

Wildlife Dynamics

An Analysis of Change in the Masai Mara Ecosystem of Kenya

Wilber Khasilwa Ottichilo

CENTRALE LANDBOUWCATALOGUS



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WILDLIFE DYNAMICS

An Analysis of Change in the Masai Mara Ecosystem

Promotores: Dr. H.H.T. Prins
Hoogleraar in het Natuurbeheer in de Tropen en de Ecologie van Vertebraten

Dr. A.K. Skidmore
Hoogleraar Vegetation and Agricultural Land Survey

Co-promotor: Dr. J. de Leeuw
Universitair hoofd docent
Environmental Systems Analysis and
Monitoring, ITC, Enschede

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WILDLIFE DYNAMICS

An Analysis of Change in the Masai Mara Ecosystem of Kenya

Wilber Khasilwa Ottichilo

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To my mother and father,
who supported and encouraged me
to pursue education

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P.O. Box 6
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Propositions (Stellingen)

Wilber K. Ottichilo

Wildlife Dynamics: An Analysis of Change in the Masai Mara Ecosystem of Kenya (PhD dissertation)

1. Proper planning and management of wildlife requires reliable and consistent data and information on their abundance and distribution.
2. To get an insight into population size trends of large wildlife herbivores, collection and analysis of long-term population estimate or abundance data is necessary. Therefore, it is necessary to establish long-term wildlife monitoring programmes in wildlife conservation areas.
3. Development of systems and analytical approaches in ecological work has been slow. The current interest in these approaches and particularly the use of geo-statistics and modelling techniques in ecological research should be encouraged and supported.
4. Development of new technologies like remote sensing, GIS, GPS, videography etc will certainly enhance collection of useful and detailed data on wildlife and their environments in the near future but they will not replace expert knowledge of ecologists.
5. Wildlife ecologists are notoriously known to study wildlife species to extinction without getting involved or participating in the species recovery programmes. They always claim that more data and information is required even in cases where there are wallowing in abundant data. Future ecologists must be proactive and must identify their research priorities in collaboration with wildlife managers but must not lose their search for novel creativity.
6. There appear to be a general consensus among most wildlife ecologists that the unprecedented worldwide decline of wildlife species (plants and animals) is mainly due to the increasing loss of their habitats to other human activities, pollution and their over-exploitation by man. To reverse this declining trend, wildlife and environmental conservation strategy for the 21st century must focus on habitat restoration and wildlife recovery programmes. This calls for increased scientific research in restoration ecology and ecological engineering.
7. To achieve sustainable wildlife and environmental conservation, it must be realized that conservation and development are interdependent and therefore the integration of the two is necessary for sustainable development. Although the concepts of sustainable development are new and not easy to implement, mankind must strive to achieve sustainable development if we have to maintain live supporting systems and processes on our planet.

8. Science being a creative activity it is impossible to predict ahead of time where a particular line of inquiry will lead. This makes science a very wasteful activity, in that most scientists spend most of their time travelling down paths that lead nowhere (*Jon fairall, editor, GIS User (Vol. 13, February-March 2000)*).
9. Increasing demand of modern age for accountability and productivity is stifling development of future scientists. More prospective scientists are increasingly becoming technologists for fear of taking the wrong road. This trend is a threat to science and must be reversed if science has to remain the main foundation of human development.
10. Embarking on PhD study is like embarking on a journey whose route is undefined but is known to be rocky and full of potholes. Therefore, to succeed one must clearly map out an achievable route at the onset and be ready to weather the hard struggle.
11. Successful completion of PhD sets you free the way truth liberates you.
12. Success is like science, that if you have the conditions, you have the results.
13. It's great nuisance that knowledge can only be acquired by hard work- *Somerset Maugham, English Writer (1874-1965)*.
14. Knowledge comes, but wisdom lingers- *Lord Alfred, English poet (1809-1892)*.
15. An idea that is not dangerous is unworthy of being called an idea at all- *Oscar Wilde, Irish Writer (1854-1900)*.
16. The further backward you look the further forward you see- *Sir Winston Churchill, Prime minister of Britain (1874-1965)*.
17. Happiness lies not in the mere possession of money; it lies in the joy of achievement, in the thrill of creative effort- *Franklin Roosevelt, President of U.S.A.*

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Abstract

W. K. Ottichilo. *Wildlife Dynamics: An Analysis of Change in the Masai Mara Ecosystem of Kenya*. Doctoral thesis: ISBN 90- 5808- 197- 4.

This thesis deals with the analysis of change in populations of large wild herbivore species in the Masai Mara ecosystem of Kenya. The total population size of all non-migratory wildlife was found to have declined by 58% in the past 20 years. Nine out of twelve species revealed significant decline. There was no significant decline in population sizes of elephant, impala and ostrich. The population sizes of livestock species did not also significantly change during the entire analysis period except for the donkey, which declined by 67%. There was surprisingly no significant difference in the decline of wildlife species and groups inside and outside the Masai Mara National Reserve except for Thomson's gazelle and warthog. For migratory species, resident wildebeest declined by 81% while resident zebra population declined by 50%.

The recorded decline of resident wildebeest population was attributed to agricultural encroachment in their former wet season grazing and breeding areas. Apart from habitat loss to agriculture, occurrence of droughts, poaching and possible competition between wildlife and livestock for scarce food may have further contributed to their decline through reduced reproduction and survival rates. These same factors are postulated here to have been responsible for the decline of other wildlife species.

The number of wildebeest migrating into the Masai Mara ecosystem from Serengeti fluctuated between years while those of the zebra increased during the analysis period. The migration of wildebeest and zebra from Serengeti to Masai Mara ecosystem was found to be related to wet season rainfall and the availability of green biomass during the dry season in the Masai Mara ecosystem. There was a strong relationship between the migrant wildebeest population size and the Normalized Difference Vegetation Index (NDVI) of NOAA-AVHRR imagery in the Masai Mara ecosystem during the migratory period (June to October). Therefore, it was concluded that NDVI could be used for monitoring and predicting the movements of migratory wildebeest populations in the Serengeti-Mara ecosystem.

Lastly, in this thesis an alarming decline of most wildlife populations in the Masai Mara ecosystem over the past 20 years is reported. This decline is mainly attributed to habitat loss, due to agricultural encroachment. Therefore, it is extremely urgent that concerned authorities and stakeholders take necessary measures that will strike a balance between wildlife conservation and agricultural development if the current downward wildlife population trend is to be reversed. Also there is an urgent need to revise both the wildlife policy and legislation so that wildlife habitats outside protected area system are protected from further undesirable destruction.

Key-words: Masai Mara ecosystem, wildlife, population trend, agriculture, rainfall, NDVI

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CHAPTER 1

General Introduction



Wildlife Management and Survey Data

Formulation of proper wildlife conservation and management strategies requires reliable data and information on their numbers, distribution and ecology. These data and information are normally collected using both ground and aerial surveys. The ground surveys provide detailed data and information on population ecology as well as behaviour, while aerial surveys provide general data and information on the abundance and distribution of animals in relation to the environment. Ground survey methods include direct observation, direct or indirect counts and mapping based on either particular area units, transects or quadrats (Riney, 1982). Aerial survey involves use of light aircraft to collect data and information on animal numbers and distribution and the environment (Norton Griffiths 1978, Caughley & Sinclair 1994). Aerial survey methods based on direct observation augmented by use of photography have been used to map the distribution of various taxonomic groups such as large mammals (Norton-Griffiths 1978, Caughley & Sinclair 1994, Seber 1996) and birds (Woodworth et al. 1997). Aerial survey methods may be more efficient and cost effective when larger areas are to be monitored while ground surveys tend to be most efficient and cost effective when used for smaller areas.

Data and information from both ground and aerial surveys has been used for different purposes in wildlife management. For example, the abundance and distribution data has been used to plan the optimum boundaries of national parks and reserves and to predict what will happen to a species if some aspects of its environment is altered (Western and Grimsdell 1979). The data and information is also used in the designation of hunting areas, allocation of wildlife species hunting quotas and in wildlife population trend monitoring (Grunblatt et al. 1996). The detailed data and information collected through ground surveys are used in formulation of comprehensive conservation, management and monitoring strategies for endangered or threatened species (Magin 1996, KWS 1992). The conservation strategies include increased protection surveillance, translocation to safe areas and institution of *in situ* and *ex-situ* breeding programmes.

The reliability and consistence of survey data is important in the successful management and monitoring of wildlife. Aerial survey is oftenly used to count large herbivores and determine their distributions because of its rapid coverage of vast areas and

ease of surveying areas where access on the ground is difficult. Further, costs per unit surveyed area are generally lower compared to most other forms of equivalent ground surveys (ILCA 1981). However, the reliability and accuracy of aerial survey data is influenced by various factors. These include the problem of controlling errors due to sampling procedures and accuracy of human observers (Taiti 1981) and bias in spotting and counting animals (Watson and Tippet 1981). Whereas it is impossible to eliminate bias from aerial surveys, its effect can be minimised at the design stage and partially corrected after survey (Norton-Griffiths 1978).

In this thesis, aerial survey data was used to analyse wildlife population trends and distributions in the Masai Mara ecosystem in south-western Kenya. The results of the analyses were deemed necessary for use in successful formulation of sustainable conservation and management strategies for wildlife in the ecosystem. First the reliability, quality and validity of the data was assessed followed by wildlife trend analyses and an investigation of possible causes of these trends.

The Masai Mara ecosystem

The Masai Mara National Reserve (MMNR) and adjoining group ranches (hereafter referred to as Masai Mara Ecosystem) in Kenya, forms the northern portion of the Serengeti-Mara ecosystem to which wild animals (especially wildebeest and zebra) migrate annually (Fig. 1). It is situated in Narok and Trans Mara districts of Kenya and lies between $1^{\circ} 00'$ and $2^{\circ} 00'$ south and longitude $34^{\circ} 45'$ and $36^{\circ} 00'$ east (Fig. 2). It is triangular in shape and covers an area of about 6000 km^2 . The ecosystem has the richest wildlife resources and offers the most spectacular wildlife watching in Kenya (Stelfox et al. 1986). It supports one of the richest assemblages of wildlife in the world (Douglas-Hamilton 1987), including over 0.5 million migratory wildebeest, over 100,000 zebra and a host of associated grazers, browsers and predators. During pre-migration and migration about 30% and 90% of total national wildlife herbivore population found within protected areas are found in Masai Mara ecosystem respectively (Grunblatt et al. 1996). These include the wildebeest, Burchell's zebra, elephant, buffalo, rhino, giraffe, eland, kongoni, topi,

waterbuck, Grant's and Thomsons gazelles, warthog and hippopotamus. The ecosystem has also the highest concentration of carnivores- especially the lion, hyena and cheetah in Kenya.

The wildebeest is the dominant species in the ecosystem and there are both resident and migratory populations. The Burchell's zebra is the second important species in terms of abundance and distribution. There are also resident and cross border migratory zebra populations in the ecosystem. The migratory wildebeest and zebra migrate annually from Serengeti National Park in Tanzania to Masai Mara ecosystem during the dry season between June and October. The animals arrive in the Masai Mara ecosystem between June and September and return to Serengeti in November (Maddock 1979). The timing of their arrival and departure is variable and is influenced by various factors (Maddock 1979, McNaughton 1990, Sinclair 1995). The migration covers an area of about 25,000km² and it is the greatest migration of large mammals in the world (Sinclair 1995). The magnitude of migrations into the Mara varies from year to year and the lowest recorded numbers for wildebeest are about 200,000 and the highest are over 500,000 animals (Brotten and Said 1995).

The annual migrations of wildebeest and zebra contribute to the density and diversity of the mammalian fauna in the ecosystem through a process known as facilitation (Bell 1970, Prins & Olf 1998). This is a process where large species alter the vegetation by grazing and trampling, with the result that a new niche becomes available for other species (Vesey-Fitzgerald 1960). Bell (1970) has described the process of facilitation in the Serengeti-Mara ecosystem as regards to the migratory wildebeest and zebra. The high diversity and density of carnivores in the Serengeti-Mara ecosystem is to a large extent dependent on wildebeest migrations as the main source of food and their overall ecology is linked to these migrations.

The diversity of wildlife and the wildebeest and zebra migrations also attract many tourists to the Masai Mara ecosystem. The ecosystem is a premier tourist attraction in Kenya, generating 8% of the national tourist revenues, 10% of all tourist bed nights and some \$20 million in foreign exchange (Douglas-Hamilton, 1988, Norton-Griffiths 1995).

Problem Statement

The Masai Mara ecosystem has undergone changes in land-cover and land-use and tenure over the past years. These changes have had profound impact on wildlife population trends in the ecosystem. Reconstruction of historic woodland dynamics in the ecosystem show that prior to 1890 the land-cover was kept in a grassland state due to both high human and ungulate populations (Dublin et al. 1990). The introduction of rinderpest in the ecosystem in the 1890's led to a decline in both wild and domestic ungulates and human population. This triggered a change in land-cover from grassland to woodland, a process further enhanced by a decline in elephant population due to ivory hunting. This led to a situation in the middle of the 20th century, where most of the Masai Mara National Reserve was covered with woodlands and shrublands. During the second half of that century the woodlands declined in Serengeti-Mara ecosystem (Glover 1968, Lamprey et al. 1967, Glover and Trump 1970). The decline was attributed to increase in human settlement, elephant encroachment and increase in fire frequency (Dublin et al. 1990). The transformation of woodlands into grasslands in the Masai Mara ecosystem starting early 1960's coincided with an increase in grazing species in the ecosystem especially the wildebeest and Burchell's zebra. This increase of grazing species was primarily attributed to improved control of rinderpest in the area (Sinclair 1995). Besides, part of this increase was attributed to higher dry season precipitation in the 1970's (Stelfox et al. 1986). In the 1960s few migratory wildebeest and zebra from Serengeti migrated into the Masai Mara ecosystem during the dry season (Pennycuick 1975). However, by late 1970s large numbers started migrating to into the Masai Mara ecosystem (Sinclair 1979). The increase was attributed partly to eradication of rinderpest and improved moisture regimes (Stelfox et al. 1986).

Major changes in land-use and land tenure in the ecosystem started in the early 1960s. The Masai Mara National Reserve was established in 1961. Prior to 1968, the land in the ecosystem was owned by the indigenous Masai people on communal basis and was held in trust as trustland for them by the local government authority (Gachugu 1996). The land was originally used exclusively for pastoral livestock and wildlife grazing. However, starting in the mid-1960s, the status of land-ownership was changed from trust lands to

group ranches through the land group representative Act, Chapter 287, 1969 of Government of Kenya (Ole Pasha 1986). The land was adjudicated and registered as freehold, private or group ranches. Due to land disputes, corruption and poor management of group ranches (Helland 1980), the Government decided to sub-divide the group ranches into individual land parcels starting early 1980s. The land sub-division in the northern parts of the ecosystem has been completed and currently the lower semi-arid areas of the ecosystem are under sub-division.

The change in land tenure system in the ecosystem led to changes in land-uses. The land in the northern parts of the ecosystem is suitable for arable agriculture because the soils are generally fertile and the climate is suitable for growing crops (FAO 1972). These areas formed the dry season grazing and breeding areas for wildebeest and zebra among other species. However, due to the agricultural potential of the land (Norton-Griffiths 1995), increasing human population in the ecosystem (about 7.5% annually) and government land and food policies for arid and semi-arid areas (Republic of Kenya 1979), these lands are increasingly being put into agricultural production. Agriculture (mainly wheat growing) in the northern parts of the ecosystem started in the early 1970s. However, it was not until the late 1970s that wheat cultivation started to spread across the areas. The land-owners, the local Masai, leased the land to commercial wheat farming enterprises (Omondi 1994). The area of land under wheat increased from about 5000 ha in 1975 (Karime 1990) to 33,000 ha in 1987 (Ottichilo 1992) to about 50,000 ha in 1995 (Serneels et al. submitted). The conversion of former wildlife and livestock dry season areas in the ecosystem into agriculture is still on-going and is expected to intensify when land sub-division in the semi-arid areas in the southern parts of the ecosystem will be completed (Ngene and Kariuki 1999).

These land use changes will have serious long-term implications on the future survival and conservation of wildlife in the Masai Mara ecosystem. Prins (1992) has outlined how competition for land between livestock, wildlife and people leads to decline in wildlife and Prins and Olff (1998) have shown that loss of parts of protected or wildlife dispersal areas to agriculture in Africa has led to decline of certain species in those areas. Therefore, if the rapid expansion of agriculture in the Masai Mara ecosystem is allowed to continue, then the following is likely to happen:

1. Loita plains which are wet season grazing and breeding areas for the wildebeest and zebra and other plains animals will be lost to agriculture (mainly wheat farming),
2. The area occupied by the migratory wildebeest and zebra in the ecosystem will drastically be reduced and this may lead to reduction in the number of animals migrating into the ecosystem annually,
3. The populations of most wildlife herbivore and carnivore species will decline and
4. The tourism industry in the ecosystem, which is heavily dependent on wildlife viewing and photography, will be negatively affected.

The Objectives of this Study

It is important that wildlife in the Masai Mara ecosystem is conserved as a national and international heritage and as a tourist attraction. The formulation and implementation of sustainable wildlife conservation strategies and programmes requires a proper understanding of the dynamics of the ecosystem. It requires monitoring of climatic variations, wildlife population trends and distributions, vegetation cover and its temporal and phenological changes, land use changes and a range of biophysical and socio-economic information. Also detailed population dynamics and ecological data is required for species that are threatened.

Although many studies have been undertaken in the Masai Mara ecosystem, none has been directed at understanding its dynamics in a holistic manner as it relates to long-term population trends and distributions, seasonal migrations and factors that influence the temporal and spatial distributions of wildlife and livestock. Also the impact of land use changes on wildlife population has not been quantitatively assessed. Studies by Broten and Said (1995), Grunblatt et al. (1996) and Leeuw et al. (1998) have shown that populations of some species in the ecosystem are declining. In these studies, all available animal count database were not used due to different reasons including lack of verification and computer entry of the data and the fact that the counts had not been conducted. The data now available on animal counts and environmental parameters in the entire ecosystem spans for a period of 20 years (1977 to 1997) and were collected by the Department of Resource

Surveys and remote Sensing (DRSRS) within the Ministry of Environment and Natural Resources, Nairobi, Kenya.

The main objective of this study was to determine the population changes of both wildlife and livestock in the ecosystem for the past 20 years (1977 to 1997) and investigate the impact of land use changes and other factors on the observed wildlife changes. Also factors influencing the migrations of wildebeest and zebra from Serengeti National Park into Masai Mara ecosystem were investigated. The specific objectives were:

1. To assess the validity and quality of aerial census data and its suitability for use in animal population trend analysis and distribution,
2. Determine the population size trends of non-migratory and migratory wildlife and livestock species in the ecosystem during the period between 1977 and 1997,
3. Establish whether there was any significant differences in population size changes of wildlife groups and species inside and outside the Masai Mara National Reserve,
4. Investigate the impact of land use changes and other factors on wildlife population trends using the resident wildebeest as the case study species,
5. Establish how the population size of migratory wildebeest in Masai Mara ecosystem has fluctuated in the last 20 years and investigate factors related to the observed fluctuations,
6. Determine the population trend and distribution of Burchell's zebra in Masai Mara ecosystem and
7. Establish whether the Normalized Difference Vegetation Index (NDVI) can be used to monitor and predict the movements of migratory wildebeest population.

The Study Area

The location of the study area is shown in Fig. 2. It is bounded by international boundary of Kenya and Tanzania in the south, the Siria escarpment (Esoit Olololo) to the west, agriculture and forest to the north, Loita hills to the east and Siana plains to the southeast. The area is roughly triangular in shape and can be divided into three range units, based on

The rainfall regime of the area has been described by Norton Griffiths et al. (1975). The rainfall pattern is loosely associated with the movement of the low inter-tropical convergence zone (ITCZ) which alternate annually between mid Sudan and northern Zimbabwe (Brown and Cocheme 1973). In addition to the very general influence of the ITCZ, local variation in topography, orographic and diurnal effects play a major role in the rainfall patterns in and around the Mara area. The annual distribution of the rainfall in the study area is bimodal, characterised by two rainy seasons as well as two dry seasons. The long rains are generally from March to May and short rains occur in November and December. The main dry period is from June to October with lesser dry spell in January and February.

The dominant topographical feature of the study area is the Siria escarpment to the west, rising to 2000- 3000 m above the Mara plains, which is the result of a fault in the basement system. The relief of southwestern, central parts of Loita, Siana and Mara plains is dominated by flat plains with an average of about 1910m above sea level. Towards the north these plains become gently undulating. Isolated inselbergs, averaging about 2000 m, rise above these plains. To the northeast, the Loita hills, which rise to over 2700 m, are the main feature. The southeast consists of Siana plains and hills. The north consists of Loita plains.

Glover and trump (1970) give detailed description of the soils. Generally the soils are shallow, sandy and rocky. Volcanic deposits dominate Loita plains. Brown clay soils, seasonally waterlogged but rather better drained than the true clays, are found in the south-particularly in the Mara National reserve. Central plains are composed of a weakly alkaline volcanic phonolitic tuff, derived from tertiary- recent volcanic activity in the Mau range to the north-east. Brown calcareous loams occur mainly in the Loita plains. Dark red friable clays occur in the south-east parts. Riverbeds and watercourses have deposits of sand, gravel and silt.

Glover (1966) gives detailed description of the drainage. The study area drains to the Southwest and all watercourses eventually join the Mara river, which itself discharges into Lake Victoria (Fig.1). The Mara River originates to the north where it is fed by numerous tributaries from the Mau range and Kipsigis area. The Mara River flows south-westwards along the base of the Siria escarpment, then south through the reserve before

turning west to discharge into Lake Victoria. The longest tributary of the Mara River is Talek, which drains the northern Siana hills and western Loita plains through two tributaries (Kaimurunya and Ol Sabukaiai). Most of the tributaries dry-up during dry season except Mara and the Talek rivers (Omondi 1994). Loita plains are drained by the Uaso Ngiri River which ends into swamps around Lake Natron to the east. The Sandy River flows along the Tanzania-Kenya border and joins Mara at Mara Bridge. Availability of water is a major factor determining the seasonal distribution of wildlife and livestock in the ecosystem. During dry season wildlife concentrate around rivers and other permanent water resources, whereas during wet season they disperse to use the forage and temporary water on the outlying plains (Douglas-Hamilton 1988).

Pastoral Maasai communities predominantly inhabited the study area. However, with change in land tenure systems in the ecosystem in the past 20 years there has been an increasing influx of people from other communities to this area. The emigrants normally come from agricultural communities and are instrumental in the introduction of agriculture in the ecosystem. They are sold land by the Maasai landowners. In 1962 the human population in the ecosystem was estimated at 10,000 (Lamprey 1984). In 1979 it was estimated at 35,000. With the rate of increase of 7.5% per annum (Lamprey 1984) through births and immigration, Douglas Hamilton (1988) estimated the population to be over 65,000 in 1987. In 1997 the population was projected at 128,000 (GOK, 1999).

Outline of the Thesis

Chapter 1 provides brief background and problem statement on the study area, the objectives of the study and description of the study area. In chapter 2, an assessment of the quality and validity of the aerial survey data used in this study is provided. The results of investigation into whether total and sample counts of elephant and buffalo in the Masai Mara ecosystem are significantly different are given in chapter 3. The population trends of non-migratory wildlife and livestock are discussed in chapter 4. Population trend and distribution of Burchell's zebra are analysed and given in chapter 5. In chapter 6 the population trends of resident wildebeest and factors influencing them are analysed. An analysis of the dynamics of the migratory wildebeest in the Masai Mara ecosystem is given

in chapter 7. The last chapter summarises the results and conclusions of the previous chapters and highlights the implications of these results on the future conservation of wildlife in Masai Mara ecosystem.

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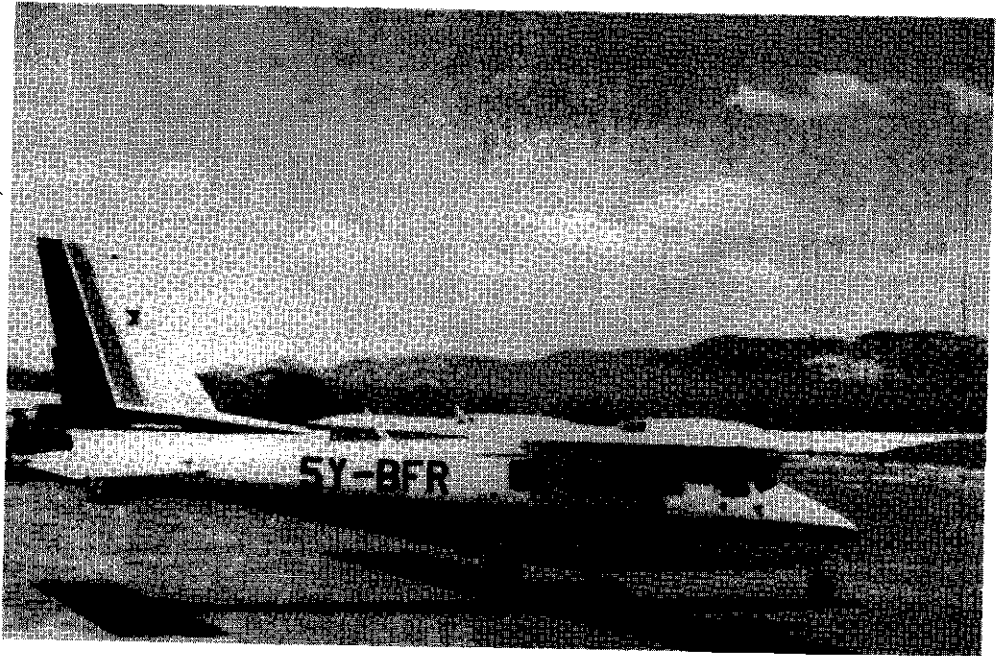
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CHAPTER 2

Validation of observer and aircraft calibration for aerial animal surveys: A case of the Department of Resource Surveys and Remote Sensing (DRSRS), Kenya

Wilber K. Ottichilo and Wilson M. Khaemba
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Abstract

Calibration procedures to determine strip widths for use by DRSRS in its aerial surveys are validated through statistical analysis. We test for differences in observer, aircraft and between using camera and naked eye in recording strip widths. We determine the relationship between strip widths measured on the ground and in the air. We also test for differences between population estimates reported by DRSRS and those recalculated using reported strip widths for elephants, kongonis wildebeests and cattle. We observe no significant differences between observers, and also none between reported and recalculated population estimates for all species except cattle. We find significant differences between strip widths obtained by camera and naked eye, with camera values being 14% higher at ground level. Strip widths measured in the air are highly correlated to those measured on the ground ($r = 0.97$). We conclude that the DRSRS calibration was carried out correctly and validate the calculation of its population estimates. Lastly we recommend that effect of wider strip widths which result from use of camera in animal surveys needs to be considered in the final calculation of population estimates.

Keywords: Aerial surveys, calibration, strip-width, population estimates

Introduction

The use of light aircraft and human observers in counting animals (both wildlife and livestock) is widely applied in Eastern and Southern Africa (Western 1976, Norton-Griffiths 1978, Steffens 1993, Grunblatt, Said and Wargate 1996). This technique is popular because of its ability to cover large areas rapidly and for providing means to survey areas where access on the ground is difficult or impossible. A detailed account of designing and conducting aerial animal counts can be found in Norton-Griffiths (1978).

Several sampling strategies can be used in aerial surveys but a modification of systematic sampling known as Systematic Reconnaissance Flights (SRF) has been adopted by several surveying organizations because of its low cost per sampled unit compared to other sampling methods. Furthermore, navigation with SRF is easy and fatigue among the crew is minimal (Norton-Griffiths 1978). This method is also used to collect spatial and temporal environmental data suitable for explaining the relationships between animals and their environment and for long-term monitoring purposes (Norton-Griffiths 1978).

Prior to conducting any animal survey, both survey and sampling zones must be clearly defined. The survey zone is defined as the whole region for which the total number of animals is to be estimated, while the sampling zone is that portion which is actually searched and all animals observed in it counted. While definition of a survey zone is not complicated, that of a sample zone involves accurate determination of the area to be searched from the air by the two Rear Seat Observers (RSOs). To minimize sampling error while reducing inter-transect variability, each RSO should scan an approximately equal area on every strip transect. Determination of this area depends on a rigorous determination of a nominal strip width through calibration of both the aircraft and observers used in aerial surveys. Calibration essentially involves determination of a desired sampling intensity (percentage of the survey zone), which can be searched comfortably and accurately by observers.

The Department of Resource Surveys and Remote Sensing (DRSRS) within the Kenyan Ministry of Planning and National Development has been using SRF in all its national aerial surveys since 1977 (Grunblatt et al. 1996). The data generated are used in national planning of wildlife and livestock resources, as well as by researchers, consultants

and various agencies for different purposes. Although DRSRS data are widely used, the calibration of procedures used to collect these data and the possible effects they may have on the overall survey results have not been independently validated. Our overall objective is to undertake this validation by studying the following questions:

- Are there significant differences in the strip width viewed by different observers?
- Is there a significant difference in strip widths obtained by using a camera or the naked eye?
- Does the observer sitting position (left or right) and aircraft type have significant influence on the strip width searched during surveys?
- What is the relationship between strip widths determined on the ground and in the air, using camera?
- How correct are the population estimates (PE) reported by DRSRS?

Materials and methods

Calibration procedure

In aerial surveys, markers fixed on windows next to RSOs as well as streamers (a pair of parallel metal rods) fastened to the wing-struts of the aircraft, define the observable strip width, which in turn defines the area sampled. An aircraft's flying height and the distance between the streamers influence this strip width, such that an increase in flying height and fixed streamers lead to increase in strip width. Calibration ensures control of the strip width in relation to streamer distance, observer sitting position and flying height. This is important because the Jolly method (1969) which is used to calculate the population estimates assumes that the RSOs search equal strip widths during surveys.

To carry out ground calibration, a light high-winged aircraft is propped in a flying position on a level surface and the RSOs are allowed to sit in such a manner that they can look out of the window in relaxed positions. The highest position of the eye level that provides near perpendicular but comfortable viewing is chosen and marked on the window.

Next, the position of the lower streamer a on the wing strut (Fig. 1) is marked in such a way that it allows the observer a line of view that is clear of the wheel but still as close to the aircraft's body as possible. The point, on the window, at which the line at point a makes with eye position E (Fig. 1) determines the lower window marker a' . The upper window marker and outer streamer are determined in such a way as to establish dependence between strip width and flying height. To ensure that all observers irrespective of their height differences maintain the determined eye level, cushions are used where necessary.

A mark A is placed on the ground so as to be in line with the lower window marker a' and lower streamer marker a (Fig. 1). The height h of the observer's eye level above the ground is measured. The distance w from A to a second mark B , placed on the ground, can be calculated using the equivalence property of triangles for a fixed strip width W and flying height H as:

$$w = \frac{h}{H} W .$$

The second streamer and upper window marker are then placed at points b and b' on the wing strut and window respectively, through the observer's line of sight to point B (Fig. 1). Distances ab and AB represent rod setting and calibrated strip width respectively at a given flying height.

Air calibration is conducted by flying and taking photographs of an airstrip marked with white lines placed at fixed intervals. Observers take photographs at fixed flying heights and streamer distance, process them and count the number of white markers between streamers, which are used to determine the average strip width. Proper air calibration requires that the aircraft is flown with minimum banking and flying height is maintained.

