Multiscale perspectives of species richness in East Africa

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To my parents and
family

and especially

Anisa, Salama and Summayah

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Multiscale perspectives of species richness in East Africa[1]

Mohammed Y. Said

This dissertation describes and analyses animal species richness in East Africa from a multi-scale perspective. We studied diversity patterns at sub-continental, national and sub-national level. The study demonstrated that species diversity patterns were scale-dependent. Diversity patterns varied with spatial and temporal scales of observation. Processes and parameters important at one scale were not as relevant at another.

At sub-continental level large herbivore assemblages revealed maximum diversity at intermediate ecosystem productivity. This finding is consistent with other studies on the relation between productivity and species richness. When furthermore comparing climatic and remotely sensed estimates of ecosystem productivity we observed the first to be a better predictor of diversity. Geographical patterns in species richness proved to be very similar among different taxonomic groupings of animal species. Most taxa revealed maximum diversity at intermediate productivity.

At Kenyan national level we analysed the coexistence of pastoralism and wildlife. A study of seventeen arid and semi arid districts revealed that the biomass of human and livestock populations was negatively related to wildlife biomass. An increase in human population density was associated with a significant decline of the density of wildlife populations. This spatio-temporal extension of the 'pastoral road to extinction' model provided more insights into the antagonistic relation between people, livestock and wildlife. Also it allowed localizing areas of conflict that need specific attention.

A further study in the arid zone of Northern Kenya revealed that wildlife distribution was negatively associated with the presence of livestock and water-points. This suggests that livestock oriented interventions in rangelands directly degrade wildlife resources. Further, we demonstrated that the local processes (competition and disturbance) have a direct link to regional patterns. In the northwestern, central and coastal areas of Kenya there are signs of local species extinction.

We finally conducted studies at sub national level in the Masai Mara ecosystem. Significant declines were recorded for of 10 out of 13 wild ungulate species between the late 1970's and the turn of the century. Further analysis provided evidence that these declines were related to changes in land use rather than climate. This suggests that the processes underlying the dynamics of wildlife in the Masai Mara ecosystem differ from those reported for the neighbouring Serengeti National Park in Tanzania.

These results indicate that conservation and rural development have arrived at crossroads. Further uncontrolled rural development will lead to a continued decline and eventual extinction of wildlife. The challenge would be to integrate rural development and sustainable wildlife conservation, with the latter defining boundary conditions for development. This would require term planning of land use, based on a realistic assessment of the interaction between wildlife conservation and other forms of land use carried out at spatio-temporal scales that transcend what appears to be achievable according to the social, economic and political agenda.

Keywords: *Ungulate, coexistence, pastoralism, NDVI, land use change, wildlife, livestock, species pool*

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Chapter 1

Multiscale perspectives of species richness

An overview

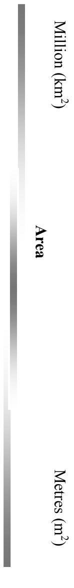
1.1 INTRODUCTION

The study of the patterns and causes of species diversity has been a focal point of ecology for more than a century. Ever since the 19th century when naturalists first visited the New and Old World tropics, they have been intrigued by the enormous latitudinal variation in the richness of plant and animal species (Brown, 1988). Since then ecologists and biogeographers have endeavoured to understand the spatial variations in the abundance and distribution of species (Myers and Giller, 1988; Ricklefs and Schluter, 1993; Huston, 1994, and references therein). Ecologists and biogeographers have hypothesized many causal environmental or biophysical factors in an attempt to explain the spatial patterns of species diversity at various scales (refer to Table 1.1 – references restricted to large mammals). Several authors have pointed out that species diversity patterns are strongly scale-dependent (Schimda and Wilson, 1985; Ricklefs, 1987; Wiens, 1989; Levin, 1992; Caley and Shluter, 1997; Gaston and Blackburn, 1999) and that the patterns vary with the spatial and temporal scales of observation and can be determined by multiple processes that function at various scales (Turner, 1989; Christensen *et al.*, 1996). Processes and parameters important at one scale may not be as important or predictive at another scale (Turner, 1989; Wiens, 1989; Levin, 1992; Wiens *et al.*, 1993; Christensen *et al.*, 1996). Wiens (1989) further points out that the 'ecological theatre' is played out at various scales of space and time and to understand the drama we must view it at an appropriate scale. The aim of this study is to develop aggregation and scaling methods for the purpose of unifying population biology, ecosystem science and applied ecology (refer to Levin's MacArthur Award lecture (1992) 'The problem of pattern and scale in ecology').

On a large scale (continental or sub-continental), species diversity is controlled by factors such as climate (Fischer, 1960; Connell and Orias, 1964), available energy (Hutchinson, 1959; Wright, 1983; Currie and Fritz, 1993; Olff *et al.*, 2002) and area (MacArthur and Wilson, 1967; Terborgh, 1973; Brown and Lomolino, 2000). These physical characteristics of environments determine the resources and capacity to support the species existence. The process leading to change in distribution patterns is based on migration, isolation, speciation and extinction rates (MacArthur and Wilson, 1967). However, changes in environment (climate and vegetation) can have an impact on both species diversity and species traits (for example physiological adaptation), as exhibited by the evolutionary radiation of the ungulates (Gwynne and Bell, 1968; Jarman and Sinclair, 1979; Janis, 1982; Sinclair, 1983; Janis, 1989; Janis *et al.*, 2002). At the landscape scale, topography diversifies the green cover of the earth into a patchwork of spatially heterogeneous biotopes (MacArthur *et al.*, 1962; Kerr and Packer, 1997). Both natural and anthropogenic disturbance can reduce the amount of resources available and accessible to species groups (such as livestock versus wild ungulates). Other physical characteristics of environments, such as climatic fluctuations or land cover/use changes, may further affect the temporal and spatial heterogeneity of the biological environment, thus influencing the interspecific interactions between species. At this level predation, diseases, facilitation and competition are important interaction processes (Pennycuick, 1975; Maddock, 1979; Sinclair and Norton-Griffiths, 1982; Borner *et al.*, 1987; Dublin *et al.*, 1990; Prins and van der Jeugd, 1993; Prins and Olff, 1998; Baird, 2001) that determine the changes in ungulate species diversity.

On the basis of the foregoing discussions it is important to understand that patterns and processes tend to emerge at different scales, and single-scale approaches often do not suffice in unravelling some of the ecological phenomena (see Dayton and Tegner, 1984; Giller and Gee, 1987; Meentemeyer and Box, 1987; Frost *et al.*, 1988; Wiens, 1989; Levin, 1992; Wiens *et al.*, 1993; May, 1994; Brown, 1995). Determining the causes of variation in species diversity requires the scales at which variation in diversity is measured to be linked to the scales at which the processes hypothesized to affect diversity actually operate (Huston, 1999).

Table 1.1: Hierarchical approach to explaining higher-order ungulate patterns and processes from low-order features. The processes are nested in time and space and are further elaborated in Figure 1.1.



Scale	Quality	Biophysical factors	Interaction	Dynamics
Epsilon (1-100 million Ha)	Physiography	Productivity (1, 2) Climatic zones and geographical ranges (3)		Glaciation (2, 4) (speciation, extinction and immigration (5)) Climate change (6)
Gamma (1000-1 million Ha)	Habitat and topographic diversity	Productivity and climate (7, 8) (precipitation, potential evapotranspiration, temperature, seasonality) Soils (8, 9) NDVI (10)		Metapopulation (20) Dynamics (patch colonization and extinction)
Alpha (0.1-1000 Ha)	Structural complexity	Productivity and climate (11, 12) (precipitation, moisture, insolation, temperature, seasonality) Soils (13) NDVI (10, 14)	(Competition and facilitation (2, 12, 15, 16)) Predation Diseases	Resource partitioning with or without exclusive niches (20) Fire (15, 17) Habitat fragmentation (17, 18)
Point (0.01-0.1 Ha)	Microhabitat factors	Soil moisture Soil nutrients		Herbivory Structure and quality of vegetation (13)

Note: The derivation of scale was based on (19). The study did not consider the diversity of species at point or microhabitat level.

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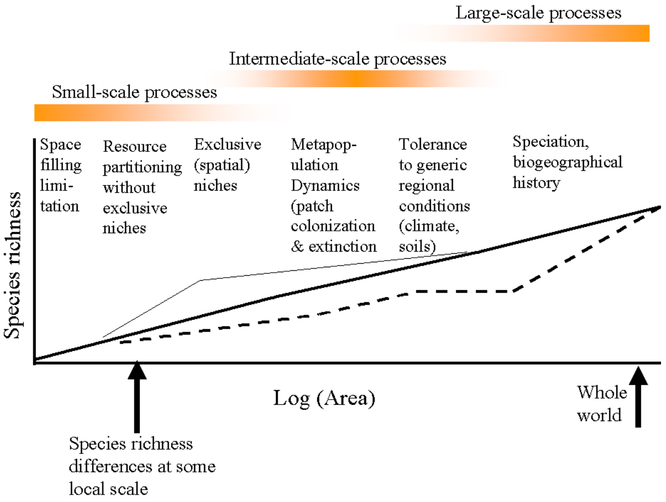


Adapted from Olff and Ritchie (2002)

Figure 1.1: Species-area curve showing how ecological processes at different scales may structure species diversity. The thin solid line represents situations where species richness is higher because of exclusive spatial niches, while the thick bold line represents less species at a local scale because of fewer exclusive niches. The dashed line indicates less species because of the processes operating at the intermediate spatial scale, such as regional conditions (climate and soils) and metapopulation dynamics allowing the persistence of less species.

Olff and Ritchie (2002) suggest that the species composition within a certain spatial extent can always be viewed as a subset of the species composition of some larger spatial extent with different structuring ecological processes (Figure 1.1). The framework of this relationship will be used in this study as a guide to link the scale of observation and ecological processes. Clearly, the choice and integration of appropriate time and space scales is important if we are to advance the understanding of patterns and processes in ecology. In addition, several authors have suggested that both historical events and ecological processes should be part of any complete explanation of patterns of species diversity (Myers and Giller, 1988b; Ricklefs and Schluter, 1993b). This forms not only the motivation for undertaking this study but also its basis.

1.2 EFFECTS OF SCALE CHANGE

In this thesis we will deal with three aspects of scale, namely the spatial, temporal and taxonomic. The spatial scale encompasses three elements: data, resolution and geographical extent. It is therefore important to understand and anticipate the implications of moving from one scale to another. Table 1.2 summarizes the implications for various parameters (adapted from Meentemeyer and Box, 1987). Perhaps the most obvious effect of scale change is the level of discernible or treatable detail that is present. Moving to a coarser scale means that one is further removed from the basic processes (Meentemeyer and Box, 1987). The number of variables useful for modelling and other analyses also changes with scale, generally becoming smaller at coarser scales.

The temporal aspect of scale changes more quickly at fine spatial scales than at broader spatial scales. However, moving to a coarser spatial scale may result in the loss of temporal detail. It also may result in the appearance of emergent properties due to synergisms at a higher level of system integration (Meentemeyer and Box, 1987). The dynamics observed at finer scales cause the equilibria observed at broader scales (Meentemeyer and Box, 1987; Levin, 1992; Huston, 1999).

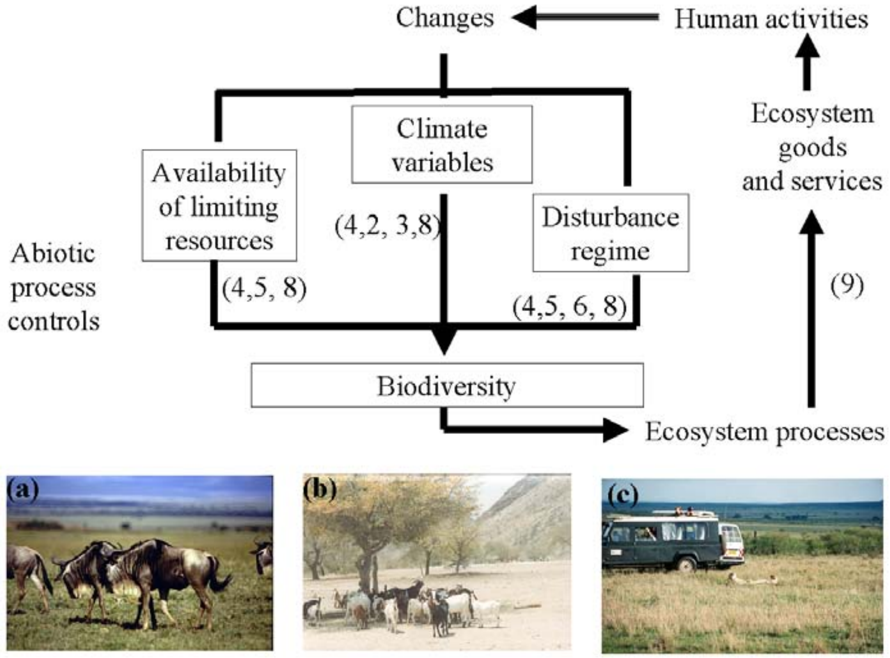
Table 1.2: Some effects of changing spatial scale on analyses and model structures.

	Size of study area	
Phenomenon	**Small**	**Large**
Level of discernible or 'treatable' detail	Higher	Lower
Potential for experimental manipulation	Higher	Lower or none
Number of important factors or variables	More	Fewer
The important variables	Biotic	Abiotic (especially physical)
Value ranges of the landscape variables	Smaller	Greater (but depends on the variable)
Importance of the temporal scale	More	Less
Emergent properties	Fewer	More

1.3 CONCEPTUAL FRAMEWORK AND THESIS OUTLINE

The conceptual model that describes the relationship between ungulate diversity, ecosystem processes and human activity, as well as the factors that control it at different scales, is presented in Figures 1.1, 1.2a and 1.2b. This lays the foundation of the research.

The dissertation is divided into three parts. The first part addresses the historical distribution of ungulate species and the factors controlling them at a large scale. The second part of the dissertation analyzes the long-term outcomes of different land use practice on the environment and wildlife (subject of present debate on projected effects of land use on biodiversity – see Lawton and May, 1995; Pimm *et al.*, 1995; Chaplin *et al.*, 2000; Newmark and Hough, 2000; Sala *et al.*, 2000; Balmford *et al.*, 2001). It examines those factors potentially driving these changes (availability of resources, increase in human population, intensification of livestock industry, socio-economic and policy changes).



Adapted and modified from Chaplin *et al.* (2000)

Figure 1.2a: Conceptual model showing the relation between biodiversity, ecosystem processes and human activity. Chapter 2 assesses the environmental variables that describe species richness, while chapter 3 tests whether species richness of terrestrial mammals measured at different taxonomic levels consistently increases with rainfall. Chapter 4 investigates the coexistence of wildlife and pastoralism in the arid and semi-arid areas. Chapter 5 assesses the links between local and regional species richness. Chapter 6 investigates the effects of developing water points on livestock and wildlife distribution. Picture (a) shows wildebeest in search of forage of high mineral content – the same areas attract wheat farming. Picture (b) shows degraded lands near settlement and water points – the vegetation is mainly composed of scattered trees with low herbaceous cover. Chapter 7 analyzes the land cover changes in the Mara ecosystem and its effects on wildlife are highlighted in chapter 8. Picture (c) illustrates the benefits of wildlife viewing through ecosystem goods and services. The links between the chapters and the processes are indicated in parentheses.

However, Wiens (1989) points out that any predictions of the dynamics of spatially broad-scale systems that do not expand the temporal scale are pseudopredictions, and mechanistic linkages will not be seen because the temporal extent of the study is too short. The problem may be particularly severe in resource management disciplines, where the application of policies to large areas is often based on very short-term studies. This issue is addressed in the third part of the thesis, at a fine scale, where the effects of climatic and land use changes on species diversity are studied. This in-depth analysis is based on 20 years of continuous monitoring of wildlife and livestock interaction in an ecosystem in Kenya.

These tasks are accomplished by analyzing the historical distribution of ungulates, conducting in-depth analysis of remote sensing, demographic and existing extensive long-term data sets on wildlife and livestock (20 years), that is linked to the existing research knowledge of community and ecosystem processes.

I - UNGULATE DIVERSITY PATTERNS

The relationship between species richness and productivity may to vary with scale (resolution, geographical extent, species group – refer to discussions in Frost *et al.*, 1988; Currie, 1991; Bohning-Gaese, 1997; Grace, 1999; Lyons and Willing, 1999) and the mechanism underlying some of these patterns still remains obscure, although many hypotheses have been suggested (Abramsky and Rosenzweig, 1984; Owen, 1988; Owen, 1990; Currie, 1991; Currie and Fritz, 1993; Wright *et al.*, 1993; Abrams, 1995; Kerr and Packer, 1997; Guo and Berry, 1998; Prins and Olff, 1998; Waide *et al.*, 1999; Olff *et al.*, 2002).

Chapter 2 assesses the environmental variables that describe species richness, while chapter 3 tests whether species richness of terrestrial mammals measured at different taxonomic levels consistently increases with rainfall. It also formalizes the rules on selecting data resolution and species richness indices for ungulate studies. The species data used in these two chapters are based on the species distribution (range), while the independent data sets are derived from climatic databases in addition to remotely sensed images. Chapter 5 assesses the links between local and regional species richness and further analyzes the trends of individual species based on meta-analysis. The aim of this analysis was to address the question of whether, based on the trends at local level (individual districts), there is a decline in individual wildlife species at a regional level (national status).

II - CHANGES IN UNGULATE DIVERSITY PATTERNS

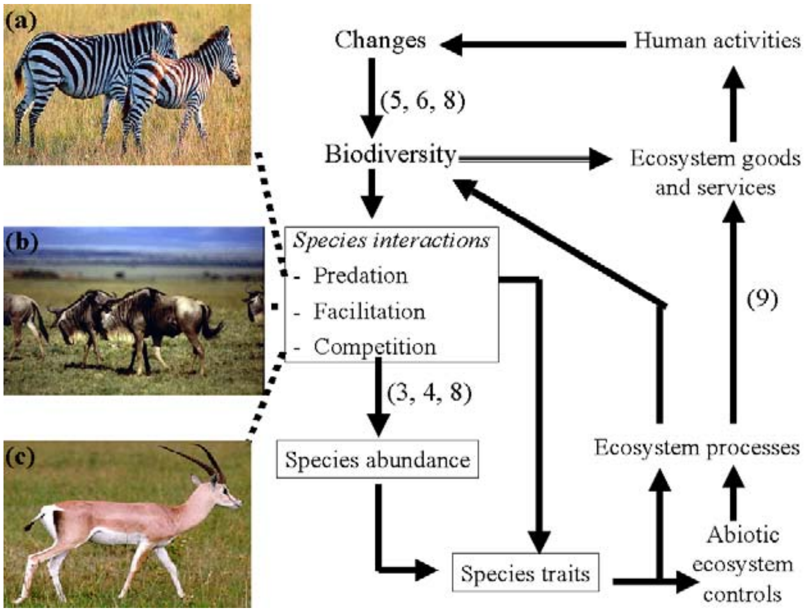
Changes in ungulate diversity can be explained by both climatic and anthropogenic activity that causes disturbance to the system. Turner (1989) defines disturbance as any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment. Apart from the climate changes, the availability of resources also limits the distribution of ungulates. The availability of resources (net primary productivity) is a function of both the quality and quantity of vegetation (Bell, 1982; McNaughton, 1985; McNaughton, 1990; Olff and Ritchie, 1998; Prins and Olff, 1998; Olff *et al.*, 2002). We hypothesized that human activities do impact on the ecosystem. These interventions can be positive and may further enhance the functioning of an ecosystem, but can also have negative effects on both the ecosystem and biodiversity.

Most of the present policies on wildlife conservation in East Africa are based on the past distribution and status of wildlife (Western and Ssemakula, 1981; Enghoff, 1990; Newmark, 1996; Norton-Griffiths, 1996; Inamdar *et al.*, 1999; Newmark and Hough, 2000). The intensification of agriculture and livestock keeping during the last half a century is increasingly having an impact on wildlife (Brown, 1971; Prins, 1992; Balmford *et al.*, 2001; Brashares *et al.*, 2001; Bruner *et al.*, 2001), and therefore the perception that wildlife and people can coexist in harmony is questionable. In chapter 4 we analyze the coexistence of wildlife and livestock based on a model proposed in Prins (1992). In this model we introduced the concept of dynamic changes, which enabled us to compare the trend, course and magnitude of change in the resources. The result revealed that livestock were increasingly displacing wildlife in more of the arid areas, and one of the contributing factors was the development of water points. In chapter 6 we investigate the impact of intensifying livestock and water management in arid and semi-arid districts on the diversity of wildlife. Such studies require more systematic, intensive and quantitative information on the various attributes under study, in terms of distribution of individual species.

In semi-arid districts pressure from land use changes (transformation of rangelands to agriculture land) are more pronounced. In Chapter 8 - we investigate in detail how local changes in land use and climate has affected wildlife in one of the key wildlife areas in Kenya – the Masai Mara.

III - INTERSPECIFIC INTERACTION OF SPECIES

The analysis in Chapter 8 on the interaction of species was conducted at a local scale. At a local level the build-up and maintenance of species diversity obviously depends largely on the structure and dynamics of interaction among the coexisting species (Brown, 1988; Huston, 1999). Interspecific competition and facilitation have both been proposed as processes promoting species separation and coexistence in African ungulates (Sinclair and Norton Griffiths, 1982; Prins and Olff, 1998; Baird, 2001). In the study at local level we investigate whether food supply, interspecific competition or facilitation (if either) determines the abundance of ungulates, given the changes in climate, land use or both in the Mara ecosystem of Kenya.



Adapted and modified from Chaplin *et al.* (2000)

Figure 1.2b: Conceptual model showing the relation between biodiversity, ecosystem processes and human activity at one level lower than Figure 1.2a. Chapter 3 assesses the relationship between various fauna groups (ungulates and carnivores) in respect to resource availability. In chapter 8 we analyze how habitat fragmentation has reduced resource availability and whether interspecific *competition* determines the abundance of ungulates. Pictures indicate the processes of grazing succession between the three key species in the Masai Mara: (a) zebra (b) wildebeest and (c) Thomson's gazelle. The outcomes of the model in Figures 1.1,1.2a and 1.2b are synthesized in chapter 9 and are discussed regarding their implications for *ecosystem goods and services* and ultimately for *human benefit*. The links between the chapters and the processes are indicated in parentheses.

In chapter 7 we analyze the land cover changes of the Mara ecosystem, based on the integration of low-resolution (8 km NOAA/AVHRR data 1982-1994) and high-resolution satellite images (30 m Landsat 1975, and TM of 1985 and 1995). The result showed that the major land cover changes (mainly wheat farms) were localized and coincided with the wet season ranges of the wildlife. Further, in chapter 8 we analyze the interaction between climate changes, land cover changes and ungulate population trends. The test was to investigate whether climate or loss of habitat had a higher effect on wildlife diversity. The aim of the test was to refine the theoretical understanding of interspecific interactions of ungulates.

The synthesis in chapter 9 puts the findings of the entire study within the perspective of unravelling the patterns and processes that determine ungulate species diversity. Finally, we draw conclusions on the implications of the results, in terms of present management and future conservation plans to maintain biodiversity in the region.

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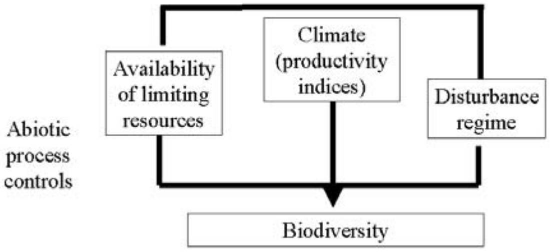
CHAPTER 2

ANALYSIS OF THE RELATION BETWEEN UNGULATE SPECIES RICHNESS IN EAST AFRICA AND CLIMATIC AND REMOTELY SENSED PRODUCTIVITY INDICES

At sub-continental or continental scale productivity or energy flow through an ecosystem is considered as a major determinant of species richness. However, the direct estimation of available energy is difficult at this scale. The aim of this chapter is evaluate whether climatic or remotely sensed indices are a better predictor of ungulate species richness. Our hypothesis is that since the remotely sensed index the normalized difference vegetation index (NDVI) integrates the influence of climatic and environmental factors, it should be a better predictor of species richness than climatic variables. Contrary to our expectation the climatic indices were better predictor of ungulate species richness than the remotely sensed normalized difference vegetation index.



Chapter 2

Analysis of the relation between ungulate species richness in East Africa and climatic and remotely sensed productivity indices

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Abstract

The aim of the study was to evaluate whether climatic or remotely sensed indices are a better predictor of ungulate species richness. Our hypothesis is that the remotely sensed index the normalized difference vegetation index (NDVI) integrates the influence of climatic and environmental factors, it should be a better predictor of species richness than climatic variables. The study was conducted in East Africa, which has high ungulate species diversity. Out of 95 ungulate species found in Africa, 55 are found within this sub-region. The vegetation is highly heterogeneous, with great variability in productivity that is influenced by the spatial and seasonal distribution of climatic variables, including precipitation and temperature. Species richness was regressed against each environmental variable, using linear, polynomial, logarithmic and exponential models. A test of the equality of two population regression coefficients was used to compare the models. The results show that the strongest correlates of species richness were rainfall and NDVI, with 69% and 55% of the variance explained. A unimodal pattern was exhibited for ungulate species richness with both rainfall and NDVI. The combination of rainfall and potential evapotranspiration (PET) best predicted the ungulate species richness. The climatic model was more predictive than NDVI (r^2 of 0.76 vs. 0.55, $t = 2.22$, $P = 0.028$) in areas with a rainfall range between 200 and 1300 mm, and (r^2 of 0.80 vs. 0.67, $t = 1.32$, $P = 0.10$) for the drier part of the rainfall gradient (<1000 mm) the difference was not significant. We concluded that NDVI was not a better predictor of species richness than integrated climatic indices. Several factors related to the reflectance of vegetation cover; soil-vegetation spectral mix and soil type /moisture limit the performance of NDVI in predicting both the primary productivity and species richness. Improvements in spectral, spatial and temporal resolutions, including information on surface radiation, ecosystem process variables (leaf area, leaf duration and primary productivity) and land cover characteristics should significantly improve the potential use of remotely sensed data in biodiversity studies.

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[*] submitted to *African Journal of Ecology*

2.1 INTRODUCTION

Species diversity varies geographically and the factors permitting the coexistence of species are scale-dependent (Levin, 1992; Prins and Olff, 1998; Grace, 1999; Waide *et al.*, 1999). At sub-continental (areas > 10^6 km^2) or continental scale the productivity or energy flow through an ecosystem is considered a major determinant of species diversity (Currie, 1991; Rosenzweig and Abramsky, 1993; Wright *et al.*, 1993). However, the direct estimation of available energy is difficult at continental or sub-continental scales (Owen, 1988; Box *et al.*, 1989; Currie, 1991). Instead, diversity has been related to other indices that are related to energy flow, for example net aboveground primary productivity (NAPP) (Abramsky and Rosenzweig, 1984; Currie and Paquin, 1987; Owen, 1990; Currie, 1991; Wright *et al.*, 1993), as well as climatic parameters such as rainfall, potential and actual evapotranspiration, temperature and solar radiation (see reviews in Ricklefs and Schluter, 1993; Huston, 1994; Grace, 1999). The development of satellites for mapping and monitoring vegetation has introduced an alternative method for estimating NAPP, and it has been empirically established that the normalized difference vegetation index (NDVI) effectively measures photosynthetically active biomass (Justice *et al.*, 1985; Tucker *et al.*, 1985; Sellers, 1985; Box *et al.*, 1989; Prince, 1991a).

In the last decade NDVI has been related to the distribution of both plant and animal species diversity. Walker *et al.* (1992) correlated plant species richness to aggregated NDVI in California, while Jorgensen and Nohr (1996) related bird diversity to landscape diversity and biomass availability in the Sahel. Recently, Oindo and Skidmore (2002) and Baird (2001) related mammalian species richness to NDVI and its variability linked to seasonality and heterogeneity. A review of literature indicates that climatic and NDVI databases represent two different ways of approximating the spatial variability in NAPP. Climatic spatial databases are based on the interpolation of point observations from climatic stations. Using spatial extrapolation techniques, a few scattered climatic station samplings characterize NAPP over a large region (Walker *et al.*, 1992). NAPP is determined in part by other factors, such as soil fertility, soil physical and chemical characteristics, soil moisture, position in the terrain, and exposure to insolation (Bell, 1982; McNaughton, 1985; Belsky, 1989; Olff *et al.*, 2002). Thus, climatic databases may well provide a biased approximation of NAPP. On the other hand, NDVI images have been largely unexplored in biodiversity studies, though they cover large areas and can be frequently updated (Walker *et al.*, 1992; Jorgensen and Nohr, 1996). Various studies have shown that NDVI integrates the influence of climatic variables and other environmental factors (Cihlar *et al.*, 1991; Nicholson and Farrar, 1994; Richard and Poccard, 1998). This suggests that NDVI is a better predictor of NAPP and, compared with climatic indices, may reveal a stronger relationship with species diversity. Since NDVI integrates the influence of climatic variables and environmental factors such as soil fertility, it is hypothesized that NDVI would better predict species diversity than would climatic variables.

Thus the aim of the study is to evaluate whether climate-based or remote sensing-based productivity indices better predict species richness. Further, the distribution of species is discussed with respect to its implications for conservation. The term 'species diversity' refers to a number of species and the relative abundance of species, while 'species richness' refers to the total number (absolute value) of species inhabiting an area.

2.2 MATERIAL AND METHODS

2.2.1 Study area and data sets

The study area is East Africa - covering Kenya (569,260 km^2), Tanzania (886,220 km^2) and Uganda (207,950 km^2). It is situated approximately between longitudes 12° South and 6° North and latitude 29° West and 42° East. The great diversity of ungulates is one of the most noticeable features of the East African region. Out of 95 ungulate species found in Africa, 55 are found within this sub-region.

The vegetation of East Africa is highly heterogeneous, with great variability in structure and productivity. The productivity is greatly influenced by the spatial and seasonal distribution of precipitation and temperature (Le Houerou and Hoste, 1977). Important vegetation types include forests, deciduous woodland, open and *Acacia* grassland, evergreen and thorn bushland, dwarf shrub grassland and sparsely vegetated grassland and shrubland in semi-desert areas.

The range of precipitation varies between and within the three countries (Brown and Cocheme, 1973; Pratt and Gwynne, 1977). Uganda has a range of 900 to 1300 mm, Tanzania 600 to 1300 mm, and Kenya 200 to 1300 mm. The three main rainfall patterns in the region are: year-long rainfall (around Lake Victoria), single season rainfall (northern Uganda, northwestern Kenya, most of Tanzania) and bimodal season rainfall (rest of Kenya).

2.2.2 Herbivore data

A total of 55 species belonging to two orders and six families were included in the analysis (Table 2.1). The orders Artiodactyla (Bovidae, Giraffidae, Hippopotamidae, Tragulidae and Suidae) and Perissodactyla (Equidae) were combined into one functional group – the ungulates. Digital data on large herbivore distribution at sub-continental level were acquired from the African Mammal Databank (Boitani *et al.*, 1999) and nomenclature was based on Wilson and Reeder (1993). The area hosts one critically endangered species (Hunter's hartebeest) and three endangered species (Ader's duiker, the Ruwenzori black-fronted duiker and Grevy's zebra). Several species are threatened, including the water chevrotain, the bay duiker, the yellow-backed duiker, Bate's pigmy antelope, the sitatunga, the bongo, and the black-fronted duiker. The rest of the species fall in the category of lower risk, but still depend on conservation programmes for their survival (IUCN, 1999).

Table 2.1: Listing of ungulate species included in the study. Nomenclature follows 'Mammals Species of the World' (Wilson and Reeder, 1993). Distribution data derived from Boitani *et al.* (1999).

Family	Common name	Species	Occurrence
Bovidae	Impala	*Aepyceros melampus* (Lichtenstein, 1812)	Kenya, Uganda and Tanzania
	Common hartebeest	*Alcelaphus buselaphus* (Pallas, 1766)	Kenya, Uganda and Tanzania
	Ader's duiker	*Cephalophus adersi* (Thomas, 1918)	Kenya, and Tanzania
	Bay duiker	*Cephalophus dorsalis* (Gray, 1846)	Uganda
	Harvey's red duiker	*Cephalophus harveyi120* (Thomas, 1893)	Kenya and Tanzania
	Blue duiker	*Cephalophus monticola* (Thunberg, 1789)	Kenya, Uganda and Tanzania
	Natal red duiker	*Cephalophus natalensis* (A. Smith, 1834)	Tanzania
	Black-fronted duiker	*Cephalophus nigrifrons* (Gray, 1871)	Kenya and Uganda
	Ruwenzori black-fronted duiker	*Cephalophus rubidus* (Thomas, 1901)	Uganda
	Red-flanked duiker	*Cephalophus rufilatus* (Gray, 1846)	Uganda
	Yellow-backed duiker	*Cephalophus silvicultor* (Afzelius, 1815)	Kenya and Uganda
	Abbott's duiker	*Cephalophus spadix* (True, 1890)	Tanzania
	Weyn's duiker	*Cephalophus weynsi* (Thomas, 1901)	Kenya, Uganda and Tanzania
	Blue wildebeest	*Connochaetes taurinus* (Burchell, 1823)	Kenya and Tanzania
	Hunter's antelope	*Damaliscus hunteri* (Sclater, 1889)	Kenya
	Topi, sassaby, tiang, korrigum	*Damaliscus lunatus* (Burchell, 1823)	Kenya, Uganda and Tanzania
	Grant's gazelle	*Gazella granti* (Brooke, 1872)	Kenya, Uganda and Tanzania
	Thomson's gazelle	*Gazella thomsonii* (Günther, 1884)	Kenya and Tanzania
	Roan antelope	*Hippotragus equinus* (Desmarest, 1804)	Kenya, Uganda and Tanzania
	Sable antelop	*Hippotragus niger* (Harris, 1838)	Kenya and Tanzania
	Common waterbuck	*Kobus ellipsiprymnus* (Ogilby, 1833)	Kenya, Uganda and Tanzania
	Kob	*Kobus kob* (Erxleben, 1777)	Uganda
	Puku	*Kobus vardonii* (Livingstone, 1857)	Tanzania
	Gerenuk	*Litocranius walleri* (Brooke, 1879)	Kenya and Tanzania
	Guentheri's dik-dik	*Madoqua guentheri* (Thomas, 1894)	Kenya and Uganda
	Kirki's damara dik-dik	*Madoqua kirki* (Günther, 1880)	Kenya and Tanzania
	Salt's dik-dik	*Madoqua saltiana* (Desmarest, 1816)	Kenya
	Bate's pigmy antelope	*Neotragus batesi* (de Winton, 1903)	Uganda
	Suni	*Neotragus moschatus* (Von Dueben, 1846)	Kenya and Tanzania
	Klipspringer	*Oreotragus oreotragus* (Zimmermann, 1783)	Kenya, Uganda and Tanzania
	Oryx or gemsbok	*Oryx gazella* (Linnaeus, 1758)	Kenya, Uganda and Tanzania
	Oribi	*Ourebia ourebi* (Zimmermann, 1783)	Kenya, Uganda and Tanzania
	Steinbok	*Raphicerus campestris* (Thunberg, 1811)	Kenya and Tanzania
	Sharpe's grysbok	*Raphicerus sharpei* (Thomas, 1897)	Tanzania
	Southern reedbuck	*Redunca arundinum* (Boddaert, 1785)	Tanzania
	Mountain reedbuck	*Redunca fulvorufula* (Afzelius, 1815)	Kenya, Uganda and Tanzania
	Bohor reedbuck	*Redunca redunca* (Pallas, 1767)	Kenya, Uganda and Tanzania
	Lichtenstein's hartebeest or konzi	*Sigmoceros lichtensteinii* (Peters, 1849)	Tanzania
	Common, grey or bush duiker	*Sylvicapra grimmia* (Linnaeus, 1758)	Kenya, Uganda and Tanzania
	African buffalo	*Syncerus caffer* (Sparrman, 1779)	Kenya, Uganda and Tanzania
	Common eland	*Taurotragus oryx* (Pallas, 1766)	Kenya, Uganda and Tanzania
	Bongo	*Tragelaphus eurycerus* (Ogilby, 1837)	Kenya and Uganda
	Lesser kudu	*Tragelaphus imberbis* (Blyth, 1869)	Kenya, Uganda and Tanzania
	Bushbuck	*Tragelaphus scriptus* (Pallas, 1766)	Kenya, Uganda and Tanzania
	Sitatunga	*Tragelaphus spekii* (Sclater, 1863)	Kenya, Uganda and Tanzania
	Greater kudu	*Tragelaphus strepsiceros* (Pallas, 1766)	Kenya, Uganda and Tanzania
Giraffidae	Giraffe	*Giraffa camelopardalis* (Linnaeus, 1758)	Kenya, Uganda and Tanzania
Hippopotamidae	Common hippopotamus	*Hippopotamus amphibius* (Linnaeus, 1758)	Kenya, Uganda and Tanzania
Suidae	Forest hog	*Hylochoerus meinertzhageni* (Thomas, 1904)	Kenya, Uganda and Tanzania
	Desert warthog	*Phacochoerus aethiopicus* (Pallas, 1766)	Kenya
	Common warthog	*Phacochoerus africanus* (Gmelin, 1788)	Kenya, Uganda and Tanzania
	Bushpig or Malagasy wild boar	*Potamochoerus larvatus* (F. Cuvier, 1822)	Kenya, Uganda and Tanzania
Tragulidae	Water chevrotain	*Hyemoschus aquaticus* (Ogilby, 1841)	Uganda
Equidae	Burchell's zebra	*Equus burchellii* (Gray, 1824)	Kenya, Uganda and Tanzania
	Grevy’s zebra	*Equus grevyi* (Oustalet, 1882)	Kenya

2.2.3 Climatic and environmental variables

The climatic and environmental data were compiled from a number of sources. The climatic, soils and land cover data were generated from the ACTS database (ACTS, 1994). Solar radiation was computed from a digital elevation model (DEM) and algorithms as described in Kumar *et al.* (1997). The climatic database was developed based on data gathered by various organizations, such as local meteorological departments, the World Meteorological Organization (WMO), research organizations including CIMMYT, the Food and Agriculture Organization (FAO), the East Anglia Climate Research Unit and Texas A&M University. The climate grids were obtained by first fitting topographically dependent climate surfaces to point climate data, using procedures in the ANUSPLIN package (Hutchinson, 1991). The surfaces were then interpolated using elevations from the DEM, using the ANUCLIM package (McMahon *et al.*, 1995). Both elevation and climate data were subjected to comprehensive error detection and correction procedures based on ANUDEM and ANUSPLIN. Complete descriptions of the topographic and climate database for Africa are being prepared (Hutchinson *et al.*, in prep.).

