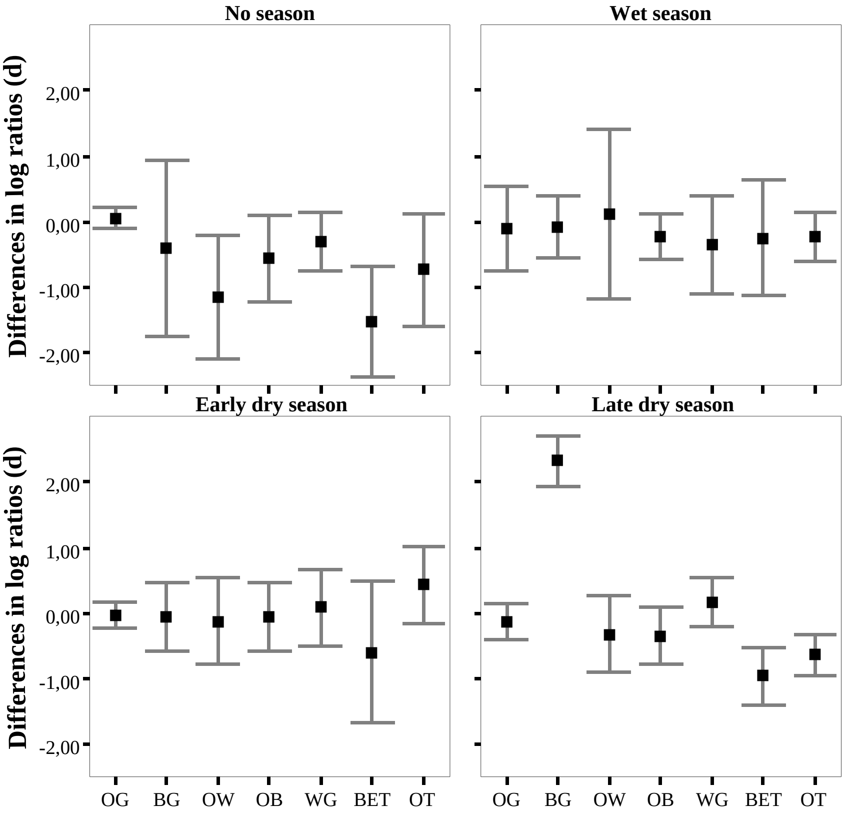
No season
Wet season
Early dry season
Late dry season
Differences in log ratios (d)
2,00
1,00
0,00
-1,00
-2,00
OG
BG
OW
OB
WG
BET
OT

Fig. 3.

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.

1987	Jarle Inge Holten	Dr. philos Bothany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants

1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)

1994 Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994 Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994 Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995 Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995 Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995 Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995 Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996 Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996 Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996 Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996 Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997 Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.

1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997 Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997 Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997 Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997 Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997 Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997 Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997 Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997 Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998 Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.
1998 Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998 Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998 Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998 Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998 Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998 Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999 Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach

1999 Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999 Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999 Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999 Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999 Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999 Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999 Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999 Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999 Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999 Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999 Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999 Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999 Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999 Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999 Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000 Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000 Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000 Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000 Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)

2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)

2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.

2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Ander Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	Phd Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	phD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	phD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	phD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	phD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	phD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	phD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	phD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine

2007 Kasper Hancke	phD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007 Tomas Holmern	phD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007 Kari Jørgensen	phD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007 Stig Ulland	phD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, */Mamestra Brassicae/* L. (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007 Snorre Henriksen	phD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007 Roelof Frans May	phD Biology	Spatial Ecology of Wolverines in Scandinavia