Both ground and air calibrations were conducted by DRSRS in 1985 using two Partenavia aircraft (5Y-BDC and 5Y-BCI) that are used regularly for surveying (Ottichilo and Sinange 1985). Seven regular observers were used in the exercise. The height h was measured as well as the strip width (AB) for different rod settings (30 cm, 35 cm, 37 cm and 40 cm for 5Y-BCI and 30 cm, 35 cm, 38 cm and 40 cm for 5Y-BDC). Measurements were taken on both the left and right side of the aircraft for each observer. Ground measurements

for AB were obtained using both naked eye and looking through a camera. For camera measurements, deviations of camera lens from the fixed eye level were also recorded.

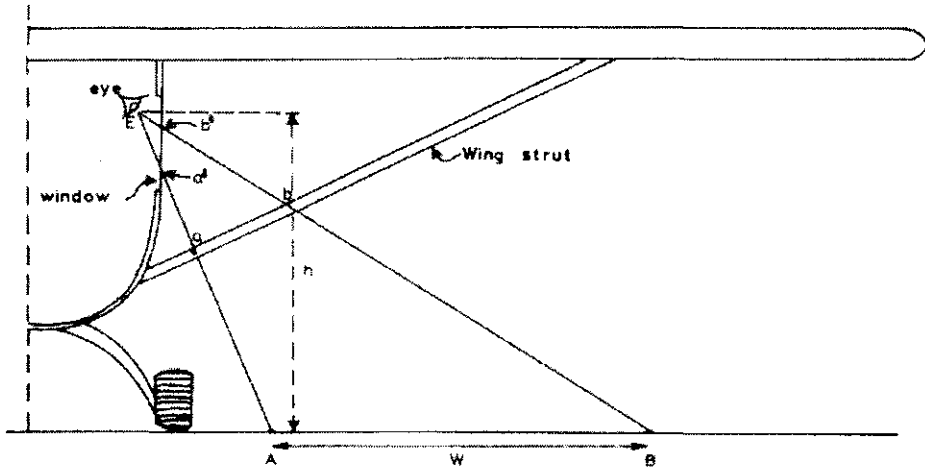


Figure 1. Determination of the proper positions of window and strut markers while the aircraft is on the ground. (Source: Ottichilo and Sinange, 1985)

Air calibration involved flying and taking photographs of an airstrip marked with white lines placed at 20 m intervals. The photographs were taken at different heights and fixed streamer settings of 35 cm and 37 cm for 5Y-BDC and 5Y-BCI respectively. The flying heights were 70 m (200 ft), 91.5 m (300 ft), 122 m (400 ft) and 152.4 m (500 ft) above ground level.

DRSRS used the results of the calibration to determine fixed strip widths and flying height for use in its regular surveys. Rod settings of 35 cm and 37 cm, which give strip widths of 282 m and 304 m at a flying height of 122 m for aircraft 5Y-BDC and 5Y-BCI respectively, were chosen (Ottichilo and Sinange, 1985). We used data collected during calibration as well as from subsequent aerial surveys for this validation.

Statistical analysis

DRSRS calculates population estimates according to the Jolly II method (Jolly 1969). In this method, an estimate \hat{D} of animal population density from n transects is given by

$$\hat{D} = \frac{\sum_{i=1}^n y_i}{\sum_{i=1}^n a_i},$$

Where y_i and a_i are the observed number of animals and area of the i -th transect respectively. In each transect, area is computed by summing the areas of all corresponding subunits (subdivisions of 5000 m along the transect). On the other hand, the subunit area is calculated using the formula

$$SArea = L \cdot \frac{H_A}{H_N} \cdot W_N,$$

Where L is the length of the sub-unit, H_A and H_N are desired and the actual flown heights while W_N is the calibrated strip width for each aircraft (which is either 282 m or 304 m in this study).

We used the analysis of variance (ANOVA) to test for difference in mean values of measured strip widths between observations taken by the naked eye versus those obtained by camera. We also used ANOVA to test for differences in mean values of strip widths between observers, sitting positions and the two aircraft used in the calibration exercise.

To ascertain the correctness of population estimates reported by DRSRS, we used data from sixteen aerial animal surveys, where the strip widths used were 282 m and 304 m, to recalculate the population estimates for elephant, kongoni, wildebeest and cattle. These were compared to the values reported by DRSRS for the same species. We used the paired t -test (Snedecor & Cochran 1980) to test for differences between the two estimates. The paired t -test is a good choice when taking into account the dependence arising from comparing two measurements taken on the same transect.

Finally, we investigated linear relationships between continuous variables using correlation analysis. We extended this investigation to regression modelling, which we used to determine the functional relationship between strip width values measured through the camera while in the air (AC), to those observed through camera but on the ground (GC) while controlling for flight height. Such a functional relation is necessary to extrapolate

strip width values in the air at different flying heights. In all cases, we tested for significance using p -values and established it for values less than the conventional 5% level.

Results

The combined mean values of strip widths (AB) determined on the ground using camera and naked eye were 1.78 m and 1.56 m respectively. These means differed significantly at all the rod settings ($p = 0.002$) indicating that strip widths observed through camera are always wider than those observed by the naked eye. Means values for AB did not differ significantly between observers ($p = 0.545$) or between the right and left position ($p = 0.455$). This indicates that the observers were well calibrated and the sitting position does not influence the strip width. Interactions between observers and position were not significant and correlation between deflection and strip width was only marginal ($r = 0.063$).

We found significant differences between strip width values observed from the two aircraft at a rod setting of 30 cm but not at a rod setting of 40 cm ($p = 0.005$ and 0.994 respectively). This is a surprising result because the two aircraft have different body configurations that lead to different streamer settings and we expected strip widths to differ significantly at all rod settings. We also found significant differences ($p = 0.0006$) between strip width values measured from the air at different heights through photography (use of a camera) (AC) and those measured using direct observation or with the naked eye (AE) (Table 1). This indicates that strip widths determined from the air, using camera, were wider than those extrapolated from ground calibrations using naked eye.

Table 1: Mean strip width values for measurements made by naked eye and by through use of a camera at different flying heights.

MEASUREMENTS	HEIGHT (m)		
	60.96	91.44	121.92
Air Eye (AE)	72.31	117.13	144.69
Air Camera (AC)	88.06	147.56	193.25
Ratio (AE/AC)	0.82	0.79	0.75

Since in calculating population estimates we use sample areas, a comparison of areas is similar to directly comparing population estimates. We found no significant differences ($p = 0.52$) between reported and recalculated areas (Table 2), indicating that DRSRS calculations are correct. However, the strip widths given in all DRSRS reports are misleading since they give an impression that each survey is conducted using only one calibrated strip width, which is not the case for most surveys. In one case, we found that the reported strip width was used in only 28% of the samples (Table 2). We did not find significant differences between recalculated and reported population estimates for the elephant ($p= 0.66$), kongoni ($p= 0.88$) and wildebeest ($p= 0.90$). However, the difference was highly significant for cattle ($p < 0.0001$), a rather surprising result.

We compared strip widths determined at different heights in the air through photography (AC) to those determined on the ground also through use of photography (GC) by extrapolating the ground measurements to respective air heights of 60.96 m, 91.54 m and 121.92 m. We found that air and ground strip widths were highly correlated ($r = 0.97$). Height was also highly correlated with both strip widths determined in the air (AC) and on the ground (GC) ($r = 0.94$ and 0.85 respectively). From the two regression models run, the first model had both height and GC ($R^2=0.9959$) and the second had GC alone ($R^2=0.948$). The change in parameter coefficients after dropping height from the model as well as the high correlation between AC and height indicated the presence of multi-collinearity in model 1.

We plotted strip widths determined on the ground through photography (GC) against those determined in the air also using photography (AC). The results showed a highly significant ($R^2 = 0.95$) linear relationship (Fig. 2). The linear relationship between AC and GC is represented by the following equation:

$$\text{Strip Width}_{AC} = 0.29 + 1.17 \text{ Strip Width}_{GC}$$

Table 2: Table showing sixteen surveys in the Mara, the reported strip width (W) for each survey, ratio of units using W to total number of units, area (Area_1) recalculated using W and sampled area (Area_2) as reported by DRSRS.

Survey	Strip Width W (m) as reported by DRSRS	Proportion of units using W	Area_1 (km^2)	Area_2 (km^2)
8505	304	0.63	397.06	389.39
8512	304	0.57	390.45	378.27
8607	304	0.63	396.34	385.80
8608	304	0.65	401.66	391.59
8615	304	0.65	399.11	389.11
8706	282	0.35	368.82	387.53
8902	282	0.64	360.18	370.17
9003	282	0.42	374.00	390.91
9102	282	0.55	375.66	388.73
9103	304	0.48	788.52	759.37
9202	304	0.48	803.04	773.04
9204	304	0.28	808.98	766.80
9306	282	0.45	752.10	784.30
9402	282	0.72	746.76	748.48
9604	282	1.00	757.20	757.20
9703	282	0.74	335.65	342.43

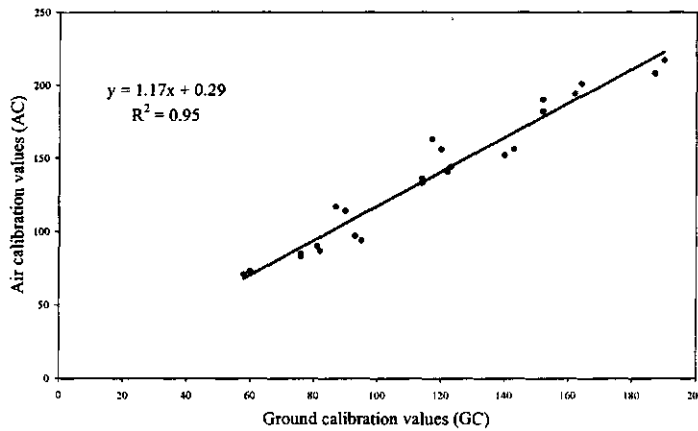


Figure 2: Regression model showing the relationship between air calibration values and ground calibration values.

Discussion

Lack of significant differences in observed strip width values (AB), interaction between observers and sitting position show that DRSRS observers are well standardized in the aerial survey counting procedures and this ensures consistency in their counting. The relationship between air and ground calibration (Fig. 2) appears to give a good fit, another indication of good calibration. Based on this relationship, strip width values can easily be calculated using the resulting regression model.

The sample areas given by the two strip widths (282 m & 304 m) and used by DRSRS in its surveys are significantly different, indicating that in cases where the two strip widths are used (i.e. the two aircraft are used), their average cannot be used in computing population estimates. In such cases, individual strip widths must be used independently to calculate the sample area and the results summed in the final computation of the population

estimates. DRSRS takes this fact into account and calculates its population estimates based on the sub-unit area calculated using formula given above. However, it reports only one calibrated strip width for each survey even when in most of its surveys (93.75%), two aircraft were used. It is therefore important that this omission is corrected in future reports.

The surprising results of significant differences between the two aircraft at 30cm rod setting but not at 40 cm may be explained by the effect of eye-level. At 30 cm rod setting, eye-level is not significantly different between the two aircraft ($p = 0.156$) whereas at 40 cm, the difference is highly significant ($p = 0.0102$). When the effect of aircraft and eye-level on strip width are simultaneously studied at both rod settings, aircraft is significant with or without controlling for eye-level at 30cm ($p = 0.0172$), but only significant at 40 cm when controlling for eye-level ($p = 0.019$). This suggests that the effect of eye-level is so strong at 40 cm rod setting that it masks the difference in strip width between the two aircraft.

Lack of significant differences between recalculated population estimates for elephant, kongoni and wildebeest and those reported by DRSRS support the reliability of DRSRS reported figures. However, the significant difference in cattle may be due to the influence of strip width used in computing the population estimate. In our analysis we used the reported strip width of 282 m but DRSRS calculations were based on both 282 m and 304 m. Because cattle are generally evenly distributed and occur in large groups, use of a narrow strip width gives higher densities and consequently higher population estimate (Peden et al. 1979). Our results indicate that using these reported strip widths blindly may result in incorrect population estimates.

The high significant difference between AE and AC may be caused by the change in eye level when the observer uses the camera to estimate strip width. Use of camera leads to backward shift in eye level and consequently increases the strip width. The results show that when a camera is used, a larger area is observed than when the naked eye is used. This difference may also be reflected in animal counts based on photos taken by RSOs during surveys. Practically, this means that a larger area is sampled when animal estimates are based on photo counts. The impact of these differences on overall PEs is not known and DRSRS does not take it into account in its calculation of PEs, assuming it to be non-significant. However, we have shown in this study that strip widths based on camera and

eye observations are significantly different, indicating that they may influence the overall population estimates.

In conclusion, this validation shows that the 1985 DRSRS calibration, on which its subsequent surveys are based, was carried out in a consistent manner and therefore observations by different observers are comparable and can be used in population estimate calculation. It should also be noted that prior to 1985, DRSRS used Cessna high wing single engine aircraft in its surveys. Strip width calibration for these aircraft have not been documented but are known to have been narrower than those reported here and varied for different surveys. De Leeuw et. al. (1998) have observed that one of the main factors which may have caused inconsistency in DRSRS data prior to 1985 calibration is variation in strip width.

There is a significant difference between the area covered, and consequently the animals seen, when counting is done using the naked eye and a camera. This has not been taken into account when computing PEs derived from aerial surveys. This is true for DRSRS and many other aerial surveys conducted in Eastern and Southern Africa. The effects of this omission need further investigation.

The information given in some of DRSRS reports regarding strip widths may be misleading. In most of its surveys, two aircraft are used. However, only one strip width is reported for each survey. Fortunately, where two strip widths have been used in a survey, both are used in the final calculation of PEs.

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CHAPTER 3

Comparison of sample and total counts of elephant and buffalo in Masai Mara, Kenya

Wilber K. Ottichilo

(African Journal of Ecology, 37/4 (1999), p. 435-438)



Abstract

Both aerial transect sample counts and total counts of elephant and buffalo were conducted in the study area during the wet season. The results from the two counting methods were tested for significant difference. The test showed that the results were not significantly different for both the elephant ($P>0.05$) and buffalo ($P>0.05$).

Key words: Masai Mara, elephant, buffalo, sample and total counts

Introduction

Aerial transect sample counts of both the elephant and buffalo were conducted in the Masai Mara ecosystem in Kenya by the Department of Resource Surveys and Remote Sensing (DRSRS) within the Kenyan Ministry of Planning and National Development since 1977 (Grunblatt et al. 1995). Aerial total counts of the same species have also been conducted in the same ecosystem by the World Wildlife Fund (WWF) in collaboration with the Kenya Wildlife Service (KWS) since 1984 (Dublin and Douglas-Hamilton 1987). Norton-Griffiths (1978) recommended that for species like elephant and buffalo, which occur in large and conspicuous herds or clumps, block or total counting be preferred to transect sample counting because transect sample counting is subject to an increase in sample error.

The objective of this analysis is to test whether the results from the two counting methods were significantly different.

Study area

The Masai Mara National Reserve (MMNR) and the adjoining areas in Narok district, Kenya, form the Masai Mara ecosystem. The area lies approximately between latitude $0^{\circ} 45'$ and $2^{\circ} 00'$ south and longitude $34^{\circ} 45'$ and $36^{\circ} 00'$ east and covers an area of about 6000km^2 .

Methods

Sample and total counts

The sample counts were conducted using systematic reconnaissance flight method (Norton-Griffiths 1978). The population estimate (P.E.) and standard errors were calculated using the Jolly 11 method (1969). The total counts were conducted using a method described by Norton-Griffiths (1978).

Data analysis

The sample and total counts data used in this analysis were collected during the wet season (between April 1 and May 30). Bar plots were used to visually display the results from the two counting methods. Descriptive statistics were also computed. Since the data were not normally distributed, the Mann Whitney U test was used to test for significant differences. The null hypothesis tested was that there is no significant difference between sample and total counts.

Results and discussion

Figs.1 and 2 show the bar plots of sample and total estimates for the elephant and buffalo respectively. Table 1 shows descriptive statistics based on elephant and buffalo population estimates. The results of the Mann Whitney U test show that population estimates derived from sample and total counts were not significantly different for both the elephant ($p>0.05$) and buffalo ($p>0.05$). The null hypothesis cannot, therefore, be rejected.

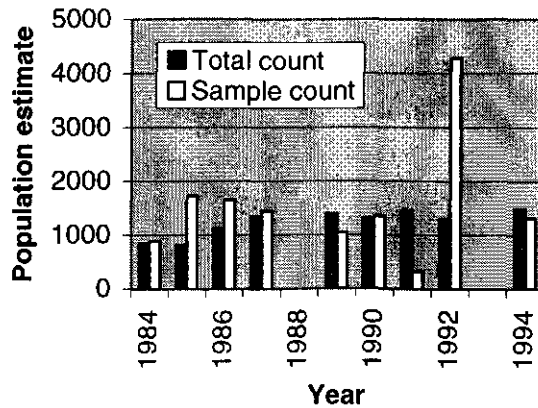


Figure 1: Bar plot of yearly of elephant population estimates

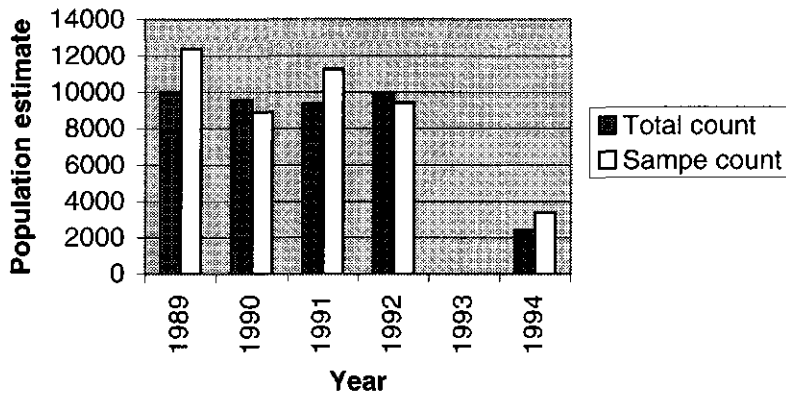


Figure 2:Bar plot of yearly of buffalo population estimates

Table1:Descriptive statistics of buffalo and elephant population estimates

Descriptive statistics	Buffalo		Elephant	
	Sample count	Total count	Sample count	Total count
Mean	9069	8264	1558	1233
Median	9427	9579	1345	1312
C.L. (-) 95%	4742	4187	706	1042
C.L. (+) 95%	13396	12342	2411	1424
S.D.	3485	3284	1109	248
S.E.	1559	1469	370	83

Yearly sample and total estimates for the elephant did not differ significantly except for 1985, 1991 and 1992 (Fig.1). The apparent differences in the estimates during the years 1985, 1991 and 1992 may be attributed to the severe drought experienced during these periods (Dublin 1994). In dry seasons or under drought conditions, aggregations of elephants in this ecosystem move into wooded and riverine areas where they can access to water and forage material. Eltringham (1977) also found that elephants in the Rwenzori National Park and Chambura Game Reserve tend to be more aggregated in the dry than in wet seasons. In such conditions, sample counting results in population underestimates. Using total counting method, Dublin and Douglas-Hamilton (1987) also reported elephant population underestimates during the dry season. In some cases, sample counting may also

give overestimates with high standard errors (e.g. in 1992). This happens when large aggregations are included in a sample count. The yearly sample and total estimates for the buffalo appear not to differ significantly (Fig. 2).

Based on the results of this analysis, the population estimates of elephant and buffalo derived from sample and total counts conducted during wet season are not significantly different and their trend is the same. This may be due to the fact that during the wet season, the distribution of elephant and buffalo in the Masai Mara ecosystem is less clumped. Dublin and Douglas-Hamilton (1987), reported that elephants counted in the ecosystem during the wet season (April 1984) were widely distributed, but contained, almost within the boundaries.

In conclusion, it appears that in more open areas like Masai Mara where elephant and buffalo populations are less clumped during the wet season, both sample and total counting methods give results that are not significantly different. However, both methods appear to give results that are less reliable. Therefore either of the methods can be used to conduct censuses of the two species during the wet season. The choice of the method will depend on the purpose of the census and available resources. Generally, total counts are more expensive than sample counts.

Acknowledgements

I am grateful to Dr. Holly Dublin of World Wildlife Fund (Nairobi Office) and Mr. Hesbon M. Aligula, the Director of DRSRS for providing me with the total and sample counts data respectively.

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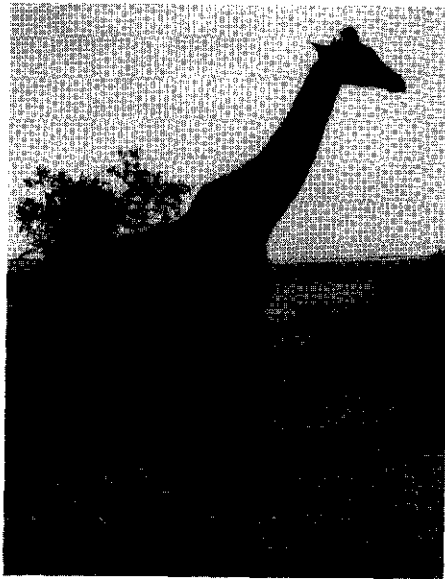
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CHAPTER 4

Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997

Wilber. K. Ottichilo, Jan de Leeuw, Andrew K. Skidmore, Herbert H.T. Prins and
Mohammed Y. Said
(African Journal of Ecology, in press)



Abstract

The total of all non-migratory wildlife species in the Masai Mara ecosystem declined by 58% in the past 20 years. The decline ranged from 49% in small brown antelopes to 72% in medium brown antelopes. In individual wildlife species, the decline ranged from 52% in Grant's gazelle to 88% in the warthog. Declines of over 70% were recorded in buffalo, giraffe, eland and waterbuck. We failed to detect any significant change in the population of elephant, impala and ostrich. Overall, there was no significant difference in the decline of all wildlife population sizes inside and outside the reserve except for Thomson's gazelle and warthog. Livestock did not significantly decline during the entire analysis period. However, livestock and cattle populations significantly declined during 1983-88 period. Donkey declined by 67%, while shoats (goats and sheep) remained stable. In case of wildlife, land use and vegetation changes, drought effects and poaching are considered to be among the potential factors that may have been responsible for the decline while the decline in livestock during the 1983-84 period was most likely due to drought effects.

Key words: Masai Mara, wildlife, livestock, population, trend, and analysis.

Introduction

The Masai Mara National Reserve (MMNR) and the adjoining group ranches (hereafter referred to as Masai Mara ecosystem) have the richest wildlife resources and offer the most spectacular wildlife watching in Kenya (Stelfox et al. 1980). It is located to the north of the Serengeti National Park in Tanzania from where wildlife (particularly common wildebeest and Burchell's zebra) migrate annually. Both Serengeti and Masai Mara ecosystem form the Serengeti-Mara ecosystem. Wild animals found in the Masai Mara ecosystem include elephant (*Loxodonta africana* (Blumenbach)), black rhinoceros (*Diceros bicornis* (L.)), buffalo (*Syncerus caffer* (Spearman)), Burchell's zebra (*Equus burchelli* (Gray)), giraffe (*Giraffa camelopardalis* (L.)), wildebeest (*Connochaetes taurinus* (Burchell)), eland (*Taurotragus oryx* (Pallas)), topi (*Damaliscus korigum* (Ogilby)), kongoni (*Alcelaphus buselaphus cokii* (Gunther)), waterbuck (*Kobus allipsiprymnus* (Ogilby)), warthog (*Phacochoerus aethiopicus* (Pallas)), Thomson's gazelle (*Gazelle thomsonii* (Brooke)), Grant's gazelle (*Gazelle granti* (Brooke)), lion (*Panthera leo* (L.)) and spotted hyaena (*Crocuta crocuta* (Erxleben)). It is the premier wildlife attraction in Kenya, generating 8% of the national tourist revenues, 10% of all tourist bed nights and some \$20 million in foreign exchange (Douglas-Hamilton 1988, Norton Griffiths 1995). However, the ecosystem is under threat due to habitat fragmentation and loss of wildlife dispersal areas to agriculture and human settlements (ACC 1997, Sitati 1997).

Globally, habitat fragmentation or complete loss is thought to have caused or is responsible for extinction of many wildlife species (Morrison et al. 1992, Caughley and Sinclair 1994, Prins and Olf 1998). Norton Griffiths (1995) also notes that the conversion of privately owned rangelands to agriculture and ranching is the most concern to wildlife managers. Lado (1996) observes that the most serious long-term threat to the future of wildlife populations in Kenya is due to the indirect effects on habitat resource destruction or alteration. Prins and Olf (1998) predicted that an ecosystem that becomes smaller due to areas being put under cultivation (where wild grazers cannot occur any more) would show a decrease in species packing. This is the result of increased competition although local extinction may play a role too. In Africa, where herbivore species-richness remains high

(Prins & Olff 1998), the increasing conversion of natural lands to agriculture and human settlements is mainly attributed to increasing human population and is thought to be responsible for the increasing decline in wildlife resources (Johan 1995).

Wildlife conservation in the Masai Mara ecosystem is increasingly coming under pressure due to changing land uses in the wildlife dispersal areas (Norton Griffiths 1995). As many other protected areas, MMNR in Masai Mara ecosystem does not encompass all wildlife dispersal areas. These areas are under private ownership and are increasingly being put under agricultural production and human settlements (Norton Griffiths 1995, Serneels *et al.* submitted). For example, between 1975 and 1995, area under agriculture (mainly wheat farming) in the Loita plains to the north of the Reserve has increased from 4875 ha in 1975 (Karime 1990) to 11,000 ha in 1985 (Serneels *et al.* submitted) to 50,000 ha in 1995 (Serneels *et al.*, submitted). The long-term impact of these land use changes on the population of different wildlife species has not been assessed. However, results of wildlife population studies undertaken in the ecosystem indicate that populations of some wildlife species are on the decline (Brotten and Said 1995, Grunblatt *et al.* 1996, Sitati 1997). The decline has been attributed to among other factors increasing loss of former wildlife grazing or dispersal areas to agriculture (mainly wheat farming) and human settlements (Brotten and Said 1995, Sinclair 1995, Sitati 1997).

The land use changes mentioned above have been taking place at a distance of over 60 kms from the reserve boundary. Given this distance one would expect higher rate of decline of wildlife species outside the reserve than within the reserve proper. So far, no analysis has been executed to test whether there is a difference in the rate of wildlife decline inside and outside the reserve.

Due to different reasons, wildlife population studies that have been undertaken in Masai Mara ecosystem (Brotten and Said 1995, Grunblatt *et al.* 1996, Sitati 1997) have not used all current available long-term census data, which spans a period of 20 years from 1977 to 1997. Our aim is to analyse these data and establish whether non-migratory wildlife herbivore and livestock populations in the ecosystem are declining or not. We further wish to establish whether there is a difference in wildlife population trends between the reserve and the outside areas. Our study hypotheses for the two objectives are: (1) that all non-

migratory wildlife herbivores have declined while livestock species have increased, and (2) there are differences in wildlife population trends between the reserve and outside areas.

Materials and Methods

Study area

The study area is situated in Narok district in Kenya. It lies approximately between latitude 1° 00' and 2° 00' south and longitude 34° 45' and 36° 00' east. The area covers about 6000km² (Fig.1). It is bounded by the international boundary of Kenya and Tanzania in the south, the Siria escarpment (Esoit Olololo) to the west, agriculture and forest to the north, the Loita plains and hills to the east and the Siana plains and hills to the south-east (Fig.1). The area is roughly triangular in shape and can be divided into three range units, based on their biogeography and climate (Stelfox et al. 1986). These units are the Mara and the Reserve (mainly composed of *Themeda* grassland), the Loita plains (composed of dwarf shrub and *Acacia drapanolopium* grassland) and the Siana (mainly hills and plains supporting *Croton* bush and other woody species interspersed with grassland).

The main land uses in the area are pastoralism, tourism and agriculture. The MMNR (1368km²) is a formal conservation area owned by Government of Kenya (GOK) and managed by Narok and Trans Mara District County Councils. Land use within the reserve is restricted to wildlife tourism. Its major conservation value is the protection of resident wildlife communities and the provision of critical dry season grazing resources for the migratory wildlife populations. The MMNR is surrounded by group ranches that are under private ownership either by groups of families (group ownership) or by individual families (individual ownership) where the main land uses are pastoralism and agriculture. The group ranches contain year-round resident wildlife, but migrants also spill onto them during the dry season.

Animal census

The animal census data was collected by the Department of Resource Surveys and Remote Sensing (DRSRS) using a systematic reconnaissance flight method (Norton Griffiths, 1978). This method as practised by DRSRS is described by Grunblatt et al. (1996). The ecosystem was surveyed along transects oriented in east-west or north-south depending on the terrain. A transect spacing of 5 km was used. The flying heights were about 90m (1977-1985) and 120 m (1985 -1997). Two experienced and well trained observers (Dirchl et al. 1981) occupied the rear seats of a high wing aircraft (Cessna 185 or Partinevia) and counted animals that appeared between 2 rods attached to the wing struts. The field of vision between these rods was calibrated by flying repeatedly across ground markers of known spacing (Ottichilo and Sinange 1988). The number of animals falling within the survey strips on either side of the aircraft along each 5 km transect segment were counted and recorded into tape recorders by two Rear Seat Observers. Groups of animals more than 10 in number were also photographed and later counted with the aid of a 10x binocular microscope and overhead projector. The population estimates (P.E.) for every species and every census were calculated using the Jolly 2 method (Jolly 1969).

The reliability of population estimates derived from aerial censuses is influenced by counting errors and biases (Jolly 1969, Caughley 1974, Norton Griffiths 1978). The animal numbers may be underestimated due to vegetation cover especially when animals occur in thick or dense vegetation cover causing visibility problems (Watson and Tippet 1981). Equally the colour contrast between vegetation cover and different animals could have an influence on the number of animals seen and counted (Dublin 1990). Counting errors may also be caused by misidentification. This is particularly likely to occur with almost similar animal species such as Grant's and Thomson's gazelles (Vitkovich et al. 1993, Dirchl et al. 1981). This may lead to increased variance of the survey statistics (De Leeuw et al, 1998).

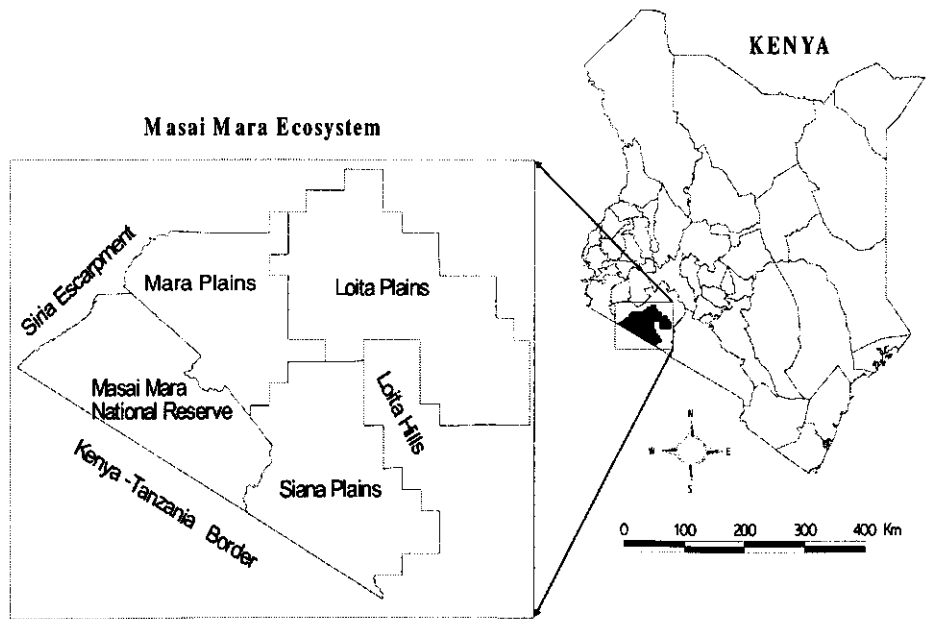


Figure 1: Map showing four range units within the Masai Mara ecosystem and the location of the study area within Kenya.