The Advanced Very High Resolution Radiometer (AVHRR) on board the National Oceanic and Atmospheric Administration (NOAA) orbiting satellites collected the NDVI images used in the study. The AVHRR collects data over the entire globe twice daily, once during the daytime and once during the night-time. The vegetation index is derived as a function of the difference between the visible and near-infrared channels over the sum of the two channels. The sub-continental data set of 8 km resolution data was used to derive the aggregated NDVI maps. The NDVI data were downloaded from the African Data Dissemination Service (ADDS). The images covered the period 1982-1999. A total of 36 images were available for each year, based on the 10 days maximum value composite images. Detailed processing procedures and the calibration of the images are discussed in Los (1998). The downloaded images were calibrated for inter- and intra-sensor degradation and effects of El Chichcon and Mt Pinatubo volcanic events.

2.2.4 Derivation of spatial data sets

The resampling of the distribution of ungulate species richness to match the environmental variables was realised at 1.5° by 1.5° or 167 km by 167 km quadrat (refer to methodology in Schall and Pianka, 1978; Owen, 1990; Currie, 1991; Anderson and Marcus, 1993). The number of ungulate species occurring in each quadrat was established by overlaying 55 species maps with a regional 1.5° by 1.5° quadrat map. The total number of species occurring in each quadrat was taken as the species richness for that quadrat. The values for rainfall, potential evapotranspiration (PET), temperature, solar radiation, NDVI and elevation variables were determined using the average value for each quadrat.

2.2.5 Statistical analysis

The relation between species richness and productivity was determined by examining bivariate plots of species richness and each of the explanatory variables. Species richness was regressed against each environmental variable, using linear, polynomial, logarithmic and exponential models. The fitting of higher polynomial order models was used if they provided a statistical improvement in fit. The best fitting model was selected based on the *F*-test (Zar, 1996). A test of the equality of two population regression coefficients (Zar, 1996) was used to compare the pair of models. Tests for independence of the residual (Durbin-Watson test) and normality (Kolmogorov-Smirnov test) were conducted for each model.

In the next stage of the analysis the most important climatic variables for explaining the variation in ungulate species richness were investigated. Using stepwise regression models the probability of each variable entering, and staying in, the model was set at $P = 0.05$. Finally a comparison between the integrated climatic model and the NDVI model was assessed. The statistical analyses were performed in Systat 7.0.1 (SPSS Inc., 1997).

2.3 RESULTS

2.3.1 General ungulate species richness patterns

Table 2.1 reveals that at country level Tanzania and Kenya host a higher number of ungulate species than Uganda. Figure 2.1 shows the spatial distribution of ungulate species richness in East Africa. A pronounced latitudinal gradient is apparent, with maximum richness between 0º North and 9º South. Longitudinal patterns were not strongly evident, though species richness was higher between longitudes 34º and 38º East. The highest species richness occurred mainly in the *Acacia* grasslands and grassy shrublands of northern and central Tanzania and southwestern Kenya, with most of the surrounding areas having medium species richness. Low species richness occurred mainly in the extreme arid environments of northern Kenya and northern Uganda. The distribution of individual species in relation to rainfall gradient is shown in Figure 2.2.

2.3.2 Species richness-productivity relationship

Figure 2.3 shows the relation between species richness and four NAPP indices. The relation between species richness and NDVI and rainfall reveals a unimodal or a hump-shaped pattern (Figure 2.3a and Figure 2.3b). A second-order polynomial regression best describes this relationship, while a third-order model did not significantly improve the fit (R^2 of 0.55 vs. 0.56; $F = 0.41$ and $P = 0.66$). A third-order polynomial best describes the pattern (R^2 of 0.69). The relationship between species richness and temperature and PET was revealed to be linear (Figs 2.3c and d). There was no significant relation between species richness and total solar radiation.

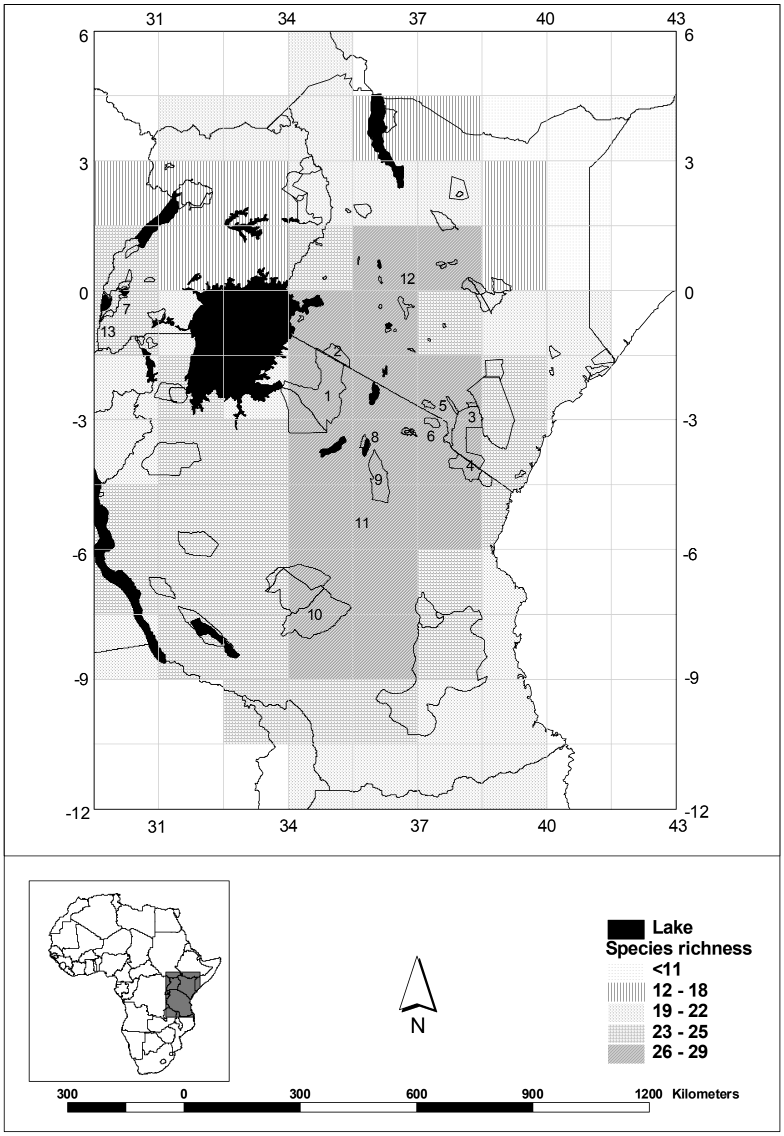

Figure 2.1: Distribution of number of ungulate species per grid cell of 1.5º by 1.5º in East Africa. The map is based on the overlay of 55 species maps. Protected and adjacent sites that have high species richness include [1]Serengeti-[2]Masai Mara ecosystem, [3]Tsavo-[4]Mkomazi ecosystem, [5]Amboseli-[6]Loliondo ecosystem, [7]Queen Elizabeth National Park and surrounding areas, [8]Manyara-[9]Tarangire ecosystem and [10]Ruaha-Rungwa ecosystem. Non-protected areas that exhibit high species richness include [11]parts of central Tanzania, [12]Laikipia-Samburu and [13]southwestern Uganda.

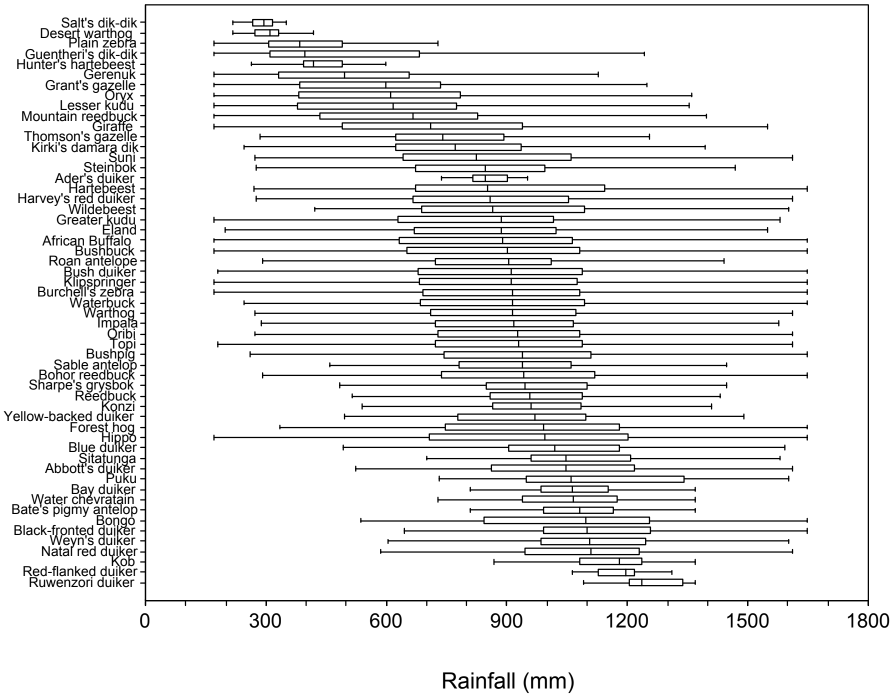

Figure 2.2: A boxplot showing the relation between species distribution and average rainfall within East Africa. The central vertical line in each box represents the median and the bars represent 1.5 of the inter-quartile range above the third quartile or below the first quartile.

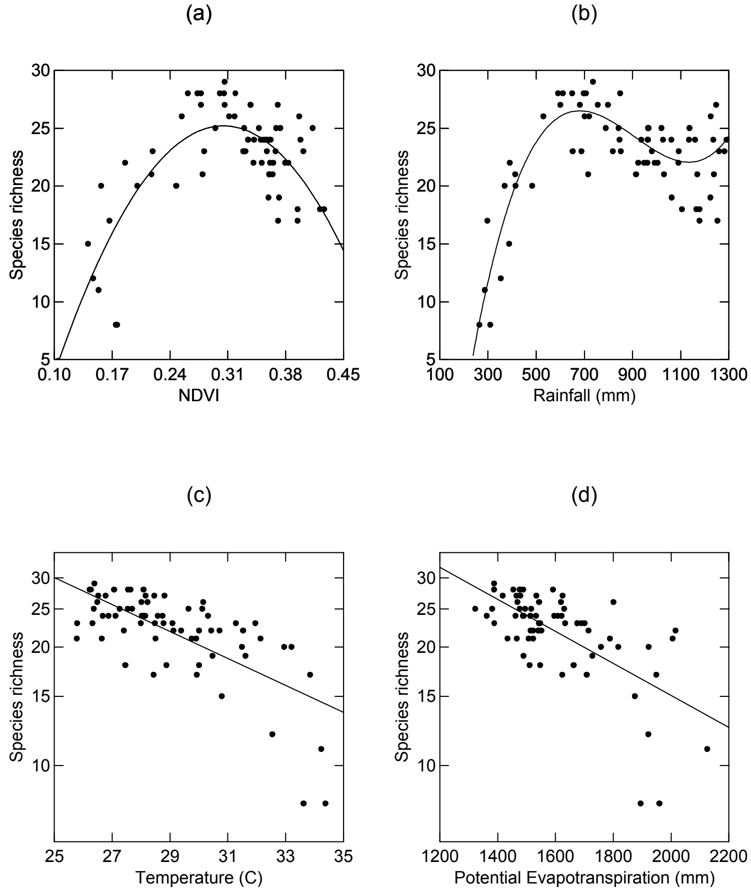

Figure 2.3: Relationship between ungulate species richness and mean annual values of four variables related to primary productivity in East Africa. Data points refer to areas of 1.5° x 1.5° (refer to Table 2.2 for detailed equations for each relationship).

The relationship between rainfall and NDVI is shown in Figure 2.4. It reveals that the NDVI value levels off at higher rainfall values, and possibly reaches an asymptote somewhere beyond 1400 mm of rainfall (NDVI = -0.7725 + 0.1613Ln(P), $P < 0.0001$, $r^2 = 0.87$, n = 69).

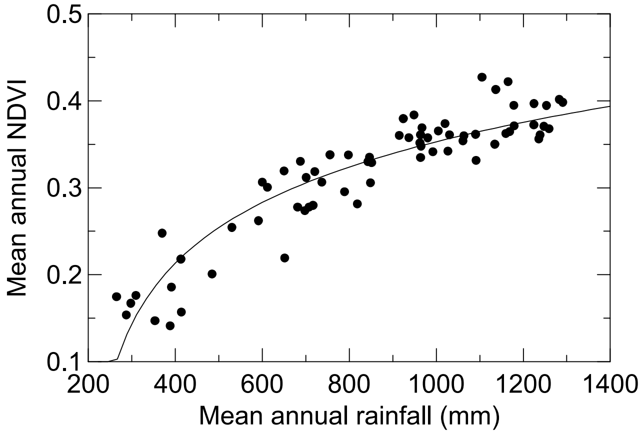

Figure 2.4: Relationship between mean annual precipitation and mean annual NDVI in East Africa; the relationships level off at higher rainfall values of about 1000 mm.

Table 2.2 summarizes the results of the statistical analysis of the relation between species richness and four environmental factors related to NAPP. The analysis was run for the whole range of rainfall (200 – 1300 mm), as well as for a shorter rainfall range (200 – 1000 mm) where rainfall and NDVI were linearly related. The strongest correlates of species richness were rainfall and NDVI, with 69% and 55% of the variance in richness explained. The variance explained increased towards 80% and 67%, respectively, when considering the drier part of the rainfall gradient.

We next compared the best-fit climatic model (including a number of climatic variables) with the best-fit remotely sensed model (Table 2.3). Rainfall and PET explained a significantly higher proportion of the variance in species composition than remotely sensed data did. This conclusion was valid for the whole range of rainfall (200 – 1300 mm; $t = 2.22$, $P = 0.028$) but not significant for the drier end of the rainfall gradient (200 – 1000 mm; $t = 1.32$; $P = 0.01$).

Table 2.2: Regression equations describing the best fitting model of polynomial (fourth order), exponential and logarithmic functions fitted between species richness and four factors related to NAPP.

Rainfall range (mm)	Factors	Model	r^2	*n*
200 - 1300	Precipitation	$-34.01 + 2.22*10^{-1}x – 2.61*10\text{-}^{4}x^{2} + 1*10^{-7}x^{3}$	.69*	69
	Temperature	$61.77 – 1.3568x$	.47*	
	Potential evapotranspiration	$49.34 – 0.0167x$	.44*	
	NDVI	$-22.22 + 311.26x – 510.71x^{2}$	.55*	
<1000	Precipitation	$-13.71 + 1.09*10^{-1}x – 7.5*10^{-5}x^{2}$	.77*	44
	Temperature	$74.19 – 1.7459x$	.66*	
	Potential evapotranspiration	$55.89 – 0.0201x$	.56*	
	NDVI	$-27.75 + 357.35x – 595.99x^{2}$	.67*	
1000 - 1300	Precipitation		ns	25
	Temperature	$41.18 – 0.79x$	.21***	
	Potential evapotranspiration	$55.40 – 0.02x$	.45**	
	NDVI		ns	

ns = not significant; * = $P < 0.0001$; ** = $P < 0.001$; *** = $P < 0.05$

Table 2.3: Regression equations describing the best fitting model between species richness and combined climatic variables, respectively remotely sensed variables, for two ranges of rainfall.

Rainfall range (mm)	Factors	Model	r^2	*n*
200 - 1300	Climatic	$-1.24 + 1.81*10^{-1}P – 22.26*10^{-4}P^{2} + 8*10^{-8}P^{3} – 1.17*10^{-2}PET$	.76	69
	Remotely sensed	$-22.22 + 311.26NDVI – 510.71NDVI^{2}$	.55	
200 - 1000	Climatic	$6.44 + 9.00*10^{-2} P – 7.57*10^{-3}P^{2} – 6.33*10^{-5}PET$	.80	44
	Remotely sensed	$-27.75 + 357.35NDVI – 595.99NDVI^{2}$	.67	

All models were significant at $P < 0.0001$. P = Precipitation; PET = Potential evapotranspiration; and NDVI = Normalized difference vegetation index.

2.4. DISCUSSION

2.4.1 Predictor of ungulate species diversity – climatic indices versus remotely sensed NDVI

The results from this study reveal that the remotely sensed index was not a better predictor of species richness than integrated climatic indices. This is contrary to our initial expectation and contradicts established literature (Nicholson *et al.*, 1990; Walker *et al.*, 1992; Stoms and Estes, 1993; Los, 1998b). The climatic model was more predictive than NDVI in areas with a rainfall range between 200 and 1300 mm; for the drier part of the rainfall gradient (<1000 mm) the difference was not significant. The difference in variance explained by the two models was investigated by reviewing the literature that related NDVI and climatic variables to NAPP. Figure 2.5 summarizes the conceptual model of primary relationships controlling species richness.

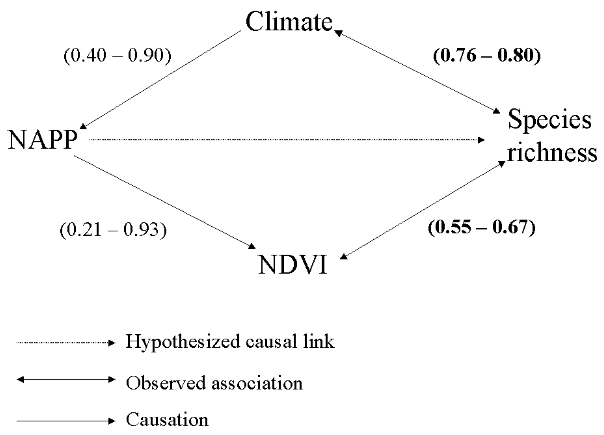

Figure 2.5: Scheme of the relation between species richness, NAPP, climate and NDVI. NAPP is hypothesized to have a causal link with species diversity. We expected that NDVI would be a better predictor of species diversity. This was not the case; climatic factors proved to be superior predictors. Values in brackets indicate range of r^2 values reported in this study (bold), respectively range of values reported in other studies (regular).

The relationship between rainfall and productivity shows that the coefficient of determination ranged between 0.40 and 0.90. In sub-Sahara Africa productivity generally relates well to average rainfall (Le Houerou and Hoste, 1977; Deshmukh, 1984; McNaughton, 1985; van Wijngaarden, 1985; Boutton *et al.*, 1988; Box *et al.*, 1989). However, the problems associated with rainfall-productivity models are linked to sampling a few points only and interpolating the data over large areas, as well as failure to incorporate all factors related to NAPP – soil and plant characteristics and resource regulators (Le

Houerou and Hoste, 1977; Box, 1978; Box *et al.*, 1989). The published information on the relationship between NDVI and productivity varies, with the coefficient of determination ranging between 0.21 and 0.93 (refer to Figure 2.5; McNaughton, 1976; Boutton and Tieszen, 1983; Tucker *et al.*, 1985; Diallo *et al.*, 1991; Prince, 1991b; Wylie *et al.*, 1991; Hobbs, 1995). The variation between rainfall and NDVI can be related to the reflectance property of the vegetation cover, as illustrated in the schematic diagram shown in Figure 2.6.

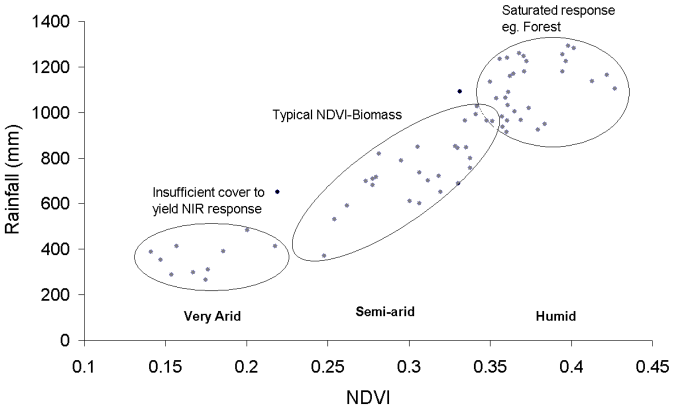

Figure 2.6: Relationship between rainfall and NDVI, which indicates poor correlation in the very arid and humid areas; a strong relation is observed in the semi-arid areas *(*refer to the text for detailed description).

The problems associated with the vegetation index in arid areas are mainly due to soil-vegetation spectral mixing (Heute and Tucker, 1991). In poorly vegetated areas there is insufficient cover to yield a reflectance response near infrared (NIR). In the semi-arid areas the relation is much stronger, with NDVI being linearly correlated with productivity. In the humid areas above a certain threshold (in this study 1000 mm), the NDVI is not sensitive to rainfall variations (Sellers, 1985; Box *et al.*, 1989; Nicholson *et al.*, 1990). In addition to vegetation cover other factors such as soils and atmospheric conditions can minimize the accuracy of predicting NAPP based on NDVI. It has been observed in partially vegetated areas (40–75% green cover) that soil darkening due to moisture or soil type can increase the NDVI by 25% (Heute and Tucker, 1991; Nicholson and Farrar, 1994). Water vapour and aerosol, however, have been reported to reduce the integrated NDVI by about 30 to 60% (Justice *et al.*, 1991). The further improvements in spectral, spatial and temporal resolutions to be introduced in the new satellite sensors, including information on surface radiation, ecosystem variables (leaf area, leaf duration and primary productivity) and land cover characteristics, should significantly improve the potential use of remotely sensed data in biodiversity studies.

This study has established that climatic model was more predictive than NDVI in areas with a rainfall range between 200 and 1300 mm; for the drier part of the rainfall gradient (<1000 mm) the difference was not significant. The factors discussed in this study indicate the limitations of NDVI in predicting NAPP and could have contributed significantly to the fact that the NDVI model did not to perform better than the climatic model in predicting species richness. This observation is supported by a number of studies relating species richness to NDVI. Most of these studies have reported lower correlations between plant or mammalian species richness and NDVI (see Walker *et al.*, 1992; Jorgensen and Nohr, 1996; Oindo *et al.*, 2000; Baird, 2001; Oindo and Skidmore, 2002; this study) than those studies using climatic variables as proxy for productivity (refer to Abramsky and Rosenzweig, 1984; Owen, 1988; Owen, 1990; Currie, 1991; Prins and Olff, 1998; Waide *et al.*, 1999; Balmford *et al.*, 2001; Olff *et al.*, 2002).

2.4.2 Ungulate species diversity pattern and its implication for conservation

The species richness in East Africa is best described as unimodal in pattern (refer to Figure 2.3b). The strongest single factor that best predicated ungulate species richness was rainfall. Contrary to expectations that high productive areas would have high species richness (energy limitation theory – see Wright, 1983), ungulates were highest at the intermediate productivity level. The pattern is consistent with studies on variations in richness (plants and animals) as functions of productivity that show species richness reaches its maximum at intermediate productivity levels (see Grime, 1973; Huston, 1980; Tilman, 1982; Abramsky and Rosenzweig, 1984; Al-Mufti *et al.*, 1984; Owen, 1988; Rosenzweig and Abramsky, 1993; Prins and Olff, 1998; Huston, 1999; Balmford *et al.*, 2001; Olff *et al.*, 2002). The hump-shaped curve of the species richness-productivity relationship appears to be composed of at least two phases: the positive (Kenya) and negative slopes (Tanzania and Uganda) that make up the two sides of the hump-shaped curve, with maximum species richness occurring in both Kenya and Tanzania.

A number of studies have shown that ungulate species diversity varies across gradients of plant abundance and quality (Western, 1975; Coe *et al.*, 1976; Bell, 1982; East, 1984; McNaughton, 1985; Prins and Olff, 1998; Olff *et al.*, 2002). Olff *et al.* (2002) further suggested that herbivore species must encounter plants of both sufficient abundance and quality to persist, and therefore may be constrained to persist only under certain conditions of plant-available moisture and nutrients. The highest herbivore density is thus expected in locations that are neither so wet and /or infertile that average plant quality would be too low to sustain smaller herbivores, nor so dry and /or infertile that plant productivity would be insufficient to sustain larger herbivores. The dry and infertile habitats have low population abundance − raising extinction rates, which may limit species diversity (Rosenzweig and Abramsky, 1993). While the low biomass of herbivore communities in moist savannas reflects the limitation imposed by vegetation quality rather than quantity (Bell, 1982; Olff *et al.*, 2002), the isolation of the population of *Cephalophus* and *Sylvicarpa* (mainly the duikers) in the forest environment over time may also have segregated the group from other ungulate species, preventing frequent mixing (Sinclair, 1983). Abrams (1995) argued that such taxonomic groups are likely to have their highest diversity in the types of environment where they have spent most of their evolutionary history.

The implication of these patterns is that both the savanna and forest ecosystems have a high diversity of ungulate species. Balmford *et al.* (2001) found high correlation between species richness and population density in Africa. These findings have been supported by local studies which have shown that increased encroachment and fragmentation of wildlife habitat through uncontrolled expansion of agriculture (Newmark, 1996; Ottichilo, 2000; Homewood *et al.*, 2001), deforestation (Chapman and Lambert, 2000), illegal killings (Caro *et al.*, 1998; McRae, 1998; Mduma *et al.*, 1998) and the introduction of artificial water points (de Leeuw *et al.*, 2001) have negatively affected wildlife diversity in East Africa. Most of these changes are occurring in the areas of high species diversity. The overall effects may be reflected in the current status of the ungulate species, where out of the 55 species studied here, one is critically endangered, three are threatened, seven are near threatened and the rest depend on the conservation status where they are located. Immediate action is needed to further manage and conserve areas of high species richness, and the models developed in this study could be used as a first step in mapping potential conservation areas that need attention.

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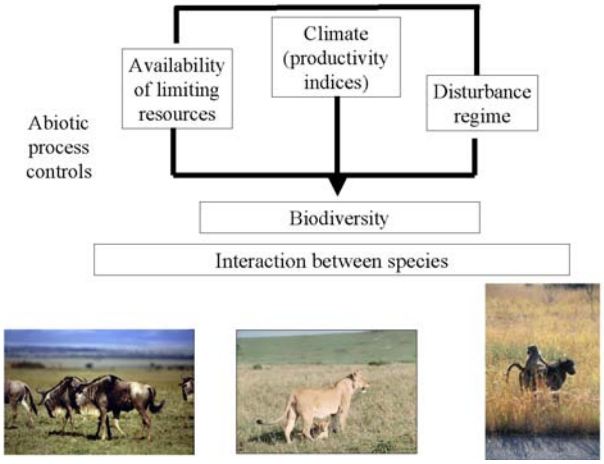
CHAPTER 3

MAMMALIAN SPECIES RICHNESS IN RELATION TO RAINFALL IN EAST AFRICA: DO SIMILAR PATTERNS EXIST AMONG TAXONOMIC GROUPS?

The aim of this study was test species richness – productivity of various taxonomic grouping (based on class, order and family groupings) *was similar. In this study we restricted our focus to mammalian species, chose a single productivity variable and conducted the study in East Africa.*



Chapter 3

Mammalian species richness in relation to rainfall in East Africa: do similar patterns exist among taxonomic groups?

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Abstract

The aim of this study was to test whether different species groupings had similar species-productivity patterns. We focused our study on East Africa, which to a large extent has retained the full diversity of its large mammal species and covers microhabitats ranging from desert-like conditions to tropical forests. The species richness of the various animal groups (11 orders and 10 families) was regressed against rainfall, using linear, polynomial, logarithmic and exponential models. The study revealed that five out of 11 orders (Artiodactyla, Hyracoidea, Rodentia, Macroscelidea and Carnivora) exhibited a unimodal pattern. The productivity-richness was dependent on taxonomic scale of the investigation, with signs of high variations at lower levels than at the level of orders and class. We conclude that species richness – productivity relationship is clearly scale-dependent. On a sub-continental scale the geographical patterns in species richness were similar among a number species groupings and tended to converge towards the same level (intermediate productivity) especially at the higher taxonomic level. The high variation of patterns at lower taxonomic level may reflect partitioning of energy gradient among families or group of species. This may be a result of different processes controlling richness at different spatial scales for various species groups.

3.1 INTRODUCTION

Studies conducted at sub-continental or continental scale have indicated that productivity and energy flows through an ecosystem are major determinants of species diversity (Abramsky and Rosenzweig, 1984; Owen, 1988; Currie, 1991; Said *et al.*, in press). Additional factors such as resource competition and facilitation (Sinclair, 1975; Sinclair, 1979; McNaughton, 1985; Prins and Olff, 1998), land use change through human

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submitted to *Ecological Indicators*

interference (Chaplin *et al.*, 2000; Sala *et al.*, 2000) and climatic disturbances (Sinclair, 1983b; Chaplin *et al.*, 2000) also contribute to variation in species diversity and assemblages of animals at this scale. Literature on the relationship between species diversity and productivity is abundant but often contradictory (see reviews Grace, 1999; Waide *et al.*, 1999), and the general theory has not been consistent (Grime, 1973; Tilman, 1982; Rosenzweig and Abramsky, 1993; Huston, 1994; Abrams, 1995).

Several studies have shown that the choice of geographical and ecological extent, taxonomic hierarchies or indices of productivity can lead to a multitude of patterns (Owen, 1990; Guo and Berry, 1998; Grace, 1999; Waide *et al.*, 1999). Waide *et al.* (1999) in their assessment of more than 200 productivity-diversity relations concluded that it requires careful attention to spatial and ecological scales to detect and understand patterns. A number of studies have addressed the effects of scaling on species diversity, with emphasis on data resolution (Anderson and Marcus, 1993; Bohning-Gaese, 1997) and sampling methods (Moore and Keddy, 1989; Rose and Legget, 1990; Lyons and Willing, 1999). Few studies have examined how groups of animals (based on taxonomic hierarchy) respond to productivity within a biogeographical area (see Currie, 1991; Kaufman and Willing, 1998**;** Rose and Legget, 1990). Such studies on interactions among the various taxonomic groups may further improve the theoretical framework of species diversity-productivity patterns.

The aim of this study was to test whether different species groupings (based on class, order and family groupings) had similar species-productivity patterns. In this study we restricted our focus to mammals, chose a single productivity variable and conducted the study in East Africa (sub-continental scale). East Africa is a natural experimental area to study species diversity-productivity interactions. It has to a large extent retained the full diversity of its large mammal species (Sinclair, 1995; Prins and Olff, 1998), and encompasses a number of microhabitats, ranging from desert-like conditions to tropical forests (Pratt and Gwynne, 1977).

3.2 MATERIAL AND METHODS

3.2.1 The study area

East Africa is situated approximately between longitudes 12° South and 6° North and latitude 29° West and 42° East. The study area covers Kenya (569,260 km^2), Tanzania (886,220 km^2) and Uganda (207,950 km^2). The vegetation of East Africa is highly heterogeneous, with great variability in structure and productivity (Coe *et al.*, 1976; Pratt and Gwynne, 1977; East, 1984; van Wijngaarden, 1985; McNaughton *et al.*, 1989). The principal modifying factors that control productivity are fire, herbivory and soil nutrient (Bell, 1982; McNaughton, 1985; van Wijngaarden, 1985; Belsky, 1986; Dublin *et al.*, 1990; Sinclair, 1995). The vegetation is composed mainly of open *Acacia* grassland, dwarf shrub grassland and sparsely vegetated xeric grasslands, shrublands, bushlands and montane forests (Pratt and Gwynne, 1977; Bourliere and Hadley, 1983).

Productivity is highly influenced by spatial and seasonal distribution of precipitation (Deshmukh, 1984; McNaughton, 1985; Nicholson *et al.*, 1990). The range of precipitation varies between and within the three countries. Uganda has the highest rainfall

(900 – 1300 mm), with moderate rainfalls in Tanzania (600 – 1230 mm), and Kenya having drier areas (200 – 1300 mm). The three main rainfall patterns in the region are: year-long rainfall (around Lake Victoria), single season rainfall (northern Uganda, northwestern Kenya, most of Tanzania) and bimodal rainfall (rest of Kenya) (Pratt and Gwynne, 1977).

3.2.2 Mammalian and climatic data

Digital data on large mammalian distributions at regional level were acquired from the African Mammal Databank (Boitani *et al.*, 1999). A total of 163 species, belonging to 11 orders and 10 families were included in the analysis (Table 3.1).

Table 3.1: Listing of order, family and the number of species included in the study. The common names for order and family are indicated in brackets. The figures in parentheses are the number of species observed at continent level.

Order	Family	Number of Species
Artiodactyla (Even-toed ungulates)	*Bovidae* (Horned antelopes)	51(79)
	Giraffidae (Giraffes)	2(2)
	Hippopotamidae (Hippopotamuses)	1(2)
	Suidae (Pigs)	5(6)
	Tragulidae (Chevrotains)	1(1)
Perissodactyla (Odd-toed ungulates)	*Equidae* (Horses)	2(4)
Hyracoidea (Hyraxes)	*Procavidae* (Rock hyraxes)	5(6)
Tubulidentata (Aardvark)	*Orycteropidae* (Aardvark)	1(1)
Carnivora (Carnivores)	*Canidae* (Dogs and allies)	5(12)
	Felidae (Cats)	7(10)
	Herpestidae (Mongoose)	15(24)
	Hyaenidae (Hyaenids)	3(4)
	Mustelidae (Mustelids)	6(10)
	Viverridae (Genets and civets)	8(15)
Insectivora (Insectivores)	*Erinaceidae* (Hedgehogs)	1(6)
	Tenrecidae (Otter shrews)	2(3)
Lagomorpha (Hares)	*Leporidae* (Hares)	
Macroscelidea (Elephant shrews)	*Macroscelididae* (Soft-furred elephant shrews)	7(15)
Pholidota (Scaly ant-eaters)	*Manidae* (Pangolins)	4(4)
Primates	*Cercopithecidae* (Monkeys)	16(39)
	Galagonidae (Bushbabies)	9(12)
	Hominidae (Man and apes)	2(3)
	Loridae (Lorisids)	1(3)
Rodentia (Rodents)	*Hystricidae* (Porcupines)	3(3)
	Pedetidae (Spring hares)	1(1)

The total number of species of these taxa in the study area are as follows: all mammalian species (*n* = 163), Artiodactyla (*n* = 60), Perissodactyla (*n* = 2), Hyracoidea (*n* = 5), Tubulidentata (*n* = 1), Carnivore (*n* = 44), Insectivora (*n* = 3), Lagomorpha (*n* = 5), Macroscelidea (*n* = 7), Pholiodota (*n* = 4), Primates (*n* = 28) and Rodentia (*n* = 4). We combined Artiodactyla, Hyracoidea, Perissodactyla, Tubulidentata, Proboscidea (note that data on the distribution of elephant and rhinoceros were not available) and Sirenia (species absent in the study area) into a larger group: the ungulates or hoofed animals. The second grouping consisted of all herbivore species. We followed the mammalian classification system of Wilson and Reeder (1993).

In this study we used rainfall as a descriptor of productivity. Studies in sub-Saharan Africa have shown that productivity generally relates well to average rainfall (Le Houerou and Hoste, 1977; Deshmukh, 1984; McNaughton, 1985; van Wijngaarden, 1985). In addition, a number of studies have related species richness to rainfall as a measure of productivity in the semi-arid and arid environments (Brown, 1973; Abramsky and Rosenzweig, 1984; Owen, 1988). The rainfall and topographic data were derived from the ACTS database developed by Texas A&M (ACTS, 1994).

3.2.3 Analytical procedures

The species richness was established by overlaying individual species maps with a 3º x 3º regional quadrat map, similar to methods used in studies conducted by Currie (1991), Owen (1990) and Schall and Pianka (1978). Earlier studies of Currie (1991) and Kerr *et al*., (1998) failed to find any indication that variation in quadrat area have a significant effect on the diversity of any vertebrate, plant, or invertebrate taxa. The total number of species occurring in each quadrat was taken as the species richness for that quadrat. Next, we examined the bivariate plots of species richness and each of the explanatory variables to determine the relationship. Later, we regressed species richness against rainfall, using linear, polynomial, logarithmic and exponential models. A higher polynomial model was fitted if there was a statistical improvement in fit based on the *F*-procedure (Zar, 1996). Tests for independence of the residual (Durbin-Watson test) and normality (Kolmogorov-Smirnov test) were conducted for each model. The statistical analysis was performed in Systat 7.0 (SPSS, 1997).

3.3 RESULTS

Maps of the spatial distribution of species richness of Mammals, Ungulates, Carnivores and Primates are shown in Figure 3.1. Descriptive and correlation statistics for species richness in the quadrat system of Figure 3.1 are as follows: Ungulates ($\overline{x}$ = 27, CV = 16) with Carnivores $r = 0.76$, with Rodentia $r = 0.72$, with Primates $r = 0.36$; Carnivores ($\overline{x}$ = 28, CV = 7) with Rodentia $r = 0.66$, with Macroscelididae $r = 0.66$, with Primates r = not significant; Primates ($\overline{x}$ = 10, CV = 42) with Insectivora $r = 0.75$, with Pholidota $r = 0.72$; Insectivora ($\overline{x}$ = 2, CV = 48) with Pholidota $r = 0.80$, with Rodentia $r = 0.56$, with Lagomorpha $r = 0.56$; significant at $P < 0.05$.