Animal species groups

To minimise counting errors, to lower potential of confusing species and to improve the chance of detecting trends, species were aggregated into categories ('guilds') based on similarity in appearance, colour and size (De Leeuw et al. 1998, Prins and Douglas-Hamilton 1990). We clustered animal species into the following categories:

Impala + Grant's gazelle + Thomson's gazelle = **Small brown antelopes**

Topi + Kongoni = **Medium brown antelopes**

Small brown antelopes + medium brown antelopes = **Brown antelopes**

All wildlife considered excluding wildebeest and zebra = **Non-migratory wildlife**

Masai giraffe + Reticulated giraffe = **Giraffe**

Sheep + goats = **Shoats**

Cattle + Shoats + Donkeys = **Livestock**

Those species that were not clustered formed their own category.

Census data aggregation

Variations among some censuses (particularly the 1979 monthly census data) were high. To minimise variations, the census data were aggregated and mean population estimated based on year and season. There were 42 censuses, and aggregation reduced this number to 26. In addition, individual population estimates were grouped into three time intervals based on historical non-drought and drought years and recovery periods (Stelfox et al, 1980, Republic of Kenya 1985, Dublin 1994). These respective time intervals were 1977-82, 1983-88 and 1989-97.

Data analysis

The data were analyzed in two ways. Firstly, regression analysis was used to identify trends. Secondly, the population estimates, which had been grouped into the three time intervals, were compared to confirm if the population had increased or decreased.

Exploratory data analysis revealed non-linear patterns in the relation between population estimates and time for some of the species. Therefore, the data was log-transformed prior to regression analysis. Regression analysis was used to analyse whether the recorded population increased, decreased or was stable over time. The null hypothesis H_0 was $\beta = 0$, the alternative hypothesis H_a was two-sided $\beta \neq 0$ where β is the slope of the regression. Since regression analysis assumes a normal distribution of the residuals and constant variance of the error component, we plotted normal probability plots and studentized residuals to check for violations of these assumptions prior to conducting the analysis. Lastly, the regression equations of log-linear models were used to calculate the decline or increase over the past 20 years as a percentage of initial population size.

The null hypothesis that the population estimates, which had been grouped into 3 time groups as outlined above, were not different, was tested using the Mann Whitney U-test since regression analysis would fail to pick up short term declines of the population, such as those caused by droughts. A non-parametric test was used because the population estimates of the time groups were not normally distributed. Box plots were constructed to visualize the change in animal numbers over time.

Log-regression was used to compare wildlife population trends between the reserve and outside areas. We used a t-test to compare slopes, with the null hypothesis H_0 : $\beta_1 = \beta_2$ and the alternative H_a : $\beta_1 \neq \beta_2$, where β_1 and β_2 are estimated slopes for the population in the reserve and outside, respectively.

Results

Figure 2 shows plots of population estimates against time. The solid lines represent the log-linear regression models. The results indicate that all species and species groups significantly declined during the analysis period except for ostrich, impala, elephant, livestock, cattle and shoats. All non-migratory wildlife declined by 58% between 1977 and 1997 while small, medium and all brown antelopes declined by 49%, 72% and 53%, respectively. Decline for individual species was as follows: warthog (88%), buffalo (82%), giraffe (79%), eland (76%), waterbuck (76%), topi (73%), kongoni (66%), Thomson's

gazelle (62%) and Grant's gazelle (52%). Donkey numbers declined significantly by 67%. We failed to detect significant changes in the populations of elephant, impala, ostrich, cattle and shoats. This suggests that the population of these species may have remained stable over time.

Figure 3 shows box plots of animal groups and individual species for the three time periods. The plots show that most wildlife groups and species declined though elephant and ostrich appear to have constant populations. The plots further indicate that livestock and cattle populations declined between 1977-82 and 1983-88 and increased slightly but not significantly between 1983-88 and 1989-97. Donkey declined while shoats remained stable during the analysis period.

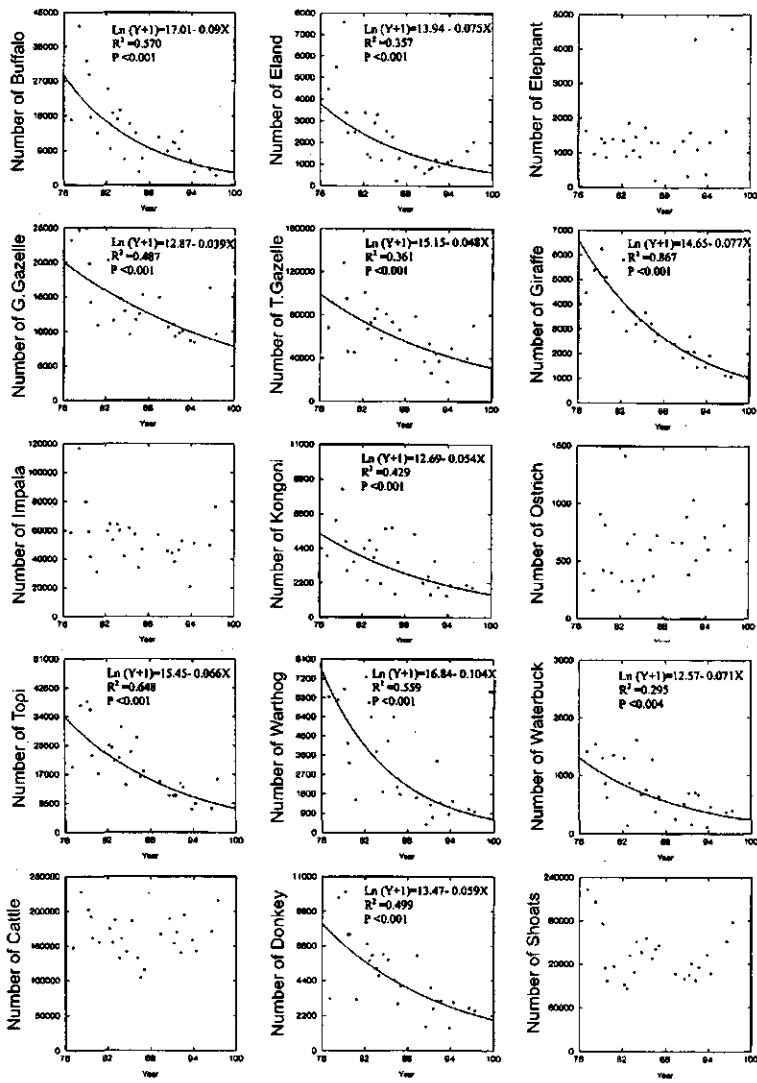


Figure 2: Relation between population estimate and year of observation for 15 wildlife and livestock species and 5 species groups in the Masai Mara ecosystem between 1977 and 1997. Solid line indicates a significant ($p < 0.05$) log-linear relationship. For categories such as “medium brown antelopes” see the methods section.

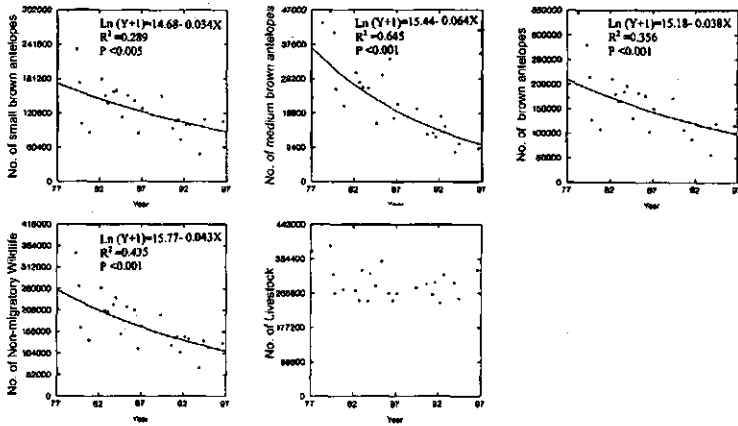
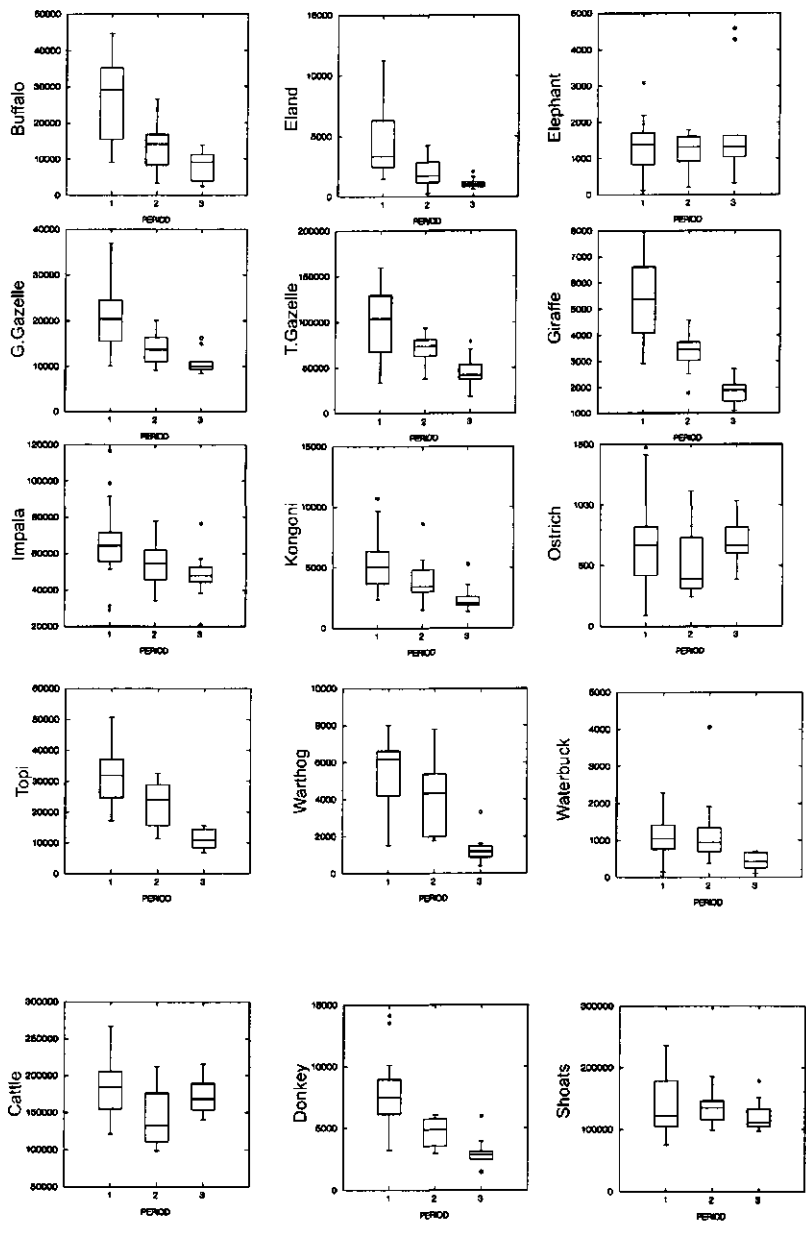


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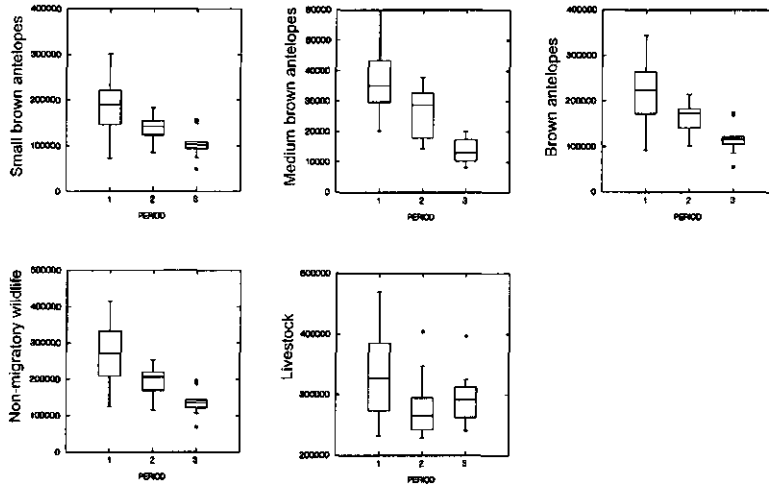


Figure 3: Box plots showing population estimate trends for 15 wildlife and livestock species and 5 species groups for three periods: 1= 1977 – 1982; 2= 1983 – 1988; 3=1989 – 1997. The asterisks and open circles in the plots show outside and far outside values, the central horizontal line in each box gives the median value and the bars or whiskers represent 1.5*IQR above the third quartile or below the first quartile.

The null hypothesis that populations of species and animal groups were not significantly different during the period between 1977-82 and 1983-88 was rejected and we conclude that most species and all animal groups significantly declined (Table 1). The null hypothesis that populations of species and animal groups were not significantly different during the period between 1983-88 and 1989-97 was either rejected or accepted for different species and groups. Between these periods, most species and all animal groups, significantly declined. The null hypothesis that populations of species and animal groups were not significantly different during the period between 1977-83 and 1989-97 was rejected for most species. Over this longer time period, all wildlife groups and species declined except the elephant and ostrich. The cattle, shoats and livestock populations were not significantly different, though the populations of donkey significantly declined.

Table 1: Results of Mann Whitney U- test for significant differences in population sizes of species and species groups between two time intervals: 1977-82 – 1983-88 ; 1983-88 – 1989-97 ; 1977-82 – 1989-97

SPECIES/ GROUP	PERIOD		
	1977-82 and 1983-88	1983-88 and 1989-97	1977-82 and 1989-97
Buffalo	**	*	***
Eland	***	*	***
Elephant	ns	ns	ns
G. Gazelle	*	*	***
T. Gazelle	*	***	***
Giraffe	**	***	***
Impala	ns	ns	**
Kongoni	*	**	***
Ostrich	ns	ns	ns
Topi	**	***	***
Warthog	ns	****	***
Waterbuck	ns	***	***
Cattle	*	ns	ns
Donkey	**	**	***
Shoats	ns	ns	ns
Livestock	**	ns	ns
S.B. Antelopes	*	**	**
M.B. Antelopes	**	***	***
Brown Antelopes	*	**	**
Non-migratory wildlife	*	***	***

P <0.05*; P<0.01**; P<0.001***; ns = Not significant

Figure 4 shows the relation between the population estimate of all wildlife in the reserve and outside the reserve against time. The figure indicates that all non-migratory wildlife declined both in the reserve as well as outside the reserve between 1977 and 1997. It further shows that more animals are found outside the reserve. Table 2 summarises the annual rate of change for the various wildlife species and species groups inside and outside the reserve and the results of the t-tests. The table shows that we failed to detect significant differences in the rate of change except for the warthog and Thomson's gazelle.

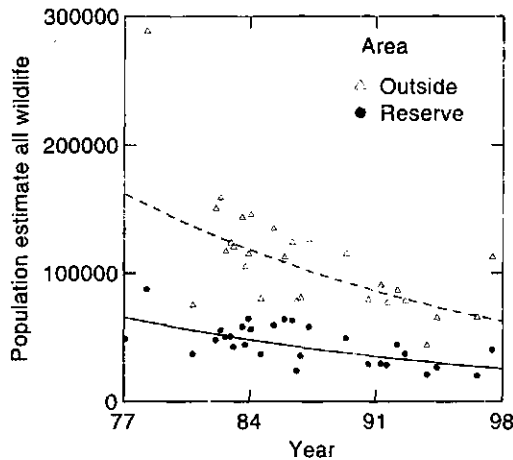


Figure 4: Relation between population estimate of all wildlife and year of observation for areas inside the reserve (black dots) and outside the reserve (open triangles). The solid and dotted lines indicate the log-linear relationship between population estimate inside and outside the reserve and time respectively. The regression equations for inside and outside the reserve lines are: $y=14.577-0.045X$; $R^2 =0.418$; $P<0.0001$ and $y=15.493-0.045X$; $R^2 =0.437$; $P<0.0001$ respectively.

Discussion

Wildlife population trends

Non-migratory wildlife herbivores in Masai Mara ecosystem significantly declined by more than fifty percent during the last 20 years. More specifically, the results show that all non-migratory wildlife and brown antelopes declined by 58% and 53% respectively. The small and medium brown antelopes declined by 49% and 72% respectively. The highest decline was for warthog and buffalo, with a decline of 88% and 82% respectively. Grant's gazelle experienced the lowest decline of 52%. We failed to detect significant decline or increase in elephant, impala and ostrich populations.

Table 2: The annual rate of change of the populations of wildlife species and species groups inside and outside the reserve between 1977 and 1997 expressed as the slope of the log-linear regression, the standard errors (s.e) of that slope, and the t-value and p-value of the test for differences in slope between the area inside and outside the reserve.

Species/Group	Inside		Outside		t-value*	p-value
	b	se	b	se		
All wildlife	-0.045	0.010	-0.045	0.010	0.000	n.s
Buffalo	-0.186	0.040	-0.109	0.027	1.48	n.s
Eland	-0.104	0.047	-0.068	0.032	0.630	n.s
Elephant	+0.036	0.027	+0.086	0.025	1.320	n.s
Giraffe	-0.093	0.014	-0.066	0.010	1.590	n.s
G. gazelle	-0.018	0.022	-0.040	0.011	1.000	n.s
Impala	-0.030	0.016	-0.014	0.011	0.842	n.s
Kongoni	-0.057	0.019	-0.057	0.017	0.000	n.s
Ostrich	-0.011	0.029	+0.062	0.024	1.342	n.s
T. gazelle	-0.021	0.013	-0.067	0.013	36.050	0.0005
Topi	-0.055	0.015	-0.076	0.012	1.000	n.s
Waterbuck	-0.140	0.038	-0.104	0.036	0.688	n.s
Warthog	-0.163	0.022	-0.091	0.025	2.25	0.02
Brown antelopes	-0.033	0.011	-0.044	0.010	0.730	n.s
M.B. antelopes	-0.055	0.014	-0.072	0.011	1.000	n.s
S.B. antelopes	-0.025	0.012	-0.041	0.010	0.800	n.s

* Critical value at 95% confidence level is 2.000 at df =58

n.s = not significant

b = slope of the log-linear equation

se = standard error

The recorded decline of most wildlife in the Masai Mara ecosystem may have been influenced by a combination of different factors. These include counting errors and biases, climatic effects, habitat changes, competition for forage resources, poaching among other factors.

Counting errors and biases (Brotten and Said 1995, Caughley 1974, Jolly 1969, Norton-Griffiths 1978, Ottichilo and Sinange 1988) may contribute to fluctuations in the population estimates. However, one of the main factors that contribute significantly to counting errors is visibility, which in turn is influenced by vegetation cover (Watson and Tippet 1981). Earlier tests of visibility bias in the Masai Mara ecosystem by DRSRS indicated that counting efficiency was 70-80% for wildlife and 80-90% for livestock (Stelfox and Peden 1981). In other words the effect of visibility errors (10- 30%) is smaller

than the reported decline (> 50%). As the method of data collection has not changed over the last 20 years, it may be assumed that the year on year visibility bias has remained constant. We therefore, consider it highly unlikely that visibility bias alone could explain the drastic decline in wildlife populations, and conclude that the decline in population estimates of all non-migratory wildlife herbivores (except the elephant and ostrich) reflect true changes in the respective population size.

Fluctuations in rainfall may have also influenced decline of wildlife populations since analysis of rainfall trends has established that the Masai Mara ecosystem experienced severe drought conditions during the periods 1984, 1986 and 1993 (Ottichilo *et al. in press*). Since there is a well-established positive relationship between rainfall and primary production of grass in semi-arid tropics up to an annual total of about 1000 mm (Phillipson 1975), it can be assumed that during these drought periods, primary production was low and limiting. Prins and Olf (1998) have shown that population dynamics of herbivores are determined by quantity and quality of food over a period long enough to enable the animal to deposit reserves of energy and protein stored in the body. Since quantity and quality of forage in semi-arid areas is largely influenced by rainfall, it is likely that frequent occurrence of droughts in the ecosystem negatively influenced wildlife populations through reduced reproductive and survival rates. Dublin (1994) reported that the population of buffalo in the reserve reduced from 10,000 to 2,400 and on the group ranches from 2,240 to 730 due to the 1993 severe drought. In the adjacent Serengeti national Park, the 1993 drought was reported to have been the most severe since 1938 and led to significant decline in wildebeest populations (Mduma *et al* 1998). The expected response to a drought would be a decline of the population estimate followed by a recovery thereafter. Visual inspection of data presented here show that there were no such dips and upswings. Hence we conclude that our data provide no evidence to support the hypothesis that the long-term decline of wildlife would have been caused by droughts.

While land use and vegetation changes (Serneels *et al.*, submitted; Dublin *et al.* 1990)), land degradation and utilization (Mwichabe 1988) have been studied and quantified, the link between these factors and wildlife population decline have not been studied. Hence, there is no direct evidence that these changes caused the reported decline in animal populations. However, Ottichilo *et al. (in press)* have shown that decline of resident

wildebeest in the ecosystem has been largely due to encroachment of agriculture (wheat farming) in former prime wildebeest wet season ranges. The loss of woodlands in the ecosystem (Dublin et al. 1990) may be responsible for the decline in giraffe population. Leuthold and Leuthold (1978) showed that reduction of woody vegetation in Tsavo National Park led to long-term decline in giraffe populations. Sinclair (1995) reported that the increasing loss of roan antelope in Serengeti and its complete disappearance in the Masai Mara ecosystem may be due to among other factors, loss of its habitats to agriculture and human settlements. Prins and Olf (1998) studied the impact of loss of wildlife habitats to other human activities in different wildlife ecosystems in Africa and reported decline in different species. Morrison et al. (1992) have noted that no single factor has been a greater cause of decline in wildlife populations than the loss of habitat. Therefore we argue that among other factors, the documented loss of wildlife dispersal areas (particularly dwarf shrubby grasslands and wooded grasslands) in the ecosystem may well have contributed to the decline in wildlife populations. The decline could have been through reduced reproduction rates, increased mortality rates and increase in competition for food resources among wildlife grazers and livestock. Prins (1992) has outlined how competition between livestock, wildlife and people may culminate into wildlife decline.

The impact of poaching remains difficult to assess because most evidence is circumstantial. However, recently Drummond (1996) reported unabated commercial poaching of wildlife on the group ranches in the Mara. Sitati (1997) reported increasing subsistence poaching of wildlife by the Maasai. A recent socio-economic survey conducted by Kenya Wildlife Service (KWS) indicated that poaching was more rampant in the ecosystem in late 1970s and early 1980s than now (Ngene and Kariuki, 1999). However, it indicated that subsistence poaching of Burchell's zebra, eland, Grant's gazelle and Thomson's gazelle is on going in the ecosystem particularly in Olchororo Oirouwa and Aitong plains and around Mararianda. Since the report does not give absolute numbers, it is not possible to calculate rates of change and confirm whether the current poaching rates are lower or higher than the previous periods. Although there is no direct evidence of poaching, we believe that it also contributed to the wildlife decline. For example, Mduma et al. (1998) has reported that in the adjacent Serengeti National Park there is a growing illegal harvest of wildebeest. They note that roughly half of the sustainable harvest is now taken in the

illegal harvest. Dublin *et al.* (1990) attributed respectively 90% and 50% declines in local buffalo populations in the north-western and western corridor areas of the park which border Masai Mara ecosystem to illegal hunting, after ruling out the effects of disease. Since there is free movements of wildlife across the border, poaching activities on either side of the border will affect the overall population sizes of concerned species. A good example is given by elephant population, which declined in Serengeti in the late 1970s and early 1980s due to poaching activities which led to the movement of elephants from the Serengeti to the Masai Mara (Dublin and Douglas-Hamilton 1987). Thus constancy of the elephant population reported in this study may reflect a reduction in poaching, as well as immigration from the Serengeti, as suggested by Dublin and Douglas-Hamilton (1987).

Livestock population trends

In contrast to the wildlife results discussed above, regression analysis showed no decline in livestock, cattle and shoats (Table 1), though donkeys had significantly decreased in population. However, the Mann Whitney U-test showed that livestock and cattle populations significantly declined between 1977-82 and 1983-88 but remained stable between 1983-88 and 1989-97. The significant decline in livestock and cattle population sizes was attributed to the 1983-84 drought (Republic of Kenya 1985). Our results on cattle trends appear to confirm what Homewood and Lewis (1987) have reported in Baringo district. They showed that cattle population recovers rapidly from drought and their fluctuations match variability of rainfall during primary productivity rather than indicating any long-term decline. In addition to the impact of drought on cattle population fluctuations, the on-going change of human activity from a pastoral to an agricultural economy is likely to have a negative impact on livestock populations and threatens to upset the entire Maasai herding economy (Sindiga 1984).

The donkey population declined by about 67%. The decline may be caused by Maasai becoming increasingly sedentary so donkeys are no longer required for carrying luggage during migration. In addition, introduction of motorized transport has reduced the need for using donkeys to transport goods (e.g., hides and skin, milk, charcoal) to markets.

The sheep and goats population did not significantly decline or increase during the period 1977 to 1997. This may be attributed to their adaptability to harsh environments and their ability to reproduce quickly. Maasai livestock management is to shift to small stock during periods of drought but reduce small stock numbers and increase cattle during periods of good rainfall. Homewood and Lewis (1987) have reported that the same management strategy is used in Baringo district.

Wildlife population trends inside and outside the reserve

We failed to detect differences in decline between areas inside and outside the reserve in almost all species and species groups. This is contrary to our expectation that the rate would be higher outside the reserve. It further raises the question what factor or factors could be responsible for the decline inside the reserve. One possible explanation could be the same factors that affect wildlife population decline outside might also be directly or indirectly responsible for the decline inside the reserve. This may be so because wildlife species in the ecosystem seasonally move between the reserve and adjoining areas (Lamprey 1984). Alternatively, some other unknown factor or factors could be responsible for the decline inside the reserve.

Except for Thomson's gazelle and warthog (Table 2) there was also no significant difference in the rate of change of individual wildlife species and species groups populations inside and outside the reserve. However, the rate of decline of all antelope groups was higher outside the reserve although not significant. Significant and higher rate of decline of Thomson's gazelle population outside the reserve may due to the fact that this species is found mostly outside the reserve (mainly in the Loita plains) and it is in these areas where most land use changes have occurred. The reason for significantly higher decline of warthog inside the reserve in comparison to the outside is not known. It could be due to a relatively higher predation by lions, cheetah and hyena since most carnivores are increasingly being confined to the reserve due to increasing human settlements in the dispersal areas.

Contrary to views that wildlife can successfully be conserved within boundaries of parks or reserves, our results appear to indicate that those views may not be true for the

Masai Mara National Reserve. In the case of the Masai Mara ecosystem, most wildlife is found outside protected area most time of the year (particularly during the wet season). Therefore sustainable conservation of wildlife in this ecosystem requires an ecosystem approach. Otherwise, with the continuing loss of wildlife dispersal areas to other human activities, it can be expected that wildlife will continue to decline both outside and inside the reserve. Complete loss of dispersal areas will reduce the reserve to an ecological island where sustainable conservation of certain wildlife species (particularly migratory) may not be possible even through active management strategies.

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CHAPTER 5

Population trend and seasonal distribution of Burchell's zebra in Masai Mara ecosystem, Kenya

W.K. Ottichilo

(submitted, Journal of Animal Ecology)



Abstract

The population trends of Burchell's zebra in Masai Mara ecosystem for the period 1977 to 1997 and their relationship with rainfall were determined using regression analysis. Changes in their distribution patterns based on all censuses conducted during the 20-year period were also determined. The wet season population size, which is composed of mainly resident zebra, declined significantly from about 70,000 to about 35,000 in the past 20 years while that of the dry season population did not decline significantly. Cross border migrations increased significantly during the same period and were also found to be significantly related to wet season rainfall. The overall distribution patterns of zebra in the ecosystem indicate that there are local seasonal migrations, which appear to be more important than cross border migrations. Their distribution patterns in the ecosystem appear to have changed over time due to changes in land use.

Key words: Masai Mara, zebra, population, trend, distribution and rainfall

Introduction

The Masai Mara National Reserve (MMNR) and the adjoining group ranches (hereafter referred to as Masai Mara Ecosystem) have the richest wildlife resources and offer the most spectacular wildlife watching in Kenya (Stelfox et al. 1980). Burchell's zebra is the second most abundant large wild herbivore species in the ecosystem after wildebeest. There are both local and cross boundary migrants and their populations are reported to be stable (Broten and Said 1995). The resident population migrate locally within the ecosystem while the migratory population migrate into the ecosystem from the Serengeti National Park in Tanzania annually (Stelfox et al. 1986, Sinclair 1995). The migration of zebra from Serengeti National Park normally occur during the dry season (June to October). The timing of their arrival and departure is variable and is influenced by various factors (Maddock 1979, McNoughton 1990, and Sinclair 1995). The migrants occupy and utilize the Masai Mara National Reserve and adjoining group ranches to the northwest of the Reserve.

Although many studies have been conducted in the Masai Mara ecosystem none has focused on the long-term population size trend analysis of zebra population. Also no recent study has focused on underlying causes of migrations within the Masai Mara ecosystem and between Masai Mara ecosystem and Serengeti National Park. Sinclair (1995) has reported that the underlying causes of migration and current movements of the migrants in the Serengeti-Mara ecosystem have not been documented.

The aims of this study are to analyze fluctuations in the population size and the distribution patterns of zebra population in the Masai Mara ecosystem between 1977 and 1997 and investigate the relationship between the magnitude of cross border migrations and rainfall. The study hypothesis is that the population sizes and distribution patterns have remained constant and cross border migrations are influenced by rainfall variations.

Study area

The study area is situated in Narok district, Kenya. It lies approximately between latitude 1⁰ 00' and 2⁰ 00' south and longitude 34⁰ 45' and 36⁰ 00' east. The area covers about 6000km². It is bounded by the international boundary of Kenya and Tanzania in the south, Siria

escarpment (Esoit Olololo) to the west, agriculture and forest to the north, Loita plains and hills to the east and Siana plains and hills to the southeast (Fig.1). The area is roughly triangular in shape and can be divided into three range units, based on their biogeography and climate (Stelfox et al. 1986). These units are Mara and the Reserve (mainly composed of *Themeda* grassland), Loita plains (composed of dwarf shrub and *Acacia drepanolobium* grassland) and Siana (mainly hills and plains supporting *Croton* bush and other woody species interspersed with grassland).