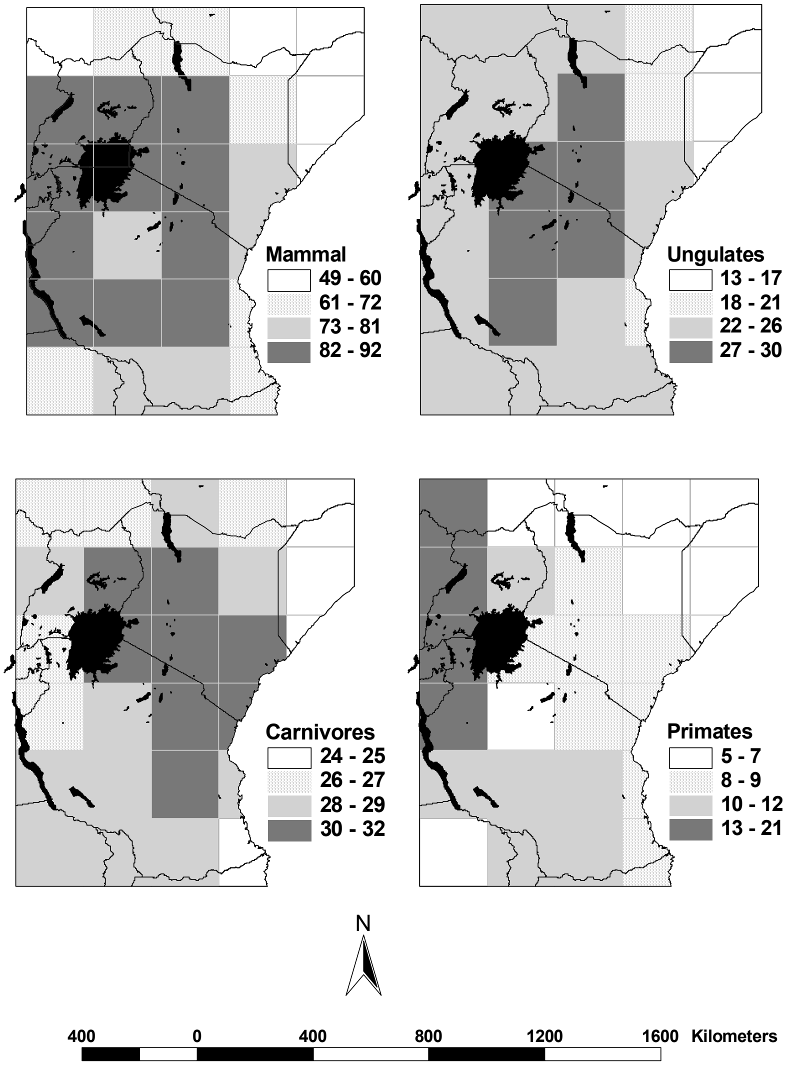


Figure 3.1: Geographical variation in species richness of mammals, ungulates, carnivores and primates in East Africa. Protected areas are symbolized in broken lines, and lakes indicated in continuous black colour. Each map is based on the overlay of species maps aggregated to 3° by 3° grids.

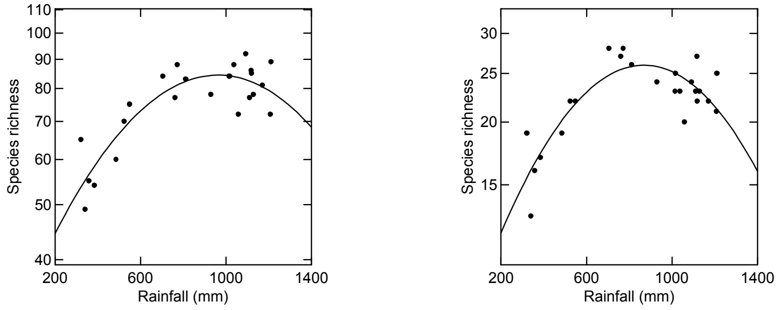
Table 3.2 present a summary of the relation between species richness of various faunal groups and rainfall. The richness of all mammals combined shows a unimodal or a humped-shaped pattern ($y = 14.99 + 0.142x – 0.0000736x^2$, $r^2 = 0.74$, $P < 0.001$, Figure 3.2a). The relationships between rainfall and species richness for five of the 11 orders (Artiodactyla, Hyracoidea, Carnivora, Macroscelidea and Rodentia) show a strikingly similar unimodal pattern (Figure 3.2b-e). The Primates (Figure 3.2f) and Insectivora revealed an exponential pattern. There was no significant relation between species richness and rainfall for the orders Perissodactyla, Tubulidentata, Pholidota and Lagomorpha.

Figure 3.3 shows the relationship between species richness at the lower taxonomic levels of the family (refer to Table 3.2 for the equations). A strong unimodal relationship between species richness and productivity was observed with the Bovidae ($r^2 = 0.81$, $P < 0.001$, Figure 3.3a). Procavidae (Figure 3.3b) and Macroscelididae (Figure 3.2d) showed similar pattern. Figure 3.4 displays combines (orders and family with similar pattern) the relationships between species richness and productivity.

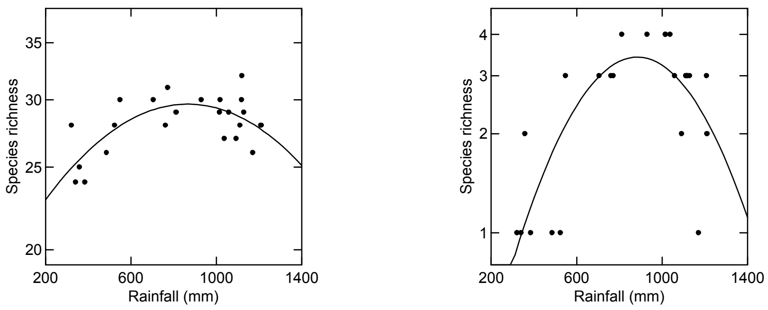
Table 3.2: Models predicting species richness as a function of productivity based on faunal grouping

Taxonomic aggregate			**Model**	**r^2**
Class	**Order**	**Family**		
Mammalia			$14.99 + 1.42*10^{-1}x – 7.36*10^{-5}x^2$	0.74***
Ungulate			$-1.32 + 7.67*10^{-2}x – 4.47*^{-5}x^2$	0.70***
	Artiodactyla		$-0.99 + 6.24*10^{-2}x – 3.63*10^{-5}x^2$	0.69***
		Bovidae	$-6.41 + 6.89*10^{-2}x – 4.04*10^{-5}x^2$	0.81***
	Hyracoidea	Procavidae	$-0.11 + 7.9*10^{-3}x – 4.52*10^{-5}x^2$	0.47**
	Perissodactyla			ns
	Tubulidentata			ns
	Rodentia		$-2.55 + 1.27*10^{-2}x – 702*10^{-5}x^2$	0.53**
	Macroscelidea	Macroscelididae	$-3.63 + 1.63*10^{-2}x – 9.38*10^{-5}x^2$	0.59**
	Carnivora		$17.74 + 2.76*10^{-2}x – 1.59*10^{-5}x^2$	0.46**
		Canidae	$5.4128e^{-0.0003x}$	0.32**
		Felidae		ns
		Herpestidae	$1.4922Ln(x) – 2.3022$	0.58***
		Mustelidae	$2.1835Ln(x) – 10.193$	0.66***
		Viverridae	$2.1037Ln(x) – 8.8128$	0.55***
	Primates		$4.037e^{0.001x}$	0.66***
		Cercopithecidae	$2.192e^{0.001x}$	0.60***
		Galagonidae	$-8.13*10^{-1} + 1.19*10^{-2}x – 6.43*10^{-6}x^2$	0.32*
	Insectivora		$0.6809e^{0.0008x}$	0.36*
	Pholidota			ns
	Lagomorpha			ns

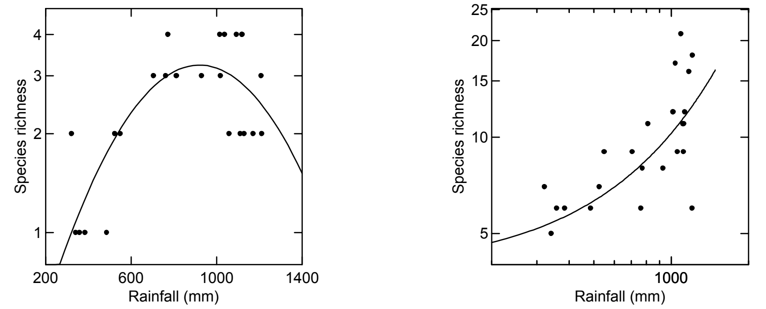
$*P < 0.05$; $** P < 0.001$; $*** P < 0.0001$


(a) Mammals

(b) Artiodactyla

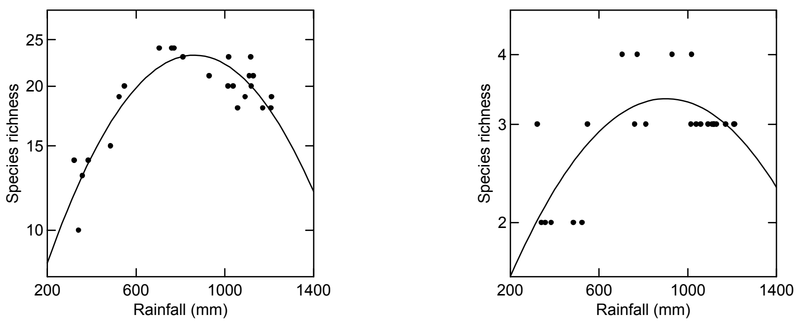

(c) Carnivora

(d) Macroscelidea

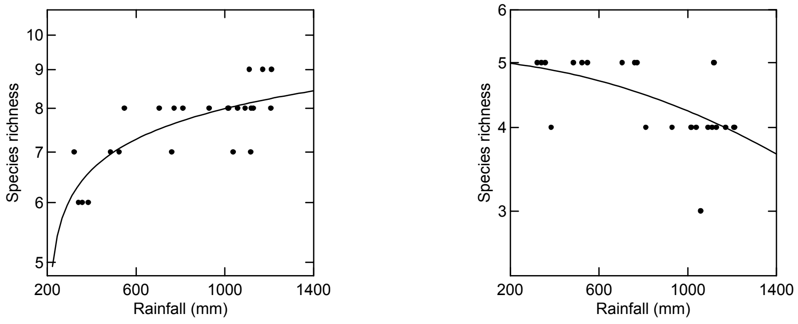

(e) Rodentia

(f) Primates

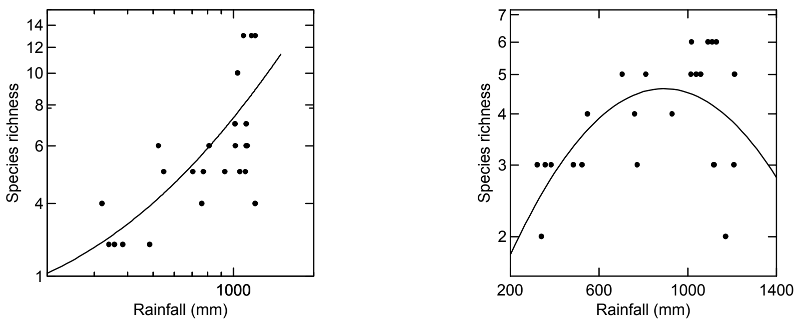
Figure 3.2: Relationship between species richness (at class and order level) and mean annual rainfall *(*refer to Table 3.2 for the detailed equation for each of the relationships).


(a) Bovidae

(b) Procaviidae


(c) Herpestidae

(d) Canidae


(e) Cercopithecidae

(f) Galagonidae

Figure 3.3: Relationship between species richness (family level) and mean annual rainfall (refer to Table 3.2 for the detailed equation for each of the relationships).

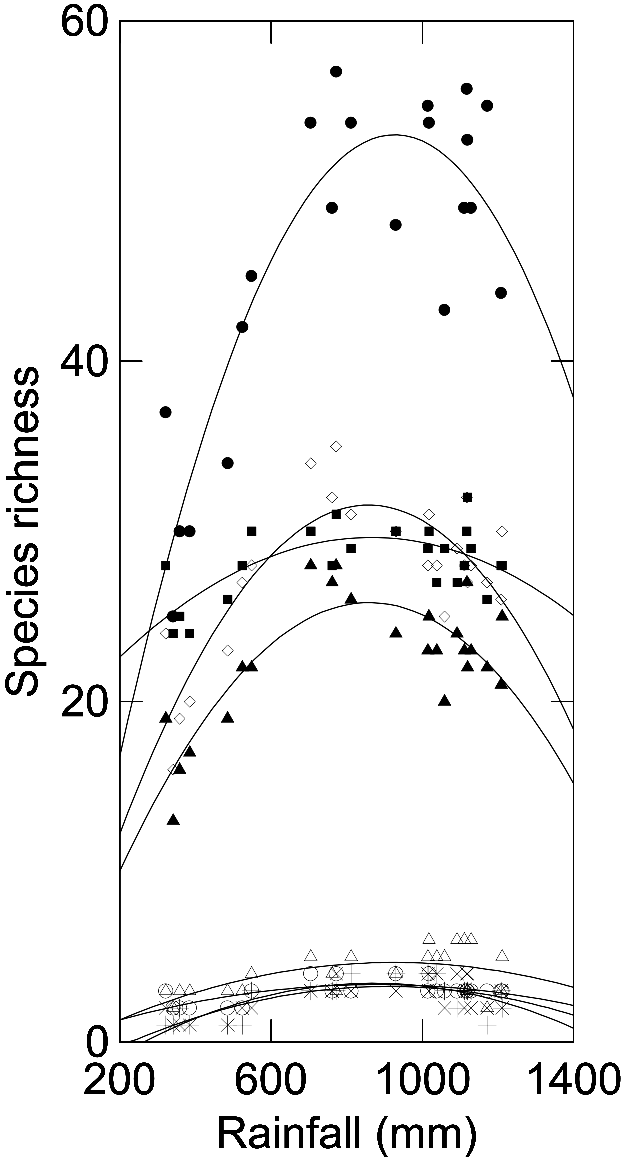


Figure 3.4: Relationship between species richness and productivity showing similar patterns among a number of fauna and taxonomic groups. The following notations represent: all Herbivores (●); Ungulates (◊); Carnivores (■); Artiodactyls (▲); Galagonidae (Δ), Rodentia (○), Macroscelidea (+), Hyracoidea (x).

The relationship between the second largest group, the Carnivora and productivity was also humped-shaped ($17.74 + 0.027x – 0.0002x^2$, $r^2 = 0.46$, $P < 0.002$, $n = 24$). The five families under the order Carnivora showed two distinct patterns: the species richness of Herpestidae (Figure 3.3c), Mustelidae and Viverridae increased as productivity increased, whereas the species richness of Canidae (Figure 3.3d) and Hyaenidae decreased as productivity increased. The Cercopithecidae or monkeys had an exponential pattern (Figure 3.3e), which was similar to its higher class the Primates, while Galagonidae or bushbabies (lower taxonomic level) showed a unimodal pattern (Figure 3.3f). For the other families the correlation was generally weaker and more variable, with no significant pattern.

3.4 DISCUSSION

3.4.1 Species diversity – productivity patterns

The result of this study shows that species richness had a different response to productivity depending on the species grouping (order and family). Five out of 11 orders (Artiodactyla, Hyracoidea, Rodentia, Macroscelidea, and Carnivora) showed a unimodal pattern. The results are also consistent with the findings of most earlier studies, showing that species richness first rises and then declines with continued increase of biomass (see also Grime, 1973; Huston, 1980; Tilman, 1982; Abramsky and Rosenzweig, 1984; Al-Mufti *et al.*, 1984; Owen, 1988; Rosenzweig and Abramsky, 1993; Prins and Olff, 1998; Huston, 1999; Balmford *et al.*, 2001; Olff *et al.*, 2002). The second important pattern revealed in this study is that the relationship between species richness and rainfall at family level was different for various species group. The pattern of carnivores was more related to food type (Schoener, 1974) than habitat type (for example highly correlated to bovine distribution. At family level the species richness of Herpesitade (Mongoose), Mustelidae (Mustelids) and Viverridae (Genets & civets) increased monotonically with productivity, whilst the Canidae (Dogs & allies) decline monotonically with rainfall. The results for the other family groups (Bovidae, Procavidae, Macroscelididae and Galagonidae or the bushbabies) were consistent with the unimodal pattern.

3.4.2 Trophic levels and secondary interactions

Competition, mutualism and trophic interactions frequently lead to secondary interactions among species (Chaplin *et al.*, 2000). The similarity in patterns in the fauna communities as presented in this study shows that assemblages of species may not be just random and the fauna of any region is attributable to several historical and ecological characteristics. A number of studies have shown that herbivore species diversity varies across gradients of plant abundance and quality (Western, 1975; Coe *et al.*, 1976; Bell, 1982; East, 1984; McNaughton, 1985; Prins and Olff, 1998; Olff *et al.*, 2002). Olff *et al.* (2002) further suggest herbivore species must encounter plants of both sufficient abundance and quality to persist, and therefore the highest herbivore density is thus expected in locations that are neither so wet and /or infertile that average plant quality would be too low to sustain smaller herbivores, nor so dry and /or infertile that plant productivity would be insufficient to sustain larger herbivores. This hypothesis was strongly supported by the relationship between the Bovidae and productivity in the study area ($r^2 = 0.81$, $P < 0.001$, $n = 24$). The carnivores on the other hand were moderately related to productivity ($17.74 + 0.027x - 0.0002x^2$, $r^2 = 0.46$, $P < 0.002$, $n = 24$). However, the strongest correlate to the carnivore density was related to ungulate distribution ($r_s = 0.76$). At the family level the strength of the relationships was greater than at the order level. This observation supports the hypothesis that carnivores are related more to food type or prey than to habitat type (Schoener, 1974). However, at the family level the patterns were different from the higher taxonomic level. This may reflect the partitioning of energy gradient among carnivores species groups as shown in this study. And an additional explanation is that particular families and orders can have differing physiological tolerances for given environmental conditions supports this pattern (Sinclair, 1983a; Currie, 1991). Earlier works have shown partitioning of energy between species or species groups do occur at a local scale, (see Jarman and Sinclair, 1979; de Boer and Prins, 1990; Illius and Gordon, 1992; Murray, 1993; Murray and Brown, 1993; Illius and O'Connor, 2000), which be reflected in regional patterns. Kingdon (1997) suggests that the diversity of carnivores is one of the surest signs identifying a high diverse ecological area. East Africa savanna ecosystems still retain about 60% of the continental carnivore species richness. Ricklefs (1990) hypothesized that predators enhance diversity among their prey by reducing populations (and hence competition for resources), thereby easing conditions for coexistence.

The other important characteristic of the savanna ecosystem is the heterogeneity of the habitat, features such as soil characteristics (texture, porosity, salt concentrations, moisture), floral composition and physiognomy result in a mosaic of habitats (Sinclair, 1975; Happold, 1983; Belsky 1986). Each produces a slightly different environment or microhabitat, which are important habitats for smaller mammalian species. In this study relationship between the rodents, shrews and hyraxes, the species richness reached its maximum at intermediate productivity level. Happold (1983) observed that habitats with a high degree of heterogeneity had more rodent species and a larger biomass of rodents than less heterogeneous habitats. Similar patterns were observed for lagomorphs and shrews (Happold 1983; Kingdon 1997). The pattern of primates was at lower taxonomic level the patterns indicated the highest concentration of bushbabies was at intermediate level, while for the monkeys the richness increased with rainfall gradient. It highest peak was observed in the extreme western parts of the study area mostly located in Uganda and Tanzania.

We conclude that species richness – productivity relationship is clearly scale-dependent. It is interesting to note that at sub-continental scale the geographical patterns in species richness were similar among a number of taxonomic and species groups and tended to converge towards the same level (intermediate productivity) especially at the higher taxonomic level. While the high variation of patterns at lower taxonomic level it may reflect partitioning of energy gradient among families or group of species. This may be a result of different processes controlling richness at different spatial scales for various species groups.

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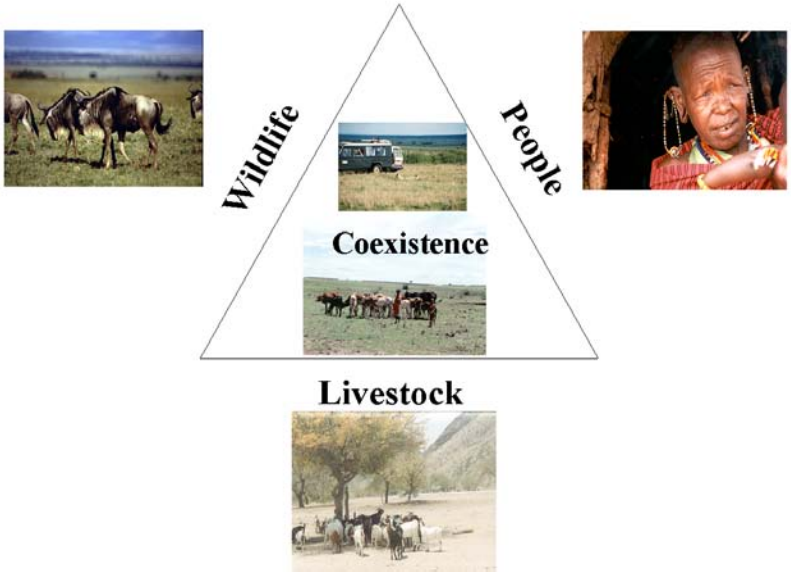
CHAPTER 4

COEXISTENCE OF PASTORALISM AND WILDLIFE IN KENYA: MOVING BEYOND PERCEPTION

A romantic notion persists that pastoralists co-exist with wildlife in a harmonious relationship. There are two contrasting perceptions with respect to the coexistence of pastoralism and wildlife in Africa. There are those who claim that pastoralism and wildlife continue to coexist harmoniously, and others who question the sustainability of this coexistence, arguing that increases in human and livestock populations would displace wildlife. The spatio-temporal extension of the model 'road to extinction)' developed in this chapter provides more insights into the conflict of resource use. The results shows we are at crossroad where some semi arid districts (with moist conditions livestock and agriculture predominates the land use, whilst in other arid and semi-arid districts the pressure to convert its land to agriculture or increasing the livestock is having an effect on the coexistence of the pastoralism and wildlife.



Chapter 4

Coexistence of pastoralism and wildlife in Kenya: moving beyond perception

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Abstract

There are two contrasting perceptions with respect to the coexistence of pastoralism and wildlife in Africa. There are those who claim that pastoralism and wildlife continue to coexist harmoniously, and others who question the sustainability of this coexistence, arguing that increases in human and livestock populations would displace wildlife. The study analyzed the spatio-temporal relation between people, wildlife and livestock in 18 arid and semi-arid districts of Kenya. The result of this study has revealed four broad patterns. The first group of districts of densely populated districts with somewhat moister climatic conditions, livestock and agriculture is rapidly replacing pastoralism as an important economic resource, as indicated in the moderate increase in the ratio of human to livestock biomass (paired t-test; $t = 1.91$, $n = 5$, $p = 0.13$) and decline in wildlife (paired t-test; $t = 1.6$, $p = 0.18$). The second group of districts - the arid to very arid districts the trends over the past two decades reveals a further intensification of pastoralism, as expressed by a significant decrease in the ratio of wildlife to livestock in all eight districts (paired t-test; $t = -2.19$, $n = 8$, $p = 0.06$) and rapid decline of wildlife (paired t-test; $t = 2.41$, $n = 8$, $p = 0.04$). The third and fourth group of districts mainly the semi-arid districts with some potential for agriculture (and with low human population density) have continued to attract the emigrant population, and agriculture is increasingly replacing wildlife. The third group mainly consisting of coastal districts of Taita Taveta (contains the Tsavo National Park) and Lamu (Boni and Dodori Game Reserve) have suffered severely from illegal hunting – particularly the hunting of elephant and rhino in the 1970s and 1980s – that decreased the wildlife population drastically. The last group of districts of Narok, Kajiado and Laikipia have both high wildlife and livestock population, but are also facing high emigration and more pressure to convert some of their rangelands into agricultural land. There is no doubt from the results presented in this study that we are at crossroads regarding the coexistence of pastoralism and wildlife in Kenya.

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* *submitted to Biological Conservation*

4.1 INTRODUCTION

There are two contrasting perceptions with respect to the coexistence of pastoralism and wildlife in Africa. Those claiming that pastoralism and wildlife continue to coexist appear to be impressed by the historical coexistence between pastoralism and wild animals (see discussions in Siegal *et al.*, 1980; Swift, 1982; Western, 1982; Ole Parkipuny, 1989; Homewood and Rodgers, 1991). Others question the sustainability of this coexistence, arguing that increases in human and livestock populations would displace wildlife (Brown, 1971; Lamprey, 1983; Osemeobo, 1988; Prins, 1992; Happold, 1995; Norton-Griffiths, 1996; Voeten, 1999; Prins, 2000). These two views reflect different traditions in analyzing eco-societal systems, focusing on different aspects of a study problem (Hjort, 1982; Prins, 1992; Happold, 1995). The proponents of the first view tend to emphasize social and ideological systems as the primary study object, whereas those of the second view tend to emphasize environmental conditions and production systems (Brown, 1971; Hjort, 1982; Happold, 1995). These two contrasting perceptions have led to contrasting approaches to the management of rangeland ecosystems and their wildlife resources.

Hjort (1982) suggests that present-day local conflicts over grazing should be analyzed not in ethnic terms that govern the contestants' perceptions, but in terms of competition between different economic systems over productive land. Prins (1992) partly addressed this problem in his model 'the road to extinction' (Figure 4.1). The model shows that at first livestock partly supplants wildlife; then, when the ratio between humans and livestock increases and wildlife is outcompeted by livestock, people switch to agriculture or horticulture and there is less and less space for wildlife. Ultimately, agriculture has to give way to urbanization. The shortcoming of this model is that it only analyzed the status and did not go further to analyze the direction of change over time. However, a fundamental problem in studying the relation between population and environment is the lack of data (Downing *et al.*, 1990; Prins, 1992; Happold, 1995). In addition to compiling comparable series of indicators on demographics and resources, the geographical regions and time intervals must be chosen to capture the underlying processes of change (Hjort, 1982; Downing *et al.*, 1990; Homewood *et al.*, 2001).

Over the past decades considerable effort has been directed at wildlife and livestock population surveys in many parts of Africa (Douglas-Hamilton *et al.*, 1992; Said *et al.*, 1995; East, 1999, and the references therein). Owing to uneven surveys at sub-national level, assessment of the status of and change in wildlife or livestock populations at national level has rarely been achieved, yet this kind of information would be crucial if more generic statements were to be formulated on the status of these resources and their relationship with human demography (Happold, 1995; Said *et al.*, 1995; Caro *et al.*, 1998; de Leeuw *et al.*, 1998; East, 1999).

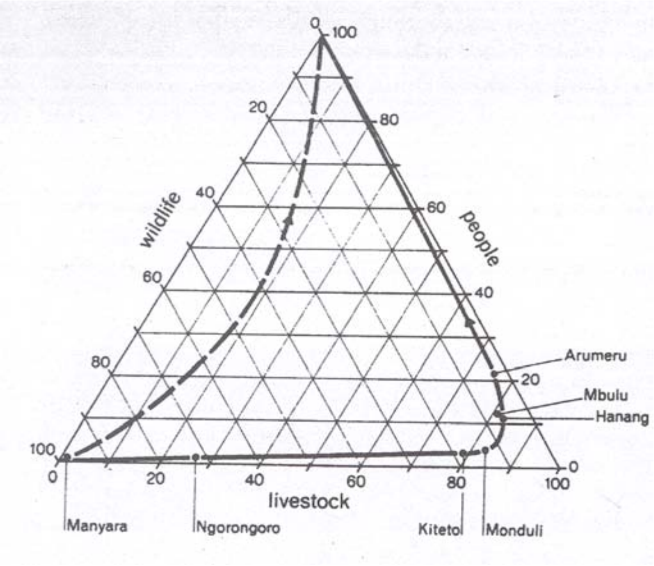

Figure 4.1: The 'pastoral road to extinction' is indicated by the black continuous line in the graph. It connects points representing the combinations of wildlife, livestock and people, as observed in different districts of East Africa based on aerial counts. The line also indicates the observed course of wildlife demise in a development from pure nature, via pastoralism, to urbanization. The broken line indicates the possible course of wildlife demise in a development from pure nature, via mixed agriculture, to urbanization. The three axes represent the metabolic weights per square kilometre of wildlife, livestock and people, respectively, as percentages of the total combined metabolic weights of these three categories. (From Prins, 1992; by permission of Cambridge University Press)

In view of the above issues, the first objective of this study was to analyze the 1978-1994 trends in wildlife and livestock in the Kenyan rangelands. Secondly, the study was intended to examine the relation between people, livestock and wildlife, based on the 'the road to extinction' model (refer to Figure 4.1) and incorporating the aspect of time (*dynamic changes in the system*). The study area consists of 19 rangeland districts that are heterogeneous in terms of land potential for wildlife, livestock and agriculture, with varying cultural backgrounds and land and land tenure policies. Aggregation of the analysis at district level and the detailed trend analysis of wildlife and livestock give a more holistic approach to comparing the status of the coexistence of pastoralism and wildlife across the country.

4.2 MATERIAL and METHODS

4.2.1 Study area

Kenya has a total area of about 581,700 km^2. Ten percent of the territory is protected under park and game reserves (Inamdar *et al.*, 1999). The size of the human population has more than doubled in the last 30 years (11 million in 1969 as against 28.7 million in 1999; CBS, 2001). The arid and semi-arid lands (ASAL) occupy about 80% of the country, and host less than 20% of the total human population (Figure 4.2). These rangelands host a unique assemblage of wildlife (Dorst and Dandelot, 1972; Stelfox *et al.*, 1979) and provide pastures for over 50% of the Kenyan livestock and a large proportion of the wildlife population (Peden, 1987; Norton-Griffiths, 1996).

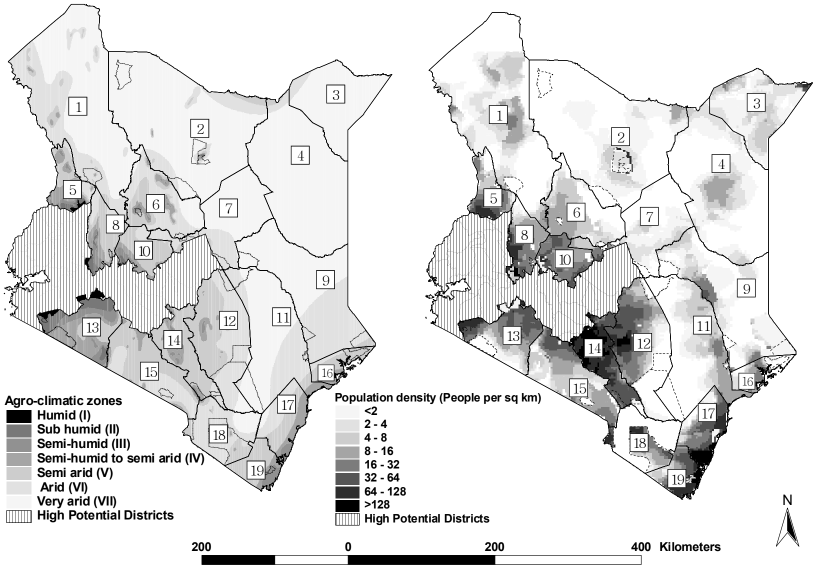

Figure 4.2: Agro-climatic zones (left) and human population density in 1999 (right) for the rangeland districts of Kenya. Protected areas are highlighted in broken line. Districts: 1-Turkana, 2-Marsabit, 3-Mandera, 4-Wajir, 5-West Pokot, 6-Samburu, 7-Isiolo, 8-Baringo, 9-Garissa, 10-Laikipia, 11-Tana River, 12-Kitui, 13-Narok, 14-Machakos, 15-Kajiado, 16-Lamu, 17-Kililfi, 18-Taita-Taveta, and 19-Kwale.

4.2.2 Data

The wildlife and livestock population data were compiled from aerial censuses conducted by the Department of Resource Surveys and Remote Sensing (DRSRS) over the period 1978-1994. Population estimates for wildlife and livestock were calculated according to Jolly

(1969). Observations derived from these surveys on elephant carcasses were used as an indicator of elephant mortality (Douglas-Hamilton and Hillman, 1981; Ottichilo *et al.*, 1987), while agricultural presence was used as an indicator of crop cultivation. The aerial census as practised by DRSRS is fully described in Norton-Griffiths (1978), Dirschl *et al.* (1981) and Ottichilo and Sinange (1985). Human population data were derived from the Kenya Central Bureau for Statistics (CBS, 1981, 1996, 2001).

4.2.3 Statistical analysis

The initial aim of the study was to address the question of whether there were declines in wildlife and livestock populations at national level. This posed a problem, since surveys had been executed at district rather than national level. First of all the number of surveys varied between the districts. Initial regression analysis at individual district level of the relation between estimated population size and time of survey led to the recognition that districts had such small sample sizes (ranging from five to 13) that there would be a realistic risk of committing a type II error. Hence we adapted the meta-analysis when analyzing the wildlife and livestock trends. This method allows many data sets to be analyzed simultaneously and thereby improves confidence in the result (see Arnqvist and Wooster, 1995; Adams *et al.*, 1997; Gurevitch and Hedges, 1999; Osenberg *et al.*, 1999).

The procedure used in this study was adopted from Arnqvist and Wooster (1995). First we regressed wildlife and livestock densities against time for each of the 18 districts (Machakos district was not included since the three surveys did not cover the whole study period). Animal densities were derived by converting the individual body weights (W in kg) of livestock and wildlife to metabolic body mass ($W^{0.75}$), which reflects energy expenditure by different groups in a comparable way (Moen, 1973). The average weights of the various wildlife species were derived from Prins and Olff (1998) and those of livestock from Peden (1987). Next we analyzed the correlation coefficients for the 18 districts in order to determine whether samples came from the same populations (Zar, 1996, pp 384). When the data were not homogenous, a Tukey test was conducted to allocate districts to homogenous groups. For groups of districts with homogenous rho, a weighted mean r and a 95% confidence interval were calculated and used to test the null hypothesis that the pooled rho equalled zero (H_o: rho = 0).

Next we used the 18 district regression equations (even when they were not significant at $\alpha'' = 0.05$) to predict the average metabolic weight ($kg.km^{-2}$) in 1978 and 1994. The metabolic weight values for the 18 districts were averaged, weighting the districts according to their area. This resulted in estimates of the national average metabolic weights of wildlife and livestock for 1978 and 1994 respectively. Based on these data, we calculated the annual rate of change in wildlife and livestock metabolic weight densities.

We then investigated the relationship between people, wildlife and livestock, using the model described in Prins (1992). The changes in the three variables for the period 1978-1994 we incorporated into the model. The non-parametric Wilcoxon signed rank test was used to investigate whether the changes in the ratio between wildlife and livestock, and in the ratio of metabolic weight between people and livestock densities differed significantly between 1978 and 1994. The ratio of metabolic weight of people to metabolic weight of livestock has been used as an indicator of people switching to other sources of food production when they cannot be sustained by the 'minimum pastoral standard of living'. A ratio of 0.045 was used as the 'threshold', as it is assumed that a family of eight in a pastoral economy needs a minimum of 6600 litres of milk and 700 kg of meat per year (see Brown 1971; Lamprey 1983; Prins 1992).

4.3 RESULTS

The distribution of wildlife and livestock in the Kenyan rangelands is shown in Figure 4.3. High densities of wildlife are found in the Narok, Kajiado, Taita Taveta, Laikipia, Lamu and Samburu districts. Livestock are mainly concentrated in the Baringo, Kajiado, Laikipia, Machakos, Mandera, Narok, West Pokot, Turkana and Samburu districts. Lamu and Taita Taveta are the only districts that show higher densities for wildlife than for livestock.

Statistical summaries of trends in wildlife densities for the 18 districts are shown in Table 4.1. Out of 18 districts, 16 had a negative sign for the regression. However, at $\alpha'' = 0.05$ the null hypothesis was rejected in seven out of the 18 cases. The test for homogeneity of wildlife densities indicated that the 18 districts did not share the same population rho ($\chi^2 = 40.29$, df = 17). A Tukey test revealed that the trends for Kajiado and Laikipia differed from those for the other 16 districts. Hence, the trends of Kajiado and Laikipia were not used for calculating the weighted mean regression for all districts. Wildlife trends in the remaining 16 districts revealed a significant decline ($r = -0.71$, df = 119, $P < 0.001$). The 95% confidence interval of the correlation coefficient was between -0.61 and -0.78. Wildlife density declined between 1978 and 1994 at an annual rate of 2.5% per annum.

Statistical summaries of the trends in livestock densities for the 18 districts are shown in Table 4.2. Livestock revealed a negative sign in 11 out of the 18 cases. However, depending on the model the null hypothesis was rejected in only one out of the 18 cases. The chi-square analysis on livestock shows the homogeneity of the data ($\chi^2 = 22.01$, df = 17, $P > 0.05$). The weighted mean regression (r) was equal to -0.23 and was highly significantly different from zero ($P < 0.001$). Livestock density in the ASAL is declining at an annual rate of 0.6% per annum.

Table 4.3 is a statistical summary of the relation between people, wildlife and livestock. At national level there was no significant difference between the 1978 and the 1994 ratio of wildlife to livestock. The arid to very arid districts, however, revealed a significant decline in the ratio of wildlife to livestock (Wilcoxon's signed rank test, $P < 0.05$; Figure 4.4) compared with the semi-arid districts (Wilcoxon's signed rank test, $P = 0.38$). The ratio of humans to livestock increased significantly between 1978 and 1994 (Wilcoxon's signed rank test, $P < 0.001$; Figure 4.4), with the semi-arid districts displaying significant changes (Wilcoxon's signed rank test, $P < 0.003$) but not the arid to very arid districts. It is noteworthy that the ratio in these latter districts remained close to 0.045, which is the theoretical threshold ratio for sustainable pastoral ecosystem.

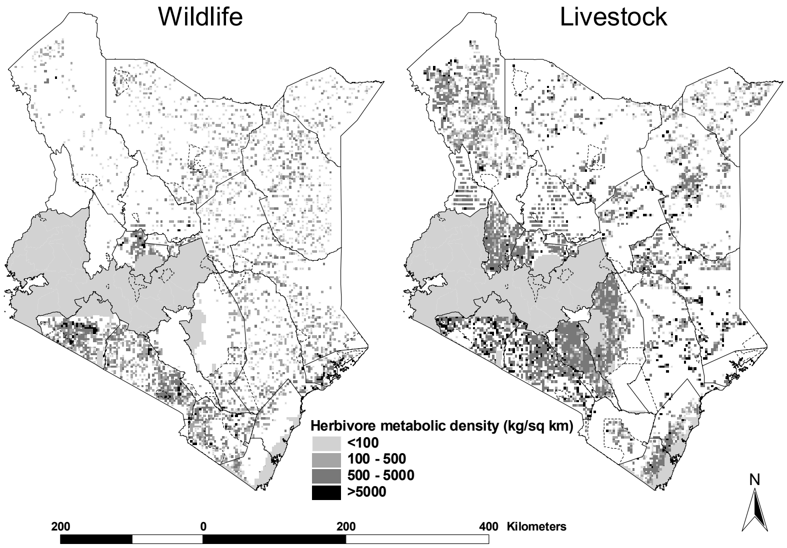

Figure 4.3: Distribution of wildlife and livestock in Kenya based on census conducted in 1994. Areas not surveyed are highlighted in continuous grey colour and protected areas in broken line.