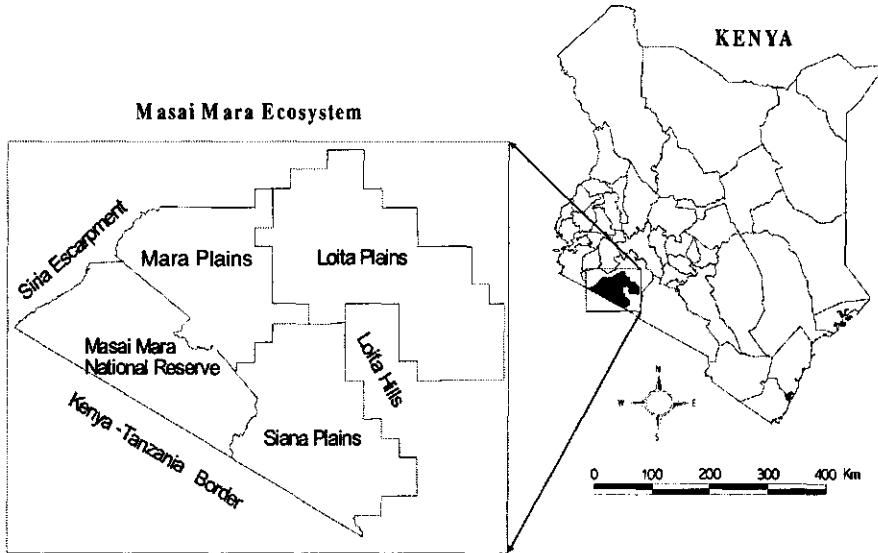


Figure 1: Map of the Masai Mara ecosystem located in the southwestern Kenya. The ecosystem is divided into 3 eco-units (Mara and the National Reserve, Siana and Loita plains) based on the biogeographical characteristics and climate.

Methods

Animal census

The animal census data was collected by Department of Resource Surveys and Remote Sensing (DRSRS) using a systematic reconnaissance flight method (Norton Griffiths,

1978). Grunblatt et al. (1996) and Ottichilo et al. (in press) give details concerning the method as practiced by DRSRS. The population estimates (P.E.) for every species and every census were calculated using Jolly 2 method (1969).

Distinguishing migratory and non-migratory period

An attempt was made to distinguish the resident zebra population from the population that migrates across the boundary. We used spatial analysis method described by Ottichilo et al. (in press). This required identification of a sub-set of censuses conducted during the non-migratory and migratory periods from the larger set of 42 censuses conducted throughout the study period. The rationale of the method is based on Lamprey (1984) who reported that during migration, migratory wildebeest and zebra concentrate in and around MMNR and adjoining group ranches, while during non-migratory periods resident populations are concentrated in the Loita plains.

Weighted centre mean (Walford 1997) for each of the 42 censuses was calculated and plotted using observed number of animals recorded on 5x5 km sub-unit basis. The distance of each weighted centre mean from the Tanzania border was calculated and the respective day number (Julian) of the year when each census was conducted plotted against them (Ottichilo et al., in press).

Population trend analysis

Regression analysis was used to analyze whether the recorded population increased, decreased or was stable over time for both the wet season and dry season populations. The time factor was expressed as year of observation, with decimals indicating the day number within the year. The null hypothesis was: $H_0: \beta = 0$, the alternative was two-sided (i.e. $H_a: \beta \neq 0$), where β is the slope for the population. An indication of the population size of the zebra population migrating across the border was calculated by subtracting the wet season population from the dry season population.

Spatial distribution

Distribution map for animals recorded on 5x5 km basis in each census was prepared and used to comment on local migrations and to establish whether there was evidence of change in the spatial distribution patterns of resident zebra population over the past 20 years. Since cattle and zebra have been shown to have large food and habitat overlap in Mara ecosystem of Northern Tanzania (Voeten 1999), cattle distribution maps of the same censuses were also prepared and compared with those of the zebra to ascertain any overlap in distribution.

Analysis of relationship between rainfall and zebra populations

Rainfall in the Masai Mara ecosystem during the study period was analyzed as described by Ottichilo et al. (submitted). Regression analysis was used to relate pooled annual, wet season, dry season rainfall to both wet and dry season population estimates.

Results

Distinguishing migratory and non-migratory period

Figure 2 shows the location of weighted centre mean of distribution of zebra recorded in 42 censuses, between 1977 and 1997. Figs. 3a&b show the relation between time of the year when the censuses were conducted and the distance of weighted mean centre of the distribution of zebra from the border and the estimated population size respectively. Although there are some identifiable patterns in weighted centre mean distribution, time of the year and distance of weighted mean from the border and the population size, it was not possible to categorically distinguish migratory and non-migratory censuses. This is because the distinction between the two was not apparent especially in terms weighted centre mean distribution. We were therefore unable to use these results to distinguish migratory from non-migratory censuses. Instead the censuses were grouped into two based on whether the census was conducted in wet or dry season and the groups were used in population trend analysis.

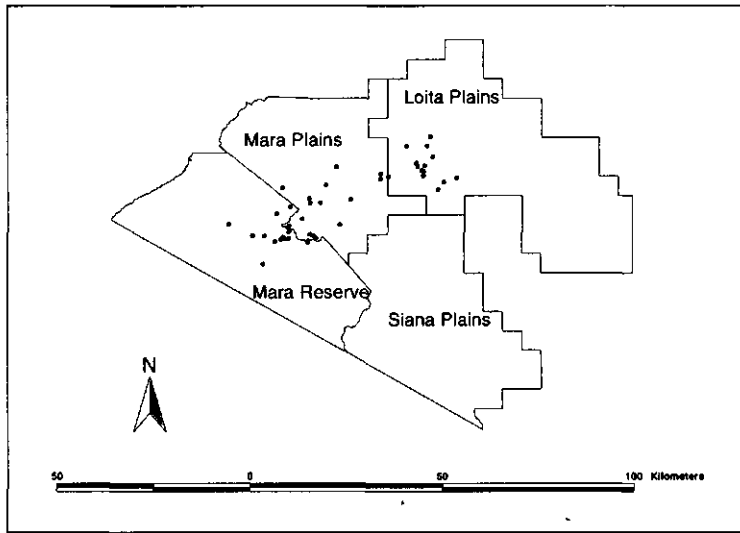


Figure 2: Weighted centre mean of distribution of zebra recorded in 42 censuses, between 1977 and 1997.

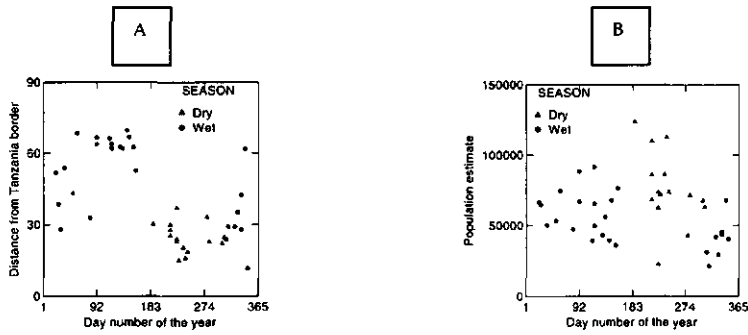


Figure 3: Relation between time of the year (Julian day number) when the censuses were conducted and a) the distance in kilometres of weighted mean centre of the distribution of zebra from the border b) the population estimate

Population trends

Figure 4 shows log-linear regression model of plot of population estimates against time for wet and dry season zebra populations. The model indicates that wet season population declined significantly ($p < 0.014$) from about 70,000 in 1977 to about 35,000 in 1997 while that of the dry season population did not decline significantly.

Figure. 5 show trends in the population size of cross border migrations between 1977 and 1998. The migrations increased significantly ($p < 0.005$) during that period. However, their size of magnitude was lower in the 1970s and 1980s in comparison to the 1990s.

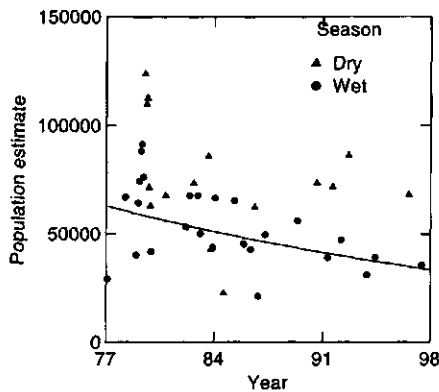


Figure 4: Relation between year of observation and the size of the wet season (represented by a dot) and dry season (represented by a triangle) zebra population. The fitted regression line represents the wet season population and corresponds to: $\ln(y) = 13.360 - 0.030X$ ($R^2 = 0.227$; $n = 26$; $P < 0.014$).

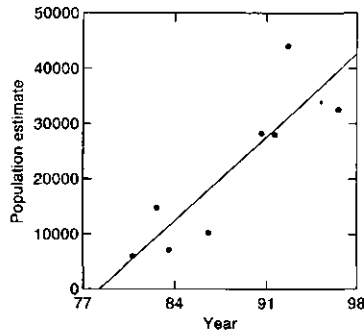


Figure 5: Trends in the size of the zebra population that migrated across the border from Serengeti into the Masai Mara ecosystem between 1977 and 1998. The fitted regression line corresponds to: $Y = -169093 + 2160.6X$ ($R^2 = 0.76$; $n=8$; $P < 0.005$).

Spatial distribution

Figure 6 shows the spatial distribution of zebra population in Masai Mara ecosystem during the period between 1979 and 1997 on census basis. The overall distribution patterns indicate that there occur some local migrations within the ecosystem. The zebra population in the ecosystem appear to occupy the rangelands (mainly the Loita plains) during the period from January to June (wet season) and Masai Mara National Reserve from July to December (dry season). These movement patterns are also discernable in Fig.3a. The movement of the zebra from the reserve into the rangelands appears to start from November and end by December.

The distribution patterns appear to indicate that there are local sub-populations which, do not migrate but are resident in certain localities (particularly in the Loita plains) of the ecosystem. They further appear to indicate that the zebra population has declined in the northern parts of the ecosystem starting from late 1980s.

Figures 7 shows the spatial distribution of cattle in the ecosystem. Cattle are distributed in all rangelands outside the Reserve and their densities appear to have increased

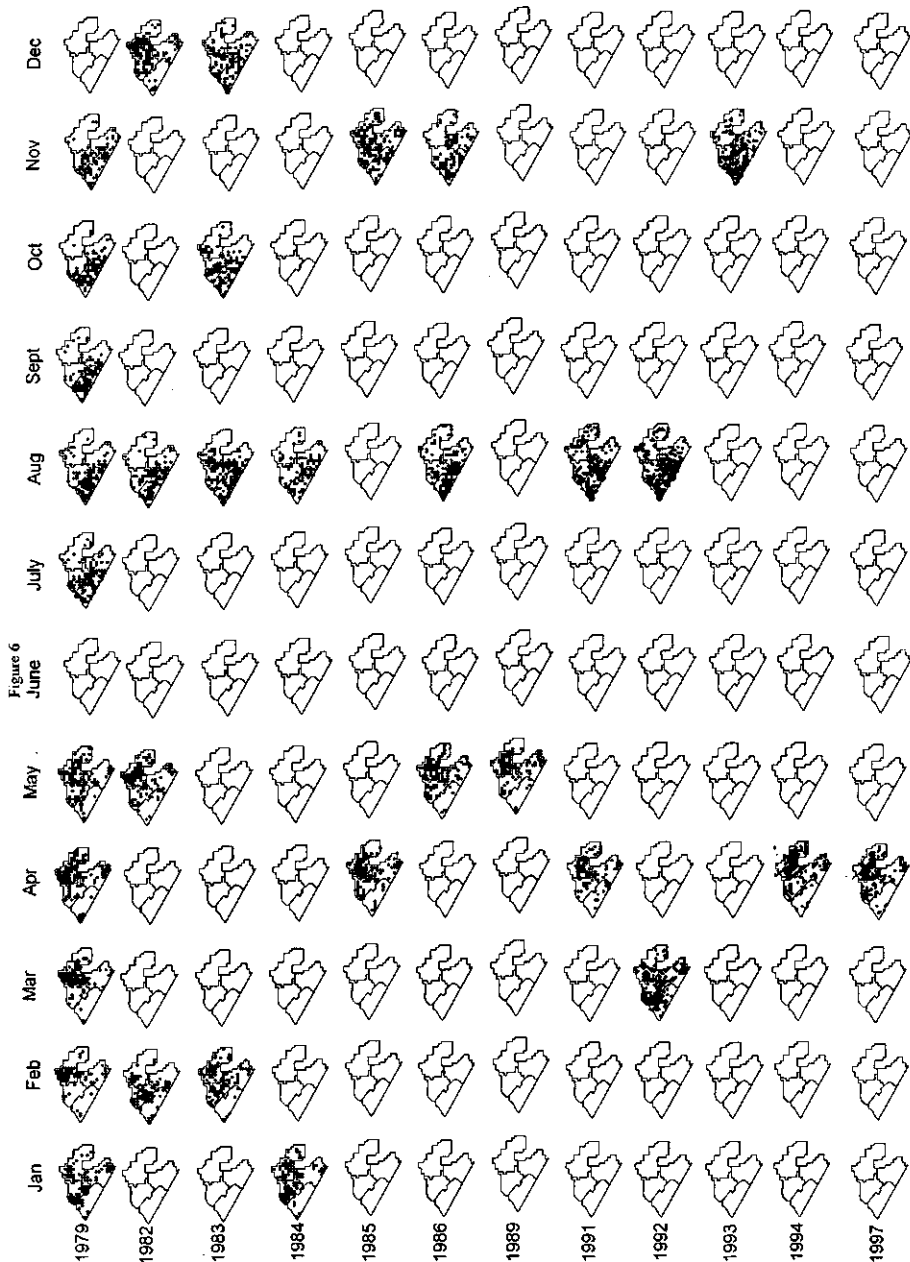


Figure 6

Figure 6

Figure 6: The distribution of zebra in the Masai Mara ecosystem between 1979 and 1997. The rows and columns show year and month of survey respectively. The dots show the spatial distributions of presence of animals observed on 5 by 5 km sub-unit basis.

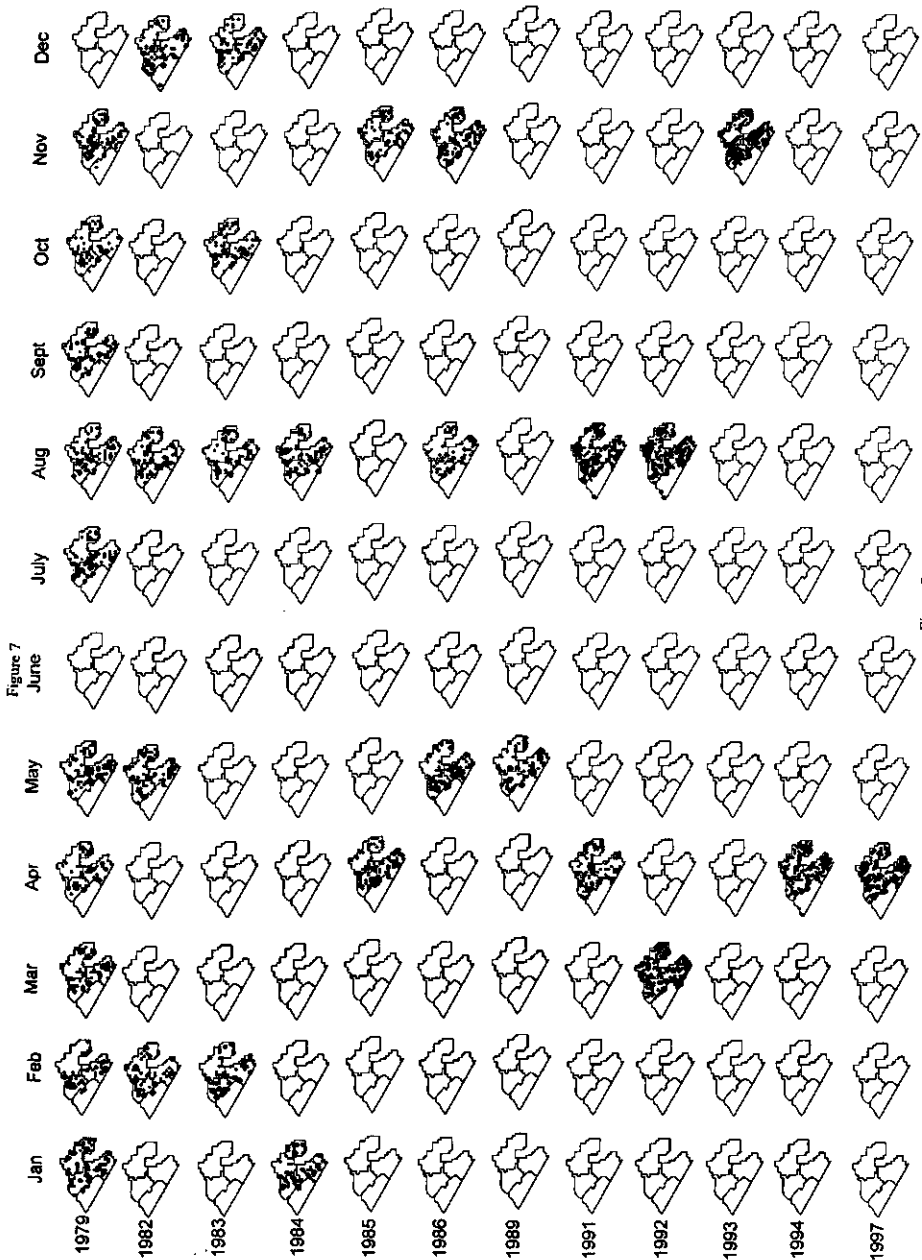


Figure 7: The distribution of cattle in the Masai Mara ecosystem between 1979 and 1997. The rows and columns show year and month of survey respectively. The dots show the spatial distribution of presence of animals observed on 5 by 5 km sub-unit basis.

particularly in the 1990s. A comparison of cattle and zebra distribution patterns show that both species occupy and utilize the same ranges. Although cattle grazing in the Reserve is prohibited, their distributions show that they do graze in some parts of the Reserve.

Relationship between rainfall and zebra populations

Dry season population size (migratory) was significantly ($p < 0.05$) correlated to wet season rainfall (Fig. 8). The population was not significantly related to annual and dry season rainfall. Lastly, the wet season population size (resident) was not significantly related to any category of rainfall.

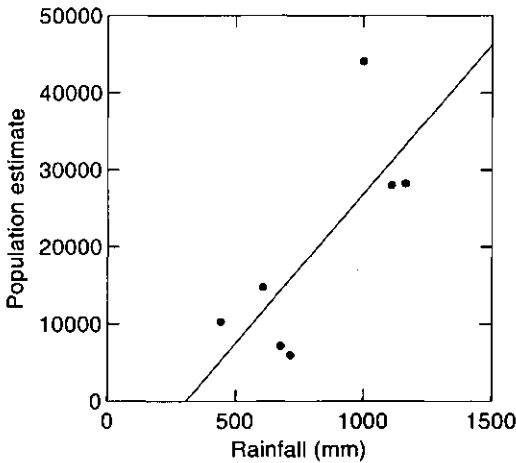


Figure 8: Relation between the dry season zebra population and the wet season rainfall in Masai Mara ecosystem. The fitted regression equation corresponds to: $Y = -11882.92 + 38.76 X$ ($R^2 = 0.57$; $n = 7$; $P < 0.05$).

Discussion

Wet season zebra population

Broten and Said (1995) reported that zebra populations in the Masai Mara ecosystem were stable. The results of this study show that the populations size trends of wet season population, which represent the resident zebra significantly declined ($p < 0.001$) from about 70,000 to about 35,000 between 1977 and 1997. The decline occurred mainly in the northern part of the ecosystem- in the Loita plains (Fig 6). These are wet season (November to May) grazing and breeding areas for the resident zebra and wildebeest (Stelfox et al. 1986). Ottichilo et al. (in press) has shown that in the past 20 years, these areas have been encroached by agriculture (mainly commercial wheat growing) and this has led to drastic decline of resident wildebeest in these areas. Since resident zebra occupied the same areas in high densities in the 1970s (Fig. 6) and their densities have over time declined in these same areas, it can be assumed that agricultural encroachment was mainly responsible for their decline. This is because complete habitat loss is thought to be responsible for the decline or extinction of many wildlife species (Prins and Olff 1998, Caughley and Sinclair 1994). Prins and Olff (1998) have shown that loss of former wildlife areas to agriculture in many areas in Africa has led to decline in populations of different wildlife species.

Apart from the impact of agricultural encroachment on the population size of resident zebra, deterioration in range conditions may have further contributed to recorded decline in these areas. Mwichabe (1988) reported that the range conditions in Loita plains are heavily degraded due to overgrazing by both livestock and wildlife. Ottichilo et al. (in press) has shown that livestock is displaced from agricultural areas in the north to more drier and degraded areas of south-east Loita plains during crop growing period. This increases competition between livestock and wildlife. Voeten (1999) has shown that there is large food and habitat overlap during the wet season between wildebeest, zebra and cattle, with zebra and cattle having the highest overlap in Mara ecosystem in Northern Tanzania. Since food in the wet season areas is reported to be limiting, and cattle numbers in the ecosystem appear to have increased over the years (Fig. 7), it was assume that competition may have occurred. Prins (1992) has outlined how competition between livestock, wildlife and people may culminate into wildlife decline.

Although there was no significant relationship between wet season zebra population size and rainfall probably due to gradual decline over time, the drought conditions that were experienced in the ecosystem in 1984, 1986 and 1993 (Ottichilo et al. In press) may also have contributed indirectly the decline. This is because during periods of drought food is normally low and limiting and this affects animals negatively through drought induced mortality or reduced reproduction rates (Prins and Olf 1998). Ottichilo et al. (in press) showed decline of resident wildebeest in the ecosystem during these periods was significantly related to wet season rainfall. Lack of significant relationship between wet season zebra population size and rainfall appear to indicate that zebra is more tolerant to drought stress than the wildebeest. The impact of poaching remains difficult to assess because most evidence is circumstantial. However, a recent socio-economic survey indicates that poaching was more rampant in the ecosystem in the late 1970s and early 1980s than now (Ngene and Kariuki 1999).

Stelfox et al. (1986) and Lamprey (1984) reported that there occurs seasonal movement of resident zebra population in the ecosystem. This study which is based on long-term census data confirms their reports. It further shows that zebra distribution patterns within the ecosystem have changed in the past 20 years. Their density distributions in the northern parts of the ecosystem appear to have declined over time. Ottichilo et al. (in press) has reported that encroachment of agriculture in these areas has led to decline in resident wildebeest population over time. Since both wildebeest and zebra formerly occupied these areas, it is postulated here that the decline in zebra distribution in these areas was also due to agricultural encroachment among other factors. With increasing agricultural encroachment (Ngene and Kariuki 1999), it is expected that density distribution patterns of the zebra population will continue to change with increasing confinement of the animals within the reserve where wildlife is officially protected. This may lead to a cessation of seasonal migrations within the ecosystem. This in turn is likely to lead to further decline in their population. Voeten et al (1999) has shown that if migratory herds of wildebeest and zebra in Masai ecosystem in northern Tanzania are forced to stay year-round in their dry season range, the current population numbers would decline.

Cross border migratory zebra population

Overall, the cross border migratory zebra population size in Masai Mara ecosystem appears to have increased from about 10,000 in the late 1970s and 1980s to about 30,000 in the 1990s. This increase may be attributed to different factors. The low migrations in the 1980s may be attributed to drought conditions which occurred in the ecosystem in 1984 and 1986 (Ottichilo et al. in press), while increase in migrations in the 1990s may be due to serious drought which occurred in the Serengeti in 1993 (Mduma et al. 1998). Apart from drought, increase in zebra migrations into the Masai Mara ecosystem may be attributed to increase in grasslands. Dublin et al. (1990) has shown that over time, the vegetation of the reserve has changed from shrubland to shrubby grassland to pure grasslands due to the impacts of fire and elephants.

Brotten and Said (1995) reported that about 10,000 to 50,000 animals appear to migrate into the ecosystem from the Serengeti annually. The results of this analysis confirm their estimate and show that in the 1970s and 1980s about 10,000 animals migrated into the ecosystem, while in the 1990s the number of animals migrating into the ecosystem increased to between 30,000 and 50,000. The probable reasons for the increase in migrations are given above.

A significant correlation between wet season rainfall and cross border migratory population indicate that the migration of zebra from Serengeti into Masai Mara may be related to wet season rainfall. The wet season rainfall influences the amount of forage biomass available in Masai Mara ecosystem for the migrating animals. Ottichilo et al. (in press) has also reported that wet season rainfall and the vegetation condition influence wildebeest migration from Serengeti into Masai Mara in the dry season. Sinclair (1995) reported that migrant movement into Masai Mara ecosystem is influenced by dry season rainfall in Serengeti. Thus when rainfall falls during early dry season period, the migrants remain longer in the Serengeti while when it does not rain they move northwards into the Masai Mara where there is occurrence of abundant grass and availability of water during the dry season. Therefore, it was concluded that wet season rainfall influences the abundance of grass in the Masai Mara ecosystem in the dry season and this in turn influence zebra migrations. The magnitudes of migrations appear to be related to the amount of rainfall.

In conclusion this study has shown that while resident zebra population in the Masai Mara ecosystem has declined by about 50%, the cross border migratory population from the Serengeti has more than trebled in the past 20 years. The study has further shown that there occur local migrations within the ecosystem, spatial distribution patterns of the resident population appear to have changed in the past 20 years and the cross border migrations are influenced by wet season rainfall. The drastic decline of resident zebra population poses threat to future conservation of the species in the ecosystem. Therefore, there is an urgent need to establish factors that are responsible for the decline and use the information to formulate sustainable conservation strategy for the zebra and other wildlife species that are found in the ecosystem.

Acknowledgements

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CHAPTER 6

Population trends of resident wildebeest (*Connochaetes taurinus hecki* (Neumann)) and factors influencing them in the Masai Mara ecosystem, Kenya

Wilber. K. Ottichilo, Jan de Leeuw and Herbert H. T. Prins
(Biological Conservation, in press)



Abstract

Population trends of resident wildebeest (*Connochaetes taurinus hecki* (Neumann)) and factors influencing them in Masai Mara ecosystem between 1977 and 1997 were investigated. Population trends were analyzed using aerial census data collected through systematic reconnaissance flights. Aerial censuses pertaining to resident wildebeest populations (non-migratory) were identified from migratory populations through spatial analysis. Regression analysis was used for population trend analysis. The impact of land use changes on wildebeest population was analyzed by comparing changes in wildebeest densities in cropped and non-cropped areas. Relationship between population size and rainfall fluctuations was used to assess the influence of rainfall on trends. Comparison of cattle densities in cropped and non-cropped areas was used to get an insight into possible competition between cattle and wildebeest for food. The results show that resident wildebeest population in Masai Mara ecosystem has declined from about 119,000 in 1977 to about 22,000 in 1997, an 81% decline. The decline is mainly attributed to loss of former resident wildebeest wet season grazing, calving and breeding ranges to agriculture. Rainfall fluctuations and possible competition between wildebeest and cattle during periods of limited food resources may have further contributed to the decline.

Keywords: resident wildebeest, population decline, trend analysis, agriculture, rainfall, competition

Introduction

The Masai Mara National Reserve (MMNR) and adjoining group ranches (hereafter referred to as Masai Mara Ecosystem) in Kenya, forms the northern portion of the Serengeti-Mara ecosystem to which wild animals (especially wildebeest and zebra) migrate annually. The ecosystem has the richest wildlife resources and offers the most spectacular wildlife watching in Kenya (Stelfox et al. 1986). These rich wildlife resources to a certain extent depend on the facilitation process maintained by annual migration of wildebeest and zebra. The wildebeest and zebra from Serengeti National Park migrate and stay in the Masai-Mara ecosystem between June and November (Maddock 1979). They occupy mainly the reserve and the adjoining group ranches. Internal migrations of resident wildebeest populations also occur within the ecosystem. This takes place between the reserve and the adjoining dispersal areas (group ranches) (Fig. 1). These migrations clearly show that the protected area (the reserve) is not adequate for the protection and viability of migratory wildlife species in the ecosystem. Rarely can wildlife parks be established so as to encompass an entire ecosystem. Because of this reason the viability of wildlife inside most protected areas is frequently influenced by outside factors (Jansen 1986)

Habitat fragmentation or complete habitat loss is thought to be responsible for many wildlife species becoming endemic or extinct (Prins and Olff 1998, Caughley and Sinclair 1994). Prins and Olff (1998) note that an ecosystem that becomes smaller due to areas being put under cultivation (where wild grazers cannot occur any more) will show a decrease in species packing. This is the result of increased competition, although local extinctions may play a role too. Norton-Griffiths (1995) also notes that the conversion of privately owned rangelands to agriculture and ranching is the most concern to wildlife managers. Lado (1996) observes that the most serious long-term threat to the future of wildlife populations in Kenya is due to the indirect effects on habitat resource destruction or alteration. In Africa, the increasing conversion of natural lands to agriculture and human settlements is mainly attributed to increasing human population and is thought to be responsible for the increasing decline in wildlife resources (Johan 1995).

The wildebeest is a flagship or keystone species in the Masai Mara ecosystem because of its occurrence in large numbers and its annual migrations within and outside the

ecosystem (Talbot and Talbot 1961, Sinclair 1995). Their migration generate, through their grazing activities, optimal conditions for other large mammals, a process generally referred to as facilitation (Bell 1970, 1971, Prins and Olf 1998). This facilitation can only be sustained through regular migrations between protected and dispersal areas. However, the dispersal areas are increasingly being converted from pastoral grazing areas to agricultural and human settlement areas (Sinclair 1995, Norton-Griffiths 1995). For example, between 1975 and 1995, the area under wheat in the Masai Mara ecosystem has increased from 4875 ha in 1975 (Karime 1990) to 11000 ha in 1985 (Serneels et al. *submitted*) to 50000 ha in 1995 (Serneels et al. *submitted*). The long-term impact of these land use changes on the population of the wildlife species (especially the migrants) has not been studied. However, a number of studies undertaken in the ecosystem indicate that populations of most wildlife species are on the decline (Ottichilo et al. *in press*, De Leeuw et al. 1998, Grunblatt et al. 1996, Broten and Said 1995). The decline is attributed to among other factors to increasing loss of former wildlife grazing or dispersal areas to agriculture (mainly wheat growing) and human settlements (Broten and Said 1995, Sinclair 1995, Sitati 1997). However, there is no evidence to support these claims.

In this study we analyze the trends of the resident wildebeest population in Masai Mara ecosystem over the past 20 years (1977-1997). We further analyze the relationship between crop (wheat) expansion, rainfall fluctuations and cattle density and wildebeest population trends.

Study area

The current study was carried out in approximately 6000 km² of the Masai Mara ecosystem, in the southern part of Narok district, Kenya (Fig. 1). Following Stelfox et al. (1986) we distinguished four range management units in the study area (Figure 1). The Masai Mara National Reserve (MMNR) and the Mara group ranches are mainly composed of *Themeda* grassland. Dwarf-shrubland and *Acacia drepanolobium* grassland characterize the Loita plains while Siana consists mainly of hills and plains supporting *Croton* shrubland and other woody species interspersed with grassland. More detailed descriptions of vegetation and land use are given by Ottichilo et al. (*in press*) and Stelfox et al. (1986).