Table 4.1: Statistics summarizing linear and log-linear regression of wildlife densities against time for the each of the 18 districts (significant p values in bold).

		Y = a + bx			Ln(Y+1) = a+ bx		
District	n	sign	r	P	sign	r	P
Baringo	13	-	0.518	0.070	-	0.497	0.084
Garissa	5	-	0.938	**0.018**	-	0.967	**0.007**
Isiolo	6	-	0.285	0.585	-	0.387	0.448
Kajiado	12	+	0.168	0.601	+	0.209	0.514
Kilifi	7	-	0.800	**0.031**	-	0.795	**0.033**
Kitui	7	-	0.598	0.156	-	0.620	0.137
Kwale	6	-	0.080	0.880	-	0.081	0.878
Laikipia	12	+	0.670	**0.017**	+	0.680	**0.015**
Lamu	11	-	0.809	**0.003**	-	0.866	**0.001**
Mandera	5	-	0.863	0.060	-	0.783	0.117
Marsabit	7	-	0.422	0.345	-	0.337	0.460
Narok	12	-	0.745	**0.005**	-	0.755	**0.005**
West Pokot	4	-	0.036	0.964	-	0.439	0.561
Samburu	7	-	0.618	0.139	-	0.511	0.241
Taita Taveta	9	-	0.658	0.054	-	0.621	0.074
Tana River	7	-	0.944	**0.001**	-	0.947	**0.001**
Turkana	5	-	0.917	**0.028**	-	0.849	0.069
Wajir	5	-	0.502	0.389	-	0.422	0.480

Table 4.2: Statistics summarizing linear and log-linear regression of livestock densities against time for the each of the 18 districts (significant p values in bold).

		Y = a + bx			Ln(Y+1) = a+ bx		
District	n	sign	r	P	sign	r	p
Baringo	13	+	0.332	0.268	+	0.379	0.202
Garissa	5	-	0.344	0.571	-	0.332	0.585
Isiolo	6	+	0.218	0.677	+	0.186	0.724
Kajiado	12	+	0.381	0.222	+	0.401	0.196
Kilifi	7	-	0.710	0.074	-	0.662	0.106
Kitui	7	-	0.097	0.836	-	0.116	0.804
Kwale	6	-	0.957	**0.003**	-	0.937	0.006
Laikipia	12	-	0.438	0.155	-	0.332	0.291
Lamu	11	-	0.347	0.295	-	0.348	0.244
Mandera	5	-	0.161	0.796	-	0.172	0.783
Marsabit	7	+	0.019	0.968	+	0.102	0.828
Narok	12	-	0.386	0.215	-	0.392	0.207
West Pokot	4	+	0.471	0.529	+	0.508	0.492
Samburu	7	-	0.683	0.091	-	0.640	0.121
Taita Taveta	9	-	0.260	0.067	-	0.275	0.473
Tana River	7	-	0.539	0.212	-	0.573	0.179
Turkana	5	+	0.110	0.860	+	0.015	0.980
Wajir	5	+	0.099	0.874	+	0.064	0.981

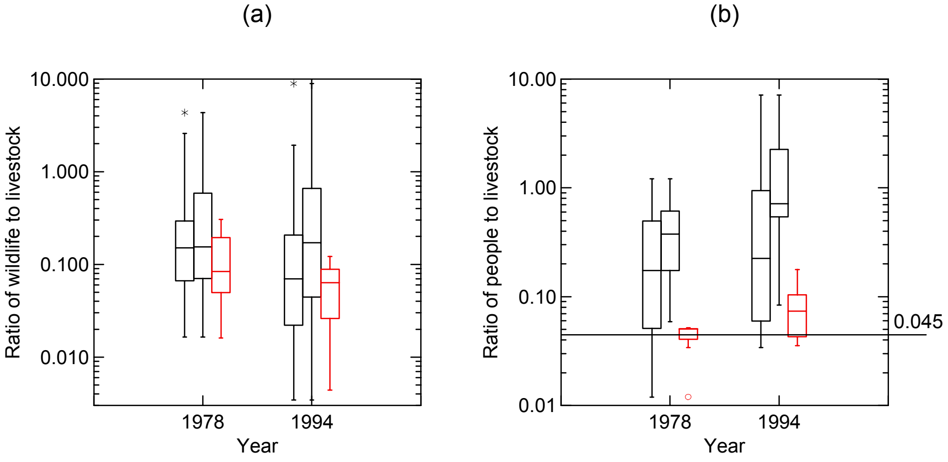

Figure 4.4: Boxplot showing the ratio of metabolic densities of wildlife to livestock and the ratio of metabolic densities of people to livestock for the semi-arid and arid to very arid rangelands (refer to text for statistical results). In both (a) and (b) the plots on the left represent all the rangeland districts, those in the middle mainly semi-arid districts (Baringo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Narok, West Pokot and Taita-Taveta) and those on the right arid to very arid districts (Isiolo, Turkana, Marsabit, Mandera, Wajir, Tana River, Samburu and Garissa). The value 0.045 in (b) is the theoretical threshold ratio for a sustainable pastoral ecosystem, and a number of arid to very arid districts fall within this category.

Table 4.3: Statistical summary of the interrelationship between people, wildlife and livestock in the Kenyan rangelands. The densities of wildlife and livestock in 1978 and 1994 were based on the interpolation of regression models.

	Wildlife density ($kg.km^{-2}$)		Livestock density ($kg.km^{-2}$)		Ratio of wildlife to livestock		Ratio of people to livestock		Human population	
District	1978	1994	1978	1994	1978	1994	1978	1994	Growth rate	Density (km^{-2})
Baringo	15	3	603	888	0.025	0.003	0.584	0.705	3.9	42
Kilifi	84	40	544	236	0.155	0.171	0.953	4.554	3.6	72
Kitui	51	13	467	446	0.108	0.030	0.645	1.240	2.5	25
Kwale	63	72	1201	492	0.052	0.146	0.423	1.923	2.6	60
West Pokot	10	11	609	748	0.016	0.015	0.308	0.599	2.7	29
Group 1	**45**	**28**	**685**	**562**	**0.071**	**0.073**	**0.583**	**1.804**	**3.1**	**46**
Garissa	154	60	591	545	0.261	0.111	0.051	0.076	0.3	3
Isiolo	60	49	634	743	0.095	0.066	0.059	0.084	5.0	5
Mandera	26	10	737	699	0.036	0.014	0.051	0.074	0.5	5
Marsabit	33	25	397	402	0.084	0.063	0.012	0.035	0.1	1
Samburu	129	77	883	631	0.146	0.122	0.052	0.142	2.6	6
Tana River	169	28	550	395	0.307	0.071	0.050	0.177	2.8	4
Turkana	12	4	756	946	0.016	0.004	0.048	0.047	1.5	3
Wajir	43	32	631	663	0.069	0.049	0.034	0.040	-1.0	2
Group 2	**78**	**36**	**647**	**628**	**0.127**	**0.063**	**0.045**	**0.084**	**1.5**	**4**
Lamu	921	361	213	40	4.331	8.913	0.377	7.110	4.5	17
Taita Taveta	633	377	244	196	2.591	1.928	1.206	2.631	2.1	13
Group 3	**777**	**369**	**229**	**118**	**3.461**	**5.421**	**0.792**	**4.871**	**3.3**	**15**
Kajiado	304	351	1091	1405	0.279	0.250	0.154	0.285	6.8	27
Laikipia	238	434	1049	721	0.227	0.602	0.184	0.716	4.6	35
Narok	2140	1084	1751	1496	1.222	0.725	0.163	0.492	6.4	43
Group 4	**894**	**623**	**1297**	**1207**	**0.576**	**0.526**	**0.167**	**0.498**	**5.9**	**35**

Figure 4.5a displays the relation between people, wildlife and livestock in the Kenyan rangelands in 1978 and 1994. Figure 4.5b reveals groups of districts with distinct patterns. The first group consists of the densely populated districts with somewhat moister climatic conditions (Kilifi, Machakos, Kitui, Baringo, Kwale and West Pokot). Here agriculture is rapidly replacing pastoral economies as an important resource. This is expressed by an upward movement of these districts along the right-hand side of the triangle and a moderate increase in the ratio of human to livestock biomass (paired t-test; $t = 1.91$, $n = 5$, $p = 0.13$). Human population growth averaged 3.1%, which was slightly lower than the national average of 3.3%. Most of these districts have a net emigration towards urban centres. Downing *et al.* (1990) observe that urban and rural areas are inextricably linked. The emergence and growth of urban areas influence the rate of population growth in rural areas, by facilitating access to inputs and markets, by creating an increased demand for agricultural goods, and by the transfer of remittances from urban workers to their rural families.

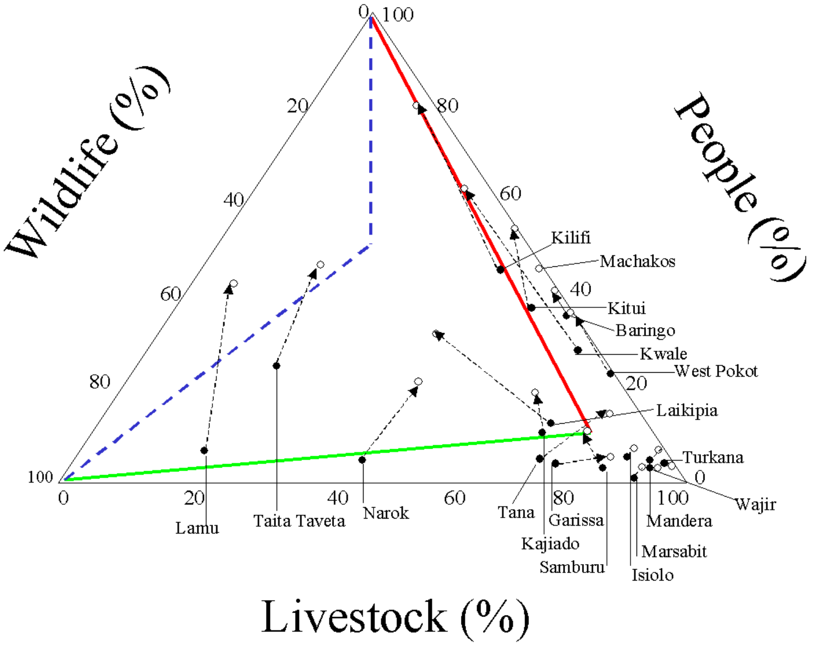

Figure 4.5a: The relation between people, wildlife and livestock in 19 Kenyan rangeland districts in 1978 (●) and 1994 (○). The three axes express the relative contribution (%) of people, wildlife and livestock to the total combined metabolic densities of the three categories. The broken line indicates a course that leads to equal proportion of wildlife, livestock and people. The continuous line indicates the observed course of wildlife demise in a development from more nature (mainly wildlife and pastoralism), via predominantly pastoralism, to mainly agriculture and urbanization. Note the figure is an extension of Prins (1992), which showed a number of other districts from Tanzania.

The second group is formed mainly of the arid to very arid districts of Mandera, Garissa, Wajir, Marsabit and Turkana, with low population growth rates (below the national average), and the trends show increased pastoralism, with more livestock and less wildlife. These districts are located in the lower right-hand corner of the figure, indicating livestock-based economies. The aridity of these districts precludes the development of rainfed agriculture (except on mountain slopes in Marsabit), while Tana River is the only district with potential for the development of irrigated agriculture. The trends over the past decades reveal a further intensification of pastoralism, expressed by a significant decrease in the ratio of wildlife to livestock in all eight districts (paired t-test; t = -219, n = 8, p = 0.06; Table 4.4).

Table 4.4: Statistical summary of the interrelationship between people, wildlife and livestock for Groups 1 and 2.

	Group 1			Group 2		
	Rate	t	P	Rate	t	P
Change in wildlife density	2.2	-1.60	0.18	3.1	-2.41	0.04
Change in livestock density	1.0	-0.69	0.52	0.2	-0.39	0.71
Change in ratio of wildlife to livestock	0.2	0.06	0.95	2.9	-2.19	0.06
Change in ratio of human population to livestock	12.3	1.91	0.13	5.1	2.52	0.04

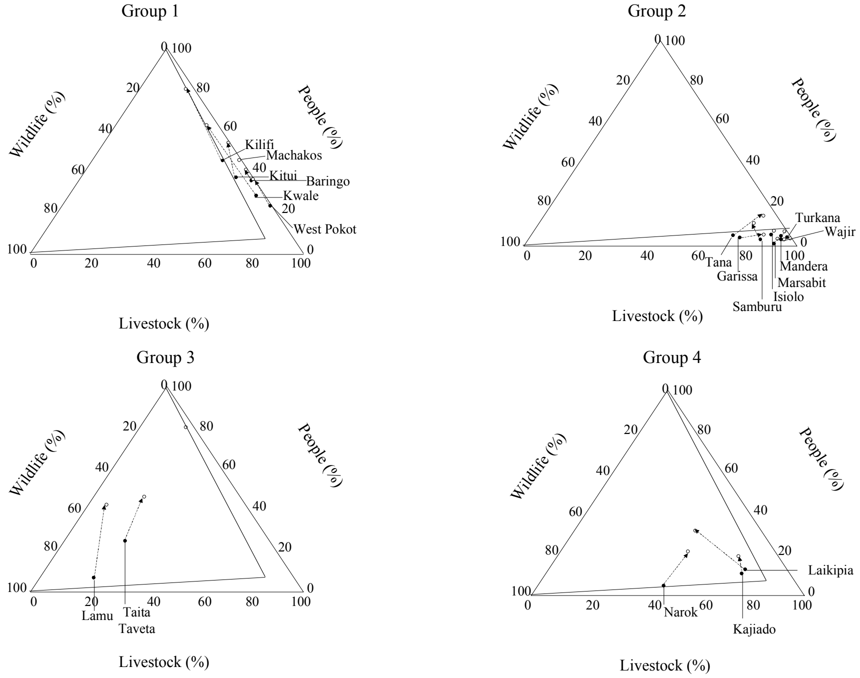

Figure 4.5b: The four broad patterns on the relation between people, wildlife and livestock in the Kenyan rangelands are highlighted in the above figure. Group 1 consists of districts with moist climatic conditions, where agriculture and urbanization are rapidly replacing pastoralism and wildlife; hence the movement of these districts along the right-hand side of the triangle. Group 2 consists of the arid to semi-arid districts with low population, which are increasingly moving towards the lower right corner, indicating more livestock. The two districts (Tana River and Samburu) with slight potential for agriculture show a slightly higher human population density. Group 3 shows districts that once were dominated by wildlife (have large tracts of parkland) but have suffered heavy poaching; later resettlement programmes increased the population in these districts. Group 4 consists of districts that have high populations of both wildlife and livestock, with the potential for agriculture. The pattern here is mixed, with Narok having a severe decline in wildlife, Laikipia having an increase in wildlife and a decline in livestock, and Kajiado having stable populations of both wildlife and livestock. All three districts continue to have an increasing human population.

The third group consists of the coastal districts of Lamu and Taita Taveta and has moved from a wildlife-dominated system towards a human-dominated system. We attribute this partly to the heavy poaching in the late 1970s and 1980s (refer to Figure 4.6 and Ottichilo *et al.*, 1987) and the severe droughts that occurred in the early 1970s (affected mostly the elephants in Taita Taveta). During the last 30 years the human population has grown rapidly in both districts (partly due to the resettlement of people – Munzinger *et al.*, 1978; Von Boguslawski and Wiese, 1992), as has the intensification of agriculture to sustain the expanding urban population on the coast and the expanding tourist market (Dijkstra, 1996).

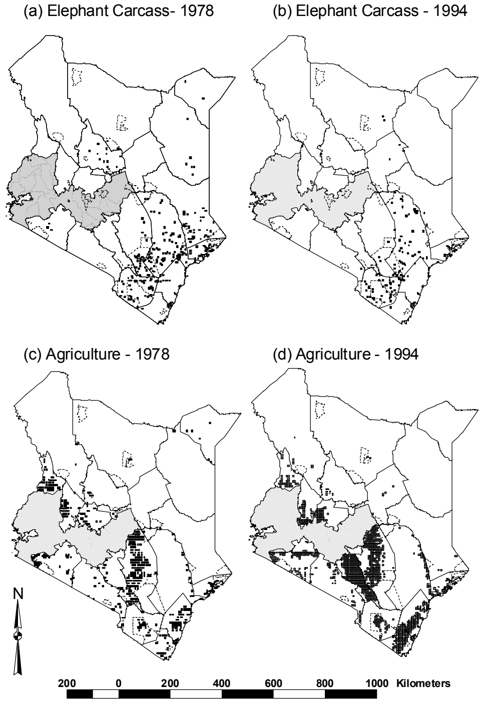

Figure 4.5: Elephant carcasses as recorded from the aerial surveys in 1978 and 1994. The carcasses indicate high levels of illegal hunting in the 1970s compared with the 1990s. The current status of agriculture indicates that coastal districts (Kilifi, Kwale, Lamu and Taita Taveta), southern rangelands (Machakos, Kitui, Kajiado and Narok) and a few northern rangelands (Baringo, West Pokot, Laikipia and Samburu) have high agricultural activities. In the arid districts of Tana River and Isiolo the agricultural activities occur mainly on river courses or on footslopes as in the case of Marsabit.

Finally, the semi-arid districts of Narok, Kajiado and Laikipia have high wildlife and livestock populations. Over the last 20 years the wildlife population has been declining in Narok district; Kajiado shows a stable population; and in Laikipia there has been an increase in wildlife and a slight decline in livestock population. All these districts have varying potential for agriculture and there is a large increase in the human population in all these districts.

4.4 DISCUSSION

The results of this study indicate that the perception of harmonious coexistence between pastoralism and wildlife is questionable. The coexistence between pastoralism and wildlife that once existed may well be the result of low human population, tribal warfare, diseases (rinderpest, cholera and smallpox), famine and droughts rather than a reflection of harmony (see Ochieng', 1980; Lamprey, 1984; Waller, 1990; Homewood and Rodgers, 1991; Prins, 1996). This seesaw of disease interaction, tribal wars, famine and restrictions on free settlement during the colonial administration (East Africa Royal Commission, 1955) may have enabled coexistence without severe competition before independence. This study has revealed that the coexistence of pastoralism and wildlife has not been harmonious in recent decades.

The spatio-temporal extension of the ‘road to extinction’ model that analyzed the regional patterns indicates that most of the semi-arid districts have already built up high human population densities through the conversion of most of their land to agriculture. Some other less densely populated semi-arid districts still retain significant populations of wildlife in coexistence with livestock (but are experiencing increased population growth, a mounting immigrant population and rapidly expanding agriculture). The arid to very arid districts appear to have completed their movement towards a pastoralist-dominated system, with marginal wildlife populations remaining. These observed changes are related to land potential and population pressure (higher population growth rates and in-migration – Downing *et al.*, 1990), land policies that encourage, exclude, restrict or give a comparative advantage to some land uses (Prins, 1992; Norton-Griffiths and Southey, 1995; Child, 2000; Homewood *et al.*, 2001), and land tenure (Norton-Griffiths, 1996). However, not all districts showed declines in wildlife; Kajiado (constant) and Laikipia (increase) showed trends in wildlife densities that are partly related to the recent intensive promotion of rural or community-based wildlife integration programmes (Western, 1982; Lindsay, 1987; Norton-Griffiths, 1996; Elliott and Mwangi, 1997).

The regional pattern presented in this study is also exhibited at continental scale. The trends in West Africa show high declines in herbivore populations that are mainly related to population pressure (Osemeobo, 1988; Happold, 1995; Brashares *et al.*, 2001). In West Africa bushmeat has also taken a toll on wildlife species, particularly in forested habitats (Anadu *et al.*, 1988; Bowen-Jones and Pendry, 1999; Fa and Garcia-Yuste, 2001). Southern Africa still retains a high diversity of wildlife outside protected areas, presumably because most of the areas are still lowly populated. The trends in East Africa appear intermediate in relation to those reported from West Africa and Southern Africa. All three East African countries are facing high declines in wildlife due to the rapid increase in human population and the expansion of agriculture onto forested and marginal lands (Kiss, 1990; Lamprey and Michelmore, 1996; Newmark, 1996; Norton-Griffiths, 1996; Caro *et al.*, 1998; de Leeuw *et al.*, 1998). This pressure will continue with either pastoralists or wildlife or both being relegated to ecologically marginal environments (Swift, 1982; Ole Parkipuny, 1989; de Leeuw *et al.*, 2001).

What is the future of the coexistence of pastoralism and wildlife in East Africa? The first view is more or less directed at improving the status of pastoralists (less emphasis on wildlife), based on ecological (mobility, habitat management, herd composition, land rights – Dyson-Hudson and Dyson-Hudson, 1980; Hjort, 1982; Swift, 1982; Western and Finch, 1986; Homewood and Rodgers, 1991) and local economic strategies. But Thornton (2002) reports that in some communities in East Africa the cultural value of nature and animals transcends economic or ecological value. The outcomes of this study shows the realization that the fabric for the coexistence of pastoralism and wildlife is at crossroads and that new initiatives are needed in promoting the harmonious coexistence of people, wildlife and livestock (more emphasis on both wildlife and livestock, but also paying attention to the social dimension). Most of the new initiatives have arisen from a concern over the last few years about economics and land use management, and about how to develop the best compromise between the needs of humans and the needs of wildlife (McNeely, 1993; Christoffersen, 1995; Happold, 1995).

These conflicting views need to be reconciled. The way forward would be to further develop a framework for ASAL that integrates the dynamics of people, wildlife and livestock in order to reduce conflicts over resource use (refer to the discussions of the various modalities in Western and Ssemakula, 1981; Kiss, 1990; McNeely, 1990; Prins, 1992; McNeely, 1993; Norton-Griffiths, 1996; Hackel, 1998; Inamdar *et al.*, 1999; Newmark and Hough, 2000; Oba *et al.*, 2000). These initiatives are based on multiple land use and on the devolution and decentralization of the proprietorship of wildlife resources and land entitlement to the local community. New strategies, apart from addressing the issues of ownership, should establish effective institutions and mechanisms for ensuring the equitable sharing of benefits that are accrued from wildlife. But equally opportunities (infrastructure, marketing, security, improved tourism facilities) should also be accorded to the arid and very arid areas that harbour pastoralism and wildlife but do not reap the benefits of their wildlife resources.

4.5 CONCLUSION

This study has revealed an increased conflict between pastoralism and wildlife and agriculture in the ASAL districts of Kenya. This spatio-temporal extension of the 'pastoral road to extinction' model provided more insights into the antagonistic relation between people, livestock and wildlife. Also it allowed localizing areas of conflict that need specific attention if pastoralism and wildlife are to coexist in harmony. The scale and perspective of the model accommodated the regional perspectives (ecological outlook) and the detailed localized information (through meta-analysis) about the pattern of land use through the long-term trends of wildlife and livestock (social and ideological changes). There is no doubt from the results presented in this study that we are at crossroads in the coexistence of pastoralism and wildlife. Immediate action is needed to address the conflict if we are to ensure the harmonious coexistence of people, wildlife and livestock in the arid and semi-arid ecosystems.

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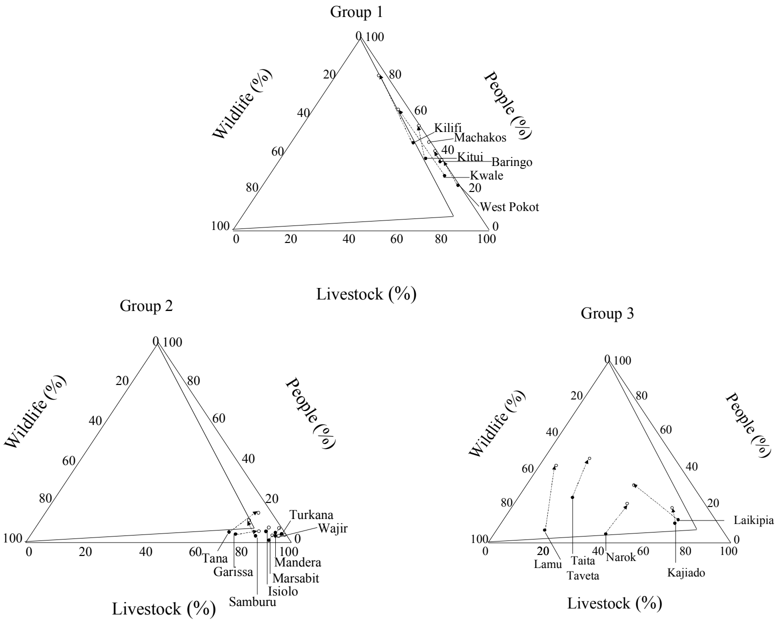
CHAPTER 5

UNGULATE SPECIES DIVERSITY IN ARID AND SEMI ARID DISTRICTS OF KENYA: THE RELATIONSHIP BETWEEN LOCAL PROCESSES AND REGIONAL PATTERNS

In chapter 4 it was shown that three broad local patterns that are related to the coexistence of pastoralism and wildlife in the arid and semi arid lands. Group 1 consists of districts with moist climatic conditions; here agriculture and urbanization are rapidly replacing pastoralism and wildlife, hence the movement of these districts along the right-hand side of the triangle. Group 2 consists of the arid to semi-arid districts with low population; these are increasingly moving towards the lower right corner, indicating more livestock. Group 3 are districts with predominate high wildlife but facing increase agriculture expansion.

The objectives of the present study are to: (1) examine how the local processes are linked to regional species diversity pattern (2) determine what it is appropriate scale of seeing the effect of local process



Chapter 5

Ungulate species diversity in arid and semi arid districts of Kenya: the relationship between local processes and regional patterns

5.1 INTRODUCTION

The role of regional and historical processes in determining local patterns of species diversity has recently regained prominence in ecological literature (see Ricklefs, 1987; Cornell and Lawton, 1992; Cornell, 1993; Ricklefs and Schluter, 1993; Westoby, 1993; Huston, 1999). Search for patterns consistent with either local or regional scale processes has provided the grist for recent debates on this topic, and most forceful conclusions have been drawn in support of the dominance of regional processes (Huston 1999). These processes, operating on large temporal and spatial scales, are likely to be important determinants of local patterns of diversity because they will determine the characteristics of the species pools from which local communities can be assembled, and because they set the upper limit on local species richness (Caley and Schluter, 1997).

It has further been argued that there seem to be relative few processes that can be considered uniquely regional in scale (e.g climate, geology, size, age and ecological evolutionary processes - Huston 1999). Then it is important to ask whether variation in the number of species between regions should be considered to be the result of regional processes, or simply the result of local processes occurring under the environmental conditions of the region? Recent studies have shown that the effects of local processes can only be detected at appropriate small scales, and at many times are obscured by large samples that aggregate environmental heterogeneity (Partel *et al.*, 1996; Huston, 1999; Ritchie and Olff, 1999).

The purpose of the present study are to: (1) assess the role of the species pool in determining the patterns of species richness and determine what it is appropriate scale of seeing the effect of local process (2) examine how regional and local richness is related to environmental gradient (3) examine how local processes is linked to the regional patterns. We tested these hypotheses using wildlife/livestock data and restricted our studied to arid and semi arid districts where there was availability of long-term aerial census data.

5.1 Study area

Kenya has a total area of about 581,700 km^2. The arid and semi arid lands (ASAL) occupy about 80% of the country, and host less than 20% of the total human population (Figure 5.1). The rangelands host a large assemblage of wildlife that are located within protected areas (comprises about 10% of the land area – Inamdar *et al.*, 1999) and adjoining areas. The country was partitioned into seven agro-climatic zones based on rainfall, soils and vegetation and it's potential to support agriculture and pastoralism (Sombroek *et al.*, 1982; refer to Figure 5.1).

The vegetation is highly heterogeneous, with great variability in structure and productivity, which can sustain high diversity of wildlife (Coe *et al.*, 1976; East, 1984; van Wijngaarden, 1985; McNaughton *et al.*, 1989). The vegetation is composed mainly of open *Acacia* grassland, dwarf shrub grassland and sparsely vegetated xeric grasslands, shrublands, bushlands and montane forests (Pratt and Gwynne, 1977; Bourliere and Hadley, 1983). Productivity is highly influenced by spatial and seasonal distribution of precipitation, where the mean annual rainfall varies from less than 250 mm in parts of northern Kenya to more than 1500mm in the southwest, and more than 2000 mm in some montane areas (Hillman *et al.*, 1988).

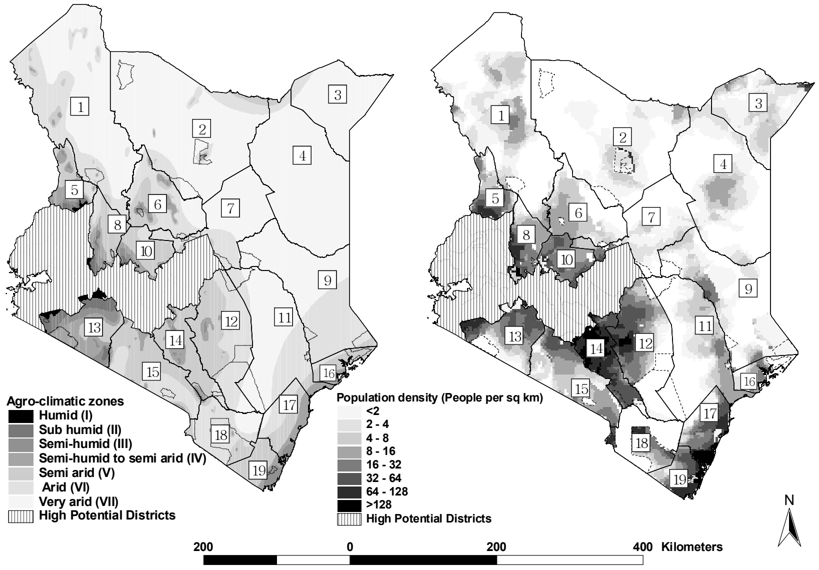
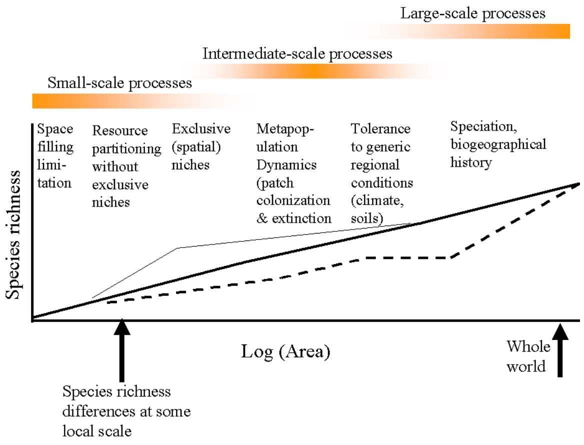


Figure 5.1: Agro-climatic zones (left) and human population density in 1999 (right) for the rangelands districts of Kenya. Protected areas are highlighted are in broken line. Districts names: 1-Turkana, 2-Marsabit, 3-Mandera, 4-Wajir, 5-West Pokot, 6-Samburu, 7-Isiolo, 8-Baringo, 9-Garissa, 10-Laikipia, 11-Tana River, 12-Kitui, 13-Narok, 14-Machakos, 15-Kajiado, 16-Lamu, 17-Kililfi, 18-Taita-Taveta, and 19-Kwale. Agro-climatic zones I, II, III are areas capable of support agriculture and also high densities of people. The ACZ IV, V, VI and VII supports low human population but sustains high densities of both wildlife and livestock.

5.2 MATERIAL AND METHODS

Olff and Ritchie (2002) hypothesised that species composition within some spatial extent can always be viewed as subset of the species composition at some larger spatial extent, with different structuring ecological processes (Figure 5.2). At local scale it has been observed that process such as competition, predation, and environmental variability may tend to reduce diversity, while mutualism, resource productivity, and resource diversity could tend to increase diversity (Ricklefs and Schluter, 1993; Caley and Schluter 1997; Prins and Olff 1998; Olff et al., 2002). This raises two possibilities where local species diversity can be either unsaturated (local diversity is linearly dependent on regional diversity) or saturated (local diversity might reach a ceiling above which it does not rise despite further increases in regional diversity – Ricklefs and Schluter, 1993; Caley and Schluter, 1997; Huston, 1999). The interrelationship between these factors and how they operate at various spatial scales is investigated in this study.



Adapted from Olff and Ritchie (2002)

Figure 5.2: Species-area curve showing how ecological processes at different scales may structure species diversity. The thin solid line represents situations where species richness is higher because of exclusive spatial niches, while the thick bold line represents less species at a local scale because of fewer exclusive niches. The dashed line indicates less species because of the processes operating at the intermediate spatial scale, such as regional conditions (climate and soils) and metapopulation dynamics allowing the persistence of less species.

5.2.1 Data

The wildlife data was compiled from aerial censuses conducted by the Department of Resource Surveys and Remote Sensing (DRSRS) over the period 1977 – 1997. The aerial census as practised by DRSRS is described in Norton-Griffiths (1978), Dirschl et al., (1981) and Ottichilo and Sinange (1985). The agro-climatic zone maps was derived from

(Sombroek *et al.*, 1982). In this study we focus on 16 species that could be observed from aerial surveys conducted in the ASAL.

5.2.2 Spatial modelling and statistical analysis

The first objective of the study was to analyse the relationship between species richness at local and regional level. We applied a standard method of testing species saturation in local communities (Partel *et al.*, 1996; Caley and Schluter, 1997; Baird 2001). We compared relationships between local and regional diversity at three spatial scales, based on locality area of 20% and 50% of the regional area (delineated at 100 by 100 km grid). We varied the locality size while keeping region size fixed, enabling comparisons of relationships between local and regional richness at different spatial scale (Partel *et al.*, 1996). Increasing the areas of the localities is expected to include more environmental heterogeneity. The goal was to examine how these different levels of heterogeneity might affect the form of the local-regional relationship, and whether different environments respond similarly to this increased variation. The original compilation of the species richness was based on a 5 by 5 km grid maps and the data was aggregated to 20 by 20 km and 50 by 50 km to represent the 20% and 50% locality species richness distributions maps. The relationship between local and regional diversity were examined for curvilinearity by comparing linear and curvilinear regressions at each scale and between all the ASAL districts, semi-humid to semi arid and arid to very arid districts.

The second objective was to test the hypothesis that local species population changes could be manifested in the regional pattern. The recent rapid increase in human population has created an environment for resource competition between people, wildlife and livestock in the ASAL. We investigated the resource competition using the model described in Prins (1992). The model assumes that in the pastoral society when they cannot be sustained by the ‘minimum pastoral standard of living’ (a family of eight needs a minimum of 6,600 litres of milk and 700 kg of meat per year - *see* Brown 1971; Lamprey 1983; Prins 1992), they there are likely to switch to agriculture or horticulture and this would out compete the wildlife as human and livestock population increases. The changes in people, livestock and wildlife were compared amongst the 19 rangelands districts between the period 1977 and 1994 based on the model of Prins (1992) – the road to extinction.

We further quantified the individual species trends based on the districts censuses that were conducted between 1977 and 1994. Since the districts censuses were not equal in terms of sample size (ranging from 5 – 13 censuses), we adapted the meta-analysis to analyse the patterns. The method allows many data sets to be analysed simultaneously and thereby improve confidence in the result (see Arnqvist & Wooster 1995; Adams et al. 1997; Gurevitch & Hedges 1999; Osenberg et al. 1999). The meta-analysis procedure used in this study was adopted from Arnqvist & Wooster (1995). The data used in the analysis (regression of each individual species against time for each of the 18 districts) was derived from de Leeuw *et al.*, (1998). We analysed the correlation coefficients for each of the species for the 18 districts to determine whether samples came from the same populations (Zar 1996 pp 384). When the data was not homogenous a Tukey test was conducted to allocate districts to homogenous groups. For groups of districts with homogenous rho, a weighted mean *r* and 95% confidence interval was calculated and used to test the null hypothesis that the pooled rho equaled zero (H_o: rho = 0).

5.3 RESULTS

5.3.1 Relationship between local processes and regional species richness patterns

Figure 5.3 shows the distribution of ungulate species richness in the ASAL at three spatial scales. The species richness in the southern rangelands is significantly higher compared to the northern rangelands (with exception of Laikipia and Samburu). The north-western districts (Baringo, West Pokot and Turkana), central (Kitui and Machakos), costal (Kilifi and Kwale) have very little wildlife left and this is reflected in both the local (Figure a-1) and intermediate species pool (Figure b-1).

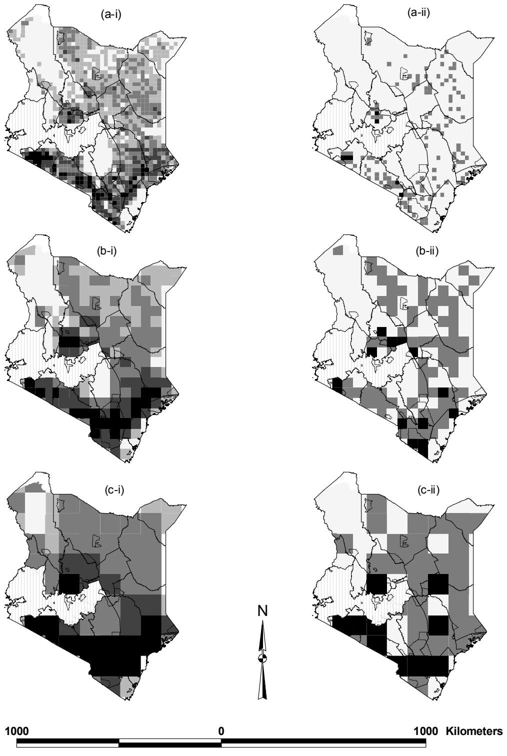


Figure 5.3: Distribution of species richness (left) and co-efficient of variation species richness (right) between local and regional species richness – local scaled maps are based (a) 20 by 20 km (b) 50 by 50 km and (c) regional species pool at a 100 by 100 km.

Figure 5.6 shows a boxplot depicting the variation of species richness based on the ACZ. At local scale of 20 by 20 km there was a high variation of species richness (Wilcoxon ranked test; P<0.001) across all ACZ. At a higher scale of 50 by 50km the variation of species richness was significant in ACZ 5 (P<0.005) and ACZ 6 (P<0.001) and moderate in ACZ 4. At regional scale (100 by 100 km) the species richness variation was significant only in very arid districts or ACZ 6 and ACZ 4 (refer to Table 5.1).

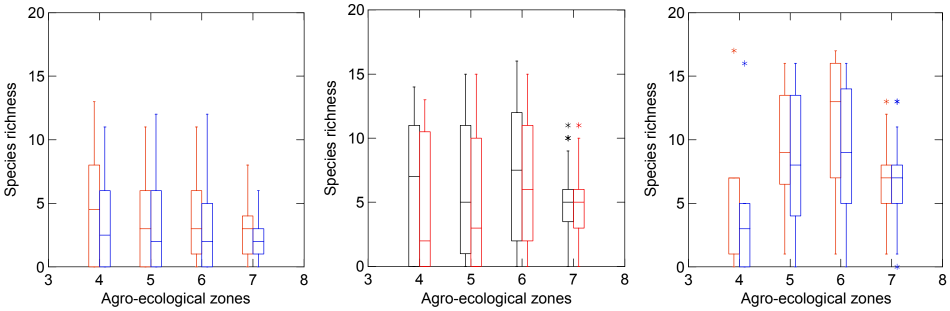


Figure 5.4: The relation between species richness for the agro-climatic zones aggregated at (left) 20 by 20 km (middle) 50 by 50 km and (right) 100 by 100 km. The bars represent the years (left) 1977 and right (1994).

Table 5.1: Multiple comparisons between species richness at three spatial scales

Agro-climatic Zone (ACZ)	20 by 20 km grid			
	4	5	6	7
4	<0.001			
5		<0.001		
6			<0.001	
7				<0.001
	50 by 50 km grid			
	4	5	6	7
4	0.09			
5		<0.005		
6			<0.001	
7				0.28
	100 by 100 km grid			
	4	5	6	7
4	0.06			
5		0.22		
6			<0.001	
7				0.16

The relation between local and regional species pool to regional species pool shows two distinct patterns (Figure 5.5). The arid to very arid areas demonstrate an asymptotic or curvilinear relationship that is consistent with limitation of diversity by local processes (could be biotic in nature), while the sub-humid to arid areas the relation was linear. At a higher scale all the relationships are linear or unsaturated.

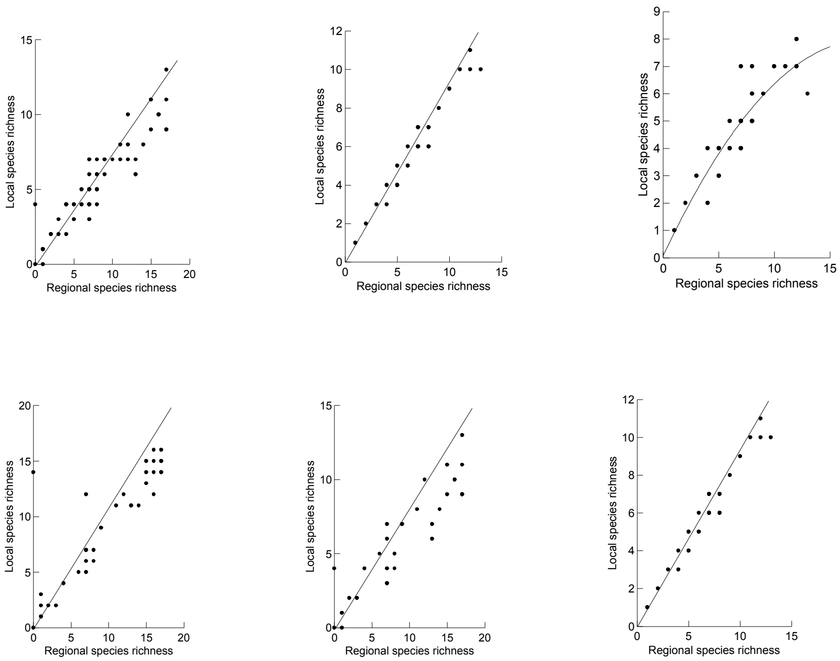


Figure 5.5: The relationship between local species richness and regional species pool for all the ASAL (left); semi arid to arid areas (middle); and very arid areas (right). Top diagram shows the relation between the local scale (20 by 20 km) with the regional scale (100 by 100 km) and lower diagram shows the relation between the intermediate scale (50 by 50 km) and regional scale (100 by 100 km).

5.3.2 Dynamics of ungulate diversity in the ASAL districts

The changes of herbivore population over time reveal three broad patterns (Figure 5.6a). The densely populated districts with somewhat moister climatic conditions (Kilifi, Machakos, Kitui, Baringo, West Pokot and Kwale), agriculture is rapidly replacing pastoralism as an important economic resource, as indicated in the significant increase of the ratio of human over livestock biomass. The arid to very arid districts (Tana River, Garissa, Mandera, Samburu, Isiolo, Marsabit, Wajir and Turkana) the trends over the past two decades revealed a further intensification of pastoralism. The species pool in these districts (Group I and II; refer to Figure 5.6b) is rapidly declining. The rest of the southern semi-arid districts (Group III - with low human population density), wildlife conservation efforts in these districts vary with some district showing decreasing (Narok, Lamu and Taita Taveta), stable (Kajiado) or increasing wildlife (Laikipia). The threat of wildlife is mainly from agriculture and intensification of livestock keeping and an increase in human population especially in the arid and semi arid lands. The total impact of these changes is reflected in the individual species trends (changes in density and distribution patterns – through colonization and local extinction of species).

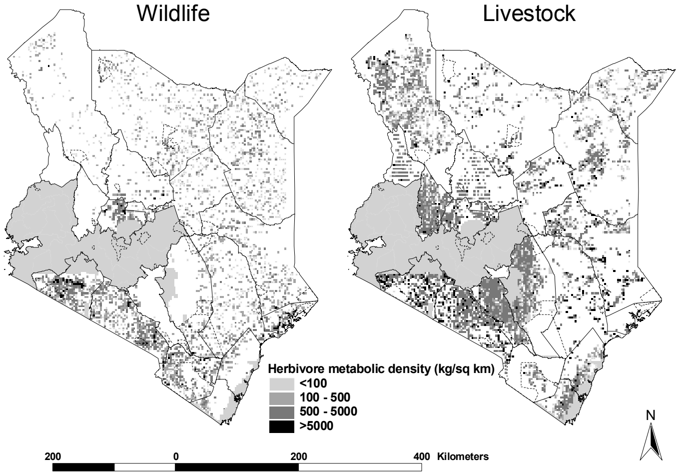


Figure 5.6a: Distribution of wildlife and livestock in Kenya. Areas not surveyed are highlighted in continuous grey colour and protected areas in broken line.

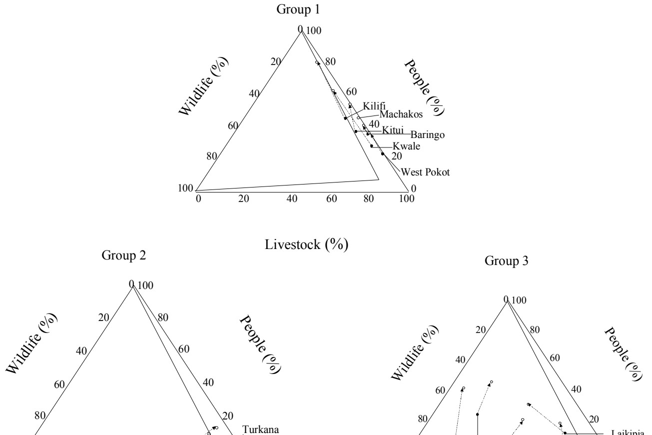


Figure 5.6b: The relation between people, wildlife and livestock in 19 Kenyan rangeland districts in 1978 (●) and 1994 (○). The three axes express the relative contribution (%) of people, wildlife and livestock to the total combined metabolic densities of the three categories. Group 1 shows the districts where wildlife is declining rapidly through conversion of land to agriculture. Group 2 are districts with high livestock and moderate wildlife populations. Group 3 are districts with both high wildlife and livestock populations that are facing increases in human population and similarly facing agriculture expansion.

The general trend of the individual species showed that some species are declining throughout the region and while other species show localised pattern (decline in some areas and increases in others). The result of the general trends of wildlife in the 18 ASAL revealed that the 18 districts did not share the same population rho (χ^2 = 40.29, df = 17). A Tukey test showed that the trends in Kajiado and Laikipia differed from the other 16 districts. Wildlife trends in the remaining 16 districts revealed a significant decline (r = 0.71, df = 119, P<0.001), with a decline annual rate of 2.5% per annum. The species that showed alarming population declines are the Hunter's hartebeest or Hirola (r = - 0.86, P<0.001) and Grevy's zebra (r = - 0.76, P <0.001). The distribution range of Grevy's zebra is much wider than hirola. Not all the Grevy's zebra range districts showed declining population - Laikipia and Tana River showed increase in numbers. The Hunter's hartebeest is localised in southern Garissa and Lamu, with small population in Tsavo (more than 70 animals – this population has grown from translocated population of less than 20 animals; Adanje and Ottichilo, 1999). There was a marginal decline in a number of species regional wide and was mainly observed in the eland with a correlation coefficient of (-0.50), elephant (0.46), wildebeest (-0.47), topi (-0.47), waterbuck (-0.47), and impala (-0.26). Mixed population changes occurred in giraffe, oryx, Grant's gazelle, lesser kudu, gerenuk, buffalo and Burchell's zebra (refer to Appendix 1 and 2 for the trends and distribution of the species respectively).

5.4 DISCUSSION

Local species diversity may be determined by local process such as competition, predation, mutualism and disturbance (Sinclair, 1973; Sinclair and Norton-Griffiths, 1982; Sinclair *et al.*, 1985; Borner *et al.*, 1987; Dublin *et al.*, 1990; Mduma *et al.*, 1999) or by regional processes such as speciation and biogeographical dispersal (MacArthur and Wilson, 1967; Bourliere and Hadley, 1983; Sinclair, 1983; Ricklefs, 1987; Janis, 1989; Janis *et al.*, 2002). Though the local trends in wildlife population in the ASAL may be partly be explained by the above factors (see Prins, 1992; Newmark *et al.*, 1994; Newmark, 1996; Caro *et al.*, 1998; de Leeuw *et al.*, 2001; Said *et al.*, in prep). Most ecological theory has focused on the local processes that determine the species pool from which members may be drawn (Caswell and Cohen, 1993). However, it has been realised that at least in part that the variation of species diversity is also directly related to the variation in size of the species pool especially at a regional level (see van de Maarel and Sykes, 1993; Sykes *et al.*, 1994; Partel *et al.*, 1996). The recognition of the role of the species pool does not conflict with ideas on the importance of the of competition and disturbance history of a particular site – although these mechanism are more important in determining species abundance relations (Partel *et al.*, 1996), they need to be linked to the regional pattern.

How do the local processes and regional pattern linked? We observed that at a local scale the relation between people, wildlife and livestock showed three broad patterns. The first group consists of districts with moist climatic conditions; here agriculture and urbanization are rapidly replacing pastoralism and wildlife. These districts consist of the coastal (Kilifi and Kwale), central (Kitui and Machakos) and north-western districts

(Baringo, West Pokot). In these districts there are signs of local extinction of species. The second group consists of the arid to semi-arid districts with low population (Turkana, Wajir, Mandera, Marsabit, Isiolo, Samburu, Garissa and Tana River); are increasingly moving towards more livestock keeping at the expense of wildlife (sign of declining population). The last group of districts (Narok, Kajiado, Laikipia, Lamu and Taita Taveta) consists of once dominated by wildlife; some of these have suffered heavy poaching, with continued expansion of agriculture. Taita Taveta, Lamu and Narok the wildlife populations are declining rapidly. These local processes were linked to the regional pattern by examining the species richness of various communities (in this study based on agro-climatic zones) and plot local diversity as function of the regional species pool.

The relation between local and regional species richness shows a direct relation between local and regional diversity when we considered all the ASAL districts. But when we analysed the two communities (sub-humid to semi arid versus arid to very arid), the results showed an asymptotic relationship that is consistent with limitation of diversity by local processes in the arid to very arid community. The limitation of species could be the result of climate or soils in that it limits species that are generic to the local condition. In sub-humid to semi arid community the relation was linear indicating local diversity is not prescribed by local conditions. Previous studies in East Africa have shown in the sub-humid to semi arid habitats being highly productive and heterogeneous (with exclusive niches) supports a high diversity of animals (see Gwynne and Bell, 1968; Bell, 1971; Jarman and Sinclair, 1979; Janis, 1989; Illius and Gordon, 1992; Murray, 1993; Murray and Brown, 1993; Illius and O'Connor, 2000). The limitation of the local species pool is reflected in the local species pattern as shown in the arid to very arid regions in Kenya. This study reveals at regional scale certain localities of Turkana, West Pokot and Baringo districts have low local species richness, and there are signs of local extinction of species. The situation is further affected by lack of in-migration of animal from the eastern neighbouring districts because of the barriers (the escarpment and the lake) and the western frontier of Karamojong in Uganda, which has already a low species pool. Mamdani (1982) and Nancholas (1987) have noted that the area was alienated from resource development for a long period of time and due to poaching and drought the wildlife has declined rapidly in Karamoja. As we move to a higher scale the relationship between the intermediate (50km) to regional (100 km) shows a linear relationship for all the ASAL, sub-humid to semi arid and also the arid to very arid areas.

The second part of study analysed the changes in species richness over time and at various spatial scales. The results shows at 20 by 20 km the variation in species richness in all agro-climatic zones was significant. Species migration or movements at this level has received attention as a mechanism of maintaining diversity (see Bell, 1971; Maddock, 1979; McNaughton, 1990; Sinclair and Arcese, 1995; Mduma *et al.*, 1999). At the intermediate scale of 50 by 50 km ACZ 4 (semi humid to arid), ACZ 5 (semi arid) and ACZ 6 (arid) showed variation in species richness, except for ACZ 7 (very arid). At the regional scale (100 by 100 km) the significance changes of species richness was reported in the semi humid to arid and arid areas. The implication of these findings is that there are significant declines in species richness in the semi-humid to semi arid (ACZ 4) and arid (ACZ 6) lands. The sub-humid to arid lands are areas that have been rapidly converted to agriculture. This process can be related to the regional patterns where a number of districts (Kilifi, Kwale, Kitui, Machakos, Baringo, West Pokot and Turkana) are facing local extinction of species (refer to Figure 5.3) through conversions of their land from rangeland use to agriculture or urban use. These patterns are further support by the declines in a number of individual species as reported in this study. The results highlights the relative contribution of regional properties and local processes vary along environmental gradient to produce-regulated pattern of species diversity. The implication of these results is that we should consider both processes of resource and species pool in investigating and also analysing species patterns. The argument is that it is easier to conserve and manage areas that have wildlife than translocating animals into habitats, which have already been destroyed through other land use activities.

We conclude that the difference between local and regional species pool depends partly on the degree of 'non disturbedness' and the integrity of the community. The closer the community has to come to reaching as steady sate, the closer the local species pool will approach the regional species spool. The impact of the disturbance on local species pool determines the changes in regional species diversity as reported in this study. The relative contributions of regional property and local processes are hypothesised to vary particularly along environmental gradient and to produce locally regulated patterns of species diversity. However, the increase in land fragmentation (through intensification and expansion of agriculture), and livestock population may contribute to the changes in local processes (through competition and disturbance), which will affect the species diversity pool at regional scale through dispersal, speciation or local extinction. The maintenance of regional species pools (be it the neighbouring district or cross border country) is crucial determinant for the persistence of local species assemblages.

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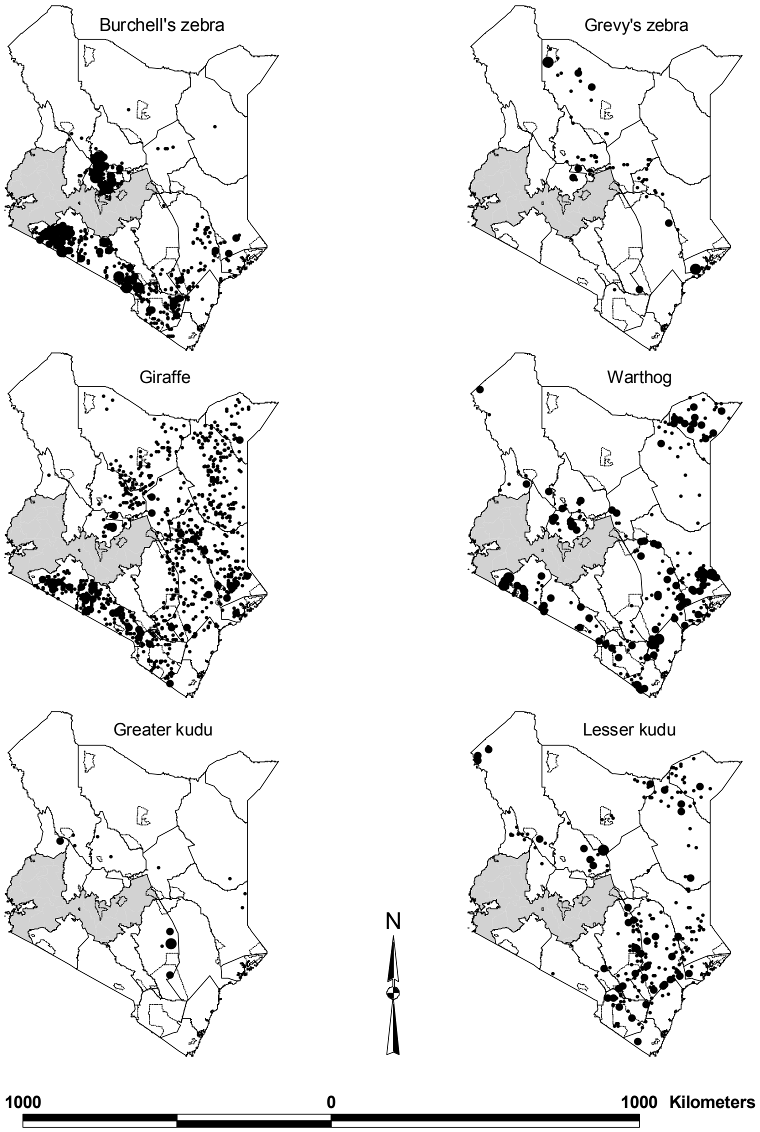
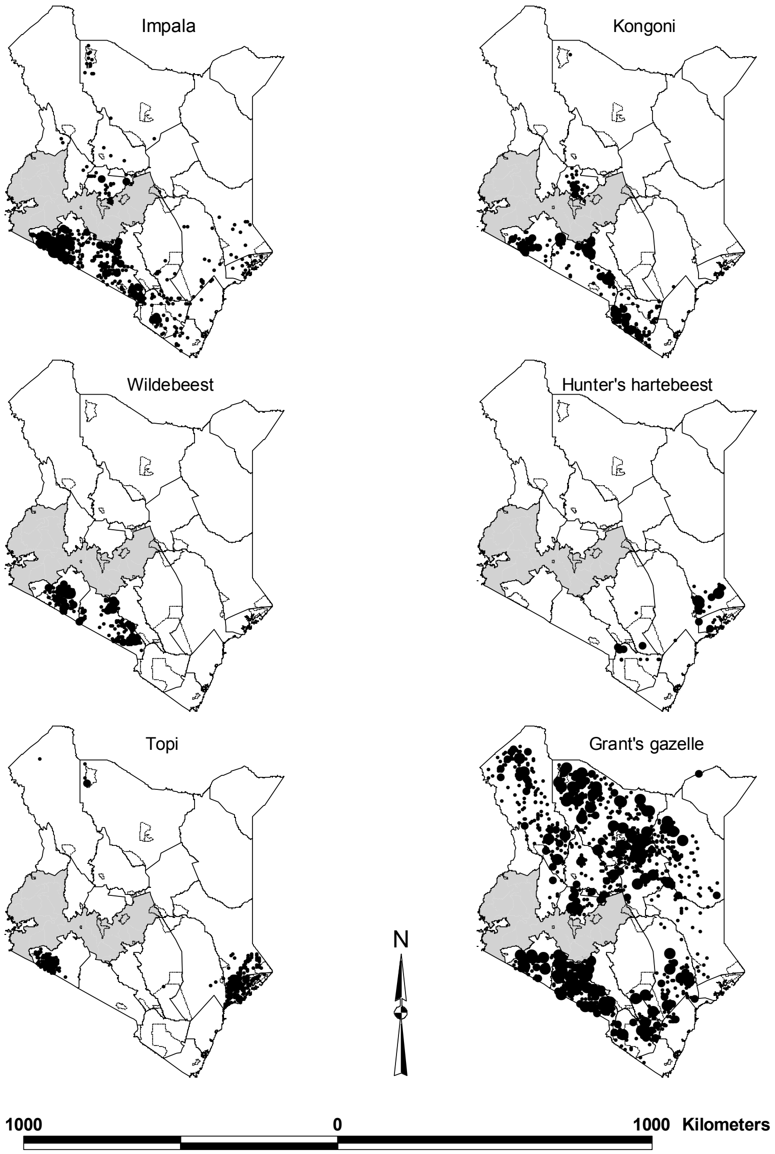
Appendix 1: The result of meta-analysis showing the regional species trend based on the local processes

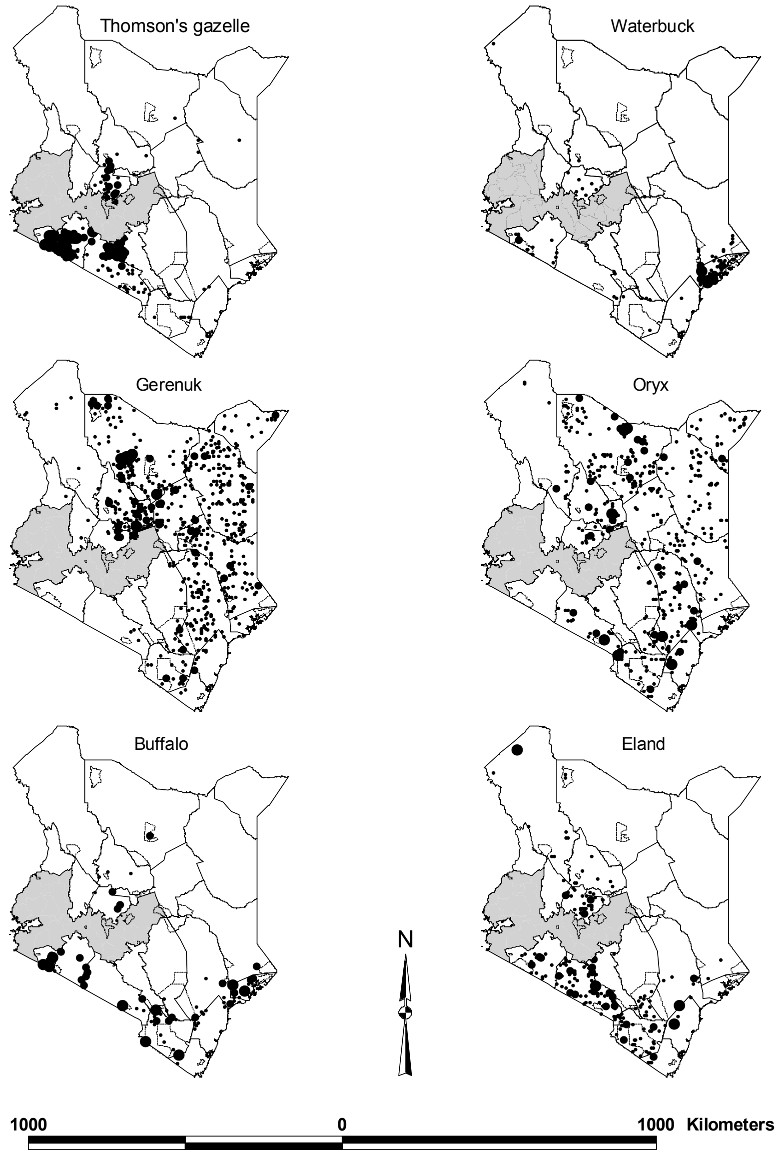
Species	Distribution of species	Stable or increase		Decline	
		Grouping I (exceptional)	r	Grouping II (all other districts)	r
Hirola	Garissa, Lamu, and Tana River			All other districts	-0.86
Grevy's zebra	Garissa, Isiolo, Laikipia, Marsabit, Samburu, Tana River and Wajir	Laikipia and Tana River	0.37	All other districts	-0.76
Kongoni	Kajiado, Kilifi, Kwale, Laikipia, Narok, and Taita Taveta,			All other districts	-0.55
Giraffe	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Mandera, Marsabit, Narok, Samburu, Taita Taveta, Tana River Turkana, Wajir, and West Pokot	Laikipia and Wajir	0.59	All other districts	-0.54
Oryx	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Mandera, Marsabit, Samburu, Taita Taveta, Tana River Turkana, Wajir, and West Pokot	Mandera and West Pokot	0.64	All other districts	-0.53
Eland	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Marsabit, Narok, Samburu, Taita Taveta, Tana River and Turkana			All other districts	-0.50
Grant's gazelle	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Marsabit, Narok, Samburu, Taita Taveta, Tana River Turkana, Wajir, and West Pokot	Kajiado, Kilifi, Kitui, Laikipia and Taita Taveta	0.43	All other districts	-0.49
Wildebeest	Kajiado and Narok			All other districts	-0.47
Topi	Garissa, Lamu, Marsabit and Narok,			All other districts	-0.47
Waterbuck	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Narok, Samburu, Taita Taveta, Tana River Turkana and West Pokot			All other districts	-0.47
Lesser kudu	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Mandera, Marsabit, Samburu, Taita Taveta, Tana River Turkana, Wajir, and West Pokot	Marsabit, Laikipia and West Pokot		All other districts	-0.45
Gerenuk	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Mandera, Marsabit, Narok, Samburu, Taita Taveta, Tana River Turkana, Wajir, and West Pokot	Lamu, Laikipia, Turkana and West Pokot	0.33	All other districts	0.40
Buffalo	Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Mandera, Marsabit, Narok, Samburu, Taita Taveta, Tana River, Turkana, and West Pokot	Kitui, Garissa, Marsabit and Tana River	0.55	All other districts	-0.38
Impala	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Mandera, Marsabit, Narok, Samburu, Taita Taveta, Tana River Turkana, Wajir, and West Pokot			All other districts	-0.26
Warthog	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Mandera, Marsabit, Narok, Samburu, Taita Taveta, Tana River Turkana, Wajir, and West Pokot			All other districts	- 0.23
Burchell's zebra	Garissa, Lamu, Marsabit, Samburu, Taita Taveta, Tana River, and Turkana,	Kajiado, Isiolo, Kilifi, Kitui, Kwale, Laikipia, Narok	0.64	All other districts	-0.51
All wildlife	Baringo, Garissa, Isiolo, Kajiado, Kilifi, Kitui, Kwale, Laikipia, Lamu, Mandera, Marsabit, Narok, Samburu, Taita Taveta, Tana River Turkana, Wajir, and West Pokot	Laikipia and Kajiado	0.41	All other districts	-0.70



Appendix 2a: Distribution of Burchell's zebra, Grevy's zebra (endangered), giraffe, warthog, Greater kudu and Lesser kudu in the arid and semi arid districts of Kenya. The grey shaded areas are the high potential agricultural areas and the protected areas are shown in dotted lines.



Appendix 2b: Distribution of impala, kongoni, giraffe, wildebeest, Hunter's hartebeest (endangered), topi (small populations of topi are found in north of Marsabit and southern parts of Ethiopia), and Grant's in the arid and semi arid districts of Kenya. The grey shaded areas are the high potential agricultural areas and the protected areas are shown in dotted lines.



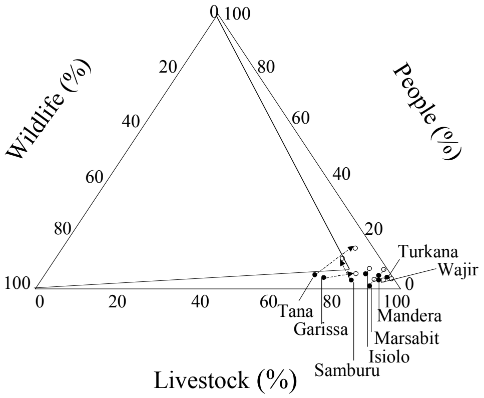
Appendix 2c: Distribution of Thomson's gazelle, waterbuck, gerenuk, oryx, buffalo, and eland in the arid and semi arid districts of Kenya. The grey shaded areas are the high potential agricultural areas and the protected areas are shown in dotted lines.

CHAPTER 6

DISTRIBUTION AND DIVERSITY OF WILDLIFE IN NORTHERN KENYA IN RELATION TO LIVESTOCK AND PERMANENT WATER POINTS

Chapter 6

In the analysis on the coexistence of pastoralism and wildlife it was shown that livestock is increasingly displacing wildlife in the arid and semi arid lands. In this chapter we analyse some of the impacts of the development of water source on wildlife diversity and distribution patterns. The analysis shows that wildlife assemblages were more diverse farther from water sources.



Chapter 6

Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points

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Abstract

Arid rangelands host a variety of drought-tolerant wildlife species, many of them requiring conservation efforts for the survival of their populations. The development of drinking water sources for people and livestock forms one of the main development interventions in these rangelands. However, the impact of availability of permanent drinking water on wildlife remains unknown. In this study we analyzed the distribution of wildlife and livestock in northern Kenya in relation to distance to permanent water. Livestock were concentrated in areas close to permanent water, while wildlife were frequently farther away from water; their distributions were inversely correlated. In addition, wildlife assemblages were more diverse farther from water. These results suggest that livestock and human activities related to water points negatively affect the distribution of wildlife.

6.1 INTRODUCTION

Arid rangelands are sensitive to degradation, which is manifested by reduced plant cover, increased exposure of bare soil and run-off, reduced rain-use efficiency and loss of productivity and diversity (Ludwig *et al.*, 1997; Milton *et al.*, 1994). Various causes have

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been put forward for such degradation, such as climatic oscillations (Hoffman and Cowling, 1990), drought (Westoby *et al.*, 1989) and more locally over-utilization in the form of overgrazing and fuel wood collection (Ayoub, 1998).

Livestock and pastoral people in arid rangelands tend to concentrate around water points. This is because most livestock species require drinking water either every day or every other day (Stoddart *et al.*, 1975). As a result, radial gradients in grazing intensity develop around water points (Andrew, 1988; Pickup, 1989; Pickup and Chewings, 1994; Pickup *et al.*, 1998). Overgrazing around water points can create local foci of severely degraded vegetation and soils (Ludwig *et al.* 1997; Ibrahim 1993; Johnson 1993; Shaabani *et al*., 1992b, 1992c; Andrew and Lange, 1986b, 1986c). Ludwig *et al*. (1997) suggest that water points, when sparsely distributed, cause severe but localized degradation while when the density of water points increases, grazing becomes less intensive and more evenly distributed. Thalen (1979), however, observed in Iraq that the opening of hundreds of new wells changed a patchwork of extensively used and highly productive rangelands interspersed with a few isolated degraded foci into a continuous stretch of degraded range. Such negative impacts have resulted in concern over the introduction of new water points. This concern, however, has focused on the control of erosion and the provision of grazing resources by the range to livestock (Shaabani *et al*., 1992a, 1992b; Andrew and Lange 1986b, 1986c). On the other hand, little is known about the impacts of water points on the abundance and diversity of wildlife.

In conservation areas, most wildlife species concentrate around water points (Owen-Smith, 1996; Western, 1975) and artificial water points are often built to attract animals. However, the impact of water points on wildlife in non-protected areas has received little attention. In these areas, livestock may compete with wildlife for both water and forage around water points and herders may intentionally or unintentionally scare away wildlife. Andrew and Lange (1986a) found that kangaroos avoided areas close to water points used intensively by sheep. Andrew (1988) suggested that animal species diversity might peak at some intermediate point along the grazing gradient away from water points. He observed that few animal ecologists had attempted to understand how water points affect faunal distribution and diversity.

In this study, we quantify the impacts of water points and livestock on the distribution and diversity of wildlife in the arid rangelands of northern Kenya. We then discuss the implications of further water point development on the future of wildlife in arid rangelands.

6.2 MATERIAL AND METHODS

6.2.1 Study area

The aim of this study was to investigate the relationship between the availability of drinking water and the presence of livestock on the one hand and the presence and diversity of wildlife on the other. We selected six arid-zone districts in northern Kenya (Figure 6.1) where information on drinking water and animal distribution was available.

People in these districts depend almost completely on livestock husbandry, mainly in the form of free-ranging pastoralism. The utilization of the rangelands is restricted by the availability of permanent drinking water, particularly in the dry season. Rangelands resources have been mapped and described in great detail for each of these six districts (Herlocker *et al*., 1993, 1994; Schwartz *et al*. 1991; Shaabani *et al*., 1992a, 1992b, 1992c).

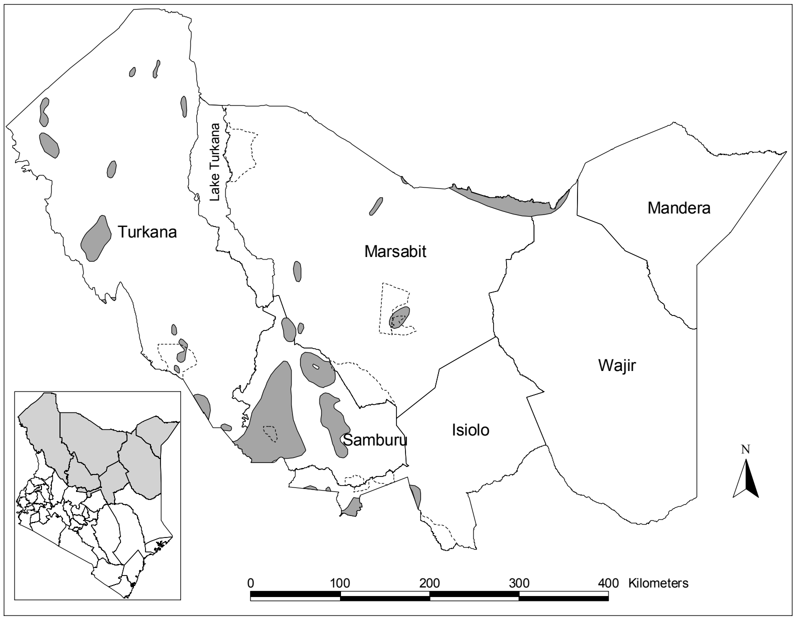


Figure 6.1 Map of northern Kenya, displaying the six districts included in this study (solid lines), the agro-ecological zones (white = arid zone, light gray = semi arid and humid zones) and the conservation areas (interrupted lines).

6.2.2. Wildlife species

The arid zone of northern Kenya hosts one endangered large herbivore wildlife species, Grevy's zebra (*Equus grevyi*). The area supports species that have less risk of extinction, but still depend on conservation programs for their survival (IUCN, 1996) such as Beisa oryx (*Oryx gazella beisa*), Grant's gazelle (*Gazella granti*), gerenuk (*Litocranius walleri*), lesser kudu (*Tragelaphus imberbis*) and giraffe (*Giraffa camelopardalis*). The latter species included both Masai and reticulated giraffe, since they could not be distinguished from the air. In this study we also considered impala (*Aepyceros melampus*), ostrich (*Struthio camelus*), warthog (*Phacochoerus aethiopicus*) and Burchell's zebra (*Equus burchelli*). Northern Kenya forms the nucleus of the distribution of Grevy's zebra, Grant's gazelle and Beisa oryx.

6.2.3. Data

Geographical information describing distance from permanent water sources in the late 1980's was taken from the Kenyan Rangeland Handbook (Herlocker *et al*., 1993, 1994; Shaabani *et al*., 1992a; 1992b, 1992c, Schwartz *et al*. 1991). In five districts maps displayed distance classes of 0-10, 10-15 and > 15 km away from the nearest permanent water sources. However, for Turkana District the map did not explicitly state whether it pertained to permanent water sources. The accompanying handbook (Herlocker *et al*., 1994) indicated that Turkana is extremely well supplied with water, having > 7000 water sources. It furthermore affirms that before the start of water development an adequate water supply existed for at least 75% of the district. This corresponded closely to the area within 15 km from water according to the map. We therefore assume that the map reflected distance to permanent water.

Information on the distribution of livestock and wildlife was collected in 1990 by the Kenyan Department of Resource Surveys and Remote Sensing (DRSRS) using the systematic reconnaissance flight method (Norton Griffiths, 1978). The northern Kenyan rangelands were surveyed using transects spaced at 5 km intervals. Flying height was c. 120 m. Two experienced observers (Dirschl *et al*., 1981) occupied the rear seats of a high wing aircraft (Cessna 185 or Partinevia). They counted all animal species recorded within 110 m on both sides of the aircraft along 5 km transect segments (Ottichilo and Sinange, 1985), here referred to as sub-units.

The animal surveys were made within three-months in 1990; Turkana District was surveyed in August, Marsabit, Samburu and Isiolo Districts in September and Mandera and Wajir in October. Together those Districts cover c. 50% of Kenya. Visual inspection of the NOAA-NDVI images of northern Kenya displayed in Eiden *et al.* (1991) revealed that these surveys were conducted during a drought in Turkana and Marsabit Districts, while the censuses in Mandera, Wajir, Isiolo and Samburu Districts were completed during the start of the 1990 short rains. The study was restricted (Figure 6.1) to the arid zone (Sombroek *et al.*, 1982). We further excluded conservation areas from the analysis, since livestock are generally excluded from these areas.

6.2.4. Species' tolerance to aridity

Tolerance to aridity is defined here as the ability of animals to withstand long periods under hot circumstances, without drinking water. We classified species as arid tolerant either when showing physiological plasticity or adaptations to conserve water or when possessing the ability, as demonstrated by ecological evidence, to live far away from watering points, or to live without drinking water for prolonged periods of time.

We listed or calculated the values of relevant physiological parameters to assess the ability of animal species to tolerate arid conditions. This information appeared to be limited to four wildlife species (oryx, impala, Grant's gazelle and ostrich) and was mostly based on laboratory experiments with confined individuals. Minimum drinking water needs are indicative of the water requirement (expressed as 10^{-2} liter of H_2O per kg of body weight per day; Taylor, 1968), and this was measured in captive animals. The evaporative water loss was measured in dehydrated, captive animals at 22 °C (night) and 40 °C (day) (Taylor, 1968). The ability to produce concentrated urine is indexed by the urine / plasma osmotic ratio (Maloiy *et al.*, 1979), usually in captive animals. Faeces with a low water content (%; Woodall and Skinner, 1993) suggest a water conservation strategy, as does a low water flux rate ($ml/kg^{0.82}$; King, 1979), and a low minimum body water turnover rate (10^{-2} l H_2O kg^{-1} d^{-1}; King, 1979). The latter three variables can be measured in free ranging animals. The water turnover rate / daily energy expenditure ratio (WTR/DEE, ml/kJ, Withers *et al.*, 1980), or water economy index (WEI, ml/kJ; Williams *et al.*, 1993), is indicative of water use efficiency during energy expenditure in the absence of drinking water.