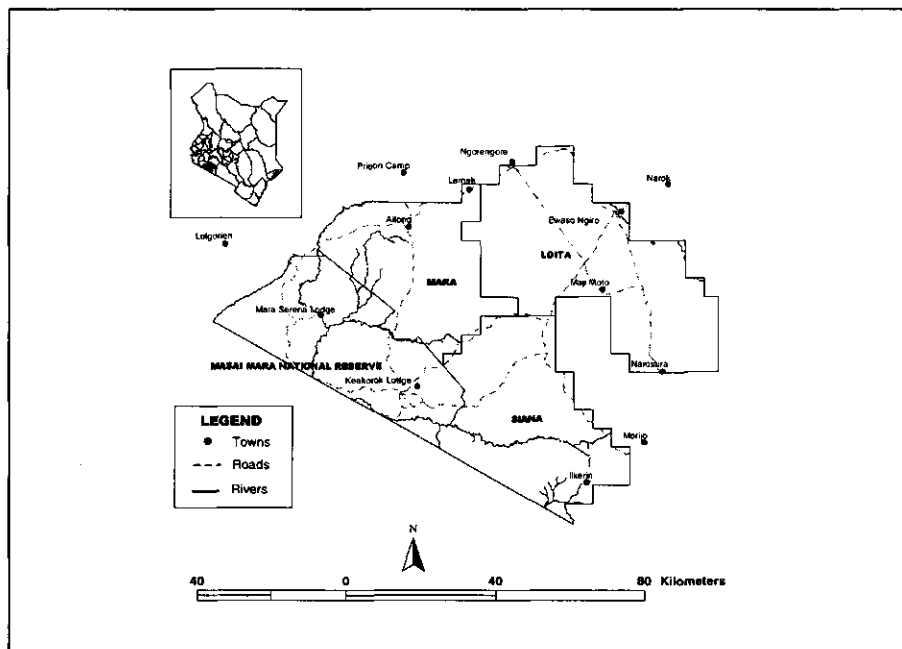


Figure 1: Map showing a) the four range units within the Masai Mara ecosystem and b) the location of the study area.

Methods

Data collection

In the current study we used animal counts from 42 censuses conducted in the ecosystem between 1977 and 1997. The data was collected by the Department of Resource Surveys and Remote Sensing (DRSRS) using a systematic reconnaissance flight (Norton Griffiths, 1978). The data and method appear trustworthy (De Leeuw et al. 1998, Ottichilo and Khaemba *submitted*). The ecosystem was surveyed along transects oriented in east- west direction and spaced at 5 km intervals. Flying heights were approximately 90 m (1977-1985) and 120 m (1985 –1997). Two experienced and well trained observers (Dirschl et al. 1981) occupied the rear seats of a high wing aircraft (Cessna 185 or Partinevia) and counted

animals that appeared between two rods attached to the wing struts. The field of vision between these rods was calibrated by flying repeatedly across ground markers of known spacing (Ottichilo and Sinange 1985). The number of animals falling within the survey strips on either side of the aircraft along each 5km transect segment were counted and recorded into tape recorders by the two Rear Seat Observers (RSO). Groups of animals more than ten in number were also photographed and later counted with the aid of a 10x binocular microscope and overhead projector. Population estimates (P.E.) for every species and every census were calculated using the Jolly 2 method (1969). Although the method gives too large standard deviations, the means are trustworthy (Khaemba and Stein *in press*).

Lastly, information on the presence or absence of agriculture and the crop species present (mainly wheat) was recorded by a Front Seat Observer (FSO) on 5*5 km sub-unit basis.

Distinguishing migratory and non-migratory period

This study analyzed trends in the resident wildebeest population. This required identification of a sub-set of censuses conducted during the non-migratory period, from the larger set of 42 censuses conducted throughout the study period. Using fixed starting and end dates for the migration as reported Maddock (1979) would have been a simpler method to allocate the censuses to either the migratory or the non-migratory period. However, we deemed this approach invalid because for the last 20 years the periodicity of the movements of migrants have not been fully described (Sinclair 1995). Also experience gained by tour operators and reserve management show that the exact month and date of the onset and end of the migration varies considerably between years.

Instead we developed a method which uses the observed spatial distribution pattern of wildebeest to decide whether there was migration or not. The rationale for this was based on Lamprey (1984) who reported that during migration, wildebeest concentrate in and around the MMNR and adjoining group ranches, while during non migratory periods resident populations are concentrated in the Loita plains. We first analyzed and verified whether this pattern which was based on analysis of 12 censuses in 1978-1979, held for the

period between 1977 and 1997, and then used the distribution pattern to differentiate between censuses pertaining to migratory and non-migratory periods.

We calculated the weighted mean centre (Walford 1997) of the distribution of wildebeest for all 42 censuses according to:

$$X_w = \sum X_i W_i / \sum W_i \quad \text{and} \quad Y_w = \sum Y_i W_i / \sum W_i$$

Where X_w and Y_w represented the weighted mean centre expressed in Universal Transverse Mercator projection (UTM), X_i and Y_i represent the UTM coordinates and W_i the weighting variable for observation point i , which corresponded to the number of animals, recorded by the RSO.

We then fitted geometric mean regression (Sokal and Rohlf 1995) through the 42 calculated weighted mean centres of the distribution of wildebeest. We subsequently projected the weighted mean centre of every census on the geometric mean regression line, and calculated the distance of these projections to the Tanzanian border. The location of these points along the geometric regression line was then used to analyze the displacement of the centre of the wildebeest population between seasons. For this purpose we plotted the day number (Julian) of the year when each census was conducted against its respective distance from the Tanzanian border. The procedures described above resulted in the selection of 21 censuses pertaining to the non-migratory period. These were used for further analysis as described below.

Analysis

Populations trends

We first regressed the 21 wildebeest population estimates against time in order to determine whether there was evidence of trend in the resident wildebeest population. The factor time was expressed as year of observation, with decimals indicating the day number within the year. The dependent variable (wildebeest population estimate) was log transformed prior to

analysis because exploratory data analysis revealed non-linearity in its relationship with time. The null hypothesis was: $H_0: \beta = 0$, the alternative was two-sided (i.e. $H_a: \beta \neq 0$), where β is the slope for the population.

We next plotted maps in order to analyze whether there was evidence of change in the spatial distribution of the density of resident wildebeest population over the last 20 years. The recorded wildebeest density ($N.km^{-2}$) for every 5x5 km aerial survey sub-unit was averaged for the following four time periods: 1977-1979, 1982-1984, 1985-1989 and 1990-1997. Arc View GIS software was used for this and other spatial analysis throughout this study.

Analysis of factors related to the observed population trends

Previous research (Sitati 1997, Douglas-Hamilton 1987) claimed that expansion of agriculture is the main factor influencing wildlife population trends in Masai Mara ecosystem. However, a decline of resident wildebeest population may be a result of more than one single factor. Therefore we analyzed the relation between size of the resident wildebeest population with rainfall and agricultural encroachment. We additionally investigated whether there was indirect evidence of increased competition between cattle and wildebeest.

We first plotted the extent of wheat farming as recorded by the front seat observers; using dots to indicate whether crop growing had been recorded (presence) or not (absence) during the four periods. We then addressed the question of whether a relation existed between encroachment of agriculture and average density of wildebeest prior to agricultural encroachment. The null hypothesis was that prior wildebeest density did not differ between areas encroached and not encroached by agriculture. A simple t-test was used to test this hypothesis.

We also addressed the question of how encroachment of arable farming has affected the density of resident wildebeest. If farming did not have an effect one would expect the same rate of decline for areas affected by farming and areas not encroached. We used FSO data to identify sub-units ever affected and those never affected by agriculture. Next, we calculated population densities for these two samples. We then separately

regressed the logarithm of wildebeest population density against time for areas occupied and not occupied by crops. Prior to the analysis, we expected that the rate of decline would be higher in areas with agriculture compared to those without. This led us to the following null and one-sided alternative hypothesis: $H_0: \beta_+ = \beta_-$ and $H_a: \beta_+ > \beta_-$, where β_+ and β_- represent the slopes for the regressions in areas with and without crops respectively. We used a T-test to test for differences in slopes between these two samples.

Rainfall is one of the main factors that influence primary production in semi-arid areas (Phillipson 1975). Its fluctuations in time and space influence the abundance and distribution of herbivores (Prins and Olf 1998). In this analysis 20-year rainfall records from two meteorological stations were used to investigate whether rainfall fluctuations during the period had any influence on wildebeest population fluctuations and whether droughts occurred during the period. Rainfall data recorded at the meteorological station in Narok, located at 15 km from the centre of the Loita plains was used in the analysis. Norton Griffiths et al. (1975) indicated that the rainfall year in the Serengeti-Mara ecosystem is considered to start in November. Therefore, to calculate annual rainfall totals, rain falling between 1 November of one year and 31 October of the following year should be used. This November-October period is more relevant ecologically than the period January- December for it represents one complete seasonal cycle (Norton-Griffiths et al. 1975, Prins and Loth 1988).

The mean annual (November- October), mean wet season (November- May) and mean dry season (June-October) rainfall and respective variability were calculated. Determination of drought or wet year was done according to Prins (1996). The resident wildebeest population estimates were regressed against the annual total rainfall as well as wet and dry season rainfall in the year of census. Lastly, the residuals of regression analysis of the relation between wildebeest densities in cropped and non-cropped areas in Loita plains and time of observation were plotted against annual, wet season and dry season rainfall to determine any relationship between them.

Increase in competition with cattle could be another factor negatively affecting the resident wildebeest population since cattle and wildebeest are known to overlap by over 60% in their forage requirements (Hansen et al 1984). During the crop- growing season (November to June), cattle are moved out of the crop fields to the adjacent non-cropped

rangelands (Livestock Officer *pers. comm.*). Hence we expect an increased density of cattle on these non-cropped rangelands during this period. These rangelands are, at this period of the year, occupied by resident wildebeest population (Lamprey 1984). The expected increased density of cattle could lead to increased competition with wildebeest. Given that the range conditions of these areas have been generally reported to be poor (Mwichabe 1988), increased competition with cattle in this particular period could in the long-term have a negative effect on the wildebeest population density.

We first analyzed the available 42 censuses, to verify whether there had been an increase in the density of cattle during the study period. Our null hypothesis was that the density had not increased: $H_0:\beta=0$ and the alternative was two sided: $H_a:\beta\neq 0$, where β is the slope of the regression line. Second, we tested the hypothesis that in the non-cropped area the difference in density of cattle between crop growing and non-growing period equaled zero. We compared censuses from the same year, one in the crop growing periods and the other in non-growing periods. We used a matched-paired test, since repeated records were made on the same sub-unit.

Results

Spatial distribution

Figure 2, which shows the weighted mean centre of the distribution of wildebeest for the 42 censuses, reveals two distinct clusters. The southwesterly cluster, situated within and around the MMNR, is located at distances of less than 40 km from the Tanzanian border. A second cluster in the Loita plains is located at distances of more than 60 km from the Tanzanian border. Two censuses are located somewhat in the middle of these two clusters.

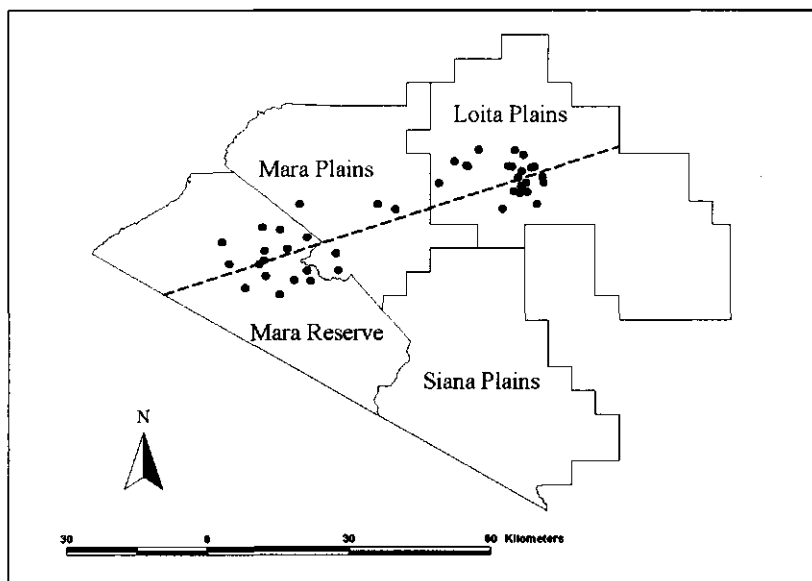


Figure 2: Location of weighted centre mean of distribution of wildebeest recorded in 42 censuses, between 1977 and 1997. The line fitted through the data represents the geometric mean regression line: $y = 555.3 + 0.338 * X$.

Figure 3a shows a relationship between the distance from the Tanzanian border and the day number, while Fig. 3b relates estimated population size and day number. Together the figures show that censuses taken between mid November (day number > 320) and late May (day number 150) correspond to wildebeest population sizes below 200,000 and occur at distances greater than 60 km from the Tanzanian boundary. We classified these 21 censuses as non-migratory censuses. Population estimates larger than 200,000 animals, at distances less than 30 km from the boundary were recorded between mid June and November. Because of period in the year, higher population sizes, and closer distance to the Tanzanian border, we classified these 19 censuses as migratory period censuses. Two censuses fell outside the two clusters mentioned above. These two censuses most likely represent transitional resident and migratory populations that have not fully dispersed. We therefore did not allocate these two censuses to the non-migratory period.

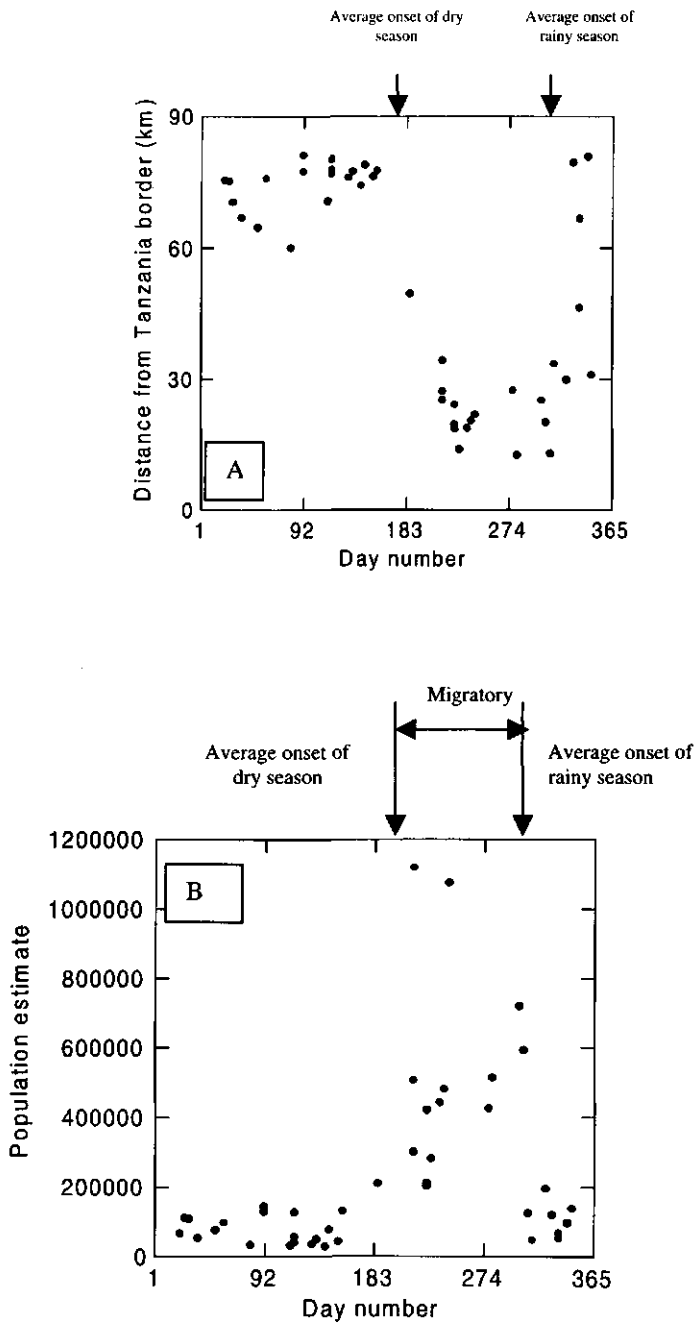


Figure 3: Relation between time of the year (Julian day number) when the censuses were conducted and a) the distance of the weighted mean centre of the distribution of wildebeest, from the Tanzania border, b) the estimated size of respective wildebeest population.

Population trends

Figure 4 shows the relation between the size of the resident population and year of observation. The fitted regression model indicated that the resident wildebeest population significantly ($P < 0.001$) declined at annual rate of 8.4% between 1977 and 1997. According to this regression model, the size of the resident wildebeest population declined from about 119,000 in 1977 to an estimated 22,000 in 1997. This corresponds to an 81% decline in resident wildebeest population in 20 years.

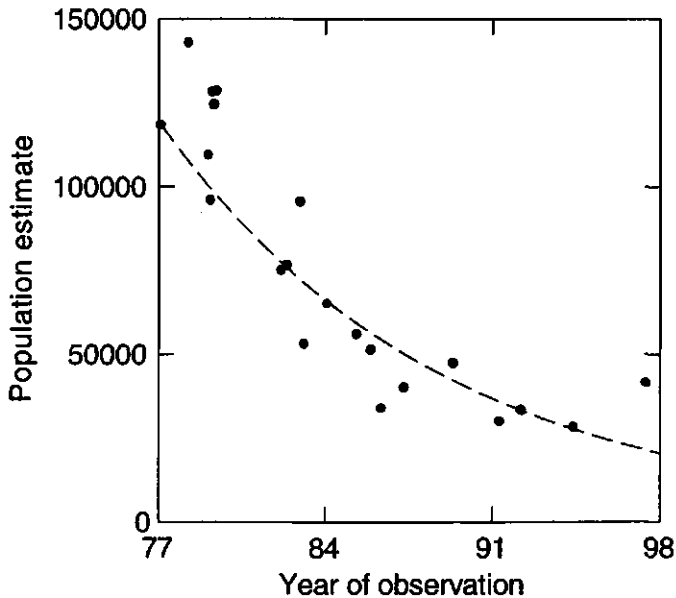


Figure 4: Relation between year of observation and the size of the resident wildebeest population. The fitted regression line corresponds to: $\text{Ln}(Y) = 18.158 - 0.084 * X$ ($R^2 = 0.794$; $n = 21$; $P < 0.0001$).

Figure 5 shows change in wildebeest density between 1977 and 1997. Initially in the late 1970s, highest densities occurred in the northern parts of the Masai Mara ecosystem particularly in the central and northwestern parts of the Loita plains. In the early 1980s

(1982-84) densities appear to have declined considerably in northern and central parts of the former 1970s high-density areas. During the late 1980s (1985-89) densities further declined in these areas including eastern parts. By the 1990s the densities appear to have declined significantly in all these areas in comparison to the late 1970s densities. Hence, this decline in wildebeest densities started in the early 1980s and continued to 1997 (Fig. 5). It appears to be most pronounced in the Loita plains.

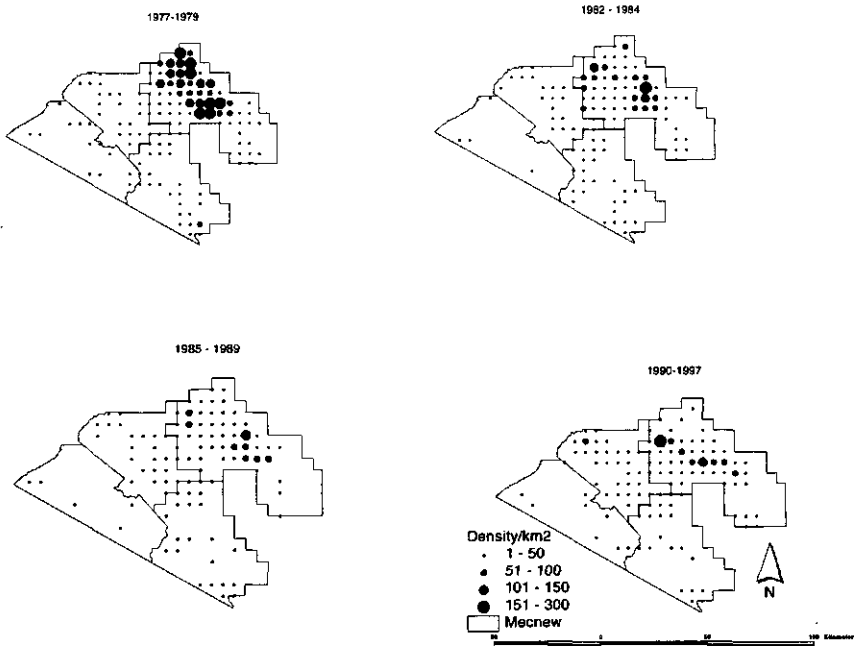


Figure 5: Average density ($N.km^{-2}$) of wildebeest recorded in the Masai Mara ecosystem for a) 1977-79, b) 1982-84, c) 1985-89 and d) 1990-97.

Factors related to observed population trends

Table 1 gives data on difference between the 20-year annual total mean, wet season total and dry season total and individual year totals. It also gives information on whether years had drought or wet years. Figure 6 shows regression models of resident wildebeest

population estimate against annual total, wet season total and dry season total rainfall respectively. The models reveal a significant relationship between resident wildebeest population estimate and annual and wet season rainfall. Plot of residuals of regression lines of wildebeest densities in agricultural and non-agricultural areas of Loita plains further showed that annual and wet season rainfall had relationship with wildebeest density trends. We failed to detect a significant relationship with dry season rainfall.

Table 1: Shows total rainfall (November-October); wet season rainfall (November-May) and dry season rainfall (June-October) for Narok Meteorological Station, and the mean of the 21 years between 1977 and 1997. The deviation of the rainfall in a particular year from the long-term mean is indicated in the columns difference 1, 2 and 3 respectively. The last column shows whether the year was wet or experienced drought. A drought year is defined as a year in which the total rainfall was less than the mean annual rainfall minus the standard deviation, while a wet year is defined as a year with more than the annual rainfall plus the standard deviation.

year	Total	Wet total	Dry total	Difference1	Difference2	Difference3	Wet or Drought
1977	905	739	166	173	133	40	
1978	1090	1024	66	358	418	-60	wet
1979	897	808	89	165	202	-37	
1980	804	635	169	73	29	43	
1981	601	546	55	-131	-60	-71	
1982	582	415	167	-150	-191	41	
1983	759	567	192	28	-39	66	
1984	406	298	108	-326	-307	-18	drought
1985	856	759	97	125	153	-29	
1986	499	459	40	-233	-146	-86	drought
1987	922	769	153	191	164	27	wet
1988	853	761	92	122	156	-34	
1989	900	718	182	168	112	56	
1990	828	709	119	96	103	-7	
1991	520	388	131	-212	-217	5	drought
1992	474	395	79	-257	-211	-47	drought
1993	774	623	151	42	18	25	
1994	547	495	52	-185	-110	-74	drought
1995	632	487	145	-99	-118	19	
1996	796	523	273	64	-82	147	
1997	719	599	120	-13	-7	-6	
Annual mean	732	606	126				
S.D of mean	181	175	56				
Variability(%)	25	30	45				

Figure 7 shows expansion of wheat growing in the Loita plains from 1978 to 1997. The highest expansion occurred during the 1986-89 and 1991-97 periods. There appears to be a remarkable coincidence between the area where wheat encroached and where wildebeest declined. Figure 8 shows original wildebeest density in 1977 for areas subsequently encroached and not encroached by agriculture. Figures 7 and 8 indicate that

wheat farming encroached in areas that had higher wildebeest densities prior to encroachment. This was confirmed by a T-test that revealed a highly significant difference in prior wildebeest densities between areas encroached and never encroached by wheat farming ($P < 0.0001$). Hence, we conclude that wheat farming encroached in particular in the areas with the original highest wildebeest densities.

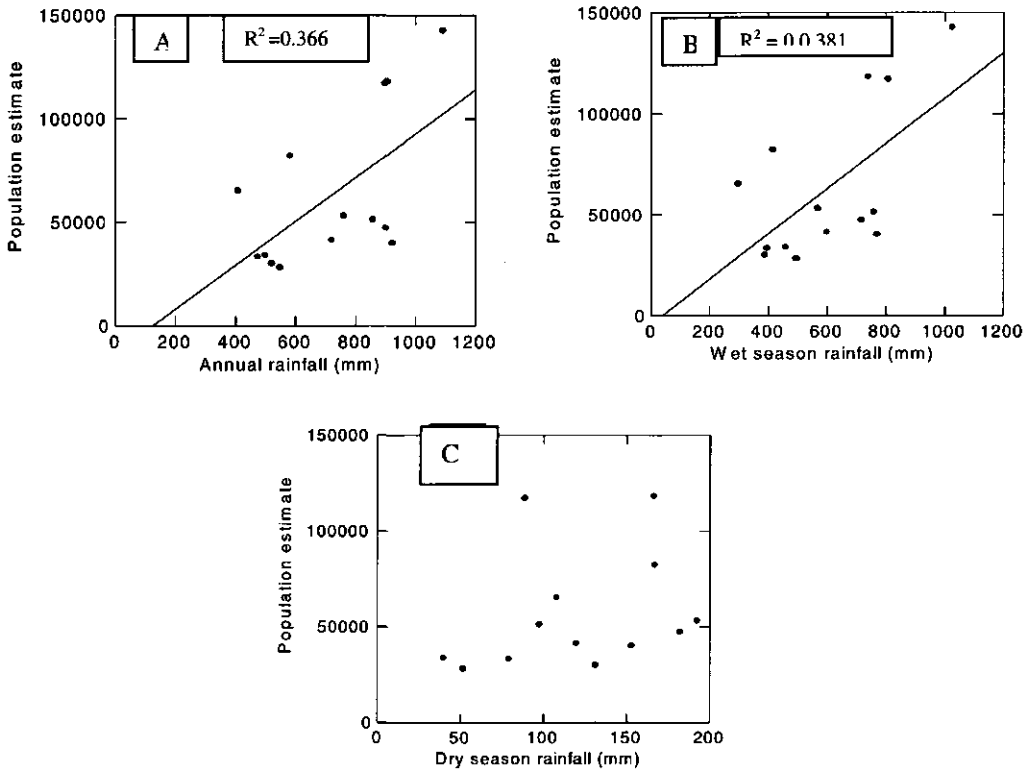


Figure. 6: Relation between wildebeest population estimate and a) annual rainfall b) wet season rainfall c) dry season rainfall at Narok Meteorological Station. Lines correspond to regression equations for annual rainfall ($y = -13.169.12 + 106.15 * X$; $R^2 = 0.366$; $P < 0.022$) and wet season rainfall ($y = -4304.02 + 112.09 * X$; $R^2 = 0.381$; $P = 0.019$).

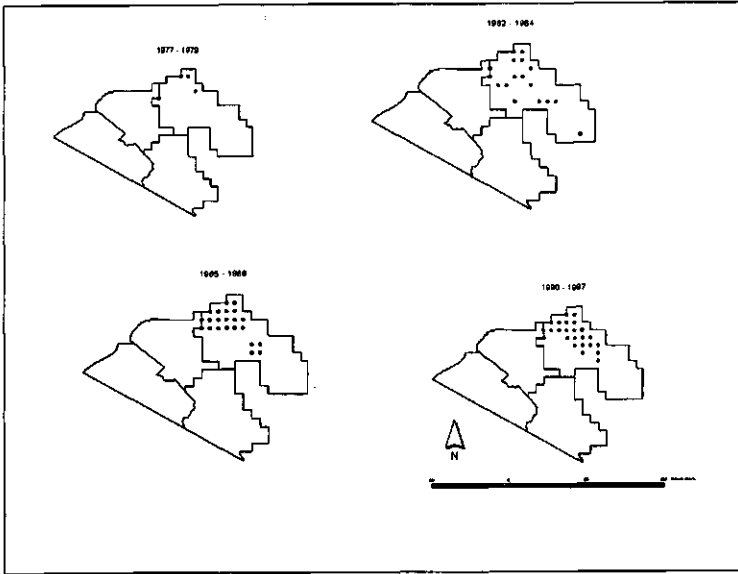


Figure 7: Presence of large scale agriculture (wheat growing) in the Masai Mara ecosystem as recorded by the front seat observer in the DRSRS airplane, in a) 1977-1979 b) 1982-1984 c) 1985-1989 d) 1990-1997.

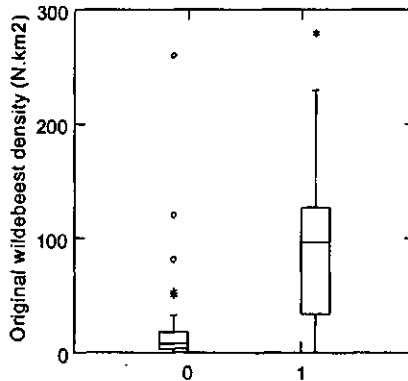


Figure 8: Box plot of wildebeest density in 1977 in the Loita plains for areas subsequently a) encroached (1) and b) not encroached (0) by agriculture.

Figure 9 shows relation of wildebeest population density in the Loita plains against year of observation for areas occupied and not occupied by crops. In both cases the log-linear regression models show significant downward trends in wildebeest densities. The

rate of decline in areas, which were encroached by agriculture of 9.8%, was higher than the rate of decline of 7.1% recorded in areas without agriculture. A test for differences in slopes of the two models was highly significant ($p < 0.0005$), indicating that the decline of wildebeest in agricultural areas was significantly higher than in the non-agricultural areas.

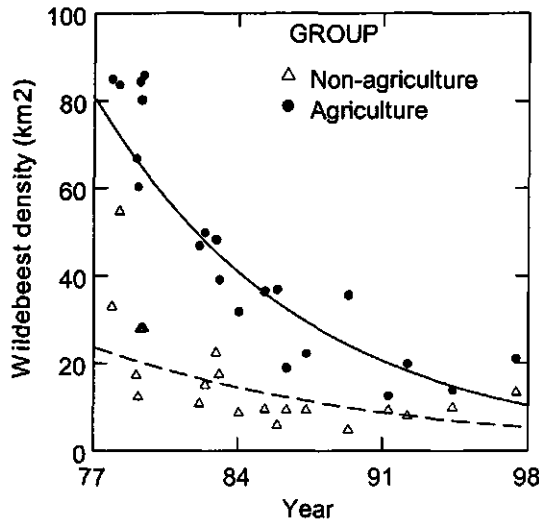


Figure 9: Relation of density ($N.km^{-2}$) of the resident wildebeest population in the Loita plains against time (year of observation) for areas occupied and not occupied by crops. Lines represent regression equations for areas occupied by agriculture (solid line, $\ln(Y) = 11.942 - 0.098 * X$; $R^2 = 0.803$; $P < 0.0001$) and areas not encroached by agriculture (dotted line; $\ln(Y) = 8.636 - 0.071 * X$; $R^2 = 0.422$; $P < 0.001$ respectively).

Regression analysis revealed no significant change in cattle densities in the Loita plains during the study period. This indicates that the cattle population size has remained relatively stable despite the fact that a significant portion of the former grazing land has been converted into agricultural land. There was also no significant difference in the cattle

density in the entire Loita plains between the dry and wet seasons, indicating that there were no significant seasonal movements outside the plains. Paired T-test of pairs of censuses for the years 1982, 1983, 1984, 1986, 1991 and 1992, where one census pertained to crop growing period and the other to non-growing (fallow) period for agricultural areas, was significant ($P>0.05$). This indicates that cattle density during crop growing period was significantly lower in comparison to non-growing period. The results of the same test for non-agricultural areas were not significant. However, cattle density in the crop-growing season was generally higher than in the non-growing period. The results suggest that in non-agricultural areas, high cattle densities occur during cropping season while their densities in agricultural areas are low during the same period (Table 2). Significantly higher densities occur in agricultural areas during the non-cropping (fallow) period. This is the period when cattle are moved in these areas to feed on wheat stubble. We therefore rejected our null hypothesis that the difference in cattle densities in cropped and not cropped areas was equal to zero. Indirectly these results imply an increase in cattle densities in non-cropped areas during the crop-growing period, since the animals are driven out of agricultural fields. However, our test failed to detect such an increase. This is because one observation (1992) there was a severe decrease instead of increase.

Table 2: Average density (N.km²) of cattle in the areas occupied and those not occupied by agriculture during the crop-growing season and during the fallow period. The analysis was restricted to those years with censuses in both seasons.

Year and compared months	No Agriculture		Agriculture	
	Cropping Season	Fallow Period	Cropping Season	Fallow Period
1982 (May&Aug.)	42.94	31.95	18.34	24.82
1983 (Feb.&Aug.)	18.57	16.85	2.77	22.43
1984 (Jan.&Aug.)	30.04	15.93	19.23	36.01
1986 (May&Aug.)	13.62	11.38	3.50	2.44
1991 (Mar.&Aug.)	35.79	17.91	17.20	37.83
1992 (Mar.&Aug.)	13.66	25.88	31.74	52.12
Mean	25.77	19.98	15.46	29.28
S.E	5.03	3.07	4.45	5.30

Discussion

Wildebeest population trends

In this study we have shown a significant decline in the size of the resident wildebeest population from about 119,000 in 1977 to an estimated 22,000 in 1997, about 81%. The decline has occurred mainly in Loita plains, which are the main calving and breeding grounds of wildebeest in southwestern Kenya (Talbot and Talbot 1963, Lamprey 1984). Population estimates from earlier counts indicate that in 1961 the resident wildebeest population in Masai Mara ecosystem was about 18,000 (Stewart and Talbot 1962). Following control of rinderpest in the late 1960's, this increased to about 94,000 in the mid 1970s (Stelfox et al. 1986). It therefore appears that the resident wildebeest population in Masai Mara ecosystem has undergone a period of increase between 1960 and 1977 and a period of decline between 1977 and 1997. The increase of the Kenyan resident population has been attributed to immigration of wildebeest from Serengeti into the Mara due to the population eruption in the Serengeti after eradication of rinderpest (Stelfox et al. 1986). Besides a change in vegetation from bushlands and thickets to open grasslands (Dublin et al. 1990) may have been contributed to the increase.

We demonstrated a remarkable association between the decline in resident wildebeest populations and the expansion of agriculture into prime and original wildebeest wet season ranges in the Loita plains. Our results further show that the highest decline of wildebeest densities in Loita plains occurred in areas that are now occupied by crops, particularly wheat. The decline has been increasing progressively mainly in northern and central parts of the Loita plains where wheat farming has become a permanent activity. We therefore conclude that the recorded drastic decline of resident wildebeest in their former prime wet season ranges in the Loita plains was caused mainly by agricultural encroachment.

Wheat growing, which started in the Loita plains in the early 1970s (Amuyunzu 1984), has continued expanding to date (Serneels et al. *submitted*). The rapid expansion of wheat growing in these areas may be attributed to the agricultural potential of the land (Norton-Griffiths 1995), increasing human population (Ngene and Kariuki 1999) and

government land and food policies for arid and semi-arid areas (Republic of Kenya 1979). It may also be due to increasing awareness of the landowners that they can realize more economic benefits by diversifying their land use activities (Norton- Griffiths 1995, Ngene and Kariuki 1999). One surprising finding was that the areas encroached by wheat had higher prior wildebeest densities compared to areas not encroached. However, one question that needs to be answered is why the encroachment was concentrated in the most suitable habitats for wildebeest?

Wildebeest transmit a deadly disease called malignant catarrh fever to cattle (Talbot and Talbot 1963, Ngene and Kariuki 1999). The disease is transmitted to cattle during the time of wildebeest calving (Talbot and Talbot 1963). As noted above, the resident wildebeest use the Loita plains as a calving and breeding ground during the wet season. To avoid transmission of the disease to their cattle, the Maasai traditionally move their livestock away from calving wildebeest. Wildebeest calving occurs in the Loita plains between November and February (Talbot and Talbot 1963).

Results of a recent socio-economic survey conducted in the ecosystem by Kenya Wildlife Service indicate that overall, wildebeest is rated by the local Maasai (over 70%, $n=178$ households) as the most problematic wild animal because it transmits disease to their cattle. This problem most likely was limited in the 1960s because of the small wildebeest population. We speculate that it increased with the ten-fold increase in wildebeest population in the 1970s. The Maasai had no other option than to accept this increase in wildebeest population, since they had no legal means to control the population particularly after the ban of wildlife hunting and control in Kenya in 1977.

Since the Maasai did not benefit from wildebeest, they decided to put their land under other beneficial uses. Starting in the early 1970s, they started leasing the land to commercial wheat growers (Azumi et al. 1993). Since then wheat growing in the area has become a profitable activity to both the landowner and the leased, hence its unabated expansion. In the Lemek area of Loita plains, where wheat farming has become dominant feature, complaints regarding wildebeest were lower (53%), compared to Olkinyei (94%), where farming is not important and cattle and wildebeest interact (Ngene and Kariuki 1999). In retrospect, it can be said that the conversion of parts of Loita plains into wheat fields solved the problem of the wildebeest plague in those areas. The wheat companies

destroyed the most suitable wildebeest habitat, which is legal under the current Kenyan law. As a result the wildebeest population size declined to the 1960s levels. This calls for serious re-examination of the rationale of making the control of wildlife populations in Kenya illegal while allowing the legal destruction of their habitats!

The impact of introduction of agriculture in the Loita plains has led to the reported decline of most wildlife (mainly wildebeest) from these areas. With the decline, the Maasai are able to use some of the non-cultivated portions of land for wet season grazing and they also graze on wheat stubble after harvest. This may be the reason why there was no significant difference in cattle densities during cropping and non-cropping periods in Loita. Apart from this they also get money for leasing part of the land to commercial wheat growers. We therefore suggest that two main reasons may have been responsible for the fast conversion of former wildebeest calving and breeding areas in the Loita to agriculture. The first was to eliminate the wildebeest from these areas to minimize disease transmission to cattle and make the areas available to livestock grazing. The second is because of economic gains they receive for leasing the land to commercial wheat farmers.

With ever increasing agricultural expansion in the ecosystem (particularly in Loita and now in the Mara ranches) (Sermeels et al. *submitted*), it can be expected that wildlife decline in these areas and consequently in the entire ecosystem will continue. Ngene and Kariuki (1999) have reported that, on the question regarding future land uses in the ecosystem, over 75% (n=178 households) of respondents indicated that more land would be put under crop farming. Voeten et al. (1999) has reported that restricted access to the wet season range could have severe consequences for migratory population numbers since quality of ungrazed vegetation in the dry season ranges does not meet herbivore requirements. Prins and Olf (1998) have shown that an ecosystem that becomes smaller due to areas being put under cultivation (where wild grazers cannot occur any more) will show a decrease in species packing. This is the result of increased competition although local extinctions may play a role too. Also Prins (1992) has shown that when human land use activities compete with wildlife, wildlife is always out-competed. Hilborn (1995) predicted that the loss of dry season grazing areas (group ranches) in Masai Mara ecosystem to agriculture could trigger migratory wildebeest population decline of some

30% but Ottichilo et al. (*submitted*) has shown that between the early 1980s and early 1990s the population has declined by about 200%.

Apart from habitat loss to agriculture, fluctuations in rainfall and increased forage competition from cattle may have further contributed to the decline of resident wildebeest population in the ecosystem. We have shown here that there is significant relationship between wildebeest population trends and annual and wet season rainfall totals in the Loita plains. Thus increase in rainfall totals (up to 1000 mm) appears to have led to increase in wildebeest numbers and vice versa. We have further established that Masai Mara ecosystem experienced severe drought conditions during the years 1984 and 1986 and less severe drought in 1993. Censuses following drought years had generally lower population estimates in comparison with previous ones while those following wet years had generally higher estimates. Since there is a well established relationship between rainfall and primary production of grass in semi-arid tropics up to an annual total of about 1000 mm (Phillipson, 1975), it is assumed that during these periods primary production in the ecosystem was low and limiting. Therefore it is possible that wildebeest population experienced food shortages and this could have in turn negatively affected their population dynamics e.g. through drought-induced mortality and reduced rate of natural increase. Talbot and Talbot (1963) reported that wildebeest breeding (or rutting) is influenced by the available food and water. Thus in drought conditions or dry season, there is rarely enough food and water to support large herds that are necessary for rutting to take place. Prins and Olff (1998) have shown that population dynamics of herbivores are determined by quantity and quality of food over a period long enough to enable the animal to deposit reserves of energy and protein stored in the body. Reproduction rates and survival therefore reflect an integrated measure of daily net intake over an extended area.

Mduma et al. (1995) have indicated that the drought that occurred in the Serengeti in 1993 was the most severe since 1938 and led to significant decline in wildebeest populations. Although the Masai Mara ecosystem experienced some drought conditions during the same year, they were not as severe as those of Serengeti (Table 1). However, the droughts of 1984 and 1986 were more severe in the Masai Mara than in the Serengeti (Ottichilo et al. *submitted*). During these droughts, high mortality of livestock was reported in the ecosystem (Republic of Kenya 1987). Since it has been shown that the energy

requirements of cattle and wildebeest are the similar (Rogerson 1966), we expect that the drought may have also affected the wildebeest population. Contrary to available evidence that wildebeest population in the Serengeti is limited primarily by intra-specific competition for dry season food (Sinclair and Arcese 1995), it appears that the resident population in the Masai Mara ecosystem is limited by wet season food or rainfall (Fig. 6). Drent and Prins (1987) found the same relationship in Lake Manyara National Park in Tanzania. This may be because it is in wet season ranges where large concentrations of resident wildebeest occur and breeding and calving takes place. Thus decline in wet season rainfall may result into poor quantity and quality of food and this in turn will affect the reproduction and survival rates of the population. Mwichabe (1988) and Said (1993) have reported that these areas are overgrazed during the wet season since they support a large biomass of wildlife and livestock during the period. Amting (1997) has reported low grass biomass in these areas in comparison to inside the Reserve. We therefore conclude that occurrence of drought conditions in the ecosystem may have further indirectly contributed to the observed decline of resident wildebeest population.

Increased competition for forage and other resources between wildebeest and cattle especially during crop growing periods could be another factor that may have also contributed indirectly to the recorded decline in resident wildebeest population. Rogerson (1966) reported that the energy requirements of both wildebeest and cattle are relatively similar; for example, the digestibility coefficient of wildebeest is close to that of cattle and the proportion of food utilized as metabolizable energy was also similar. Therefore, at a time that both wildebeest and cattle have similar requirements of the resources available and the resources were limiting, then competition is expected to occur.

Our analyses show that cattle populations in the Loita did not vary significantly between 1977 and 1997 and that their movements were mainly restricted within the Loita plains. The analysis further shows that during the crop-growing period, higher densities of cattle are found in non-cropped areas. These are the same areas occupied by resident wildebeest. Mwichabe (1988) and Said (1993) have showed that these areas (eastern and southeastern parts of Loita plains) are overgrazed and have very little or no grass during certain periods of the wet season. We therefore expect intense competition for forage resources between cattle and wildebeest during this period. Hansen et al. (1984) has shown

that cattle and wildebeest in the ecosystem have over 60% overlap in their food resources. When food is limiting and food overlaps between the two species is high, it is likely that the two species compete for the same food resources particularly during drought periods. Andere (1981) observed in Amboseli National Park that, during dry periods when food in restricted grazing areas became limiting, cattle displaced wildebeest from these areas. Prins and Olf (1998) indicated that in those cases where species loss has occurred, this loss and the patterns of loss could be related to resource competition. We therefore suggest that the encroachment of agriculture triggered increased competition between cattle and resident wildebeest, in rangeland areas adjacent to those occupied by agriculture. We postulate that this process has been responsible for the reported decline of wildebeest in those areas not encroached by wheat farming.

Conclusions

Overall, we have shown in this study that the resident wildebeest population in the Masai Mara ecosystem has gone from a low population of about 18,000 in the 1960s to a maximum of over 100,000 in the late 1970s to a renewed low of around 22,000 in the late 1990s. The decline in population is attributed mainly to agricultural encroachment in former wildebeest wet season grazing and breeding areas. Wildebeest form a keystone species for the Masai Mara ecosystem and are considered to contribute to the density and diversity of the mammalian fauna through facilitation. The conversion of former wildebeest habitat into agriculture is continuing and the Maasai community is intending to convert more land in the nearby future. This paints a gloomy perspective for the future of the Kenya's largest wildebeest population and the fauna and flora of Masai Mara ecosystem, which according to the facilitation theory, depends on its migration. Therefore, it is extremely urgent that a balance be struck between wildlife conservation and agricultural development if the current downward wildlife population trend is to be reversed.

Lastly the current Kenyan legislation prohibits on one hand the killing of wildlife, while on the other hand leaving the option open for unlimited destruction of its habitat. It is strongly argued that the current wildlife policy be reconsidered and its legislation modified

such that it would be possible to protect wildlife habitat outside protected area system from further undesirable destruction.

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CHAPTER 7

The dynamics of migratory wildebeest in the Masai Mara ecosystem, Kenya: 1977-1997

W. K. Ottichilo, M. Y. Said, H.N. Koster, H.H.T Prins , J.de Leeuw and I.M.A. Heikonig
(Submitted)



Abstract

The population trends of migratory wildebeest in Masai Mara ecosystem and factors influencing them are analyzed and discussed using aerial census data collected between 1977 and 1997. Rainfall and Normalized Difference Vegetation Index (NDVI) data for the same period were analyzed and correlated with the trends. The trend analysis showed that the populations of wildebeest had fluctuated over time between 1977 and 1997. Overall, wildebeest migrations into Masai Mara ecosystem declined significantly from about 750,000 in 1979-82 to 283,000 in 1983-90 and increased slightly to 311,000 in 1991-96. The fluctuations in migratory wildebeest populations was found to be strongly related to the amount of annual and wet season rainfall in Masai Mara ecosystem and dry season rainfall in the Serengeti. A strong correlation was also found between wildebeest population trends and NDVI, indicating that NDVI which, appears to be a good indicator of vegetation condition, could be used to monitor vegetation condition and predict temporal and spatial distributions of migratory animals. Lastly, the overall decline in wildebeest numbers that migrate into the Masai Mara ecosystem could be attributed to drought effects, changes in land use and poaching activities in the Serengeti-Mara ecosystem.

Key words: Wildebeest – Migratory – Population fluctuations – Rainfall – NDVI

Introduction

The Masai Mara National Reserve (MMNR) and the adjoining group ranches (hereafter referred to as Masai Mara ecosystem) have the richest wildlife resources in Kenya and offer spectacular wildlife watching (Stelfox et al. 1980). The gnu or wildebeest (*Connochaetes taurinus hecki* (Neumann)) is the most abundant species and both the resident and migratory populations of this species are found in the ecosystem. The migratory populations move within an area of about 25,000km² which encompass Serengeti National Park in Tanzania and Masai Mara ecosystem (both areas form the Serengeti-Mara ecosystem) (Sinclair 1995). Although wildebeest migration from Serengeti into the Masai Mara ecosystem has existed for many decades (Bell 1970), significant migrations involving large number of animals started during the early 1970s when the wildebeest population in the Serengeti erupted after the eradication of rinder-pest in the Serengeti-Mara ecosystem (Sinclair 1979). The migration, which is a regular annual event, has a significant ecological influence on the Serengeti-Mara ecosystem (Bell 1970, McNaughton 1989).

Maddock (1979) has described the spatial and temporal migration patterns of wildebeest in the Serengeti-Mara ecosystem. The migration from Serengeti to the Masai Mara ecosystem normally occurs during the dry season (June to October). The animals arrive in the Masai Mara ecosystem between June and September and return to Serengeti in November (Maddock 1979). The timing of their arrival and departure is variable and is influenced by various factors (Maddock 1979, McNaughton 1990, Sinclair 1995). Although studies have been conducted on wildebeest migrations in the Serengeti-Mara ecosystem, the underlying causes of migration are still not fully established (Sinclair 1995). Various reasons have been advanced to explain why the species migrate (McNaughton 1979, 1990 & 1995, Sinclair 1979 and 1995, Maddock 1979). The overall migration pattern is thought to be related to food supply, which is dependent on the uneven distribution of rainfall (Pennycuick 1975, Maddock 1979). It has been suggested that the principal northwesterly movement from Serengeti at the start of the dry season is in response to the need to find surface water (Sinclair and Fryxell 1985). However, according to Watson (1967), in some years the movement may begin before the wet season has ended, despite continued growth of grass and abundant supplies of drinking water. It has also been suggested that wildebeest

movement could be influenced by changes in the requirements for specific nutrients (McNaughton 1989 and 1990, Kreulen 1975). McNaughton (1989,1991) observes that wildebeest and its companions confront a highly variable and complex environment. Therefore, their responses to this complex environment are probably to a certain extent genetically programmed, but may also undoubtedly be learned to a considerable extent (McNaughton and Banyikwa 1995) as is demonstrated by the absence of migratory behaviour in populations residing in the Ngorongoro Crater and the Western Corridor (Prins 1996).

Wildebeest population in the Serengeti increased five-fold between 1962 and 1971 due to the disappearance of rinderpest (Sinclair 1973, 1974, Norton-Griffiths 1973, Prins 1996). In 1962, the population of wildebeest was estimated at 263,000 and it increased to 773,000 in 1972. This population doubled by 1977 to 1.44 million (Sinclair and Norton-Griffiths 1982, Dublin et al. 1990, Mduma et al. 1998). Between the late 1970s and early 1990s the wildebeest population in Serengeti stabilized at *ca* 1.32 million. The 1993 drought reduced the wildebeest population in the Serengeti significantly ($p < 0.001$) to 920,000 animals (Mduma et al. 1998).

In the 1960s, few migratory wildebeest from Serengeti entered Masai Mara ecosystem during the dry season (Pennycuick 1975). However, by 1979 large numbers of wildebeest started migrating into the Masai Mara ecosystem from late June to late October (Stelfox et al. 1986). This migration increased wildebeest numbers from about 18,000 in 1961 (Stewart and Talbot 1962) to 820,000 in 1979 (Stelfox et al. 1986). The question we ask is that if the population of wildebeest in the Serengeti stabilized in the last 20 years, what causes the migration of wildebeest populations in the Masai Mara ecosystem to fluctuate?

To be able to get an insight into the factors that may be influencing the annual migrations of wildebeest from Serengeti to Masai Mara ecosystem, an understanding of their long-term population trends in the two areas and possible relationship between the trends and the then prevailing environmental conditions is necessary. In this study, population trends and distribution patterns of migratory wildebeest in the Masai Mara ecosystem and Serengeti National Park between 1977 and 1997 are analyzed and the relation between rainfall and vegetation condition and the size of the migratory wildebeest

population and distribution patterns are investigated. Our research hypothesis is that the size of the population of migratory wildebeest recorded in the Masai Mara Ecosystem has fluctuated over time due to differences in the amount of rainfall and vegetation conditions between the Masai Mara ecosystem and the Serengeti.

Study area

Description of the study area

The study area is situated in Narok district, Kenya. It lies approximately between $1^{\circ} 00'$ and $2^{\circ} 00'$ south and $34^{\circ} 45'$ and $36^{\circ} 00'$ east. The area covers about $6,000 \text{ km}^2$ and is bounded by the international boundary of Kenya and Tanzania in the south, the Siria escarpment (Esoit Olololo) to the west, agriculture and forest to the north, the Loita plains and hills to the east and the Siana plains and hills to the south-east (Fig. 1). The area is roughly triangular in shape and can be divided into three range units, based on their biogeography and climate (Stelfox et al. 1986, Ottichilo et al. in press). These units are Mara and Masai Mara National Reserve (MMNR) (mainly composed of *Themeda* grassland), Loita plains (composed of dwarf shrub and *Acacia drepanolopium* grassland) and Siana (mainly hills and plains supporting *Croton* bush and other woody species interspersed with grassland).

The main land uses in the area are pastoralism, tourism and agriculture. The MMNR ($1,368 \text{ km}^2$) is a formal conservation area owned by the Government of Kenya (GOK) and managed by Narok and Trans Mara District County Councils. Land use within the reserve is restricted to wildlife tourism. Its major conservation value is the protection of resident wildlife communities and the provision of critical dry season grazing resources for the migratory populations. The MMNR is surrounded by group ranches that are under private ownership either by groups of families (group ownership) or by one individual family (individual ownership) where the main land uses are pastoralism and agriculture.

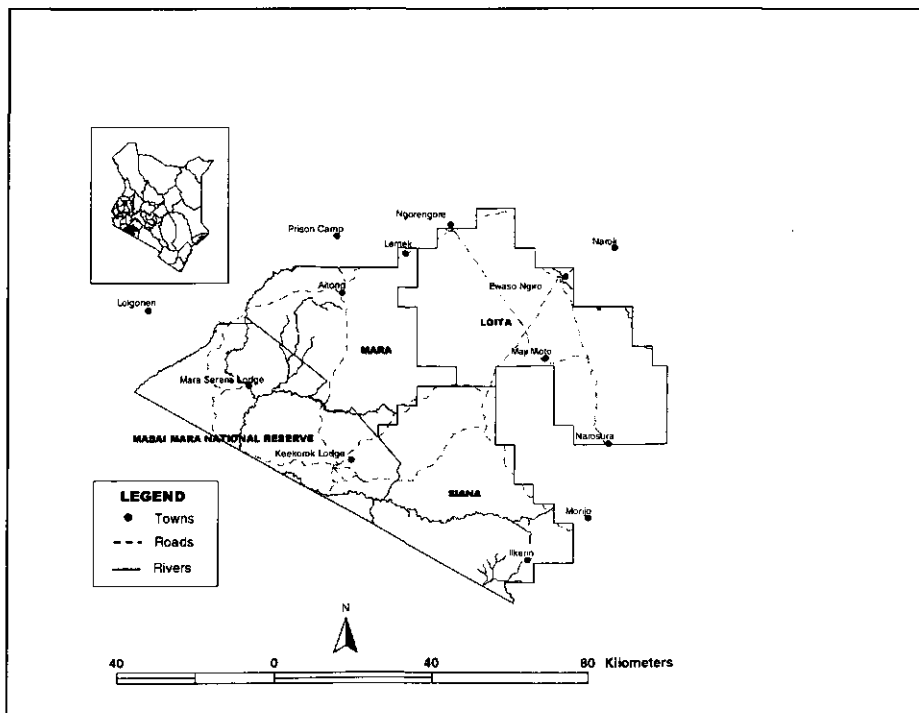


Figure 1. The Masai Mara ecosystem located in the southwestern Kenya. The ecosystem is divided into 3 eco-units (Mara, Siana and Loita) based on the bio-geographical characteristics and climate. The study area encompasses about 6,000 km² of which the 1,368 km² forms the Masai Mara National Reserve

The group ranches contain year round communities of resident wildlife and livestock, but migrants also spill onto them during the dry season.

The rainfall patterns of the study area

The rainfall pattern in the Masai Mara ecosystem is basically controlled by the low level monsoon winds associated with the annual movements of the low pressure inter-tropical convergence zone (ITCZ) interacting with the local synoptic processes (Brown and Cochemé 1973, Norton-Griffiths et al. 1975, Prins and Loth 1988). The mean annual rainfall distribution pattern for some of the major stations in the study area during the study period are shown (Fig. 2). The annual distribution of rainfall is bimodal in pattern, characterized by two rainy seasons and two dry seasons (Epp and Agatsiva 1980, Broten

and Said 1995). The main rains are from March to May with a peak in April and a second peak (although not as noticeable) in the November-December period. The main dry season is from mid-June to mid-October with a lesser dry season in January and February.

In addition to the very general influences of the ITCZ, local variations in topography plus orographic and diurnal effects play a major role in the rainfall patterns within the study area (Norton-Griffiths et al. 1975). The lowland Loita and Siana receive a mean annual rainfall of about 400-mm. The highlands composed of the Loita Hills and the Siria escarpment receive high amounts of rainfall of more than 600 mm and 1000 mm respectively. The Mara plains receive between 500 and 700 mm of rainfall annually. The southwestern part of the study area receives annual amount of rainfall between 375 and 500 mm.

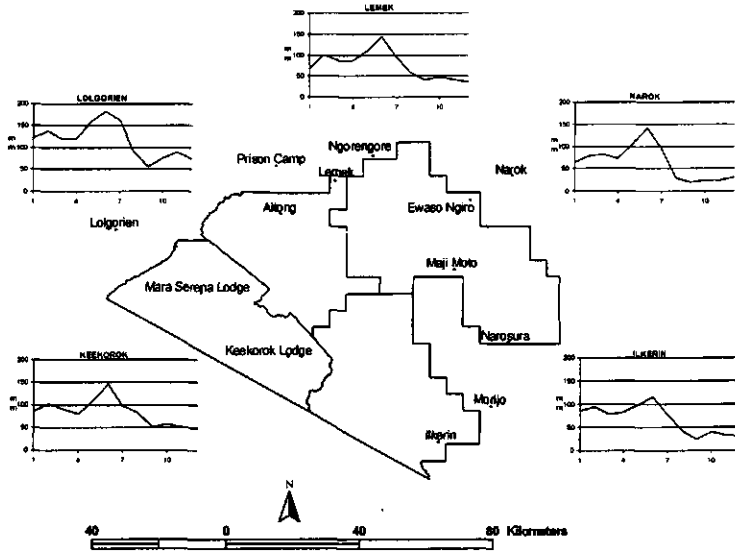


Figure. 2. The mean annual pattern of rainfall in 5 rain stations in the Masai Mara ecosystem. There is a general increase in rainfall from east to west and northwards. The wet season is from November-May and dry season from June-October. The 1st month represents November and the 12th month represents October.

Materials and Methods

Animal census and population trends

The animal census data in Masai Mara ecosystem was collected by the Department of Resource Surveys and Remote Sensing (DRSRS) using systematic reconnaissance flights (Norton - Griffiths 1978). Details of the method as implemented by DRSRS are given in Grunblatt et al. (1995) and in De Leeuw et al. (1998) and the analytical considerations in Ottichilo et al. (in press). The surveys were conducted during the dry season period and the majority of them (80%) were done during August when peak migrations normally occur in Masai Mara ecosystem. The censuses included both the migratory and resident wildebeest population. A total of fifteen surveys were conducted between 1977 and 1997. The population estimates for each species and every survey were calculated using the Jolly 2 method (Jolly 1969). In 1979 and 1983 several surveys were conducted in the dry season. Population estimates of each of the monthly counts were tested for significant difference and those that were not significant were merged into one using the method described by Norton- Griffiths (1978). A total of ten surveys were used in the the analysis.

The migratory wildebeest population was determined by subtracting resident wildebeest population from the total population determined during the migratory or dry season period. The resident population was analyzed using a total of 21 counts conducted over the period 1977-1997 during non-migratory period. Log-linear model was used in the analysis of the data. The details of the model are given in Ottichilo et al. (*in press*). Both the migratory and total wildebeest populations were used in the trend analysis.

Exploratory data analysis revealed linear patterns in the relation between wildebeest population and time. The data was tested for various regression models and a polynomial model best described the trends.

Based on non-drought, combination of drought and wet and drought periods, the data was grouped into 3 periods: 1978-1982, 1983-1990 and 1991-1996. Box plots for the three periods were made and Mann Whitney U-test was used to test for significant differences in population estimates between the various periods. Distribution maps for

wildebeest in the Masai Mara ecosystem for the periods were prepared by averaging the observed number of animals and calculating the density per 5 by 5-km grid for each period. The densities were represented on a map by graduated dot symbols. ArcInfo (ESRI 1998) software was used for spatial analysis and mapping. The Serengeti wildebeest population was analyzed using data derived from published literature. Censuses that were not significantly different were merged accordingly to Norton-Griffiths (1978).

The temporal and spatial analysis of rainfall patterns

Monthly rainfall data for Masai Mara ecosystem and Serengeti National Park were acquired from Kenya Meteorological Department and Serengeti Ecological Monitoring Programme. The data were evaluated for typographical errors, missing data and consistency. A total of 32 stations in Masai Mara ecosystem for the period 1977 and 1997 and 39 in Serengeti for the period 1977 and 1994 were selected for data analysis. Some stations had shorter records of rainfall data or some months were missing. Linear regression as described by Prins and Loth (1988) was used to estimate values of missing data. Due to spatial variability in rainfall distribution between rainfall stations, all stations surrounding the master station were used for interpolation. Stations with an excessive number of missing values were excluded from the analysis.

Annual, wet and dry total rainfall values and their respective coefficient of variation (standard deviation as percentage of the mean reported here as variability) were calculated for the Masai Mara ecosystem and Serengeti National Park. The annual totals were derived from November of one year to October of the next year. This period is more relevant ecologically than the period January-December for it represents one complete seasonal cycle (Norton-Griffiths et al. 1975, Prins and Loth 1988). The wet season falls between November and May and the dry season falls between June and October (Norton-Griffiths et al. 1975, Broten and Said 1995). The annual totals were classified into normal, wet and drought years according to Prins (1996). A drought year is defined as a year in which the total rainfall was less than the mean annual rainfall minus the standard deviation, while a wet year is defined as a year with more than the annual rainfall plus the standard deviation. In addition to the yearly rainfall analysis, detailed monthly analysis of rainfall

patterns was conducted for the Masai Mara ecosystem and Serengeti. The means, standard deviation and cumulative deviation were analyzed for annual, seasonal and monthly totals. The means and cumulative deviations were then plotted against time and fitted with a model that best related them. Lastly, pooled annual, wet season, dry season and monthly cumulative deviations were related to wildebeest populations using Spearman rank correlation (r_s) test and regression analysis.

Temporal and spatial analysis of vegetation condition

The Normalized Difference in Vegetation Index (NDVI), derived from NOAA satellite data, is widely used for monitoring green vegetation over large areas and provides an index of primary productivity (Justice et al. 1985). NDVI or "greenness index", is a ratio of red and infrared channels which contrasts the two signals and effectively expresses the degree of pixel greenness. Several studies have indicated some relationships between NDVI, rainfall and biomass in the drylands. Prince (1991) demonstrated that there is a strong linear relationship between the satellite observation of vegetation indices and the seasonal primary production. Farrar et al. (1994) and Richard and Pocard (1998) have reported a linear relationship between rainfall and NDVI in most savanna ecosystems in Africa where rainfall is the limiting factor (<900 mm). NDVI has been used in monitoring East African and African vegetation dynamics (Justice et al. 1986, Townshend et al. 1991, Serneels et al. *submitted*), desert locust monitoring (Hielkema 1981), evaluation of suitability of vegetation characteristics in arid lands (Huete and Jackson 1987) and determination of herbaceous biomass (Prince and Tucker 1986). However, there are few studies that have attempted to relate NDVI to animal temporal and spatial distribution (i.e. Muchoki, 1995).