The physiological values were contrasted among species, and compared with ecological literature on arid zone distribution of our study species, to assess each species' tolerance to aridity. In the case of giraffe, warthog, lesser kudu, gerenuk, Grevy's zebra and Burchell's zebra, no relevant physiological data were found in the literature, so we had to rely exclusively on authoritative ecological information to decide on the aridity tolerance of those species.

6.2.5. Statistical analysis

We used a χ^2 test to determine if there was an association between the presence/absence of livestock and the distance to permanent water points (expressed in three distance classes, see above).

The relationship between *presence/absence* of wildlife (Y) and presence of livestock (X_1) and distance to permanent water (X_2) was studied by the following logistic regression model using 9432 aerial census sub-units:

$$Y = e^z/(1+ e^z)$$

$$\text{with} \quad z = a + b*X_1+c*X_2 + d*X_1*X_2$$

To see whether the *diversity* of wildlife was affected by these two variables we made log-linear analyses, again using just these 2243 sub-units. Systat 7.0 was used for all statistical analyses.

6.3. RESULTS

Most of the land in the six districts is classified as arid zone (Figure 6.1), with only 2.7% of the land designated for conservation. The 1990 survey revealed that > 93% of all wildlife in the arid zone was residing outside this protected area system where the mean density of livestock was 33 times higher than the mean density of wildlife (20.06 versus 0.61 animals km^{-2} respectively).

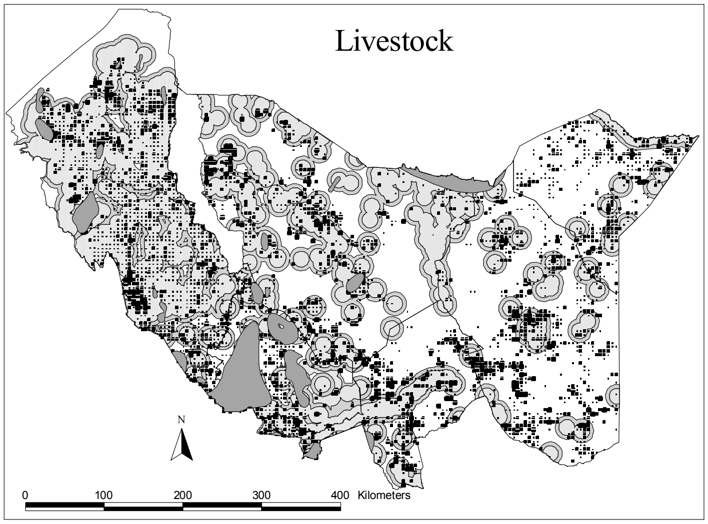
In the late 1980s there were strong differences in the availability and accessibility of permanent drinking water resources for animals across northern Kenya (Figure 6.2). The northwestern region (Turkana and parts of Marsabit) had a dense network of permanent water sources. Consequently, most of this region was located within 15 km of permanent water. The central and northeastern regions (Isiolo, Mandera, Wajir and parts of Marsabit) showed a much lower density of water points. Here large stretches of land were situated at distances > 15 km away from permanent drinking water.

Livestock were evenly spread across the northwestern region and were more clustered in the central and northeastern regions (Figure 6.2a). Livestock were also clustered near permanent water sources. In areas > 15 km from water livestock were present in only 25% of the census units; within 10 km livestock were observed in nearly 50% of the sub-units. Statistically there was a highly significant association between the presence/absence of livestock and distance to water (χ^2-test, χ^2=431.9, d.f. = 2, $p < 0.001$). Livestock were clustered more closely to water in the northwestern region than in the other regions. In the northeastern region several clusters of livestock occurred at distances > 15 km from water (Figure 6.2a).

In contrast to livestock, wildlife occurred more frequently in areas > 10 km from water (Figure 6.2b). The relation between the presence of livestock, the distance to water and the presence of wildlife is shown in Table 6. 1. The values in the cells of the table display the percentage of aerial survey sub-units where wildlife had been recorded. For example, the number of sub-units <10 km from water where livestock was present was 1867 of which wildlife were recorded in 438, i.e. 23.46%. On average, wildlife were one-third less frequent, at any distance from water, when livestock were present than when they were absent in a census sub-unit. Table 6. 1 furthermore shows that wildlife avoided areas within 10 km of water, but were attracted to areas 10-15 km from water. Logistic regression confirmed these patterns: the presence of wildlife was negatively associated to the presence of livestock and significantly related to distance from water (Table 6. 2).

Table 6. 1. Frequency (%) of aerial survey sub-units where wildlife were recorded in relation to distance to permanent water and the presence/absence of livestock. The ratio is the absence value divided by the presence value at each distance; a ratio > 1 indicates a negative association between livestock and wildlife. Significance levels: * p<0.05; ** p<0.01; *** p<0.001.

Livestock	Distance to permanent water		
	0-10 km	10-15 km	> 15 km
Absent	23.46	29.58	28.41
Present	14.97	21.28	19.15
Ratio	1.57^{***}	1.39^{***}	1.48^{***}



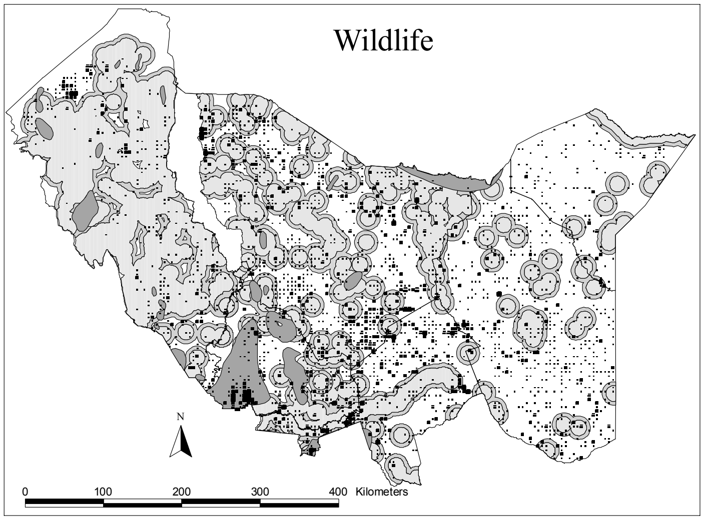


Figure 6.2 Maps of northern Kenya displaying the density and distribution in 1990 of (top) livestock and (bottom) wildlife in relation to the distance to permanent water sources as recorded in the late 1980s. Dark gray represents the semi-arid zone, which was excluded from further analysis. White, medium and light gray represent areas at distances from permanent water sources of more than 15km, 10-15 km and less than 10 km respectively. Dot sizes represent the following animal densities/km^2: Livestock: small = > 0-50, medium = > 50-250, large = > 250; wildlife: small = > 0-5, medium = > 5-25, large = > 25.

Some wildlife species were significantly affected by the presence of livestock while others were not (Table 6.2 and 6.3). Only Burchell's zebra was more frequent in the presence of livestock at close distances from water (Table 6.3), leading to a significant interaction term in the model. Six species (giraffe, oryx, ostrich, lesser kudu, gerenuk and Grant's gazelle) were significantly reduced in the presence of livestock. Grevy's zebra, impala and warthog were not affected by the presence of livestock. The significant interaction term in the model for oryx indicates an increased negative effect of livestock on this species in the proximity of water. In addition, the presence of Grant's gazelle, gerenuk, ostrich and giraffe was significantly related to both the presence of livestock and the distance from permanent water.

Table 6.2 Statistics describing the relationship (logistic regression) between the presence of wildlife and two explanatory variables; presence/absence of livestock (L), and three distance classes ($D_{0\text{-}10}$, $D_{10\text{-}15}$ and $D_{>15}$) at 0-10 km, 10-15 and >15 km away from water*.

Species	Constant	L	$D_{0\text{-}10}$	$D_{10\text{-}15}$	$L{*}D_{0\text{-}10}$	$L{*}D_{10\text{-}15}$
Wildlife	-0.99^{***}	-0.52^{***}	-0.21^{***}	0.14^{**}	-	-
Grevy's zebra	-	-	-	-	-	-
Burchell's zebra	-6.97^{***}	-	-	-	1.97^{***}	-2.04^{ns}
Giraffe	-3.13^{***}	-0.88^{***}	-0.27^{**}	-0.03^{ns}	-	-
Warthog	-4.72^{***}	-	-	-	-0.60^{*}	0.11^{ns}
Oryx	-3.06^{***}	-1.06^{***}	-	-	-1.21^{***}	0.80^{***}
Ostrich	-3.35^{***}	-0.55^{***}	-0.56^{***}	0.36^{***}	-	-
Lesser kudu	-4.16^{***}	-0.87^{***}	-	-	-	-
Impala	-5.97^{***}	-	-	-	-	-
Gerenuk	-2.92^{***}	-0.59^{***}	-0.21^{**}	0.09^{ns}	-	-
Grant's gazelle	-1.98^{***}	-0.30^{***}	-0.03^{ns}	0.18^{**}	-	-

*The analysis tested for significance between $D_{>15}$ (which obtained a coefficient of zero) and the other two distance classes. $L{*}D_{0\text{-}10}$ and $L{*}D_{10\text{-}15}$ represent interaction terms in the model. Positive and negative coefficients indicate a positive respectively negative influence of the variable concerned. Dashes (-) indicate variables not included in the model. ns, Not significant; *P<0.05; **P<0.01;***P<0.001.

Similarly, the relationship of wildlife with distance from water varied among the species. Giraffe, ostrich and gerenuk avoided areas within 10 km of water, while ostrich and Grant's gazelle were attracted to areas at intermediate distances (10-15 km) from water. The significant interaction term in the model for warthog indicates that the presence of this species tends to be reduced closer to water in the presence of livestock.

Overall, the statistical analysis showed that six wildlife species avoided the presence of livestock, three were unaffected, while Burchell's zebra was positively associated (Table 6.2). Four species (giraffe, gerenuk, oryx and ostrich) appeared to stay away from water points. Table 6. 4 provides information on the water physiology and drinking water requirements of several species according to the literature. Comparison of this table with the results summarized above reveals that water-dependent species such as the two zebra species and warthog, tend to show no or a positive relation to distance to water. Gerenuk, ostrich, oryx and giraffe, aridity tolerant species that are less dependent on drinking water tend to be observed more frequently away from water.

Table 6.3 Distribution of wildlife in relation to distance to permanent water (km) and the presence/absence of livestock*.

Species	Livestock present			Livestock absent			Ratio		
	0-10 km	10-15 km	>15 km	0-10 km	10-15 km	>15 km	0-10 km	10-15 km	>15 km
Grevy's zebra	0.60	0.97	0.47	0.64	0.71	0.31	1.06^{ns}	0.73^{ns}	0.66^{ns}
Burchell's zebra	0.66	0.00	0.09	0.21	0.09	0.03	0.32^{*}	∞^{ns}	0.33^{ns}
Giraffe	1.27	1.35	2.75	3.32	4.25	5.46	2.61^{***}	3.15^{**}	1.99^{***}
Warthog	0.48	0.97	1.42	0.75	0.80	1.00	1.56^{ns}	0.82^{ns}	0.70^{ns}
Oryx	0.48	3.48	2.37	3.43	5.40	4.77	7.15^{***}	1.55^{ns}	2.01^{***}
Ostrich	1.03	3.48	2.28	2.09	4.52	4.15	2.03^{*}	1.30^{ns}	1.82^{**}
Lesser kudu	0.54	0.00	1.14	1.61	1.24	1.59	2.98^{**}	∞^{*}	1.39^{ns}
Impala	0.12	0.19	0.19	0.48	0.18	0.25	3.98^{ns}	0.92^{ns}	1.31^{ns}
Gerenuk	2.05	2.71	3.98	4.45	5.76	5.52	2.17^{***}	2.13^{**}	1.39^{*}
Grant's gazelle	9.35	11.99	6.92	11.41	13.55	11.07	1.22^{*}	1.13^{ns}	1.60^{***}

*Each value shows the percentage of the aerial census sub-units where the species was observed. The ratio was calculated and statistically tested as in Table 6. 1; values > 1 indicate a negative association between livestock and wildlife. ns, Not significant; *P<0.05; **P<0.01;***P<0.001.

Individual species showed contrasting distribution patterns in northern Kenya (Figure 6.3). Grant's gazelle, which was the most widespread species, occurs throughout northern Kenya including Turkana District, but not in Mandera. Gerenuk, giraffe, oryx and ostrich are very rare or absent from Turkana apart from one area without water in the northern part of the district. Warthog are observed more frequently in the Islamic districts of Isiolo, Wajir and Mandera than in the Christian districts of Turkana, Marsabit and Samburu (1.7 Vs 0.2%, χ^2 - test, $\chi^2 = 54.31$, d.f. = 1, $p < 0.001$).

The diversity of wildlife, expressed as the frequency of sub-units with two or more wildlife species, was reduced in the presence of livestock (Table 6.5). The table reveals that sub-units with two or more wildlife species were more frequent farther from water. This pattern did not hold for sub-units with three or more wildlife species farther than 15 km from water. Here the relative frequencies were reduced compared to distances closer to water. Log-linear analysis of these data confirmed this significant negative association between wildlife diversity and the presence of livestock and distance to permanent water.

Table 6.5 Frequency (expressed as row percentages) of aerial survey sub-units where one, two or >2 wildlife species were recorded in relation to distance to permanent water and the presence/absence of livestock*.

Distance	Livestock	Number of wildlife species			Total
		1	2	>2	(%)
0-10 km	Present	90.32	7.66	2.02	100
	Absent	81.96	13.47	4.57	100
10-15 km	Present	84.55	11.82	3.64	100
	Absent	79.94	15.87	4.19	100
> 15 km	Present	86.63	12.87	0.50	100
	Absent	81.45	16.47	2.09	100

*The analysis was restricted to those sub-units where wildlife were present (n=2243).

Table 6. 4 Water physiological parameters (see Section 2.4) in wildlife and livestock species, as derived from the literature*.

Species	Water requirement[1] 10^{-2} l kg^{-1}d^{-1}	Water loss dehydration 22-40[2]	Urine / Plasma osmotic ratio[2]	Faecal water[3] %	Water flux rate[5] ml/kg$^{0.82}$	Min. body water turn-over rate[7] 10^{-2} l kg^{-1}d^{-1}	WTR/DEE[8] = WEI[9] ml/kJ	Tolerance to aridity
Ostrich			2.7	55			0.107-0.17[9]	yes[20]
Oryx	2.85[10]-3.00	2.15	8.0	55[4]	78-70	3.0	0.142	yes[21]
Impala	2.98[2]	1.92	7.3	53-57[6]		7.2[11]	0.335	weak[22]
Zebu cattle	3.22	2.10	4.0		177	7.3	0.241	weak[23]
Sheep	3.74[6]	3.12	8.0	50[6]	197[6]	7.2	0.377[12]	yes[24]
Grant's gazelle	3.87	3.25	8.0				0.102	yes[25]
Goat	4.18[6]	3.24	8.0	50[6]	185[6]	7.7	0.371[12]	yes[26]
Giraffe								yes[27]
Warthog								unclear[28]
Lesser kudu								yes[29]
Gerenuk								yes[30]
Grevy's zebra								no[31]
Burchell's zebra								no[32]

*Tolerance to aridity was based on the physiological evidence summarized here and the reported ability, as demonstrated by ecological evidence referred to below, to live far away from watering points, or to live without drinking water for prolonged periods of time.

[1]) Taylor (1968)

[2]) Evaporative water loss in dehydrated laboratory animals at 22° - 40°C; expressed in 10^{-2} liter H_2O per kg body mass per day; Maloiy *et al.* (1979), from various sources

[3]) Woodall and Skinner (1993), measurements in animals from South Africa and Namibia

[4]) Measured in gemsbok

[5]) Listed from various sources by Grenot (1992); a low water flux rate suggests a water conservation physiology.

[6]) Maloiy (1973)

[7]) King (1979). A low minimal body water turnover rate suggests a water conservation physiology.

[8]) Calculated by Withers *et al.* (1980) as water turnover rate (ml/d) / daily energy expenditure (kJ/d) = ml/kJ. A low ratio suggests tolerance to aridity.

[9]) Williams *et al.* (1993); but their estimated energy intake values are 10x larger than those by Withers (1983)

[10]) King *et al*. (1975)

[11]) Fairall and Klein (1984)

[12]) Calculated as min. body water turnover rate / estimated DEE , with estimated DEE = $0.82*2.0*405*BW^{0.75}$ kJ

[20]) Western (1975); Williams *et al.* (1993), but juveniles drink regularly

[21]) This table; Western (1975); Smithers (1983)

[22]) This table provides contradictory information, often suggesting that the species is potentially capable of conserving water well, yet ecological evidence strongly suggests that impala need to drink regularly: Fairall and Klein (1984), Smithers (1983), Vrba (1984) *in* Fairall and Klein (1984); Maloiy (1979)

[23]) This table suggests that zebu are potentially capable of conserving water reasonably well, but the urine concentrating capacity is very low; see also Maloiy (1979)

[24]) This table; Maloiy (1979)

[25]) This table; Maloiy (1979); Western (1975)

[26]) This table; Maloiy (1979)

[27]) Smithers (1983); Scheepers (1992)

[28]) Smithers (1983): independent of water; Western (1975): water dependent

[29]) Leuthold (1978a): also has a very small home range.

[30]) Leuthold (1978b)

[31]) Becker and Ginsberg (1990): females very water dependent during lactation, from March to September <5km from water

[32]) Western (1975); Smithers (1983): almost invariable <12km from water

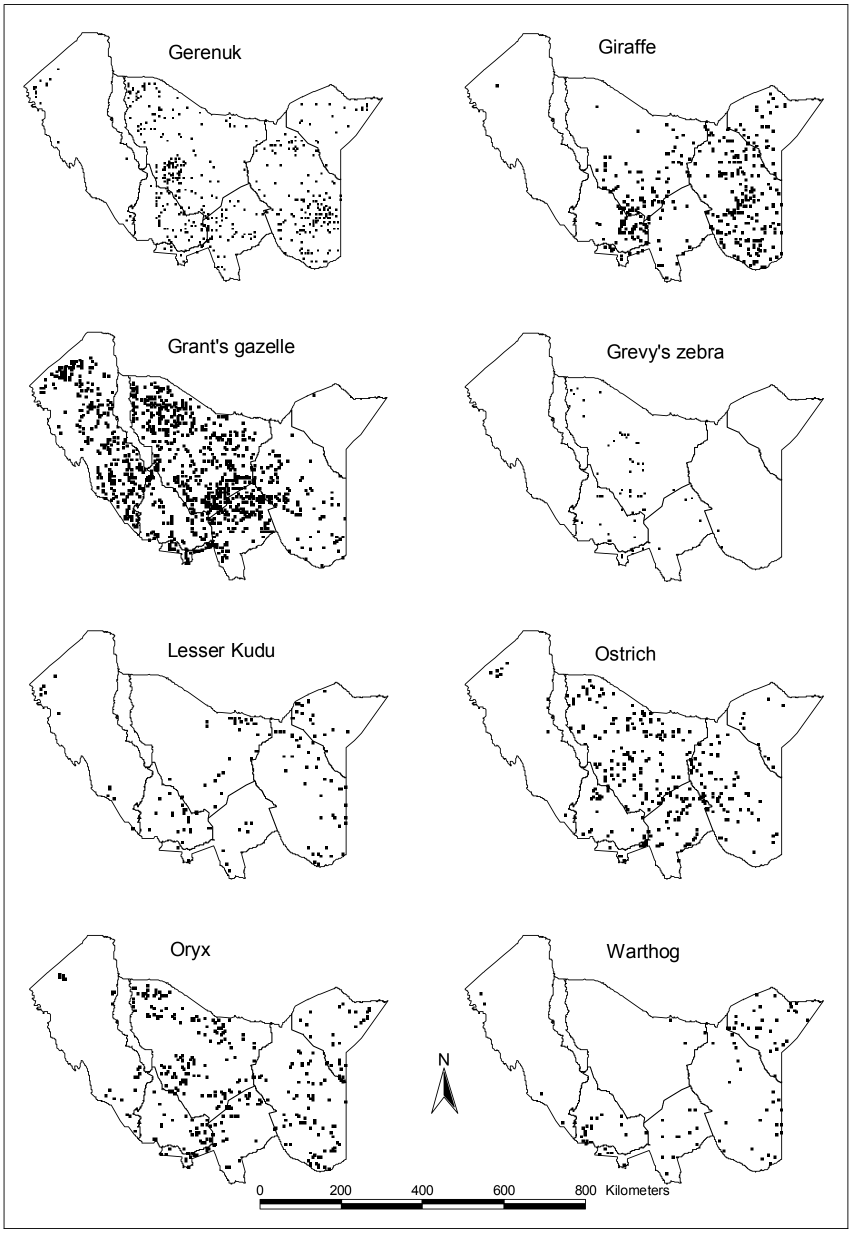


Figure 6.3 Maps displaying the distribution of Reticulated giraffe, Grant's gazelle, gerenuk, Lesser kudu, ostrich, oryx, warthog and Grevys zebra in northern Kenya in 1990.

6.4. DISCUSSION

In northern Kenya, different species of livestock need to drink once every 1-3 days (Coppock *et al*., 1988), which forces herdsman to remain close to permanent water in the dry season (Shaabani *et al*., 1992b). The likelihood of encountering livestock drops by half (47% to 24.8%) as the distance from water increases from < 10 km to > 15km. This assessment of the magnitude of the impact of distance to water is strongly determined by the fact that our distance data were classified into three classes. The actual impact of distance to water on the presence of livestock would have been more pronounced if we had been able to use a continuous variable for distance to water. A second factor affecting the magnitude of the impact of distance to water is the fact that in the northeastern area several clusters of livestock were observed at distances > 15 km from water. An under-reporting of the permanent water points in this area could cause this. At the time of data collection for the Kenyan Rangeland Handbook the northeastern districts were not safe, and intensive field-checks for water points may not have been possible. In addition, the animal censuses in the northeastern region were conducted at the start of the short rains. Hence, ephemeral bodies of surface water may have accumulated in the rangelands, thus allowing herdsman temporarily to graze their animals away from permanent water.

The observed reduced frequency of wildlife > 15 km from water conforms to the decrease in wildlife numbers farther away from water commonly observed in conservation areas (Owen-Smith, 1996, Western, 1975). The reported depressed frequency of wildlife within 10 km of water points differs from the expected distribution of wildlife in relation to water points. Depending on the water dependency of the species, one would expect the frequency of wildlife near the water points at least to be equal to that further away. Burchell's zebra and also Grevy's zebra and to some extent impala confirm this expectation, with an increased presence in the vicinity of water. Giraffe, gerenuk, oryx and ostrich, however, were significantly more frequent further away. Hence we suggest that some other factor, related to distance to water, deter these wildlife species from coming closer to the water points.

To our knowledge this is the first case where a negative association has been reported between livestock and the distribution and diversity of wildlife. This might lead to an intuitive conclusion that livestock exerts a negative impact on wildlife. Competition for food resources between livestock and wildlife could be a possible mechanism. Prins (1992) for example argued that livestock husbandry could wipe out wildlife, as a result of competition for resources. In a more recent review on competition between livestock and wildlife in African rangelands Prins (in press) indicates that there is little evidence for competition although diffuse competition cannot be excluded. Competition for forage appears to cause wildlife to avoid areas near pastoral settlements in the Mara region of southern Kenya (Reid *et al*., unpublished results). The reverse, wildlife competing with livestock, seems highly unlikely since wildlife densities that are reported in this study are very small compared to those of livestock.

The observed negative association between livestock and wildlife may well reflect the impact of people associated with livestock rather than the impact of livestock itself. There are many, mostly anecdotal, references claiming a negative impact of people on wildlife in the arid zone. Cramp and Simmons (1977) reported that ostrich avoid regions frequently disturbed by humans, while Folch (1992) attributed the reduction in range of ostrich to hunting for feather, eggs, meat and skin, and to habitat destruction caused by overgrazing. Kingdon (1982) reported that, to the west of Lake Turkana, oryx had been virtually exterminated by hunting. Interviews in the late 1980s with Turkana indicated that wildlife hunting was a common subsistence activity at that time (Reid, unpublished data). A case in point in our study was the observation that warthog, which is not eaten by Muslims, was more frequent in the Islamic districts in the northeastern region compared with the Christian districts in the North-West. This would suggest that Christians are hunting warthog while Muslims do not. Furthermore, firearms are widely available in northern Kenya (JdL, pers. obs.). In 1998, the then Director of KWS, suggested that the so called bush meat industry (poaching) intensified following an earlier rise in the price of meat (Dr. Leakey, pers. comm.).

When water points are sparsely distributed livestock cluster around them and wildlife occupy the more remote areas in between. When water points are in a denser network, livestock is more evenly distributed across the landscape and wildlife is virtually absent. We suggest that such patches of less intensively used rangeland form a refuge for a number of wildlife species. Further development of water points will lead to a more even spread of livestock across the landscape and ultimately to the disappearance of these wildlife refuges.

The development of drinking water resources for livestock and people forms one of the major interventions in rangelands. Such interventions tend to be executed without consideration for their impact on wildlife. Our data do not allow us to establish causal relationships but strongly suggests that these interventions exert a negative impact on the distribution and diversity of wildlife. We argue that sustainable conservation of wildlife resources requires a coherent land use policy that balances wildlife and livestock and the further development of water points. We recommend that the impacts of water points on wildlife (and vegetation and soils) be assessed before new water points are constructed in arid rangelands. Only then can local communities and national policy makers objectively assess the trade-off between increased livestock production and conservation of wildlife.

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CHAPTER 7

LAND COVER CHANGES AROUND A MAJOR EAST AFRICAN WILDLIFE RESERVE: THE MARA ECOSYSTEM (KENYA)

Chapter 7

In chapter 4 we showed that land use/land cover changes occurred in the rangelands districts that have potential to sustain agriculture as indicated in aerial censuses conducted in the rangelands over the last 20 years. In this chapter we investigated the dynamics of those changes over time by integrating both high and low resolution image to map out the land use/cover changes in one of key wildlife and livestock area facing high declines in wildlife - the Masai Mara

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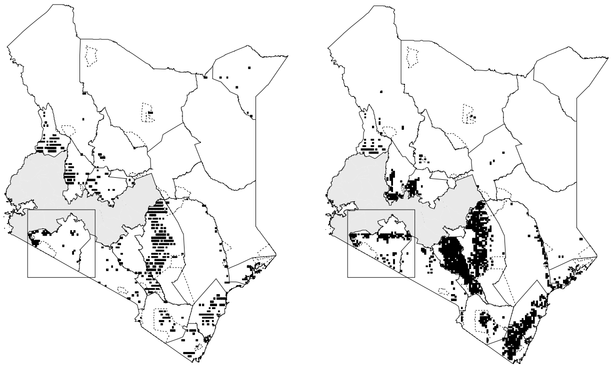

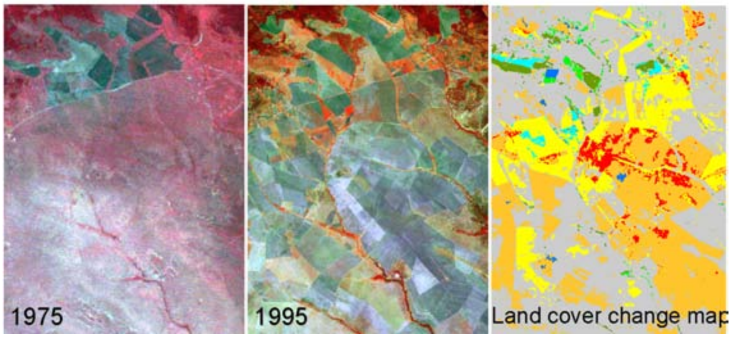

Chapter 7

Land-cover changes around a major East-African wildlife reserve: The Mara Ecosystem (Kenya)

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Abstract

Dynamics of savannah vegetation are still poorly understood. This study aims at analysing land cover changes over the past 20 years in the rangelands area of Narok District, Kenya. To analyse the impact of inter-annual climate variability and human activities on land cover modifications in the area, change detection techniques based on remote sensing data at different spatial and temporal resolutions were used. Coarse spatial, high temporal resolution NOAA data were analysed to investigate the role of inter-annual climate variations on the ecosystem. A combination of time contextual and spatial contextual change detection approaches was used on a set of 3 high spatial resolution Landsat images to map land cover modifications over the past 20 years. Both data sets are highly complementary in the detection of land cover dynamics. On the one hand, the coarse spatial resolution data detected areas that are sensitive to inter-annual climate fluctuations, but are not subjected to land-cover conversion. On the other hand, the high spatial resolution data allowed detecting land-cover conversions or modifications between two consecutive dates that have a more permanent character and are independent of climate-induced fluctuations in surface attributes.

7.1 INTRODUCTION

There still is considerable debate about the relative importance of anthropogenic, climatic and other factors shaping savannah vegetation, ecology and biodiversity. The interplay of different land tenure and management systems, and of national and international economic factors in changes in resource uses, in biodiversity and of livelihoods is poorly understood. Climate driven fluctuation characteristics of savannah ecosystems make it difficult to investigate causal relationships of land-cover changes in short-term studies.

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The objective of the overall project is to use the Serengeti-Mara Ecosystem as a natural experiment to study the impacts of land use policy and land use strategies on the relations between wildlife, farming and herding in East African savannahs. The ecologically and ethnically continuous rangelands of the Serengeti-Mara Ecosystem straddle the Kenya - Tanzania border, comprising wildlife conservation areas and joint conservation/pastoralist land use areas in each of two radically different economic contexts. The Serengeti National Park and Masai Mara National Reserve are surrounded by areas of largely pastoralist and agro-pastoralist land use which act as buffer zones, playing a major role in maintaining wildlife populations. As human populations grow and land use intensifies, the interaction of conservation with development in the buffer zones surrounding the protected areas becomes more complex. In the buffer zone, habitat conversion is particularly evident in high-potential areas of central importance to farmers, livestock and wildlife alike. Land use policy is a major factor influencing the conversion of rangelands to cultivation, but the same policy can produce different outcomes in different national and regional contexts. The relative importance of policy in producing these outcomes, as compared to biophysical, socio-economic and demographic factors, varies in different parts of the Serengeti-Mara Ecosystem.

This paper deals with the first step in the analysis of the ecosystem dynamics, namely the study of the changes in land cover over the past three decades. We attempt to measure, at a fine level of spatial aggregation, land-cover changes in the Kenyan part of the Serengeti-Mara Ecosystem. The study area in Kenya is subject to a large variety of changes, ranging from natural successions in the Masai Mara National Reserve, through intensification of rangelands use in the Loita plains, to the expansion of subsistence agriculture in the northern part of Narok district and the large-scale development of mechanised agriculture.

The objective of this study is to develop and test a change detection technique based on high-resolution satellite imagery that allows detecting land-cover changes that display a certain level of permanence in the landscape while controlling for the short term and highly reversible effects of inter-annual climate fluctuations. This study combines the detection of land-cover changes at fine spatial resolution with the analysis of a time series of coarse resolution satellite data.

7.2 BACKGROUND

7.2.1 Change detection

Digital change detection based on satellite images is a process of identifying differences in the state of an object or phenomenon by observing it at different times (Singh 1989). Several authors have reviewed remote sensing change detection techniques, in general (Singh 1989) or for specific applications (Coppin and Bauer 1996). Singh (1989) describes normalised difference vegetation index (NDVI) image differencing as one of the more straightforward techniques, which gives accurate results for forest change detection. Recently, image-differencing techniques, sometimes in combination with post-classification comparison, have been implemented using multi-temporal satellite data in a wide range of ecosystems (Pilon *et al* 1988, Sader 1995, Coppin and Bauer 1996, Michener and Houhoulis 1997, Washinghton-Allen *et al* 1998). Macleod and Congalton (1998) preferred image differencing change detection to post-classification and principal component analysis to detect changes in submerged aquatic vegetation. Lyon *et al* (1998) used NDVI image differencing with thresholding to detect land-cover changes in Chiapas, Mexico. Prakash and Gupta (1998) applied the technique in a land-use change detection exercise in a coal mining area in India.

Few authors have published results on change detection studies with high-resolution remote sensing data in the Serengeti-Mara ecosystem. Mwalyosi (1992) used aerial photographs to map land use changes and resource degradation in south-west Maasailand, Tanzania. Lamprey (1984) used satellite data to examine the relationship between vegetation change, livestock distributions and settlement distributions in the Mara region. He used several Landsat-MSS images to relate different phenological states of the grasslands to cattle density. Land use changes in Ngorengore-Loita plains in Kenya were mapped by Karime (1990), using visual interpretation of Landsat images.

Previous studies have mainly observed African vegetation at high temporal but low spatial resolution, using NOAA-AVHRR time series. Justice *et al* (1986) used AVHRR data for vegetation monitoring in east Africa and Tucker *et al* (1994) used AVHRR-GAC time series to determine the extent of the Sahara Desert and its inter-annual variation from 1980 to 1990. Lambin and Ehrlich (1997) studied land-cover changes in Sub-Saharan Africa between 1982 and 1991. They calculated a multi-temporal change vector index based on monthly composites of AVHRR-GAC NDVI and land surface brightness temperature data. Analysing the resulting annual land-cover-change magnitude images, they found that about 2.6% of sub-Saharan Africa is subjected to a continuous loss in vegetation over the study period. Several authors (Davenport and Nicholson 1993, Richard and Poccard 1998, Eklundh 1998) studied the sensitivity of NDVI to inter-annual variations in rainfall. While the first two studies came up with good correlation of NDVI with bimonthly antecedent rainfall, the last study contests the validity of these relationships, stating that most of the correlation might be due to auto-correlation in the data and non-stationarity of the data.

7.3 STUDY AREA

7.3.1 Geographical context

Narok District is located in south-western Kenya, between 34°45'E – 36°00'E and 0°45'S – 2°00'S (Figure 7.1). The Transmara Plateau, in the west, is separated from the Masai Mara National Reserve by the Siria Escarpment. The plateau naturally supports a mixture of forest and woodland with scattered bushes, but is rapidly being transformed into cultivated land. The Mau Uplands in the north are the result of recent volcanic activity with highly porous and fertile volcanic ash soils (Said *et al* 1997). The uplands are part of what is known in Kenya as the "high potential lands" and were extensively opened up for agriculture.

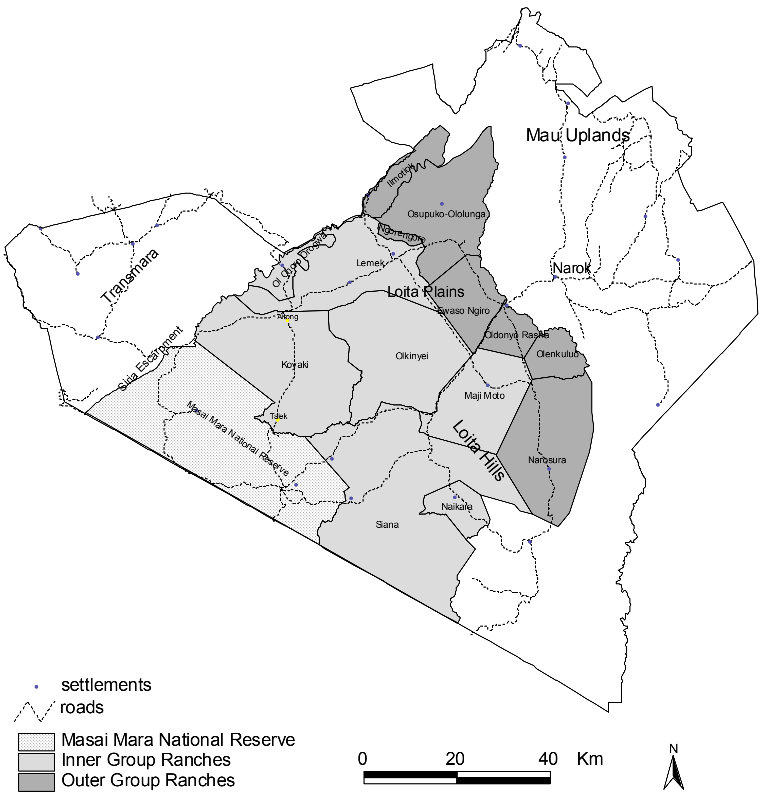


Figure 1

Figure 7.1: Study area is situated in Narok district. It lies approximately between 1° and 2° south and longitude 34° 45′ and 36° 00′. It covers an area of approximately 6000 km^2 of which 1368 km2 forms the Masai Mara National Reserve.

The rangelands of the southern part of the district are bounded on the east by the Rift Valley, on the south-west by the Kenya-Tanzania border and on the north-west by the Siria Escarpment. This roughly triangular area can be divided into three range units, based on biogeographic and climatic differences. The Mara eco-unit consists mainly of grasslands in the western part of the study area and comprises the Masai Mara National Reserve. The Loita Plains stretch out in the north-eastern part of the study area and are covered by dwarf shrub and whistling thorn grasslands. Siana (east) is an area of hills and plains supporting *Croton* bush and several other woody species interspersed with grasslands (Stelfox *et al* 1986).

The Masai Mara National Reserve was established in 1961, bordering Tanzania's Serengeti National Park. The 152 300 ha reserve is a formal conservation estate, where land use is restricted to wildlife tourism. Surrounding this area of fortress conservation are the vast rangelands of former Maasailand. The rangelands were intended to act as a buffer zone between the National Reserve and the high potential areas in the northern part of Narok District that have now almost completely been brought under cultivation. The rangelands surrounding the Masai Mara National Reserve contain year-round communities of resident wildlife, but migrating wildlife also spills out onto them during the dry season. These dry-season grazing resources in the buffer zone are important to the migrant wildebeest and to livestock alike. The Land Group Representatives and Land Adjudication Act of 1968 enabled the land of Narok District to be demarcated into Group Ranches. By the end of the 70s, most of the land in Narok had been adjudicated and ranches were owned and under private title by a group of registered members and managed by an elected committee. Since then, many of the group ranches have been subdivided into individual land titles (Singida 1984).