Temporal and spatial NDVI changes in the study area were analyzed and related to migratory wildebeest population trends and distributions patterns. We also analyzed the seasonal behaviour of vegetation in relation to rainfall patterns in the area. The NOAA/NASA Pathfinder AVHRR 8-km Land Data Set (PAL) spanning the period 1981-1994 was used (Smith et al. 1997). The analysis entailed finding relationships between NDVI and rainfall. Monthly composite images were analyzed using WINDISP3 (Pfirman 1999). The images were registered to a common Universal Transverse Mercator (UTM)

projection and placed into their original units, from -1 to 1, using Eidenshink and Faundeed (1994) algebraic statements:

$$NDVI_{real} = \frac{NDVI_{given} - 128}{128}$$

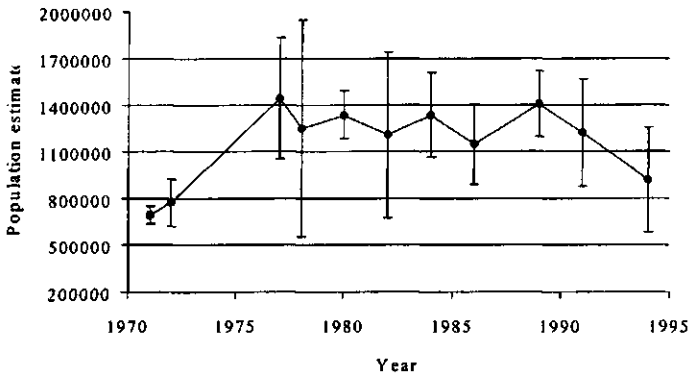
Total annual NDVI means were extracted for the Masai Mara ecosystem and the Serengeti National Park starting from December to end of October. This calendar year period was chosen due to the one-month time lag between rainfall and NDVI. Correlation analysis between NDVI and rainfall based on annual means, dry season means and wet season means was then undertaken. Finally, NDVI was also related to wildebeest population trends over the period 1981 to 1994.

Results

Wildebeest population trends and distribution

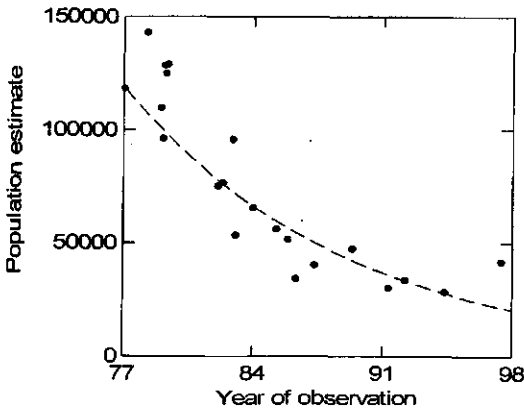
The wildebeest population recorded in the Serengeti (Fig. 3) increased from *ca.* 250,000 in the early 1960s to an average of *ca.* 703,000 ± 52,900 (95% c.l.) in the early 1970s. This population increased by twofold to *ca.* 1,320,000 ± 94,900 (95% c.l.) animals in late 1970s. Since then, the population has remained constant between 1.1 - 1.4 million except for a significant decline in the early-1990s to 917,000 ± 340,000 animals ($P < 0.01$).

The resident wildebeest population trend model used in the determination of migratory population in Masai Mara ecosystem is given in Fig. 4. The population trend of the migratory wildebeest in the Masai Mara ecosystem is shown by the dotted line on Fig 5. The same figure shows the trend (in solid line) of both migratory and resident wildebeest during migration period. The polynomial fit curve for migratory wildebeest had r^2 of 0.67 indicating that time alone could explain about 67% of the observed population fluctuations.



Source: Sinclair (1979); Sinclair & Norton-Griffiths (1982); Sinclair et al. (1985); Dublin et al., (1990); Campbell & Borner (1995); Farm & Woodworth (1994), Mduma (1996) and Mduma et al. (1998).

Figure 3: Wildebeest population trends in the Serengeti ecosystem between 1971 to 1995. The error bars indicate 95% confidence limits.



Source: Ottichilo et al. (*in press*)

Figure 4: Resident population trends of wildebeest in the Masai Mara ecosystem between 1977 and 1997 ($\ln Y = 18.158 - 0.084X$, $r^2 = 0.79$, $n = 21$, $P < 0.001$).

The population trends of migratory wildebeest show two peaks in the early 1980s and early 1990s and two dips in mid 1980s and mid 1990s (Fig. 5). The peak in the early 1980s was about 800,000 animals and in early 1990s were about 400,000 animals. The mean wildebeest population estimates for the periods 1979-82 was 750,000 and this declined significantly (Man Whitney test, $p < 0.05$), to 270,500 in 1983-90 (Fig. 6). Between the periods 1983-1990 and 1991-96 population increased slightly but not significantly to about 311,000.

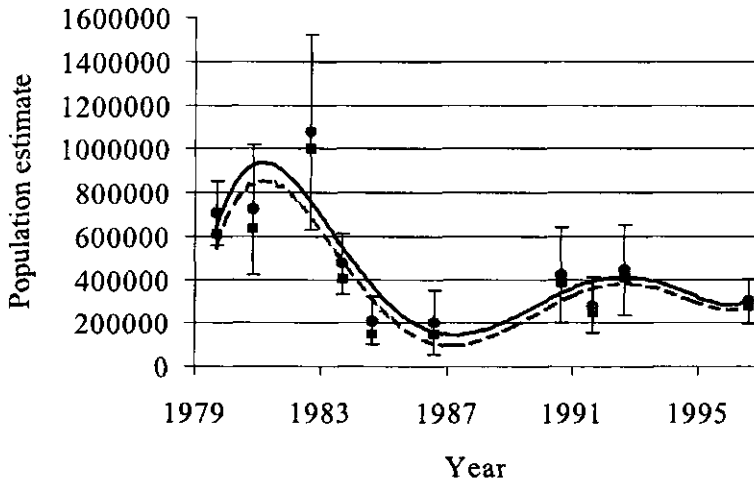


Figure 5: Migratory population size trends of wildebeest in the Masai Mara ecosystem (dotted lines) between 1979 and 1997 ($y = 40.28x^5 - 400631x^4 + 2*10^9x^3 - 3*10^{12}x^2 + 3*10^{15}x - 1*10^{18}$, $r^2 = 0.67$, $n = 10$). The trend for combined migratory and resident wildebeest population estimates (bold line) for the same period is ($y = 40.28x^5 - 179751x^4 + 3*10^6x^3 - 3*10^8x^2 + 3*10^{10}x - 2*10^{11}$, $r^2 = 0.70$, $n = 10$). The error bars indicate 95% confidence limits of this population. The migratory was estimated as the total population in the Mara less the resident population.

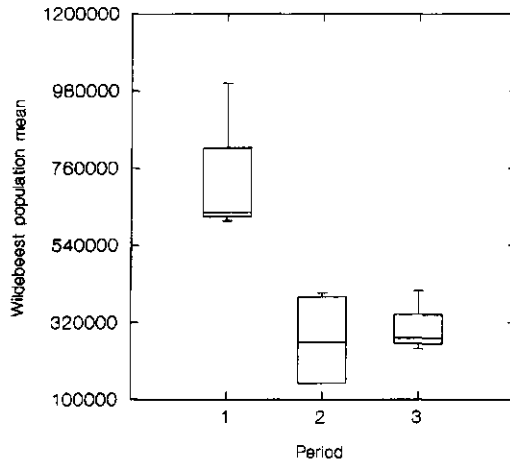


Figure 6: Box plot of wildebeest population means for the periods: 1 = 1979-1982; period 2= 1983-1990; and period 3 = 1991-1996. The mean for the period 1 was significantly differently from the means of the period 2 ($p < 0.05$).

Fig. 7 shows the spatial distribution and densities of wildebeest in the Masai Mara ecosystem during the periods 1979-82, 1983-90 and 1991-96 and reflects the population trends discussed above. The spatial distribution patterns of wildebeest appear to have changed over time. Since early 1980s, the migratory population appears to concentrate in the Masai Mara National reserve, whereas before 1980s it used to spill into the ranches north and northwest of the reserve.

The long term rainfall patterns and variability

Total rainfall variability of all stations in the Masai Mara ecosystem and Serengeti show significant and negative correlation with the totals of annual, wet, and dry season rainfall means for the same periods (Fig. 8). These results indicate that areas with higher rainfall total are less variable than those areas with lower rainfall total.

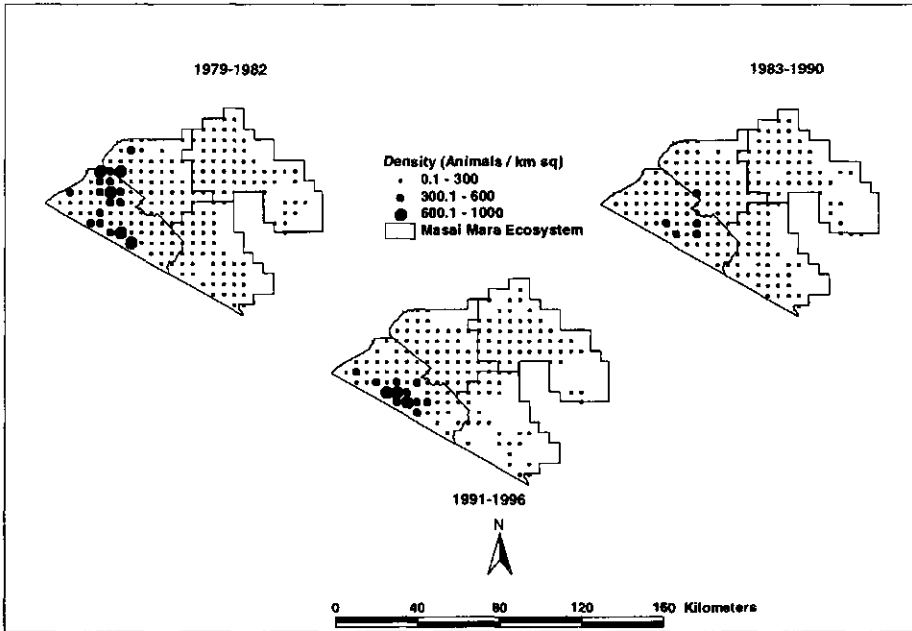


Figure 7: Spatial distribution and average density ($N.km^2$) of wildebeest in the Masai Mara ecosystem for the period:1979-1982, 1983-1990and 1991-1996. The density was calculated on 5 by 5 km sub-unit basis.

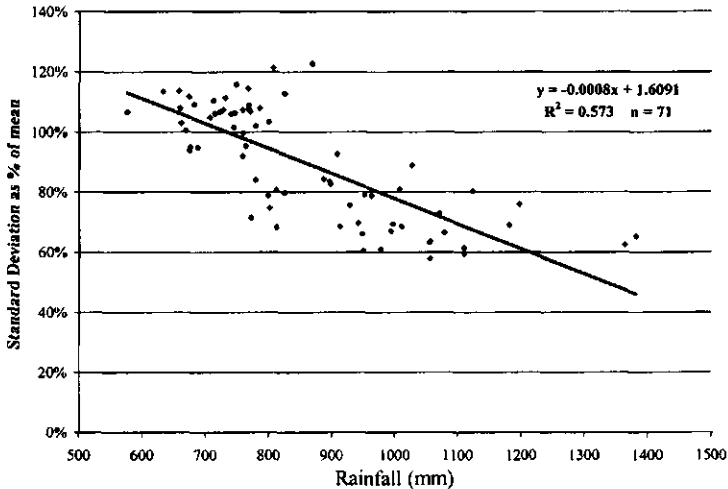


Figure 8: Rainfall distribution and variability for all rain stations in the Serengeti-Mara ecosystem between 1977 and 1997.

The results of long-term rainfall trend shows that both Masai Mara ecosystem and Serengeti experienced dry conditions between 1981 and 1987 and between 1991 and 1994 (Fig. 9). Detailed analysis (Table 1) further showed that Masai Mara ecosystem suffered severe droughts in 1984, 1986 and 1993. The 1984 and 1986 droughts were more extreme than the 1993. The pooled cumulative deviation (annual and monthly means) was used to reveal the periodicity in rainfall in the Masai Mara ecosystem and Serengeti (Fig. 9). The pooled annual cumulative deviations indicate that both Masai Mara ecosystem and Serengeti experienced increase (peaks) and decrease (dips) in rainfall during the twenty years. Between 1975 and 1986, the deviations between the two areas were marginally different ($p < 0.08$), with Masai Mara ecosystem having the highest positive deviation, indicating occurrence of a higher mean rainfall. Between 1986 and 1992 both areas experienced positive deviations and were significantly different ($p < 0.017$) with Serengeti having the highest positive deviation. The polynomial model gives high correlation between mean annual rainfall cumulative deviations and time for both the Masai Mara ecosystem ($r^2 = 0.91, n = 20$) and the Serengeti Ecosystem ($r^2=0.96, n= 18$).

The Serengeti ecosystem received a mean of 751 mm of rainfall with an annual variability of 17% during the period 1976-1993. During the same period, it received a mean of 614 mm of rainfall in the wet season and 137mm in the dry season. The mean annual rainfall for the Masai Mara ecosystem during the period 1977-97 was 965 mm with an annual variability of 14% (Table 1). The wet and dry season means were 708 mm and 259 mm respectively. Figure 2 shows the mean annual rainfall of five rainfall stations in Masai Mara ecosystem for the period between 1977 and 1997. The figure shows a clear gradient of increasing precipitation from east to west and northward. The annual and pooled cumulative deviation of the mean annual rainfall for both Serengeti and Masai Mara ecosystem are given in Fig. 9. The figure also shows periods when the areas experienced wet and drought conditions. Overall, Masai Mara ecosystem receives higher annual, wet and dry rainfall than Serengeti.

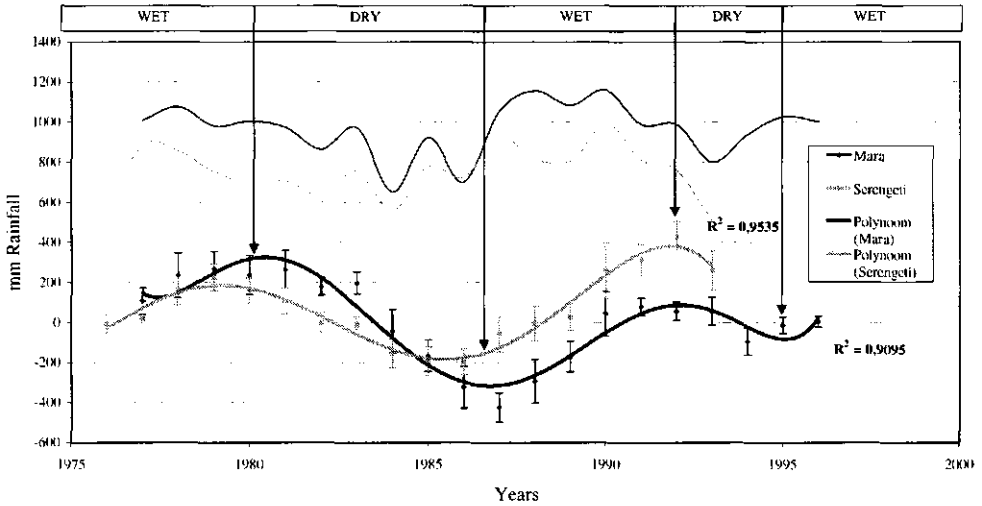


Figure 9: Mean annual rainfall and pooled cumulative deviation of mean annual rainfall of 32 rainfall stations in the Masai Mara ecosystem and 39 in the Serengeti ecosystem.

The influence of rainfall on wildebeest population trends

Table 2 summarizes the results of Spearman rank order correlation between the size of the wildebeest population and rainfall parameters in the Masai Mara ecosystem. A significant correlation was established between the wet season mean and annual mean cumulative deviation and population size only. There was a strong but not significant correlation between dry season cumulative deviation and wildebeest population size. Regression analysis further revealed that the population size of wildebeest in the Masai Mara ecosystem was significantly related to the mean annual rainfall ($r^2=0.91$, $n = 9$, $p < 0.01$) (Fig. 10), and mean wet season rainfall patterns ($r^2=0.58$, $n = 9$, $p < 0.05$).

Table 1. Summary of rainfall patterns and condition of six rainfall stations in the Masai Mara ecosystem. A drought years is defined as a year in which the total rainfall was less than the mean annual rainfall minus the standard deviation, while a wet year is defined as a year with more than the annual rainfall plus the standard deviation.

Years	Keekorok	Narok	Ilkerin	Lolgorien	Lemek	Average *	Condition	# Wet Months	# Dry Months
1977	1134	1018	945	1396	-	1008	Normal	1	1
1978	1090	1115	1001	1419	1027	1075	Normal	4	2
1979	1014	897	863	1503	822	981	Normal	3	2
1980	1141	698	783	1588	999	1003	Normal	3	4
1981	1035	602	850	1162	1046	973	Normal	3	2
1982	653	582	662	1379	866	862	Normal	1	1
1983	1154	759	757	1446	870	971	Normal	1	1
1984	731	404	484	1132	564	651	Dry	0	4
1985	874	857	760	1294	849	922	Normal	2	4
1986	892	519	692	701	568	700	Dry	0	4
1987	1060	961	731	1330	1026	1055	Normal	3	0
1988	1300	850	644	1669	1182	1156	Wet	2	0
1989	1148	899	1029	1646	1071	1083	Normal	2	0
1990	1287	826	970	1991	1157	1160	Wet	4	0
1991	999	623	760	1565	734	987	Normal	1	0
1992	925	548	872	1081	-	985	Normal	1	0
1993	634	774	584	1172	-	800	Dry	0	2
1994	784	759	887	-	-	940	Normal	1	2
1995	1031	805	909	-	-	1026	Normal	2	0
Mean	993.93	762.95	799.11	1380.82	912.93	965.04			
Std Dev	193.79	183.19	146.35	289.28	195.53	134.66			

* Annual rainfall average of 33 rainstations in Masai Mara ecosystem

Table 2. Correlation between wildebeest population estimates and rainfall parameters in the Masai Mara Ecosystem based on Spearman (r_s) rank order correlation

Rainfall Parameters	$n = 9$ r_s -value
Annual average	0.417
Annual average cumulative deviation	0.950**
Wet season average	0.717*
Wet season cumulative deviation	0.650
Dry season average	-0.017
Dry season cumulative deviation	0.583

Significant at p -value $< 0.05^*$ and p -level $< 0.001^{**}$

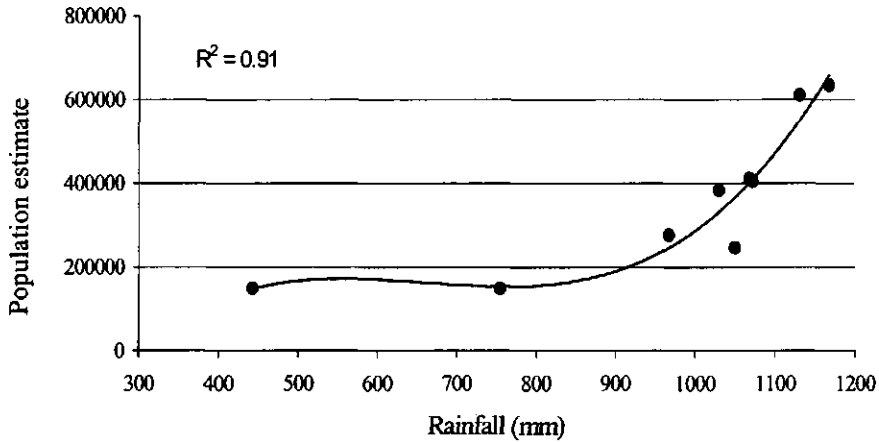


Figure 10: Relationship between annual cumulative deviation rainfall and wildebeest population in the Masai Mara ecosystem ($y = 0.0044x^3 - 8.6572x^2 + 5581.5x - 1 \cdot 10^6$, $n = 9$, $r^2 = 0.91$).

The temporal relations between rainfall and NDVI

Mean NDVI and its variability was calculated for year, as well as for the wet and dry season, both for the Masai Mara ecosystem and the Serengeti (Table 3). There was a highly significant relation (Fig 11) between mean annual NDVI and rainfall for both the Masai Mara ecosystem ($r^2 = 0.90$, $n = 12$, $p < 0.001$) and the Serengeti ($r^2 = 0.88$, $n = 12$, $p < 0.001$) (Fig. 11). The mean annual NDVI total for the Masai Mara was 0.368 with an annual variability of 7.0%. The mean NDVI for the wet season was 0.405 and 0.330 for the dry season. The mean annual NDVI for the Serengeti was 0.356 with an annual variability of 6.4%. The mean NDVI for the wet season was 0.447 and 0.266 for the dry season. The wet season NDVI shows less variance than the dry season in both areas (Table 3). The NDVI values were significantly higher ($P < 0.05$) in the Masai Mara ecosystem during the dry season and higher in the Serengeti during the wet season (Fig.12). Overall the NDVI was higher in the Masai Mara ecosystem than the Serengeti, though not significant ($n = 17$, $p = 0.056$).

Table 3. Summary of the annual and seasonal NDVI in the Masai Mara ecosystem and the Serengeti National Park.

Years	Masai Mara		Serengeti		Masai Mara		Serengeti		Masai Mara		Serengeti		Masai Mara	Serengeti
	Mean	Var %	Mean	Var %	Wet	Var %	Wet	Var %	Dry	Var %	Dry	Var %	Condition *	Condition *
1982	0.348	7.8%	0.317	7.7%	0.363	8.6%	0.393	7.7%	0.333	7.5%	0.240	8.7%	Normal	Poor
1983	0.363	7.5%	0.352	7.0%	0.419	7.2%	0.446	6.1%	0.306	8.3%	0.257	8.7%	Normal	Normal
1984	0.333	8.6%	0.352	6.5%	0.380	8.4%	0.441	6.2%	0.285	9.0%	0.264	7.6%	Poor	Normal
1985	0.396	7.3%	0.367	6.6%	0.441	7.1%	0.453	6.4%	0.350	8.1%	0.281	8.2%	Normal	Normal
1986	0.318	6.6%	0.318	6.3%	0.329	6.0%	0.394	6.3%	0.307	7.8%	0.242	6.9%	Poor	Poor
1987	0.380	7.6%	0.401	5.8%	0.400	7.5%	0.512	4.9%	0.360	8.1%	0.291	7.8%	Normal	Good
1988	0.408	6.0%	0.392	6.8%	0.445	5.5%	0.488	5.4%	0.370	6.9%	0.295	8.8%	Good	Good
1989	0.414	6.1%	0.378	6.0%	0.452	5.7%	0.457	5.2%	0.375	7.1%	0.299	7.6%	Good	Normal
1990	0.413	6.4%	0.388	6.5%	0.466	5.4%	0.480	6.2%	0.361	7.9%	0.297	7.5%	Good	Good
1991	0.321	6.9%	0.322	5.9%	0.360	8.3%	0.414	6.6%	0.285	5.8%	0.230	6.0%	Poor	Poor
1992	0.349	6.5%	0.331	5.7%	0.373	6.1%	0.398	4.6%	0.325	7.2%	0.266	7.7%	Normal	Normal
1993	0.369	6.9%	0.356	6.1%	0.436	6.1%	0.484	5.8%	0.302	8.1%	0.229	7.4%	Normal	Normal
Mean	0.368	7.0%	0.356	6.4%	0.405	6.8%	0.447	5.9%	0.330	7.6%	0.266	7.7%		
Std	0.035	0.8%	0.030	0.6%	0.044	1.2%	0.040	0.8%	0.033	0.8%	0.027	0.8%		

* A poor year is defined as a year in which the NDVI was less than the mean annual NDVI minus the standard deviation, while a good year is defined as a year with more than the annual rainfall plus the standard deviation.

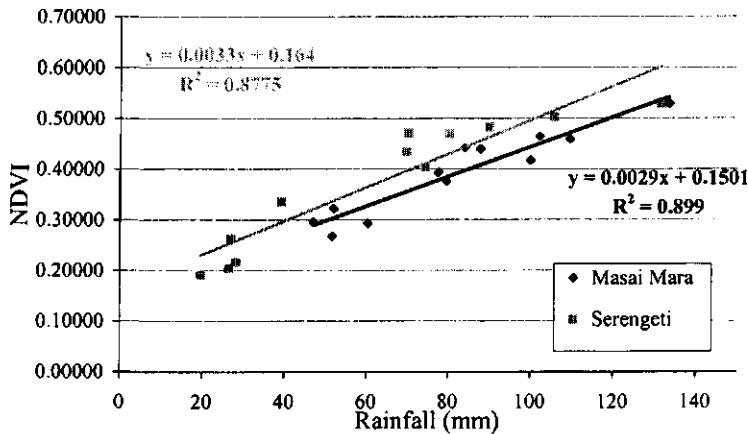


Figure 11: Linear relationships between mean month rainfall and NDVI for the Masai Mara ecosystem and Serengeti National Park. A time lag of one month was used in the analysis because it has been shown that it takes about one month for vegetation to fully respond to the effect of rainfall.

The results of the analysis of the NDVI profiles between 1982 and 1993 show that both the Masai Mara ecosystem and Serengeti suffered two poor vegetation conditions between 1982 and 1986 and between 1990 and 1993 (Fig.12). These are the same periods when both areas experienced drought conditions. The profiles further show that 1984 and 1986 drought had more severe negative effect on Masai Mara ecosystem vegetation than on that of Serengeti. Between 1986 and 1990 both Masai Mara and Serengeti showed general recovery of NDVI (Fig. 12). However, between 1990 and 1993 the vegetation condition declined in both areas with the highest decline occurring in Serengeti. Overall, these results indicate that NDVI is a good indicator of vegetation condition.

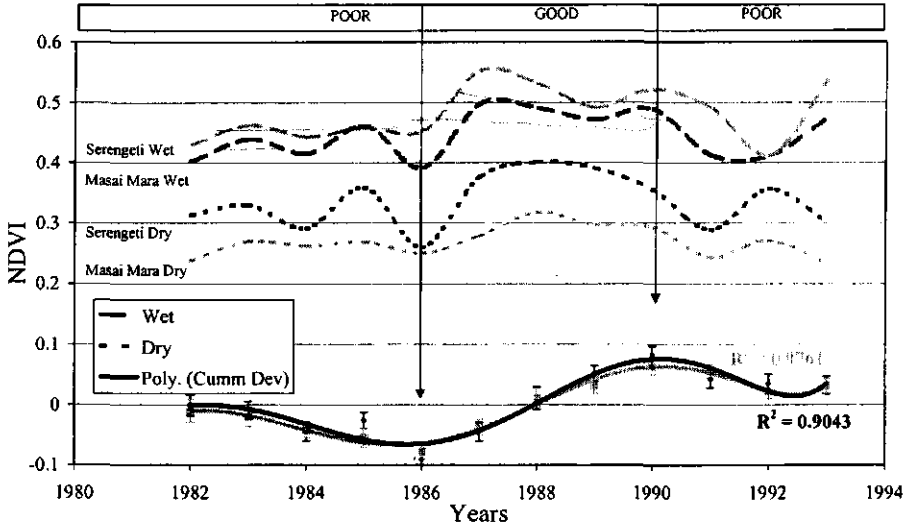


Figure 12: Dry & Wet Season NDVI and pooled annual cumulative deviation for the Masai Mara ecosystem and Serengeti

Rainfall (annual and wet mean) and NDVI in both Masai Mara ecosystem and Serengeti were significantly correlated (Table 4). Although there was no significant correlation between rainfall and NDVI in the Masai Mara ecosystem and Serengeti in the dry season, the correlation was relatively higher in Masai Mara ecosystem than in

Serengeti. This indicates that Masai Mara ecosystem receives more rainfall and has greener biomass during dry season than Serengeti.

Table 4: Correlation between NDVI and rainfall parameters based on Spearman (r_s) rank order correlation and linear regression (r)

RAINFALL	NDVI Masai Mara $n = 12$		NDVI Serengeti $n = 12$	
	r_s -value	r-value	r_s -value	r-value
Annual average	0.706*	0.732**	0.622*	0.514
Annual average cumulative deviation	0.622*	0.737**	0.776**	0.811**
Wet season average	0.713*	0.688*	0.476	0.413
Wet season cumulative deviation	0.615*	0.698*	0.860**	0.733**
Dry season average	0.273	0.251	0.105	0.147
Dry season cumulative deviation	0.378	0.366	0.224	0.321

Significant at p-value < 0.05* and p-level < 0.001**

Correlation of NDVI with wildebeest population trends

Regression and correlation analyses were conducted to find out whether there was any relationship between population size of migratory wildebeest and NDVI (or vegetation condition) in Masai Mara ecosystem (Table 5). The analysis revealed a strong and significant relation between dry season and annual NDVI mean and wildebeest population size ($r^2 = 0.84$, $p < 0.01$ and $r^2 = 0.69$, $p < 0.05$ respectively). Figure 13 shows the relationship between dry season NDVI and wildebeest population size. These results indicate that the movement of wildebeest from Serengeti into Masai Mara ecosystem is strongly influenced by dry season vegetation condition, which in turn is influenced by rainfall.

Table 5: Correlation between wildebeest population estimates and NDVI parameters based on Spearman (r_s) rank order correlation and linear regression (r)

	Masai Mara Ecosystem	
	Wildebeest $n = 6$	
	r_s -value	r -value
Annual average	0.771	0.697
Annual average cumulative deviation	0.486	0.609
Wet season average	0.600	0.673
Wet season cumulative deviation	0.543	0.563
Dry season average	0.257	0.594
Dry season cumulative deviation	0.486	0.629

Significant at p -value $< 0.05^*$ and p -level $< 0.001^{**}$

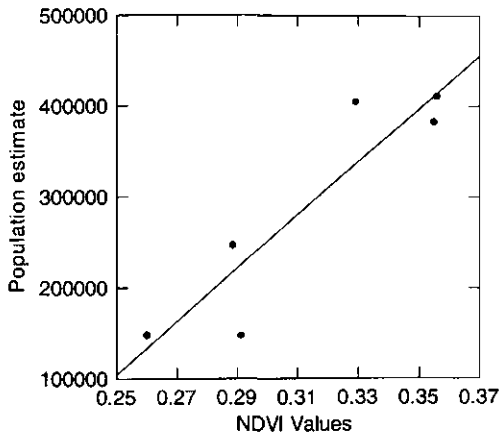


Figure 13: Relationship between dry season mean NDVI and wildebeest population estimates in the Masai Mara ecosystem ($y = -626383.135 + 2924091.376x$, $n = 6$, $r^2 = 0.84$)

Discussion

Migratory wildebeest population trends

Overall, the population size of wildebeest migrating annually into Masai Mara ecosystem from Serengeti declined in the past 20 years. It declined from about 750,000 animals in 1979-82 to about 271,000 in 1983-90. Between the periods 1983-90 and 1991-96, the population size increased slightly to 311,000. Unlike in Masai Mara ecosystem, the population size of wildebeest in Serengeti steadied in the late 1970s and the population has remained constant between 1.1m – 1.4m except for a significant decline in the early 1990s to about $917,000 \pm 340,000$ animals. The decline was caused mainly by drought (Mduma et al. 1995). Factors that influenced wildebeest migrations and fluctuations in their population sizes in Masai Mara ecosystem during the period between 1977 and 1997 are discussed below.

The relationship between rainfall and population trends

We hypothesized that the variation in rainfall and vegetation condition between the Serengeti and the Masai Mara ecosystems was responsible for fluctuations in population sizes of migratory wildebeest in Masai Mara ecosystem. Our results indicate that differences in rainfall regimes in the two areas appear to have a significant impact on the wildebeest population fluctuations in the Masai Mara ecosystem (Figs. 5 & 9). The differences can be discerned from the monthly and annual cumulative deviations from the mean for the two areas. Thus in the late 1970s and early 1980s, Masai Mara ecosystem received significant increase in mean monthly and annual rainfall. This increase in rainfall corresponds with significant increase of migratory wildebeest into the Masai Mara ecosystem during the same period. During the early and mid-1980s rainfall declined drastically in the Masai Mara ecosystem and this also corresponds with drastic decline of migratory wildebeest into the Masai Mara ecosystem during the same period. From 1986 to 1992 rainfall increased steadily in the Masai Mara ecosystem but at a lower rate in comparison to the Serengeti. Although the number of animals migrating into the Masai Mara ecosystem increased steadily, the rate was much lower than that of late 1970s and

early 1980s, indicating that other factor(s) rather than rainfall were impacting on the migrating population.