7.3.2 *Climate*

Rainfall in the area is generally influenced by the Intertropical Convergence Zone, but local variations in topography together with orographic and diurnal effects play a major role in rainfall patterns in the study area (Brown and Cocheme 1973, Norton-Griffiths *et al* 1975). The main rain shadow areas encompass the Loita Plains and part of the Siana Plains, with a mean normal rainfall of approximately 400mm. There is a rainfall gradient from the dry south-eastern plains (500mm/yr) to the wet north-west (1200mm/yr) (Sinclair 1995). In the Loita Hills and the Siria Escarpment, there is a sharp increase in rainfall with altitude. The rainfall pattern is weakly bimodal, with the "short rains" occurring during November-December, followed by the main rains from March to May. The main dry season runs from mid-June to mid-October, with sometimes a lesser dry period in January-February. Often, the short and long rains are merged into one season, or the short rains fail completely.

7.3.3 *Historical changes in land cover*

The entire Mara ecosystem has been subject to considerable vegetation changes since the beginning of this century. Explorers and hunters from the early 1900s encountered a Mara characterised by broad, open expanses of grassland studded by occasional *Acacia* trees, much as the Mara is today. Waller (1990), Dublin *et al* (1990) and Dublin (1995) give an overview of ecosystem dynamics in this century. Over the past century, the ecosystem of south-western Narok has passed through successive stages of transformation as the result of the interaction between four distinct, and probably cyclical, processes of change: change in vegetation, climate, tsetse and tick infection and pastoral occupation and management. At the end of the 19th century, Maasai pastoralism was supported within an extensive grassland ecology (Waller 1990).

Following the great rinderpest epidemic of 1890, human and animal populations were reduced to negligible numbers in the Mara region. These natural disasters disrupted the grazing and patterns of displacement of Maasai pastoralists. Up until the 1950s, the Maasai settlements and grazing patterns concentrated human and stock population away from the Mara Plains (Waller 1990). With low fire frequency due to recurrent droughts and with low animal numbers, the prevailing conditions saw the establishment of dense woodlands and thickets in the Mara Plains (Dublin *et al* 1990). This dense, woody vegetation was a habitat for tsetse flies and prevented significant human settlement. In the 1950s and 60s, the woodlands were again converted into grasslands (Waller 1990). At that time, the human population in the area was rapidly increasing and fire was used by Maasai herdsmen to improve grazing pastures and to clear tsetse-infested bush. Increased elephant densities further maintained the woodland decline in the Masai Mara National Reserve as the animals moved to the protected areas from the surrounding, more densely inhabited areas. By the mid-70s the wildebeest population had increased to about 1,5 million and has fluctuated around 1 million ever since (Dublin 1995). The wildebeest remove the majority of the available standing biomass in the grassland plains and thus help to maintain the grassland vegetation.

7.4 METHODS AND MATERIALS

7.4.1 *Data*

For the coarse spatial resolution analysis, two data sets of satellite imagery have been used:

- the NOAA/NASA Pathfinder AVHRR 8-km Land Data Set (PAL) (Smith *et al* 1997), spanning the period 1981-1994, and
- The land-cover change data obtained by Lambin and Ehrlich (1997) using the NOAA-AVHRR GAC data set processed at the Joint Research Centre (Malingreau

and Belward 1994) and covering the period 1982-1991 at a spatial resolution of 5 km.

- Daily rainfall data were collected at Narok meteorological station from 1977 onwards and aggregated to monthly totals.

For the fine spatial resolution analysis, a time series of three satellite images has been acquired for the area. The data set consists of one Landsat-MSS image (29-07-1975) and two Landsat-TM scenes (09-01-85, 21-01-95), all acquired with an interval of 10 years. All images have been geometrically co-registered with a high accuracy (RMS error below the pixel size, using a second-order polynomial based on more than one hundred ground control points) and registered to a common UTM projection, based on the 1/250 000 topographic map of Narok District, Kenya. Differences in sensor parameters and solar illumination conditions were taken into account in the radiometric correction, transforming the digital numbers into at-satellite reflectance (Markham and Barker 1986).

7.4.2 *Land-cover change analysis*

The high inter-annual variability of ecological conditions at a variety of spatial and temporal scales is a distinctive aspect of savannah ecosystems. To detect and categorise land-cover changes in East African savannahs, one has to take into account the inter-annual climate variability and the fluctuations in land cover conditions. Assessing the broad scale inter-annual fluctuations in rainfall distribution, and in the timing and length of the growing season allows understanding the impact of inter-annual variability in vegetation conditions on the change detection at a finer scale. We used NOAA-AVHRR Pathfinder (PAL) time series to analyse the seasonal behaviour of the vegetation signal at a regional scale. We then detected changes at a finer spatial resolution, using a time series of three Landsat images. The resulting land-cover change map was validated in the field and the spatial organisation of the different change processes around the Masai Mara National Reserve was analysed and mapped.

The analysis at both coarse and high spatial resolution was based on the normalised difference vegetation index (NDVI). The NDVI was calculated from reflectances in the red and near infrared (NIR) parts of the electromagnetic spectrum as (NIR-Red)/(NIR+Red). Empirical studies and simulations with radiative transfer models support the interpretation of the NDVI in terms of fraction of photosynthetically active radiation absorbed by the vegetation canopy, canopy attributes (e.g. green biomass or green leaf area index) and state of the vegetation (i.e. vegetation vigour or stress). (e.g. Kumar and Montheit 1981, Asrar *et al*. 1992, Myneni *et al*. 1995).

7.4.2.1 *Climate-induced fluctuations in vegetation at coarse resolution*

Monthly maximum value composites of NDVI from the AVHRR-PAL data set were extracted over the study area. Several authors (Davenport and Nicholson 1993, Richard and Poccard 1998), have linked NDVI to rainfall in Africa and concluded that there is a high correlation between vegetation performance and rainfall in areas were rainfall is the limiting factor (<900mm/year) and that have a marked dry and wet season. To characterise climate-driven fluctuations in the net primary production of grasslands of Narok district, a rangeland area of 96 000ha was selected in a region with low human impact. The monthly NDVI data for this area were spatially averaged. Monthly NDVI anomalies were calculated for the entire time series using the z-transform $((x_i - \mu)/ std)$, with x_i being the NDVI value for a given month in year i, μ the mean NDVI value for that month across all years, and *std* the standard deviation of the NDVI values for that month across all years. Inter-annual variations in vegetation conditions over the study period could thus be analysed. This information helped us in assessing the vegetation conditions during the growing season preceding the acquisition of the Landsat-TM images (1985 and 1995). As the high-resolution images only provide a snapshot of the state of the land cover, it is important to place these snapshots in their temporal context.

While the former approach qualitatively identifies the temporal behaviour of the vegetation, the use of change vector magnitude images (Lambin and Ehrlich 1997) allows to quantify the magnitude and spatial extent of deviations in seasonal behaviour of vegetation, e.g. due to drought impacts. Yearly change vector magnitude (ChM) images for the area, calculated for the period 1982 – 1991, were investigated. The ChM images depict the intensity of the change in land cover, measured in terms of deviation between the temporal development curve of a land-cover indicator for a given pixel, for a given year, and a temporal development curve of reference for that pixel (Lambin and Strahler 1994). For drought years, the ChM will be higher for the entire scene, but some vegetation types are more affected than others. To isolate the regions that are very susceptible to climate variations, we thresholded each ChM image at the mean ChM + 1,5 standard deviation. Pixels with a ChM above that threshold for a given year correspond to resolution cells that are considered to be affected by vegetation conditions which are deviating from the reference state in a more pronounced way compared to the average deviation in vegetation conditions for that year. The number of times that a pixel had a high ChM value during the 1981-1991 period is depicted in Figure 7.4.

7.4.2.2 *Land cover conversions and modifications at fine spatial resolution*

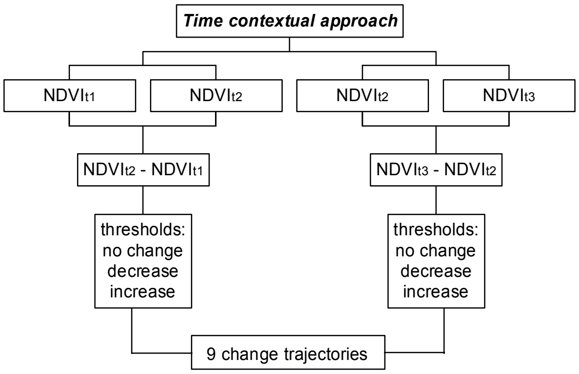
For the high-resolution data analysis, a combination of a time contextual and spatial contextual approach was adopted (Figure 7.2). The time contextual approach allows to detect changes in vegetation cover, while controlling for inter-annual variability. This technique is complemented by the spatial contextual approach, allowing delineation of small areas of human-induced disturbance within larger homogeneous zones, that themselves might have been subject to climate-induced changes in surface conditions. In combination with the time contextual technique, it allows us to accurately delineate small plots opened for cultivation or other local scale activities, without overestimating change in other areas.

In the time contextual analysis, the image differencing technique was applied to pairs of observation years, subtracting NDVI values measured at successive dates. The band differencing method measures change along a continuum of change intensity. The difference image depicts the degree to which the vegetation cover was modified, using the NDVI as a proxy. Only the areas with a high change intensity were retained, after application of a threshold value of change intensity. These thresholds were interactively defined based on areas of known change. They allowed classification of each difference image into one of three categories: increase in NDVI, no change, decrease in NDVI. The resulting change images for paired dates were joined, regrouping the class combinations into nine land-cover change trajectories (Table 7.1).

To detect the small patches of agriculture in the mountainous areas and other small features of human impact, a spatial contextual approach was designed. If, in the image differencing technique, conservative thresholds are chosen to minimise the commission error in change detection, the change map mainly indicates the centres of areas that are subjected to change, rather than delineating the exact boundaries of the changed areas. This implies that small plots are often not detected, or at least not clearly delineated.

The spatial contextual approach compares changes at two scales. It identifies areas that behave differently through time at the pixel level as compared to their spatial context. The pixel level is referred to as local scale while the spatial context is referred to as landscape scale. The method detects areas subjected to local scale, high magnitude (e.g. anthropogenic) change in a situation where more subtle, landscape scale changes (e.g. due to climate fluctuations) are also taking place. To analyse the landscape scale changes, each NDVI image is smoothed with a low pass filter (101*101 pixels). The size of the filter is determined based on the average size of landscape units in the area. Image differencing is applied to each pair of smoothed NDVI images to detect landscape-scale changes. Local-scale change patterns are detected by image differencing between the unsmoothed, full resolution NDVI images. Subsequently, the local-scale change image is subtracted from the landscape-scale change image.

In the resulting image, all pixels that behaved differently through time at local and landscape level have a high value. These high difference values can be caused by three situations. Firstly, they may correspond to local changes in an otherwise unchanged landscape. Secondly, they may correspond to local changes in a landscape affected by more subtle, climate related fluctuations in land cover. These two situations lead to a detection of change. Thirdly, in exceptional cases, they may correspond to large magnitude landscape-scale changes (e.g. large-scale conversion for mechanised agriculture), with a few spots remaining unchanged at the local scale. To avoid integrating this situation in the change detection, a mask was applied to the landscape-scale image difference map to exclude from the analysis those areas that have been subjected to large magnitude, anthropogenic landscape-scale changes. This was performed by applying a threshold to the smoothed difference image.



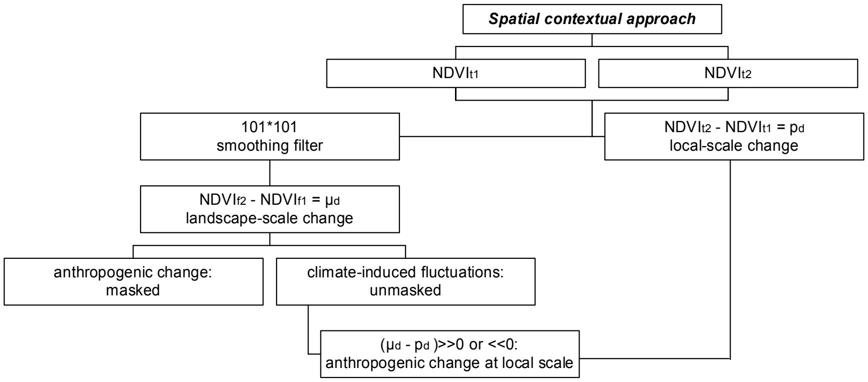


Figure 7.2: Flowcharts describing the time contextual and spatial contextual approach used to detect land-cover changes with high-resolution satellite imagery.

Table 7.1: Land cover change trajectories

Change trajectory	*Change class*
$NDVI_{75} = NDVI_{85} = NDVI_{95}$:	Stable vegetation
$NDVI_{75} > NDVI_{85} = NDVI_{95}$:	Decrease1975-85
$NDVI_{75} = NDVI_{85} > NDVI_{95}$:	Decrease1985-95
$NDVI_{75} < NDVI_{85} = NDVI_{95}$:	Increase1975-85
$NDVI_{75} = NDVI_{85} < NDVI_{95}$:	Increase1985-95
$NDVI_{75} > NDVI_{85} > NDVI_{95}$:	gradual decrease
$NDVI_{75} < NDVI_{85} < NDVI_{95}$:	gradual increase
$NDVI_{75} > NDVI_{85} < NDVI_{95}$:	Fluctuation
$NDVI_{75} < NDVI_{85} > NDVI_{95}$	Fluctuation

On the final difference map (i.e. difference between the local-scale and landscape-scale image difference maps), the sign of the change pixel depends on the type of local-scale change (e.g. decrease or increase in vegetation cover). The final change map can be simplified into three classes: local-scale decrease in NDVI, no change, local-scale increase in NDVI. Analogous to the procedure followed in the time contextual approach, the two change maps (corresponding to the 1975-85 and 1985-95 periods) are joined to identify nine land-cover change trajectories. Finally, the land-cover change maps based on the temporal and spatial-contextual methods were combined, taking into account the changes detected on any of the two maps. Finally, a manually digitised cloud mask was applied to the land-cover change map, masking all pixels that were cloud-obscured at one of the 3 dates.

Note that the earliest MSS image does not cover the westernmost part of the study area as covered by the TM scenes. The area for which there were no data for 1975 (MSS image) was treated as if there were no changes in land cover for the area between 1975 and 1985.

The final land-cover change map was validated with field observations made in August 1998. Each of the areas where significant changes in land cover were detected was visited, as well as a number of areas of no change, as a control. The current state of the vegetation was analysed and, where possible, short interviews with local people were held to collect qualitative information on past ground cover. For some sites, the work was facilitated through the use of aerial photographs from the 80s. In the rangeland areas, information was collected on the presence or absence of plant species indicating changes in the species composition of grassland communities. Each visited site was documented with photographs. Together with the degree and nature of change, the areal extent of change was validated.

7.5. RESULTS

7.5.1 *Inter-annual climate fluctuations*

Figure 7.3a shows the temporal behaviour of the NDVI for the sample rangelands area in the Mara region. The mean seasonal profile of NDVI for the period 1981-1994 is also reproduced, to allow for a visual interpretation of the yearly deviations in NDVI. Standardised NDVI anomalies were compared with rainfall anomalies for Narok station. A significant correlation was found ($r=0.50$, $p<0.001$) between the rainfall anomalies and the NDVI anomalies with a two month lag (Figure 7.3b). NDVI is thus a good indicator of the impact of inter-annual climate variability on vegetation conditions. Figure 7.3a shows a lower than average net primary production for 3 consecutive years in the early eighties. After drought conditions between 1981 and 1983, the wet season in 1984 also knew a low net primary production. Despite a very early greening up during the short rains (in August instead of October 1984), NDVI was slightly below average in February 1985, at the moment of acquisition of the first TM scene. Thus, the vegetation in Narok District was still recovering from previous droughts and not in optimal condition when the 1985 TM image was captured.

The period between 1985 and 1995 can be split up in two phases in terms of climatic conditions. After an initial failure of the rains in 1986, the last part of the decade was very good, with average to above average net primary production. A new drought was most noticeable in the very low NDVI values at the end of 1991 and beginning of 1992. The vegetation recovered during the wet season. After initial abundant rains in the '92-93 short wet season, 1993 was another drought year. Abundant rainfall during the 1994 wet season, resulted in high NDVI values and large amounts of standing green biomass at the start of the dry season. The short rainy season at the end of 1994 received above average rainfall amounts, but concentrated in a short period, followed by a dry period of three months before the main wet season started in March 1995. Thus the Landsat TM image acquired in February 1995 also depicts below optimal vegetation conditions. We can thus conclude that vegetation conditions represented on the 1985 and 1995 Landsat-TM images are highly comparable. This will facilitate the change detection analysis at a fine spatial resolution. Note that for the beginning of the study period (1975-1981), no coarse resolution satellite data were available. Rainfall data for Narok were only available from 1977 onwards, but records from rain gauges in the Masai Mara National Park indicated that the 1975 wet season had slightly below average rainfall. As the 1975 image was captured in July, after the wet season, the vegetation was also in sub-optimal condition and thus comparable with the other Landsat data.

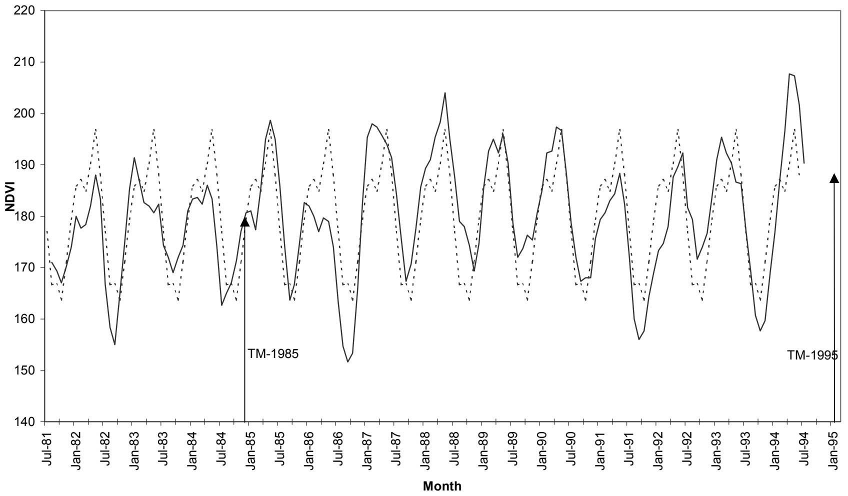


Figure 7.3a: Temporal behaviour of NDVI for rangelands in the Mara region (____: NDVI time series; ------: average NDVI profile)

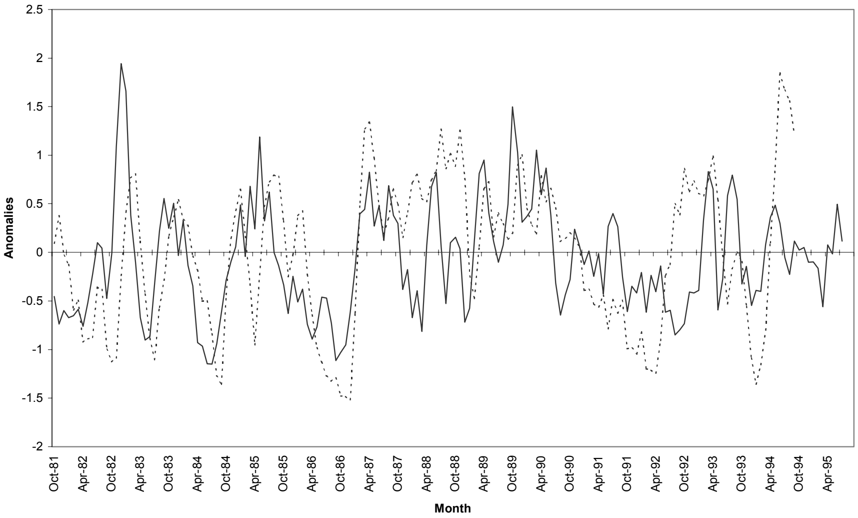


Figure 7.3b: Correlation between the NDVI anomalies and rainfall anomalies for Narok station. The correlation coefficient r = 0.50 for a lag of 2 months between rainfall and NDVI anomalies (____: rainfall anomalies ------: NDVI anomalies)

7.5.2 *Change vector magnitude analysis*

Figure 7.4 represents the areas that are frequently characterised by a high yearly change vector magnitude. Most of the low-lying areas had at least one high value of the change vector magnitude over the study period (1981-1991). During years of serious drought (e.g. 1986), most vegetation types are affected by drought stress and have high change vector magnitudes. In general, the upland areas and the wetter grasslands in the Masai Mara National Reserve seem to be less sensitive to climate fluctuations. These areas receive higher rainfall amounts (>1000mm/yr) and it was shown by others (Davenport and Nicholson 1993, Goward and Prince 1995) that NDVI becomes less sensitive to rainfall fluctuations when rainfall is not the limiting factor for vegetation growth.

Two areas in Narok District frequently have high values of the change vector magnitude. One is the south-eastern part of the Loita Plains, lying in the rain shadow of Loita Hills. The other is an area in the open plains stretching east of Talek to Entingaser, at the western edge of the Loita Hills. Both areas show a large inter-annual variability in vegetation cover, but neither of them is picked up as an area of change in the high resolution change detection analysis. Both are grassland areas, which are sensitive to fluctuations in rainfall but also a highly resilient land cover type. In years of drought, the vegetation cover is very sparse and of poor quality. In years with average or abundant rainfall, the grasslands recover quickly and display a low value of change vector magnitude.

7.5.3 *High resolution land-cover change map*

7.5.3.1 *Statistics on land cover change*

Figure 7.5 shows the land-cover change map derived from high resolution data from 1975, 1985 and 1995 for the study area. The field validation of the initial results has led to some minor adjustments of the map (mostly a downward revision of the spatial extent of the class 'vegetation increase'). A surface of about 116 360 ha or 8.2% of the study area has undergone some form of land-cover change over the past 20 years. Certain types of change, such as conversion towards agriculture, can be mapped with a high accuracy, due to the nature of the change and the sharp boundaries characteristic for cultivated fields. Mapping accuracy depends on the size of the fields. Plots smaller than the pixel size are often not detected. However, other phenomena such as natural vegetation succession or decrease of vegetation cover in rangelands are a gradual process and boundaries between the changed and unchanged areas are fuzzy.

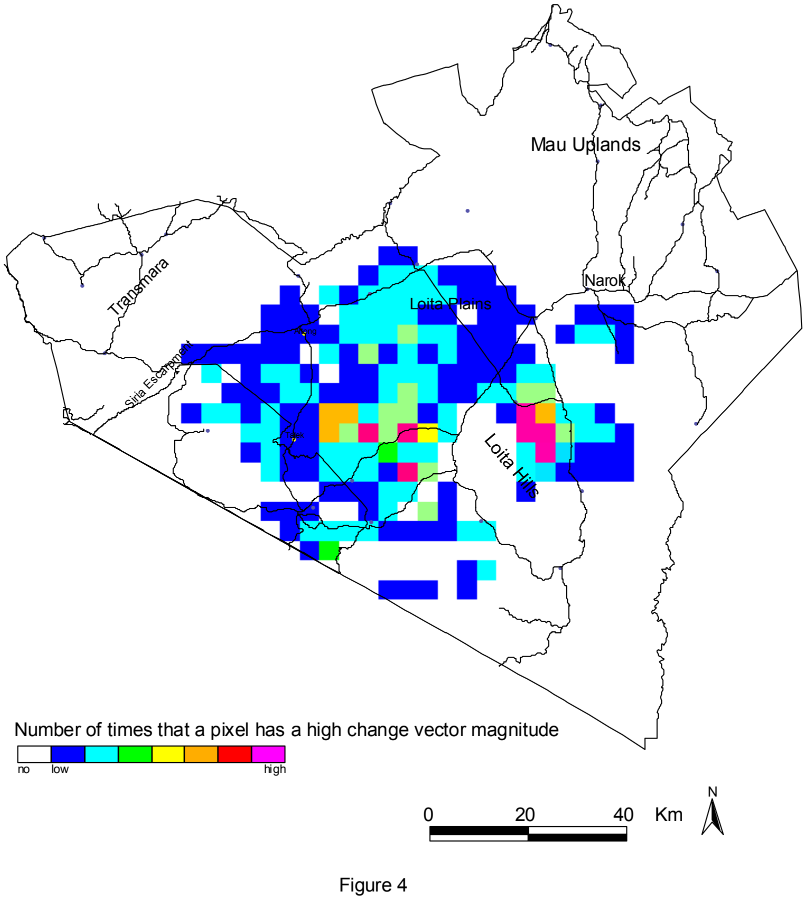


Figure 7.4: Areas having experienced a high change vector magnitude (ChM) over the period 1982-1991. The colour range indicates the number of times that the ChM was high.

To evaluate the contribution of each of the two change detection techniques to the final land-cover change map, we calculated the total area of change detected by each of the techniques within the study area. In the further explanation, we will always refer to the 'study area' as the part of Narok District that is covered by the satellite images. This excludes parts of the image that cover Tanzanian ground as well as part of the north-western highlands that fall outside Narok District. Part of the Transmara area is not covered by the satellite images, hence the change detection statistics only refer to the eastern part of the Transmara area. The time contextual approach (image differencing) detected 97 250 ha of change (Table 7.2). The spatial contextual approach detected a total of 60 890 ha of change, of which 19 110 ha were not detected by the time contextual approach. 47.7 % of the changes are detected by the time contextual approach only. These are mainly large-scale changes, which have been masked deliberately in the spatial contextual approach. Another 35.9% of the changes is detected with both techniques and 16.4% of the small-scale changes is picked up exclusively by the spatial contextual technique. Thus, the spatial contextual change detection method contributes a significant amount of information to the overall land-cover change map.

The majority of the changes detected consist of an alteration in vegetation cover. Few of the vegetation changes observed between 1975 and 1985 return to the "original" vegetation cover at the end of the observation period. Likewise, there are only small areas that are subjected to a continuous loss or gain in vegetation over the study period. Figure 7.6 summarises the sequences of land-cover changes between 1975 and 1985 and between 1985 and 1995. Most of the changes detected are characterised by a decline in vegetation cover. The area affected by a decrease in vegetation cover during the second decade of the observation period was three times larger as compared to the first decade. During the first decade, a total surface of 24 518 ha was subject to a decline in vegetation cover. 86% of the areas that were affected by a decline in vegetation cover remained as such after the initial modification. Only 1 200 ha recovered and gained in vegetation cover in the subsequent observation period and another 2 200 ha (9.1%) were subjected to a further loss in biomass in the second decade of the study period. In the first decade, a total area of 7 571 ha gained in biomass. One third of this area suffered a loss in vegetation in the second decade, the rest of the surface remaining stable afterwards.

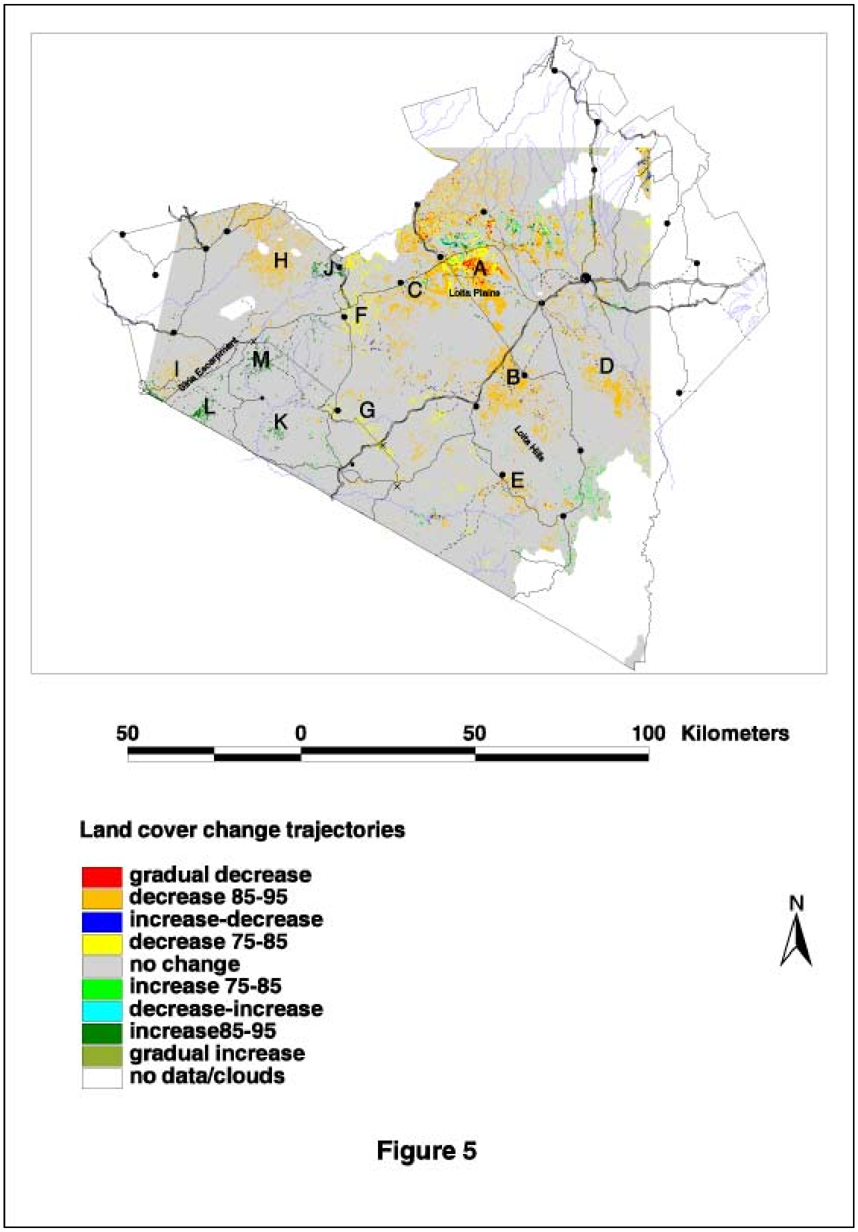


Figure 7.5: Land-cover change map derived from 1975-1985-1995 Landsat images. Nine change trajectories are depicted.

Table 7.2: Land cover changes detected with the different techniques

	time	spatial contextual	time + spatial contextual
total # ha detected	97250	60890	116360
% detected by one technique only	47.7	16.4	
% detected by both techniques			35.9

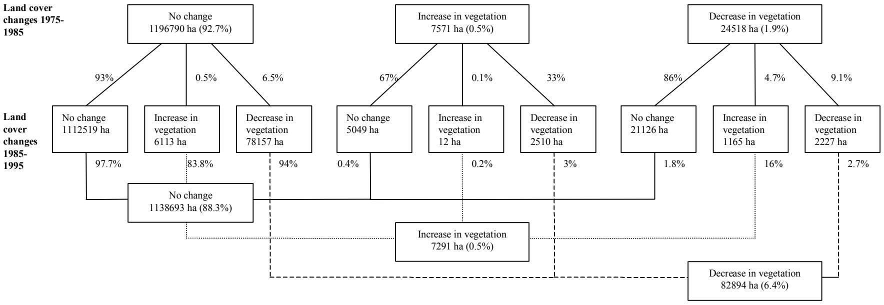


Figure 7.6: Land-cover change trajectories

Land cover conversion and modification expanded considerably in the 1985-1995 period. A total of 82 894 ha was characterised by a decrease in vegetation in that decade. Of this area, 4 700 ha had already known a conversion in land cover during the first decade of the study period. During this period, also 7 290 ha were subjected to an increase in biomass. This surface is similar to the total area that increased in vegetation in the first decade. 1 200 ha have recovered from previous vegetation loss, the remaining surface gaining in vegetation cover after a stable period.

7.5.3.2 *Types of land cover changes in Narok District*

The areas affected by land-cover changes (as depicted in Figure 7.5) have been calculated per administrative unit (Table 7.3a and b). Narok District is subdivided in 102 Group Ranches. For ease of interpretation, those group ranches were clustered in 4 units:

- the Inner Group Ranches surround the Masai Mara National Reserve;
- the Outer Group Ranches are forming a band around the inner Group Ranches;

- the Transmara Group Ranches lie west of the Masai Mara National Reserve in the Transmara region; and
- the Narok Group Ranches include the remaining Group Ranches.

In the following explanation, we will either refer to one of these units or to individual Group Ranches.

The largest area of land-cover changes can be found in the Outer Group Ranches. The conversion of land for large-scale cultivation started in Lemek and Osupuko/Ololunga Group Ranches and spread out in the second decade into Ewaso Ngiro Group Ranch and the Narok area (Figure 7.5-A). In 1975, an area of 4 875 ha north of the Ngorengore-Ololungu road and in the Mau Uplands was cultivated (Karime 1990). From the change map, we calculated that by 1985, at least an additional 11 000 ha were converted into large-scale wheat growing.

In the second half of the study period, another 33 000 ha were converted to large-scale wheat cultivation (Figure 7.5-A). The surface brought into cultivation in the second decade of the study period tripled compared to the area converted in the first decade. Hence, the process of agricultural expansion is clearly accelerating. Based on the change detection analysis, we calculated that in 1995, a total area of about 50 000 ha was used for wheat farming. Expansion still continues, as was ascertained during the field survey in 1998 (Figure 7.7-A). Wheat fields were found well beyond the zone detected on the 1995 images.

Land-cover changes that indicate a conversion to large-scale cultivation can relatively easily be separated from other types of land-cover changes. The change patches are regularly shaped and form closed areas. This contrasts with land-cover changes indicating a decrease in vegetation cover in rangelands. They are characterised by a patchy appearance, forming clusters of small change spots in an unchanged “background”.

The most apparent loss in vegetation cover in rangelands is found in Maji Moto Group Ranch (Figure 7.5-B). Here, an area of 8 400 ha has known a decline in ground cover between 1985 and 1995. The presence of low cover and sparse vegetation in these areas as compared to other rangelands was confirmed by fieldwork (Figure 7.7-b). The affected area stretches out into the adjacent Olkinyei Group Ranch. Other areas with a decrease in vegetation cover in rangelands can be found south-west of the cultivated area near Lemek (Figure 7.5-C) and in the eastern part of the study area, in the rangelands straddling the border of Olenkuluo and Narosura group ranches (Figure 7.5-D). Another important area of vegetation decrease in rangelands is found in Naikara Group Ranch (Figure 7.5-E). The pattern of land cover changes, occurring mainly during the second decade of the observation period, is quite complex, being a mosaic of patches indicating a decline in vegetation cover in rangelands and plots of land that have been brought under small-scale cultivation.

Closer to the park, land cover changes occurred mainly during the first decade of the observation period (Figure 7.5-F). Rangeland areas that knew a decrease in vegetation cover between 1975 and 1985 are found in the area around Aitong. Along Talek River, areas with a decrease in vegetation cover are following the park boundaries. Close to the park boundary, between Talek and the eastern gates (Figure 7.5-G), patches with a decreased vegetation cover can be found. Change pixels close to Talek River denote a decline in riverine forest, whereas the majority of the change pixels refer to a decrease in vegetation cover in rangeland areas. At Talek and towards the eastern gates, permanent settlements are found.

Table 7.3a: land-cover change trajectories summarized per Group Ranch

#ha/Group Ranch	gradual decrease	1985-95 decrease	increase-decrease	1975-85 decrease	no change	1975-85 increase	decrease-increase	1985-95 increase	gradual increase
Masai Mara Nat. Reserve	0	386	15	537	148038	251	6	3066	0
Inner Group Ranches	12	20254	1031	6343	373735	721	42	859	0
Koyaki	1	2182	260	2314	88667	67	0	316	0
Siana	3	2024	137	2427	150015	411	2	61	0
Olkinyei	0	5882	224	424	73721	114	0	39	0
Naikara	0	1602	50	152	13257	46	2	0	0
Ol Choro Orogwa	8	158	0	925	8027	7	37	443	0
Maji Moto	0	8405	359	101	40047	76	0	0	0
Outer Group Ranches	1919	33822	734	10242	217123	2177	676	874	11
Lemek	208	9996	183	4253	45789	270	233	148	2
Ngorengore	9	303	64	96	1863	119	156	314	7
Narosura	0	3757	111	49	61953	823	13	16	0
Ewaso Ngiro	147	5766	5	400	21740	93	1	105	0
Oldonyio Rasha	0	623	23	38	13061	17	0	0	0
Olenkuluo	0	1195	83	0	14144	73	0	0	0
Ilmotiok	167	2772	22	938	12647	38	6	2	0
Osupuko/Ololunga	1388	9410	242	4468	45926	744	266	288	1
Transmara Group Ranches	0	11295	0	0	155926	0	0	1097	0
Narok Group Ranches	295	12401	730	4004	217696	1899	442	217	1
Narok District	2227	87785	2842	21556	1237696	5935	1166	6164	12

Table 7.3b: Total land cover change per group ranch

	Number of hectares per Group Ranch		
	Total surface	Total change	Change (%)
Masai Mara National Reserve	**152299**	**4261**	**3**
Inner Group Ranches	**405080**	**29263**	**7**
Koyaki	93808	5141	5
Siana	155081	5065	3
Olkinyei	80413	6684	8
Naikara	15110	1852	12
Ol Choro Orogwa	11662	1578	14
Maji Moto	49006	8942	18
Outer Group Ranches	**272188**	**50454**	**19**
Lemek	64998	15294	24
Ngorengore	2932	1069	36
Narosura	67419	4769	7
Ewaso Ngiro	28259	6518	23
Oldonyio Rasha	13762	701	5
Olenkuluo	15496	1352	9
Ilmotiok	16591	3944	24
Osupuko/Ololunga	62732	16806	27
Transmara Group Ranches	**235562**	**12392**	**5**
Narok Group Ranches	**403019**	**19991**	**5**
Narok District	**1582453**	**127688**	**8**

In Transmara and the Mau Uplands, changes in land cover are related to small-scale cultivation (Figure 7.5-H). The northern part of Transmara is almost completely cultivated and agriculture is encroaching more and more upon the forested areas. Data for the first decade of the observation period are not available, but small-scale cultivation spread considerably during the second decade. Although agriculture was present in the uplands of Transmara even before the beginning of the study period (Omondi 1995), it has considerably expanded in areas bordering the Masai Mara National Reserve. Cultivation is now practised right upon the Siria Escarpment, which forms a natural barrier on the western side of the Masai Mara National Reserve (Figure 7.5-I).