Our results further show that the total annual and wet season rainfall are strongly correlated and have a strong influence on the wildebeest migration into the Masai Mara ecosystem. This is due to the fact that it is the wet season rainfall that largely determines the amount of biomass production, which forms the bulk of the forage utilized by the migrants during the dry season. Drent and Prins (1987) also found that wet season rainfall rather than dry season rainfall largely influenced movement of wildebeest in Lake Manyara National Park. The Lake acts as a refuge for animals when it is very dry in northern and the rest of the Masai Ecosystem. Hence if there is a drought in the ecosystem, more wildebeest move in Manyara during the dry season. Sinclair and Arcese (1995) reported that wildebeest population in the Serengeti is limited primarily by intra-specific competition for dry season forage whose availability is influenced partly by dry season rainfall. Boutton et al (1987) also reported that wild herbivores in East Africa are limited by forage and nutrient shortage during the dry season. The question is therefore what makes the wildebeest to find it necessary to migrate to Masai Mara ecosystem during the dry season? Sinclair (1995) argues that migration depends on the dry season progress in the Serengeti. The progress in turn depends on the on-set, duration and intensity of the wet and dry season rainfall. The progress may set-in, as early as June and in late seasons it might not occur until September. Pennycuik (1995), in her analysis of eleven years of data on wildebeest movements, showed that they can respond to short-term (i.e. monthly) changes in rainfall distribution and how their movement north into Mara is affected by rainfall. Our analysis shows that wildebeest migrations into Masai Mara ecosystem are strongly linked to rainfall variations between Masai Mara ecosystem and the Serengeti.

Based on these evidence and our results, we conclude that the status of both dry season rainfall in Serengeti and wet and dry season rainfall in the Masai Mara ecosystem influences the movement of the migrants into the Masai Mara ecosystem.

The relationship between rainfall, vegetation, population trends and NDVI

The quantity of biomass in the herb layer of grasslands varies during the course of the year in response to seasonal rainfall. These fluctuations in primary biomass are important in determining food habits, movement patterns, and habitat utilization by large mammalian herbivores (Boutton et al. 1987). NDVI can be used to study vegetation phenology and quantify the changes in biomass production in both temporal and spatial context. Boutton and Tieszen (1983) using a hand held spectrometer found a significant correlation ($r^2 = 0.70$) between NDVI and primary biomass production in the Masai Mara National Reserve. McNaughton (1979) using a hand held spectrometer observed a higher correlation ($r^2 = 0.90$) between NDVI and primary biomass production in the Serengeti National Park. Boutton and Tieszen (1983) also found that the spectral reflectance technique does not give reliable estimates of plant biomass in grasslands where proportion of live to total vegetation does not exceed 30%. Prins and Beekman (1989) found a good correlation (0.62-0.91) for green leaf biomass but a weak correlation for other sward components.

We found a strong and significant linear relationship between mean monthly rainfall and NDVI. Our results confirm findings by Farrar et al. (1994) and Richard and Pocard (1998). We also found a strong correlation between annual and wet season rainfall and NDVI in both Masai Mara and Serengeti. However, there was a weak correlation between the dry season rainfall and NDVI in Serengeti. According to McNaughton (1985) there is very little available forage remaining anywhere in the Serengeti at the end of the dry season. The mean standing crop of green forage was estimated at $8 \pm 1 \text{g/m}^2$ (95% c.l.) and standing crop of dead material was $22 \pm 3 \text{g/m}^2$. This is probably the reason why we did not find strong relationship based on the satellite observed NDVI values and dry season rainfall.

Our results show that Serengeti has higher wet season NDVI values than Masai Mara ecosystem, while the Masai Mara ecosystem has higher dry NDVI values than Serengeti (Table 3). This appears to indicate that there are two important primary production systems in the Serengeti-Mara ecosystem and these systems could be used to explain why wildebeest migrate between the two systems. The overall reason why animals migrate in the Serengeti-Mara ecosystem is thought to be related to food supply (Pennycuik 1975 and Maddock 1979). Therefore, we would expect wildebeest to migrate to Masai Mara during the dry season due to availability of relatively good vegetation

conditions and occurrence of dry season rainfall and return back to Serengeti during the wet season because of good vegetation condition and rainfall. However, their migration will vary in time and space depending on the on-set and duration of wet and dry season rainfall in the Serengeti. Our expectations are supported by the strong relationship that we found between dry season NDVI and wildebeest population size in Masai Mara ecosystem (Fig. 13). Since NDVI was found to have a strong linear relationship with rainfall, we conclude that differences in vegetation condition between Masai Mara ecosystem and Serengeti largely influence the migration of wildebeest between the two areas.

Lastly, we have established in this study that there is a strong relationship between rainfall and NDVI in both Masai Mara ecosystem and the Serengeti. Since NDVI is a good indicator of vegetation and other abiotic attributes of the landscape, it can be used effectively in monitoring the range conditions and also to analyze the inter-annual variability in production across ecosystems. This study has also demonstrated that it can also be used in predicting wildebeest movements between Masai Mara ecosystem and Serengeti.

Factors that influence the population size of migratory wildebeest

In the above discussion we have attempted to establish mechanism that explain the annual wildebeest migration from Serengeti into Masai Mara ecosystem. However, we have not addressed the question why the overall population size of wildebeest migrating into the Mara has declined in the past 20 years.

Results of our rainfall analysis show that both Masai Mara and Serengeti experienced severe drought in 1984, 1986 and 1993. The 1984 and 1986 droughts were more severe in the Mara than Serengeti, while the 1993 was more severe in Serengeti than in the Mara. Mduma et al. (1998) observes that the 1993 drought in Serengeti was the most severe since rainfall records began in 1938, with dry season rainfall being the lowest record. This drought is thought to have been responsible for the decline in wildebeest numbers in Serengeti from around 1.3million to 917,000 (Mduma et al. 1998). In Masai Mara ecosystem, Ottichilo et al. (*in press*) concluded that the occurrence of drought conditions indirectly contributed to the recorded decline in resident wildebeest population. This is

further thought to have also affected the migratory population as shown earlier in this paper.

A part from drought, land use changes and poaching may also have been also responsible for the recorded decline in migratory population. Sinclair (1995) has reported progressive decline in area available to wildebeest during the dry season due to human settlement and agriculture which is particularly severe in the Maswa and Grumeti areas in the west and Ikorongo in the northwest in Serengeti and in the Loita in the Masai Mara. The loss of these critical habitats could have led to the recorded decline in migratory wildebeest numbers. Prins and Olff (1998) have shown that when an ecosystem becomes smaller due to areas being put under cultivation, wild grazers will show a decrease in species packing. Ottichilo et al. (*in press*) have shown that drastic decline of resident wildebeest population in the Masai Mara ecosystem is mainly due to loss of former wet season and breeding habitats to agriculture. It has also been shown in this paper that migratory wildebeest population is increasingly being concentrated in the Masai Mara National Reserve. This is because their former dry season dispersal areas in the north and northwest are increasingly being settled and converted into agriculture.

Poaching may also have contributed to the decline in migratory wildebeest population in the Serengeti- Mara ecosystem. Mduma et al. (1998) has reported that poaching off-take in Serengeti is approaching maximum sustained yield for wildebeest and therefore changes in the level of poaching in the next few years will determine whether the wildebeest population will collapse or not. In Masai Mara ecosystem, poaching is reported to have been rampant during late 1970s and early 1980s and is now again on the increase (Ngene and Kariuki 1999).

Conclusion

Overall, wildebeest migrations into Masai Mara ecosystem from Serengeti have declined in the past 20 years. The magnitude of migration was largely influenced by wet and dry rainfall in the Masai Mara ecosystem and the status of dry season in the Serengeti and by the dry season vegetation condition in Masai Mara ecosystem. NDVI was strongly related

to rainfall and migratory wildebeest population trends. It can therefore be used as an indicator of effectiveness of rainfall on primary production and in predicting wildebeest spatial and temporal movements. Lastly, the overall decline in migratory wildebeest population may be attributed to drought effects, land use changes (habitat loss) and poaching among other factors.

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CHAPTER 8

SYNTHESIS:

Analysis of Change in Population Size and Distribution of Wildlife in the Masai Mara Ecosystem, Kenya



Formulation of sustainable wildlife conservation and management strategies requires reliable data and information on their population numbers and distributions. The Masai Mara National Reserve (MMNR) and adjoining areas which are all referred to here Masai Mara ecosystem have the richest wildlife resources and offers the most spectacular wildlife watching in Kenya. They form the northern portion of the Serengeti-Mara ecosystem (Masai Mara ecosystem and Serengeti National Park) to which wild animals (especially wildebeest and zebra) annually migrate. The wildebeest and zebra migrations from Serengeti to Masai Mara ecosystem normally occurs during the dry season (June to October). According to the facilitation theory, the grazing sequence in the ecosystem depends on this migration.

Due to increasing human population and changes in land tenure system, former wildlife and livestock ranges in the Masai Mara ecosystem are being converted to agriculture and other land uses at a fast rate. The impact of these changes on the overall population size trends and distributions of main wildlife and livestock species have not been fully investigated and quantified using long-term monitoring data. The main objective of this study was to analyze population size trends of selected wildlife and livestock species and factors influencing them in the Masai Mara ecosystem in the past 20 years using aerial survey data collected from 1977 to 1997.

The specific research questions investigated in this study were:

1. What was the quality and validity of aerial survey data used in this study and how do population estimates derived from total count differ from sample count?
2. How did the population sizes of non-migratory and migratory wildlife and livestock species change during the period between 1977 and 1997?
3. Were there any differences in population size changes of wildlife groups and species inside and outside the Masai Mara National Reserve during the study period?
4. What factors were responsible for wildlife population size changes?
5. How did the population size of migratory wildebeest in the Masai Mara ecosystem change and what factors were responsible for the observed changes,
6. How did the population size of resident and migratory Burchell's zebra in the ecosystem change and what factors were responsible for the observed changes,

7. Can Normalized Difference Vegetation Index (NDVI) be used to monitor and predict the movements of migratory wildebeest population?

The results of data quality and validity assessment are given in chapter 2. Overall, the aerial survey data was found to be consistent and based on survey method that was executed in accordance with standard procedures described by Norton-Griffiths (1978). Independent evaluation of the DRSRS aerial survey database by Capricorn Consultants (1994) concluded that the data could reliably be used in monitoring of wildlife and livestock populations and distributions. Also independent evaluation of the same database and method of data collection indicated that both are trustworthy (De Leeuw et al. 1998). Khaemba and Stein (*in press*) evaluated the Jolly 2 method (1969) used in the data analysis of population estimates and showed that although the method gives too large standard deviations, the means are trustworthy. Therefore, due to consistence of the data and availability of large number of surveys (42) conducted in Masai Mara ecosystem between 1977 and 1997, the data was found to be suitable for animal population size trend analysis. This is because it is known that if bias is held constant by rigorously standardizing sampling methods and maintaining consistence, then population estimate indices obtained can be used for monitoring changes in animal population size and distribution over time (Seber, 1996).

A total of 42 surveys each consisting of 212 sub-units (5x5 km) were used in this analysis. These units were chosen because they were common in all the surveys. The methods used in data analysis were Jolly 2 method for population estimate analysis, linear and log-linear regression analysis for population size trend analysis, Spearman rank correlation, t-tests, ANOVA and Mann Whitney U test.

In chapter 3 comparisons between wet season total and sample counts of elephant and buffalo were undertaken. The counts from the two different counting systems were found not to be significantly different for both the elephant and buffalo. This is contrary to the assumption that total counts are more accurate than sample counts. These results appear to indicate that both methods are less reliable. It therefore appears that either of the method can be used in counting these species in Masai Mara during the wet season. The choice of the method will depend on the purpose of the census and available resources. Generally, total counts are more expensive that sample counts.

In chapter 4 we analyzed the changes in non-migratory wildlife and livestock species in the Masai Mara ecosystem. The total of non-migratory wildlife species was found to have declined by 58% in the last 20 years. The decline ranged from 49% in small brown antelopes to 72% in medium brown antelopes. In individual wildlife species, the decline ranged from 52% in Grant's gazelle to 88% in the warthog. The population sizes of elephant, impala and ostrich were not significantly different indicating that their population remained constant during the analysis period. Overall, there was no significant difference in population size decline of wildlife species and groups both inside and outside the Masai Mara National Reserve except for Thomson's gazelle and warthog. Livestock did not significantly decline during the entire analysis period. However, individual species population fluctuated with time but not significantly except for the donkey. Their distribution patterns remained the same during the analysis period. Land use and vegetation changes, drought effects and poaching were considered to be among the potential factors that may have been responsible for the recorded wildlife decline in the ecosystem.

In chapter 5 the population trend and distribution of Burchell's zebra in the Masai Mara ecosystem were analyzed. Since it was not possible to distinguish between resident and migratory population, population size changes were analyzed on seasonal basis. The wet season population mainly represented resident population while the dry season population represented both resident and cross border migratory population. The results of population trend analysis show that the wet season population declined significantly from about 70,000 in 1977 to about 35,000 in 1997 while that of the dry season population did not decline significantly. Cross border migrations appear to have increased from about 5,000 in the 1970s and 1980s to between 30,000 and 50,000 in the 1990s. The spatial distribution patterns indicate that there occur local seasonal migrations of the zebra population in the ecosystem. They occupy the rangelands (mainly the Loita plains) outside the Masai Mara National Reserve during the period from January to June (wet season) and reserve from July to December (dry season). The distribution patterns in the ecosystem appear to have changed over time due to changes in land use among other factors. The migrations within the ecosystem and from the Serengeti into the Masai Mara ecosystem appear to be influenced by wet season rainfall.

In chapter 6 we analyzed population trends of resident wildebeest and factors influencing them in the Masai Mara ecosystem. The results showed that their population size had declined from about 119,000 to about 22,000 in 1997, an 81% decline. A part from decline in population size, their distribution patterns were found to have changed over time during the same period. Loss of former wet season and breeding ranges to agriculture was found to have significantly contributed to the drastic decline in population size of resident wildebeest. There was a remarkable association between the decline in resident wildebeest populations and the expansion of agriculture into prime and original wildebeest wet season ranges in the Loita plains. Our results further showed that the highest decline of wildebeest densities in Loita plains occurred in areas that are now occupied by crops- particularly wheat. Apart from habitat loss to agriculture, occurrence of droughts and possible competition between resident wildebeest and cattle for scarce food may have contributed to their decline through reduced reproduction and survival rates.

In chapter 7 we analyzed the dynamics of migratory wildebeest in the ecosystem. Overall, wildebeest migrations into the Masai Mara ecosystem declined significantly from about 750,000 animals in 1979-82 to 283,000 in 1983-90 and increased slightly to 311,000 in 1991-96. Reasons why wildebeest migrate annually to Masai Mara ecosystem from Serengeti were investigated through the analysis of rainfall and vegetation condition data. Rainfall directly influences primary production of vegetation and vegetation forms the main food source for animals. Since it has been suggested that animal migrations are related to food supply (Pennycuick 1975, Maddock 1979), we analyzed and related rainfall and vegetation condition as expressed by NDVI to fluctuations in population sizes of migratory wildebeest. Comparison of annual rainfall cumulative deviations from the mean in Masai Mara ecosystem and Serengeti showed that the two areas experienced different rainfall regimes and these differences were related to changes in wildebeest migrations into the Masai Mara ecosystem. We found a significant relationship between annual and wet season rainfall with migratory wildebeest population size changes in Masai Mara ecosystem. We also found significant relationship between cumulative dry season NDVI and migratory wildebeest population size changes in Masai Mara ecosystem. Overall, these results indicate that migration of wildebeest into Masai Mara ecosystem from Serengeti is influenced by differences in rainfall received in the two areas and more specifically by the

annual and wet season rainfall received in Masai Mara ecosystem. It is also strongly influenced by the availability of green and abundant food supply in the Masai Mara ecosystem during the dry season. Lastly, the reported decline in migratory wildebeest into Masai Mara ecosystem may be attributed to drought effects, land use changes (habitat loss) and poaching among other factors.

Results of the investigation into whether Normalized Difference Vegetation Index (NDVI) can be used to monitor and predict the movements of migratory wildebeest population are discussed in chapter 7. The investigation first established whether there was a relationship between rainfall and NDVI in Masai Mara ecosystem and the Serengeti. Second, cumulated NDVI for different periods was related to migratory wildebeest population size fluctuations in Masai Mara ecosystem. We found significant relationship between rainfall and NDVI in both Masai Mara ecosystem and the Serengeti. We also found significant relationship between dry season NDVI and migratory wildebeest population size changes in Masai Mara ecosystem. Since NDVI has been shown to have a strong relationship with rainfall and migratory wildebeest population size fluctuations during migratory period (dry season), it may be used for monitoring and predicting the movements of migratory wildebeest populations in the Serengeti-Mara ecosystem.

Analysis of wildlife population size trends in Masai Mara ecosystem has shown that populations of many species are declining to levels where in the near future, it will not be possible to monitor their population numbers using aerial surveys. Already the population numbers of certain species for example the rhino and wild dog have become so low in the ecosystem that they are no longer detected through aerial surveys. In case of the rhino a special ground-monitoring programme has been put in place to monitor their numbers, movements, feeding habits etc. It is therefore imperative that detailed population studies of fast declining species (e.g. warthog, giraffe etc.) are instituted in order to understand their population dynamics and use the information to formulate their conservation strategies.

Lastly, with the continuing loss of wildlife dispersal areas to agriculture and other human activities, it can be expected that wildlife will continue to decline both inside and outside the Masai Mara National Reserve. Complete loss of dispersal areas will reduce the

reserve to an ecological island where sustainable conservation of certain species (particularly migratory) may not be possible even through active management strategies. And cessation of migratory movements of the wildebeest will lead to a breakdown in facilitation, which is essential for the maintenance of the grazing sequence in the ecosystem. It may also lead to a decline in carnivore populations whose food supplies partly depend on it. Therefore, it is urgent and important that a balance be struck between wildlife conservation and different land use activities through integrated land use planning. Also appropriate wildlife conservation measures need to urgently be put in place by concerned authorities and stakeholders to reverse the current downward population trend of most wildlife species in the ecosystem.

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Summary

This thesis deals with the dynamics of large herbivores in the Masai Mara ecosystem in Kenya. The study area is famous for the annual migration of wildebeest and common zebra from and back to the Serengeti in Tanzania. In this study a distinction was made between these two migratory species and the other non-migratory wildlife species. The results reported are based on animal population estimates derived from counts made on board of small light aircraft. The study covers the period from 1977 to 1997.

The total of non-migratory wildlife species in the Masai Mara ecosystem declined by 58% in the last 20 years. The decline ranged from 49% in small brown antelopes to 72% in medium brown antelopes. In individual species, the decline ranged from 52% in Grant's gazelle to 88% in the warthog. The population sizes of the elephant, impala and ostrich remained constant during the analysis period. There was no significant difference in the decline of wildlife inside and outside the Masai Mara National Reserve except for Thomson's gazelle and warthog. The population sizes of all livestock species except for the donkey did not significantly change during the entire analysis period.

A large proportion of wildebeest migrates between the Serengeti and the Masai Mara ecosystem. A smaller population migrates between the Masai Mara National Reserve and the Loita plains in the north. Statistical analysis revealed that the size of this so-called "resident" wildebeest population declined by 81% over the last 20 years. Further analysis revealed a remarkable association between the decline in resident wildebeest population and the expansion of wheat farming into prime and original wildebeest habitat in the Loita plains. It was therefore concluded that loss of former wildlife habitat to agriculture was responsible for the drastic decline of resident wildebeest population.

Apart from habitat loss to agriculture, droughts, poaching and possibly competition between wildlife and livestock may have further contributed to the decline. It is argued that these factors and agricultural encroachment might have been responsible for the reported decline of the non-migratory species as well.

In the last chapter of this thesis a number of environmental factors that could be associated to the migration of wildebeest and common zebra were studied. A significant relationship was found between wet season rainfall in Kenya and the size of the wildebeest and zebra population migrating into the Masai Mara ecosystem. Also a significant relationship was found between dry season NDVI and the size of wildebeest population migrating into the Masai Mara ecosystem. It was concluded that wet season rainfall and availability of food in the dry season influence the migration into the Masai Mara ecosystem. It was also concluded that NDVI could be used for monitoring and predicting the movements of migratory wildebeest populations in the Serengeti-Mara ecosystem.

In this thesis an alarming decline of most wildlife populations in Masai Mara ecosystem over the past 20 years is reported. Furthermore, it was made plausible that this decline was related to habitat loss, due to agricultural encroachment. Socio-economic surveys not analyzed in this thesis but reported elsewhere, indicated that the local people in the areas adjoining the Masai Mara national Reserve anticipate that they will put their hands to the plough once the on-going land adjudication process is completed. The impact of this would be a further decline and possibly a complete collapse of the wildlife populations for which the Masai Mara is reputed. Therefore, it is extremely urgent that a balance be struck between wildlife conservation and this alternative land-use if the current downward wildlife population trend is to be reversed.

Lastly the current Kenyan legislation prohibits on one hand the killing of wildlife, while on the other hand leaving the option open for unlimited destruction of its habitat. The reported decline of the resident wildebeest population is in my view a direct result of this gap in the legislation. It is argued that the concerned authorities urgently reconsider the wildlife conservation policy and adjust its legislation such that it would be possible to protect wildlife habitat outside the protected area system from further undesirable destruction.

Samenvatting

Dit proefschrift behandelt de dynamiek van grote herbivoren in het Masai Mara ecosysteem in Kenya. Het studiegebied is beroemd vanwege de jaarlijkse migratie van wildebeest en Burchell's zebra vanuit de Serengeti in Tanzania. In het proefschrift wordt onderscheid gemaakt tussen deze twee migrerende soorten en de overige wildsoorten die niet migreren. De resultaten zijn gebaseerd op visuele waarnemingen van het wild verricht vanuit kleine vliegtuigen. De studie beslaat de periode van 1977 tot 1997.

De totale populatie van het niet migrerende wild nam in twintig jaar af met 58%. De afname varieerde van 49% in kleine bruine antilopen tot 72% in middelgrote bruine antilopen. Voor individuele soorten varieerde de afname tussen de 52% voor Grant's gazelle en 88% voor het wrattenzwijn. Voor olifant, impala en struisvogel kon geen significante afname worden aangetoond. Voorts bleek er geen significant verschil in afname te bestaan tussen de wildpopulaties binnen en buiten het Masai Mara nationaal reservaat. De populatie van koeien, alsmede die van schapen en geiten bleek in deze periode niet te zijn veranderd, terwijl er voor ezels een significante afname optrad.

Een groot deel van de wildebeest populatie migreert tussen de Serengeti en het Masai Mara ecosysteem. Een kleiner deel van de populatie migreert tussen het Masai Mara nationaal reservaat en de ten noorden hiervan gelegen Loita plains. Tussen 1977 en 1997 nam de grootte van deze residente populatie af met 81%. Verdere analyse onthulde een bijzonder sterke relatie tussen deze afname en de uitbreiding van landbouw in voormalig wildebeest habitat. Op grond hiervan concluderen wij dat verlies van habitat aan de oprukkende landbouw verantwoordelijk moet worden gesteld voor de drastische afname van deze residente wildebeest populatie. Naast het verlies aan habitat hebben droogte, stroperij en competitie met vee wellicht een verdere bijdrage geleverd aan de gerapporteerde afname van de residente wildebeest populatie. We argumenteren verder dat deze factoren ook verantwoordelijk zouden kunnen zijn voor de hierboven gerapporteerde afname van de niet migrerende soorten.

In het laatste hoofdstuk van dit proefschrift bestudeerden wij de relatie tussen een aantal milieufactoren en de trek van wildebeest. Wij vonden een significante relatie tussen de regenval in zuid Kenya in het natte seizoen en de grootte van de migrerende populaties van wildebeest en zebra in het Masai Mara ecosysteem. We vonden voorts een significante

relatie tussen de NDVI (normalized differential vegetation index) en de populatie van migrerende wildebeesten in het Masai Mara ecosysteem. We concluderen dat de regenval in het natte seizoen en de beschikbaarheid van voedsel in het droge seizoen de migratie naar het Masai Mara ecosysteem beïnvloedt. We concluderen verder dat NDVI gebruikt kan worden voor het monitoren en voorspellen van de verplaatsingen van de migrerende wildebeest populaties in het Serengeti-Mara ecosysteem.

Samenvattend, in dit proefschrift tonen wij een alarmerende afname aan van de wildstand in het Masai Mara ecosysteem. Er wordt voorts aannemelijk gemaakt dat deze afname ten dele valt toe te schrijven aan verlies van habitat onder invloed van de oprukkende landbouw. Elders gepubliceerd socio-economisch onderzoek heeft aangetoond dat de lokale bevolking die leeft in het randgebied van het reservaat van plan is om in de nabije toekomst de hand aan de ploeg te slaan, zodra het land dat nu in collectief beheer is, aan hen zal zijn toegewezen. Dit zou een verdere afname en wellicht een compleet in elkaar storten van de wildstand teweeg kunnen brengen. Voor het keren van deze negatieve trend in wildstand is het daarom extreem belangrijk dat er een evenwicht wordt geschapen tussen deze alternatieve vormen van landgebruik en het beheer van wild.

De huidige Kenyaanse wetgeving verbiedt aan de ene kant het doden van wild terwijl zij aan de andere kant de mogelijkheid open laat tot een ongelimiteerde vernietiging van haar habitat. De gerapporteerde achteruitgang van de residente wildebeest populatie valt ons inziens direct toe te schrijven aan deze lacune in de wetgeving. We betogen dat het noodzakelijk is dat het beleid ten aanzien van wildbeheer wordt heroverwogen en de wetgeving dienaangaande zodanig wordt aangepast dat het mogelijk wordt om buiten beschermde gebieden gelegen habitat te behoeden voor verdere ongewenste vernietiging.

Résumé

Cette thèse porte sur l'analyse de la dynamique des espèces de grands herbivores sauvages dans l'écosystème du Masai Mara au Kenya. Il a été trouvé que la taille de la population totale de la faune non migratoire a diminué de 58% depuis ces 20 dernières années. Neuf des douze espèces ont diminué de façon significative. Nous n'avons pas pu déterminer de façon significative la diminution de la taille du troupeau des éléphants, des impalas, et des autruches. Les quantités des différentes espèces du bétail n'ont pas changé de façon significative au cours de la période de l'analyse, à l'exception des ânes qui ont diminué de 67%. De façon surprenante, il n'a pas été trouvé une différence fondamentale dans la diminution des espèces et des groupes tant à l'intérieur qu'à l'extérieur de la Réserve Nationale du Masai Mara, à l'exception des gazelles de Thomson et des phacochères. En ce qui concerne les espèces migratoires, la diminution de la population résidante de gnous a été de 81% tandis que celle des Zèbres a été de 50%. La diminution du nombre de Zèbres et de gnous a été attribuée à l'empiétement de l'agriculture sur leurs zones traditionnelles de pâturage en saison humide. Outre la transformation de leur habitat en zone d'agriculture, les sécheresses, le braconnage et la compétition éventuelle entre la faune et le bétail pour les maigres ressources fourragères, ont probablement contribué à leur diminution à travers la baisse de la reproduction et des taux de survie. Ces mêmes facteurs sont probablement la cause de la diminution du nombre des autres espèces fauniques.

Le nombre de zèbres et de gnous migrant de l'écosystème de Serengeti à celui de Massai mara a montré une fluctuation au cours des années. Il a été trouvé que la migration est liée à la pluviométrie en saison humide et à la disponibilité de la biomasse verte en saison sèche dans l'écosystème de Masai Mara. Il y avait une forte relation entre la taille de la population des gnous et la différence normalisée de l'indice de végétation (NDVI) de l'imagerie satellitaire NOAA AVHRR dans l'écosystème de Massai Mara pendant la période migratoire (juin octobre) Nous avons conclu que le NDVI pourrait être utilisé pour le suivi et la prédiction des flux migratoires des populations de gnous dans l'Ecosystème Serengeti-Mara.

Enfin, cette thèse fait mention de la baisse alarmante de la population faunique. Cette diminution est essentiellement liée à la perte de leurs habitats, due à l'empiétement de

l'agriculture. De ce fait, il est extrêmement urgent que les autorités et toutes les parties directement impliquées prennent les mesures adéquates pour trouver un juste équilibre entre la conservation de la faune et le développement agricole, si on veut que la tendance actuelle soit inversée. Il est aussi urgent de réviser la politique et la législation en matière de faune de façon à mieux préserver les habitats contre toutes les intrusions indésirables.

Mots Clés : Ecosystème du Masai Mara, faune, tendance de la population, agriculture, pluviométrie, NDVI.

Curriculum vitae

Wilber Khasilwa Ottichilo was born on the 23rd of September 1952 in Vihiga District, Kenya. Between 1968 and 1972 he attended secondary and high school at Emusire and Kagumo respectively. He studied and obtained B.Sc. (Hons) in Botany and zoology at the University of Nairobi during the period between 1974 to 1977.

He was employed as a Biologist in the Department of Resource Surveys and Remote Sensing (DRSRS) within the Ministry of Environment and Natural Resources as from April 1977. He was among the pioneers who established an ecological monitoring programme for the Kenya rangelands and he was responsible for the planning and execution of wildlife and livestock aerial surveys and collection of a variety of environmental data.

In 1979 he registered for a part-time M.Sc. course in Biology of Conservation and Ecology at the University of Nairobi. His thesis research work was on the population dynamics of the elephant in Tsavo National Park, Kenya. He was awarded a Dutch Government Scholarship to study Geographic Landscape Analysis (Rural Survey) and Remote Sensing at ITC, Enschede in 1981. He successfully completed his studies in April 1982 and returned to Kenya to continue with his duties at DRSRS. He obtained his M.Sc. in 1983.

In 1984 he was awarded one year U.S.A Government Scholarship to study natural resource planning and management at Colorado State University. On completion he returned to Kenya and was promoted to a position of Senior Surveys Biologist within DRSRS. Between 1987 and 1989 he coordinated a joint Government of Kenya and United Nations Environment Programme (UNEP) project on, Desertification Mapping and Assessment. He was promoted to the position of Deputy Director in 1990. He left DRSRS in 1991 to take up a position of Project Counterpart (remote sensing specialist) within FAO's Project on, Remote Sensing Component of the Early Warning System for Eastern Africa. The project ended in December 1993 and in 1994 he was appointed to the position of Chief Scientist at Kenya Wildlife Service (KWS). He was responsible for the coordination of wildlife research and planning programmes within the organization.

In 1996 he was appointed to the position of Deputy Director in charge of biodiversity conservation and planning. He resigned from this position in 1997 to pursue P.hD studies in ecology and environmental conservation at ITC, Enschede, the Netherlands.

He has published over ten papers in peer reviewed internationally journals, he is a senior author of a book published by Stockholm Environmental Institute on, Climate Change and Investment in Kenya. He has written numerous technical reports on ecological monitoring, wildlife ecology and population dynamics, land use mapping using remote sensing techniques and food security and early warning systems. He has attended many short courses in remote sensing, GIS, planning and management and he is a member of several professional and social organizations.