Several small patches of increase in vegetation cover are found in the study area. With the exception of some areas of vegetation increase found on cultivated land (e.g. in the Mau Uplands or Ol Choro Orogwa), all increase in vegetation cover can be defined as natural vegetation successions. Most of the natural vegetation successions occurred in the second part of the study period and are found mainly within the Masai Mara National Reserve. During fieldwork in the hills in the southern part of the central plains of the reserve (Figure 7.5-K), we found scattered clumps of *Croton dichogamus* bushes distributed in patches with a radius of a few hundreds of meters. All thickets were relatively young and occurred only at the hilltops and upper slopes. *Croton dichogamus* is resistant to fires (Lamprey 1984) and has a relatively high capacity to regenerate.

Although the regeneration in this area is still patchy, it might be significant for certain wildlife species, as the thickets provide shade and resting places for the big cats (Figure 7.7-c).

In the Mara triangle, close to the Tanzanian border, a second stretch of increased vegetation is found (Figure 7.5-L). Unfortunately, the area was inaccessible at the time of fieldwork. One hypothesis framed by a game warden is that there is regeneration of the Acacia woodlands in the area. Other workers (Sinclair 1998) have found regeneration of Acacia woodlands in parts of the Serengeti. However, further research and a more detailed terrain visit is needed to confirm or reject this hypothesis.

A third area of vegetation increase can be found close to the borders of the Mara River. In this area, a combination of regeneration of riverine forest and bushes in the surrounding grasslands results in a mosaic of small areas with increase in vegetation cover (Figure 7.5-M).

7.6 Discussion

The inter-annual fluctuations in net primary production detected on the low-resolution data, are not picked up by the three "snapshots" provided by the high-resolution imagery as: (i) there are no major land-cover conversions in these areas and (ii) the Landsat TM data happened to be collected during periods with similar vegetation conditions. Conversely, areas that have changed in the high-resolution analysis do not have high values of the change vector magnitude over several successive years. This is related to the fact that most land-cover conversions in Narok District are permanent at the time scale of a few decades and only occur once. Grassland that is turned into agricultural land shows a high value of change vector magnitude in the year of conversion, but behaves as a stable land cover afterwards. The AVHRR time series therefore provides information on land-cover changes that is highly complementary to the information provided by the high-resolution data.

Figure 7.7 gives a schematic representation of the most important land cover changes in Narok District and their spatial organisation. This Figure 7.7 was produced by generalising the remote-sensing based land-cover change map and by adding information on change processes derived from field observations. Not all areas affected by land-cover changes are displayed on the map. It provides an abstract representation of the regional dynamics of land cover in Narok District. The Masai Mara National Reserve is represented in light grey and is surrounded by two circular areas. They represent the rangelands that were designed to act as buffer zones between the protected area and the high potential agricultural uplands. The darker, inner circle that immediately surrounds the reserve, roughly corresponds to the territory of the Inner Group Ranches. The lighter, outer circle covers the area made up by the Outer Group Ranches and part of the Transmara Group Ranches. The different land-cover change processes are represented by different symbols (Figure 7.7 a, b and c).

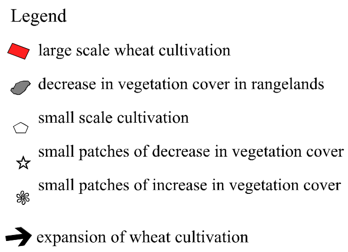
Land cover changes in the outer ring are mainly caused by the expansion of large-scale wheat cultivation in the lowlands and small-scale cultivation in the uplands. The inner ring is characterised by a patchwork of decrease in vegetation cover in rangelands, whereas the main land cover change within the protected zone is an increase in vegetation cover in small patches. The spatial pattern can thus be described as:

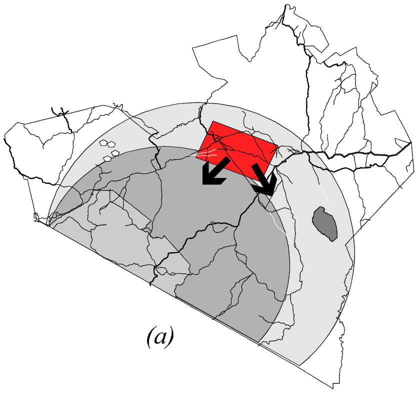
- an outer ring characterised by the centripetal expansion of cultivation (either large-scale wheat cultivation or smallholder agriculture) that is compressing the spatial system;
- an inner ring that acts as a buffer zone and is subjected to rangeland modifications with local patches of decrease in vegetation; these mainly occur close to the outer ring and along the boundaries with the National Reserve; and
- the Reserve itself that is relatively stable, except for some patches of natural vegetation successions.

This regional scale pattern of land-cover changes suggests that the expansion of cultivation in the outer ring has driven livestock and wildlife towards the park. This constriction of the buffer zone might have led to an increase of the grazing pressure in the inner ring and thus to the observed land-cover modifications in that territory. This hypothesis should indeed be tested rigorously through a combination of socio-economic, demographic and wildlife surveys, to be related in a spatially explicit way to the analysis of land-cover changes. These analyses will be reported in forthcoming publications.

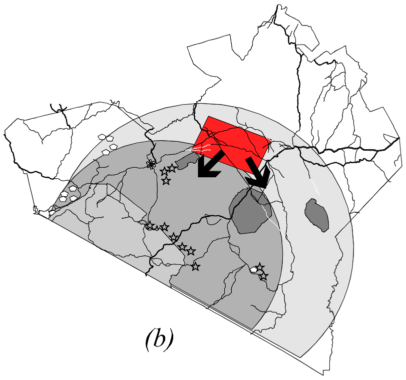
7.7 CONCLUSIONS

Advanced change detection techniques applied to coarse and fine spatial resolution remote sensing data have led to the detection of a regional scale pattern of land cover changes in the buffer zones around the Masai Mara National Reserve. Analysis of an image series with a high temporal and low spatial resolution in combination with the analysis of a set of three snapshots of high spatial resolution images, has shown that both data sets are highly complementary in the detection of land cover dynamics. On the one hand, the coarse spatial resolution data detected areas that are sensitive to inter-annual climate fluctuations, but are not subjected to land-cover conversion. On the other hand, the high spatial resolution data allowed to detect land-cover conversions or modifications between two consecutive dates that have a more permanent character and are independent of climate-induced fluctuations in surface attributes.

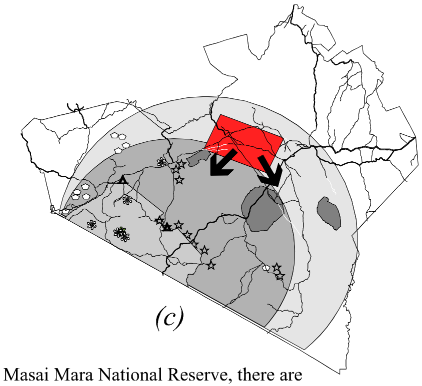




Changes in land cover in the outer ring are mainly large scale wheat cultivation, small scale cultivation and some patches of decrease in vegetation cover in rangelands.



Changes in land cover in the inner ring are related to patches of decrease in vegetation cover and small scale cultivation.



In the Masai Mara National Reserve, there are several patches of natural vegetation succession.

Figure 7.7: Schematic representation of land-cover changes in Narok District.

It remains to be investigated whether the changes in land-cover have had a measurable impact on the spatial distribution of livestock and wildlife, or have influenced total numbers of animal species through time (this is reviewed in chapter 8). There is also a need to analyse the socio-economic and spatial determinants of land-cover change trajectories in order to determine the importance of the different factors that are driving and controlling land-cover changes. Furthermore, the socio-economic factors that cause local people to change their livelihood need to be investigated, in order to understand how the system might evolve in time and what the impact of these changes would be on people, livestock and wildlife.

ACKNOWLEDGEMENTS

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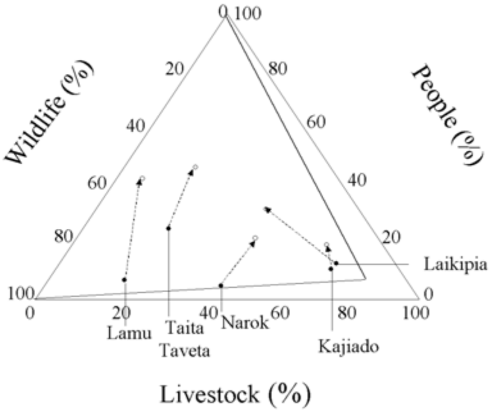
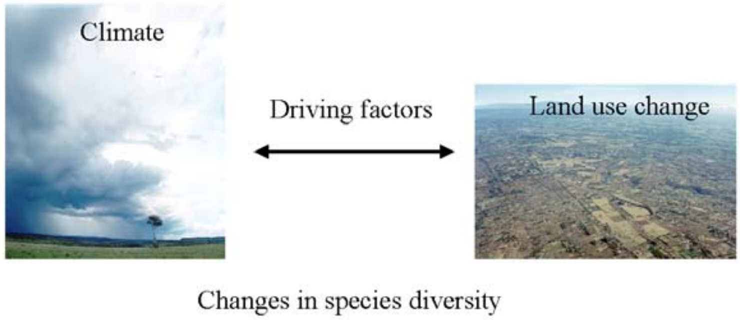
CHAPTER 8

DECLINING POPULATION OF WILD UNGULATES IN THE MASAI MARA ECOSYSTEM: A SIGN OF RESOURCE COMPETITION

In chapter four it was observed that the semi-arid districts of Lamu, Taita, Narok, Kajiado and Laikipia have a high diversity of ungulates and in some districts the declines are higher either due to illegal hunting or changes in land use. One of the districts that exhibited high declines in wildlife was Narok district.

The aim of this study is first to establish the temporal and spatial changes in land cover/use and rainfall pattern in the Serengeti-Mara Ecosystem. Secondly, the study will assess the significance of changes in the ungulate population density by using general linear model that incorporate the effects of (i) season and (ii) climate and/or period of land cover changes. The question is it the climate or the land use changes or both that has driven to the declines of wildlife in the Masai Mara





Chapter 8

Declining population of wild ungulates in the Masai Mara ecosystem: a sign of resource competition

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Abstract

This study reveals that loss of wildlife wet season range and habitat fragmentation through land use changes has a much wider impact on the dynamics of wild ungulates than do the effects of climatic variations. If climate were the only factor affecting the wild herbivores in the Serengeti-Mara ecosystem (SME), we could expect similar changes in species population in both the Masai Mara ecosystem (MM) and the Serengeti ecosystem (SE). But the results shows a higher of wild ungulates in the MM, with most declines occurring after 1985, whereas the decline in the Serengeti has involved only a few species. The declines were more rapid among the larger-bodied ungulates than among the smaller-bodied ones during the non-migratory period. There are signs of possible competition between species during the non-migratory (decline of 10 out of 13 wild ungulates) or periods of limited food supply than in the dry season (decline of 6 out of 13 wild ungulates). The declines in wildebeest and buffalo were mainly associated with intraspecific competition for food. The resident wildebeest population declined heavily during the period 1977-85, which was a period of low rainfall. The resident zebra population remained stable, dominating in areas of poor vegetation production (the Loita plain), and wildebeest dominated areas of high productivity (the Mara range unit). Thomson's gazelle, topi, kongoni, warthog, and buffalo declined as the zebra, wildebeest and elephant populations levelled off after 1985. The decline of Thomson's gazelle and topi was steeper during the migratory season than during the non-migratory season. The buffalo, kongoni and warthog the decline was steeper in the wet season than in the dry season. The study concludes that the loss of the wet season habitat (the Loita plains) has had a major impact on the population dynamics (changes in population densities and distribution) in the MM. Further loss of wildlife habitat to agriculture and the fragmentation of land will cause more declines wildlife population through resource competition as indicated in the high declines during both the non-migratory (low forage) and migratory periods (high forage).

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[*] *submitted to Journal of Animal Ecology*

8.1 INTRODUCTION

The Serengeti-Mara ecosystem (SME) is renowned for its abundant and diverse assemblage of wild ungulates (Talbot and Steward, 1964; Gwynne and Bell, 1968; Sinclair, 1979a; McNaughton, 1985; Stelfox *et al.*, 1986). Studies of ungulates in the SME have provided one of the longest time series of population data in East Africa. Changes in the populations of several species over the last 30 years suggest several hypotheses for the regulation of ungulates in the SME, that consists of competition, facilitation, predation and diseases (Sinclair, 1973; Sinclair and Norton-Griffiths, 1982; Sinclair *et al.*, 1985; Borner *et al.*, 1987; Dublin *et al.*, 1990; Mduma *et al.*, 1999). However, the underlying processes of resource exploitation and resource supply (Sinclair, 1975; Western, 1975; McNaughton, 1985; Sinclair *et al.*, 1985; McNaughton, 1990; Mduma *et al.*, 1999), and their interaction with wildlife species, are still poorly understood (Sinclair and Norton-Griffiths, 1982; Prins and Douglas-Hamilton, 1990; Prins and Olff, 1998; Du Toit and Cumming, 1999; Voeten and Prins, 1999; Murray and Illius, 2000; Baird, 2001).

Recent studies in the SME indicate a sharp decline in the population numbers of ungulates in the Masai Mara (MM) (Broten and Said, 1995; Ottichilo *et al.*, 2001a; Ottichilo *et al.*, 2001b; Serneels and Lambin, 2001) compared with the Serengeti (Campbell and Borner, 1995; Sinclair, 1995a; Sinclair, 1995b; Homewood *et al.*, 2001). The MM, which consists of the Masai Mara National Reserve (MMNR) and adjoining group ranches in Kenya, forms the northern portion of the Serengeti-Mara ecosystem. In the MM there has been a rapid conversion of rangeland (pastures mainly used by wildlife and livestock) to agriculture in the last 20 years (Epp and Agatsiva, 1980; Lamprey, 1984; Karime, 1990; Homewood *et al.*, 2001; Serneels *et al.*, 2001). Apart from the changes in land cover, the rainfall pattern has changed from what was observed in the late 1960s and 1970s (Mduma *et al.*, 1999; Ottichilo, 2000; and this study), and its effect on the ungulate population still needs to be investigated. Previous studies in the SME on interactions between species or on the interactions of species with other parameters (such as food supply) generally focused on a single species (Sinclair and Norton-Griffiths, 1982; Sinclair *et al.*, 1985; Borner *et al.*, 1987; Dublin *et al.*, 1990; Mduma *et al.*, 1999; Ottichilo *et al.*, 2001a; Serneels and Lambin, 2001) or on a number of species but for a single season (Broten and Said, 1995; Campbell and Borner, 1995; Ottichilo *et al.*, 2001b).

In this paper we extend the study to 16 ungulate species and analyze the trends and spatial distribution patterns for both the wet (non-migratory) and dry (migratory) seasons. The aim of this study is first to establish the temporal and spatial changes in land cover/use and rainfall pattern in the SME. Secondly, the study will assess the significance of changes in the ungulate population density by using general linear models that incorporate the effects of (i) season and (ii) climate and/or period of land cover changes (time period derived from the first objective).

8.1.1 Study area

The MM, which is part of the large SME, is located in southwestern Kenya, between 34° 45'E to 36° 00'E and 0° 45'S to 2° 00'S. The area is roughly triangular and covers about 6500 km^2. It can be divided into three range units, based on their biogeography and climate (Stelfox *et al.*, 1986). These units are the Mara (composed mainly of *Themeda* grasslands – the reserve forms part of this unit), the Loita plains (composed of dwarf shrub and *Acacia drapanolobium* 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 recently agriculture. The Loita plains are the main wet season range for the wildebeest and zebra populations in the MM, while the Mara range unit forms the dry season range for the migratory wildebeest and zebra populations, in addition to a number of resident species.

The description of the land cover changes is based on remotely sensed time series change analysis conducted by Serneels *et al.* (2001) and previous land cover studies in the MM (refer to Epp and Agatsiva, 1980; Lamprey, 1984; Karime, 1990). There were minor land cover changes in the MM between 1975 and 1985, but the period 1985-95 showed small patches of intensively cultivated land spreading across the Mara and Siana range units (refer to Figure 8.1 and Table 8.1). However, the largest changes in the land cover occurred in the Loita plains. The large-scale cultivation of wheat in the Loita started in the 1970s and increased extensively during the period 1985-95 (Ottichilo, 2000; Homewood *et al.*, 2001; Serneels *et al.*, 2001). The area under cultivation increased fivefold between 1975 and 1995 (4,800 ha versus 26,700 ha), which accounted for about a 13% loss of wet season wildlife habitat or range to agriculture (refer to Table 8.1).

The rainfall pattern in the SME is described in detail in Brown and Cocheme (1973), Norton-Griffiths *et al.* (1975) and Pennycuick and Norton-Griffiths (1976). The annual distribution of rainfall is bimodal, characterized by two rainy seasons and two dry seasons (Stelfox *et al.*, 1986; Broten and Said, 1995; Ottichilo, 2000). The main rains fall from March to May, with a peak in April and a second peak (although not 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 (see Figure 8.2). The long-term rainfall pattern in the SME shows changes over time. Sinclair (1979b) linked the increase in dry season rainfall in the 1970s (upwards of 250 mm) to the increase in wildebeest and buffalo populations in the SME. The rainfall pattern in time and space within the SME was studied using the rainfall data of 71 stations within the area. The cumulative deviations of the mean can be used to reveal periodicity in annual rainfall (refer to the methodology in Prins and Loth, 1988; Ottichilo, 2000). The pooled rainfall data for the different stations show a series of wet and dry years. The period 1977-97 experienced a decline in rainfall between 1977 and 1985 and an increase between 1986 and 1997 (Figure 8.3a). Coincidently, the period of increased rainfall also reflects the phase of increased agricultural activities. The MM received a mean of 965 mm of rainfall, with a dry season mean of 215 mm for the period 1977-85 and 295 mm for the period 1987-93. The Serengeti received an annual rainfall of 750 mm, with a dry season mean of 140 mm for the period 1977-93 (no significant change was observed before or after 1986 – see also Mduma *et al.*, 1999). This would partly explain the stability of most of the ungulate species populations in the Serengeti ecosystem (Dublin *et al.*, 1990; Campbell and Borner, 1995; Mduma *et al.*, 1999; Homewood *et al.*, 2001).

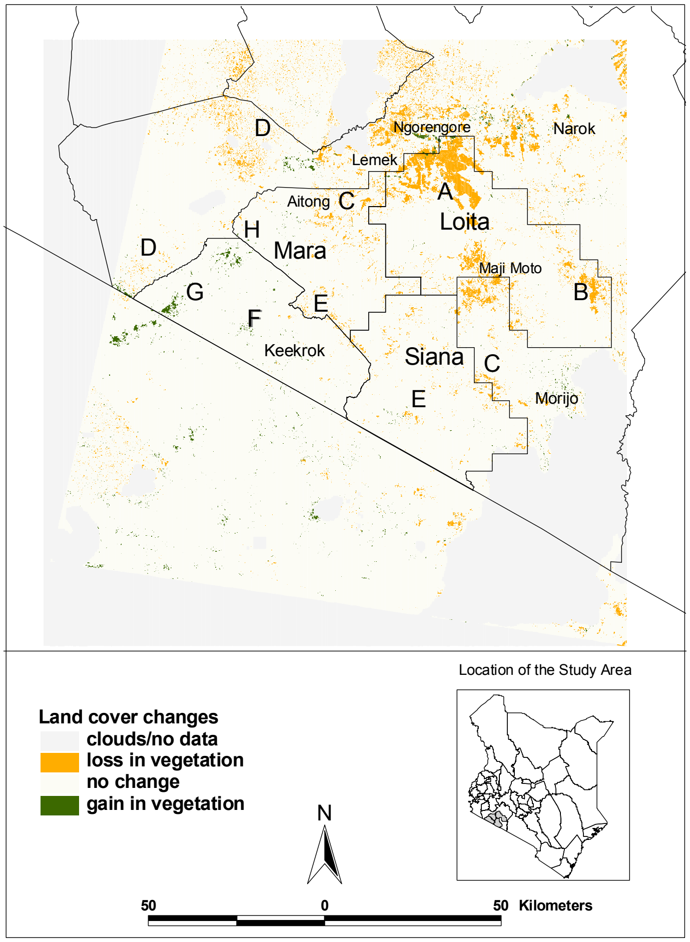

Figure 8.1: Land cover changes in the Mara ecosystem derived from 1975-1985-1995 TM and Landsat satellite images. Intensive agriculture was observed in the Loita plains (A) and (B). Patches of mosaic small-scale cultivation are developing in the Mara and Siana eco-units (C). Intensive small-scale cultivation replacing woodlands occurs in the Trans Mara region (D). Heavy decline in riverine vegetation was observed during the period 1975-85 near the Talek and Sekanali (E) gates. Increased vegetation in the park consisted of small bushes of *Croton dichogamus* (F), *Acacia* woodlands (G) and bushlands (H).

Table 8.1: Land cover changes in the Masai Mara ecosystem and the three range units, based on the three satellite images of 1975-1985-1995 (the figures in parenthesis are land cover changes in percentage).

	Range units			**Ecosystem**
Land cover changes	Loita (ha)	Mara (ha)	Siana (ha)	(ha)
gradual decrease	1000 (0.5%)	20 (<0.1%)	10 (<0.1%)	1030 (0.2%)
decrease 1985-95	26,710 (12.3%)	4690 (1.7%)	3000 (1.8%)	34,400 (5.2%)
increase-decrease	550 (0.3%)	420 (0.1%)	190 (0.1%)	1,160 (0.2%)
decrease 1975-85	4830 (2.2%)	4040 (1.4%)	2110 (1.3%)	10,980 (1.6%)
no change	183,840 (84.3%)	270,200 (95.5%)	157,540 (95.8%)	611,580 (91.9%)
increase 1975-85	470 (0.2%)	360 (0.1%)	440 (0.3%)	1,270 (0.2%)
decrease-increase	170 (0.1%)	10 (<0.1%)	10 (<0.1%)	190 (<0.1%)
increase 1985-95	350 (0.2%)	3330 (1.2%)	70 (<0.1%)	3750 (0.6%)
gradual increase	10 (<0.1%)			10 (<0.1%)
clouds	110 (<0.1%)		1210 (0.7%)	1320 (0.2%)

The monthly normalized vegetation difference index (NDVI – a proxy index for primary production; refer to Justice *et al.*, 1985; Justice, 1986; Box *et al.*, 1989) anomaly patterns clearly highlight the response of the plants and grass growth to rainfall. The pattern shows lower than average primary production for the period 1982-85. The decade 1987-97 had above average net primary production, with a sharp drop in plant biomass in 1991 and 1993 due to drought events (Figure 8.3b). The NDVI anomalies were calculated from the time series data by using the z-transform $((x_i - u)/\text{std})$, with x_i being the NDVI value for a given month in year i, u the mean NDVI value for that month across all years, and std the standard deviation of the NDVI values for that month across all years (Anyamba *et al.*, 2001; Serneels *et al.*, 2001).

A review of the land cover and rainfall changes establishes that the period 1975-85 experienced fewer changes in land cover and that the rainfall was lower than in the preceding decade, which had experienced an increase in the number of wildlife species in the Serengeti ecosystem. The period after 1985 experienced a significant change in land cover, especially in the Loita (wet season range for resident wildebeest and zebra populations). The rainfall pattern and vegetation response during this period show mostly above average production of biomass, except in the drought years of 1991 and 1993. We hypothesize that the wild ungulate population should show a declining trend between 1977 and 1985 if food supply is the limiting factor. However, the period 1986-97 should show either an increase or decrease, depending on the effects of interaction between climate and land cover change on ungulate populations.

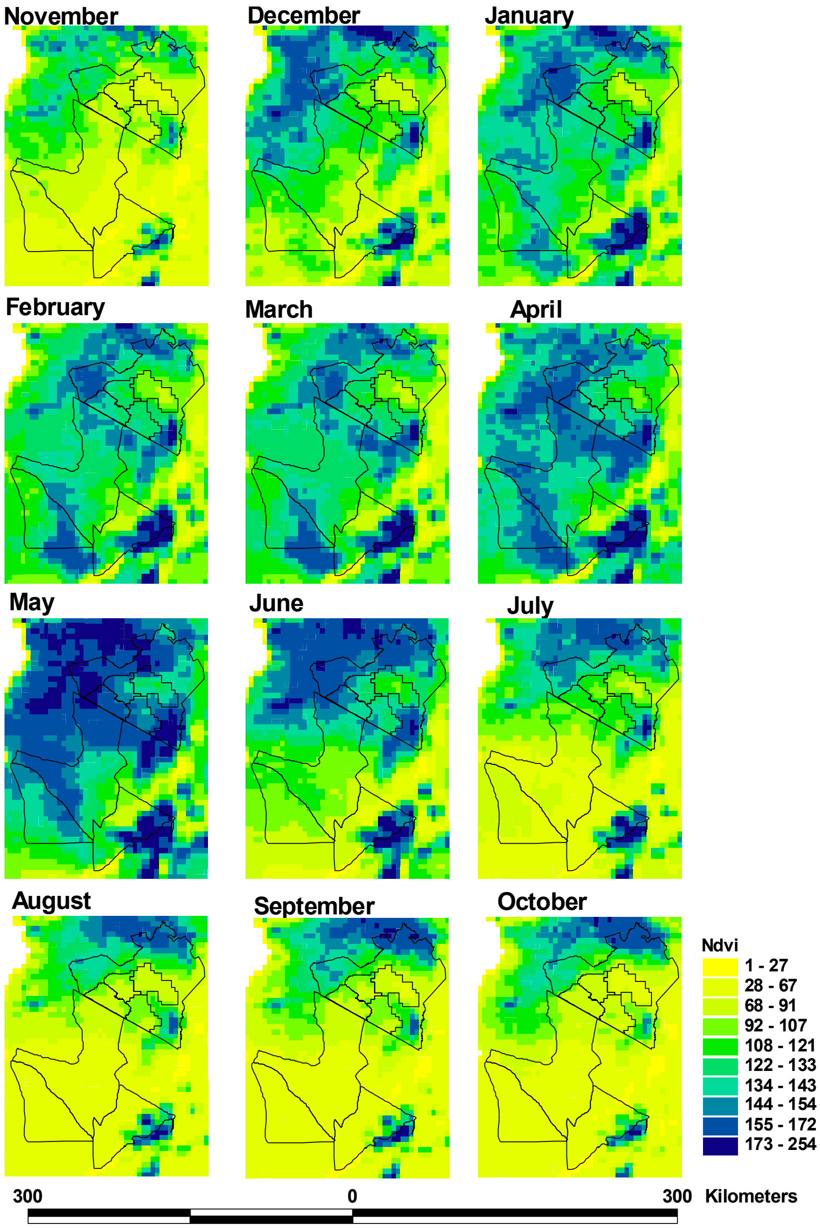

Figure 8.2: Spatial monthly variation in NDVI in the Serengeti-Mara ecosystem. The migratory species of wildebeest, zebra and Thomson's gazelle move between the Serengeti ecosystem and the Mara during the dry season (June-July), when the vegetation in the Serengeti is drier than in the Masai Mara. The animals move back to the Serengeti after October, when it starts to become green. The movements are dictated by local rainfall events and differ from year to year.

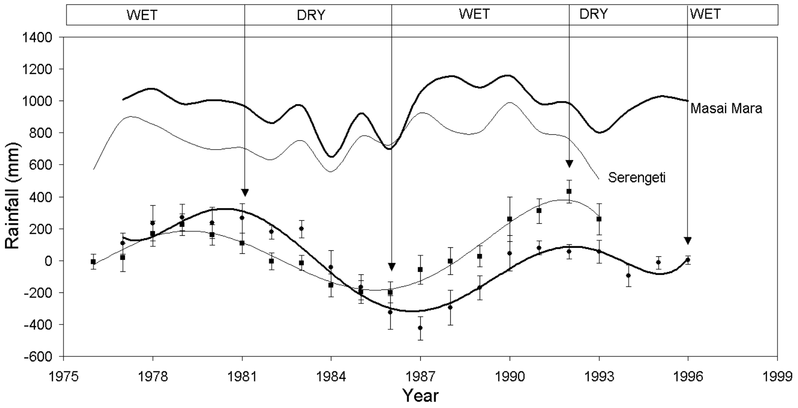

Figure 8.3a: Temporal changes in mean annual rainfall and cumulative deviation of rainfall in the Masai Mara (39 stations) and Serengeti (32 stations) between 1976 and 1996. Pooled cumulative deviations of the annual rainfall of wet and dry periods alternate but the length of the period varies.

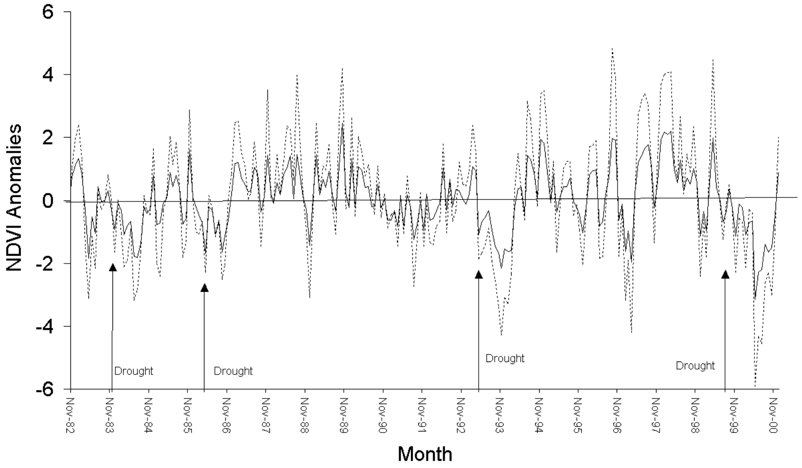

Figure 8.3b: Temporal monthly changes of NDVI in the Masai Mara (—) and Serengeti (------) ecosystems between 1982 and 2000. The severest droughts occurred in 1993 and 2000 and the impacts were felt more in the Serengeti ecosystem.

8.2 MATERIAL and METHODS

8.2.1 Data

The wildlife and livestock populations and distributions were compiled from aerial censuses conducted by the Department of Resource Surveys and Remote Sensing (DRSRS). The method as used and adapted by DRSRS is described in detail in Norton-Griffiths (1978), Dirschl *et al.* (1981) and Ottichilo and Sinange (1985). Population estimates for wildlife and livestock were calculated using Jolly (1969). Between 1977 and 1997 a total of 42 counts of ungulates in the Mara were undertaken, with regular wet (15 surveys) and dry (12 surveys) season counts (12 surveys were conducted in 1979 on a monthly bases). Three surveys were conducted in between the wet and dry seasons and could not be classified as either wet or dry season. The classification of the seasons was based on Ottichilo *et al.* (2001a).

8.2.2 Analysis of species trends

We analyzed the changes in ungulate populations between 1977 and 1997 for both dry and wet seasons for the entire MM. Secondly, we assessed the significance of changes in the population density by incorporating the effects of season and the significance of changes in linear trends before and after the land cover and climatic changes. We identified the time period of change to be between 1977-85 (a declining rainfall period) and 1986-97 (a period of increased rainfall and land cover activities). We tested how these factors impact on the trends of the individual or groups of species by analyzing the trends before and after 1985. Animal densities were derived by converting the individual body weights (W in kg) of wildlife and livestock to metabolic body mass ($W^{0.75}$), a value that reflects energy expenditure by different species in a comparable way (Moen, 1973). The average weights of the various wildlife species were derived from Prins and Olff (1998) and those of livestock from Peden (1987).

8.3 RESULTS

8.3.1 Long–term population trends of the ungulates

The long-term population trends of both wild ungulates and livestock are summarized in Table 8.2. All species except zebra, elephant, impala and cattle showed significant population changes in either the wet or dry season, or in both periods. Wildebeest, Grant's gazelle, eland and waterbuck showed a decline in population in the wet season and a non-significant change in population in the dry season. Thomson's gazelle, topi, buffalo, warthog, giraffe and kongoni showed a declining population in both periods. The populations of Thomson's gazelle, topi, warthog, giraffe and kongoni were higher in the wet season, and only wildebeest showed a higher population during the dry season. We did not find any significant seasonal changes in zebra, buffalo, Grant's gazelle, eland, waterbuck, elephant and impala populations. The trends in livestock populations were mixed with the cattle population remaining constant throughout the study period. Sheep and goats showed an increase in population during the dry season. The donkey trends were mixed, with declines in the wet season and increases in the dry season.

The marked changes in the population sizes of individual species were reflected in the total change in wild ungulate biomass over time. There were moderate declines in wildlife (though these were not significant) in the wet season ($\text{In}(Y) = 13.16 - 0.050x$, $r^2 = 0.75$, $P < 0.001$) compared with the dry season ($\text{In}(Y) = 14.99 - 0.027x$, $r^2 = 0.32$, $P < 0.052$). The declines in the wet season were reflected in a greater loss of the large-bodied (>100 kg) wild ungulates ($\ln(Y) = 13.79 - 0.081x$, $r^2 = 0.87$; $P < 0.001$, $n = 15$) than of the small-bodied (<100 kg) ungulates ($\text{In}(Y) = 8.37 - 0.03x$, $r^2 = 0.45$, $P = 0.006$, ($t = 97$, $P < 0.0001$, $df = 26$), whereas in the dry season there was no significant differences between the two populations ($t = 1.81$, $P = 0.08$, $df = 20$). Livestock population remained constant during both the wet and the dry seasons.

The large-bodied ungulates that showed sharp declines in their populations are the wildebeest, buffalo and giraffe (Table 8.2). The wildebeest population suffered declines during both the wet ($\text{In}(Y_{\text{wet}}) = 17.02 - 0.13x$, $r^2 = 0.86$, $P < 0.001$, $n = 8$) and dry seasons in the period 1977-85 ($\text{In}(Y_{\text{dry}}) = 31.89 - 0.29x$, $r^2 = 0.65$, $P < 0.001$, $n = 6$). The resident wildebeest population declined from an average of 120,000 animals in the late 1970s to less than 50,000 in the 1990s. The period 1977-85 had a moderate impact (declining trends approaching statistical significance) on the buffalo population, but the numbers dropped sharply during the wet season in the period 1986-97 ($\text{In}(Y_{\text{wet}})$ $18.15 - 0.15x$, $r^2 = 0.64$, $P < 0.05$, $n = 7$). The buffalo population crashed from more than 20,000 animals observed in the late 1970s to a population of less than 5000 buffalo observed in the 1990s. The giraffe population continued to decline throughout the study period ($\text{In}(Y) = 10.645 - 0.076$, $r^2 = 0.87$, $P < 0.001$, $n = 15$), dropping from more than 5000 animals in the 1970s to less than 2000 in the 1990s. The long-term trends of both Thomson's gazelle and topi seem to be similar. Both have a higher wet season population and their populations declined significantly in the dry season, and especially after 1985. The declines in the dry season were significantly higher than those in the wet season for both Thomson's gazelle ($t = 53.44$, $P < 0.001$, $df = 12$) and topi ($t = 18.78$, $P < 0.001$, $df = 12$). The decline in kongoni was significantly higher in the wet season than in the dry season ($t = 51$, $P < 0.001$, $df = 12$) and a similar pattern was observed for Grant's gazelle ($t = 24$, $P < 0.001$, $df = 12$).

Table 8.2: Wildlife ungulates and livestock population trends in the Masai Mara.

	Wet Season			Dry Season				
	Trends 1977-97 (n = 15)	Change in slope of linear trend before and after 1985		Trends 1977-97 (n = 12)	Change in slope of linear trend before and after 1985		Season	
Species	r^2 of model	Trends	r^2	r^2 of model	Trends	r^2	Season with a high population	P
Wildebeest	0.75***	B: decline	0.86***	0.31^{ns}	B: decline	0.65*	Dry	**
		A: no	0.01^{ns}		A: increase	0.03^{ns}		
Burchell's zebra	0.15^{ns}	B: no	0.22^{ns}	0.01^{ns}	B: decline	0.54^{ns}		ns
		A decline	0.45^{ns}		A: no	0.01^{ns}		
Thomson's gazelle	0.46**	B: no	0.03^{ns}	0.78***	B: no	0.13^{ns}	Wet	**
		A decline	0.36^{ns}		A: decline	0.69*		
Topi	0.48**	B: no	0.01^{ns}	0.73***	B: no	0.25^{ns}	Wet	*
		A: decline	0.53^{ns}		A: decline	0.63*		
Buffalo	0.80***	B: decline	0.44^{ns}	0.35*	B: decline	0.46^{ns}		ns
		A: decline	0.64*		A: no	0.17^{ns}		
Warthog	0.77***	B: decline	0.32^{ns}	0.40*	B: no	0.02^{ns}	Wet	**
		A: decline	0.47^{ns}		A: no	0.01^{ns}		
Grant's gazelle	0.51**	B: decline	0.16^{ns}	0.25^{ns}	B: no	0.11^{ns}		ns
		A decline	0.36^{ns}		A: no	0.05^{ns}		
Eland	0.50**	B: decline	0.42^{ns}	0.22^{ns}	B: decline	0.41^{ns}		ns
		A no	0.02^{ns}		A: increase	0.82*		
Giraffe	0.87***	B: decline	0.55*	0.61**	B: no	0.01^{ns}	Wet	*
		A decline	0.80**		A: decline	0.36^{ns}		
Waterbuck	0.37*	B: no	0.01^{ns}	0.07^{ns}	B: no	0.16^{ns}		ns
		A decline	0.29^{ns}		A: no	0.01^{ns}		
Elephant	0.11^{ns}	B: no	0.09^{ns}	0.01^{ns}	B: increase	0.41^{ns}		ns
		A no	0.12^{ns}		A: no	0.15^{ns}		
Impala	0.16^{ns}	B: no	0.16^{ns}	0.16^{ns}	B: no	0.01^{ns}		ns
		A: no	0.01^{ns}		A: no	0.03^{ns}		
Kongoni	0.38*	B: no	0.02^{ns}	0.37*	B: decline	0.42^{ns}	Wet	**
		A: decline	0.74*		A: no	0.24^{ns}		
Cattle	0.02^{ns}	B: no	0.23^{ns}	0.01^{ns}	B: decline	0.75*		ns
		A: no	0.03^{ns}		A: no	0.21^{ns}		
Sheep and goats	0.16^{ns}	B: decline	0.31^{ns}	0.36*	B: no	0.01^{ns}		ns
		A: no	0.02^{ns}		A: no	0.01^{ns}		
Donkey	0.44**	B: no	0.14^{ns}	0.48*	B: increase	0.51^{ns}		ns
		A: decline	0.47^{ns}		A: no	0.01^{ns}		

Note: Significance assessed by log-linear models (P values: *<0.05; **<0.01; ***<0.001; ns = not significant). Notation B represents before and notation A after 1985. A total of 15 censuses were conducted in the dry season, with eight censuses surveyed before and seven after 1985. As for the wet season there were 12 censuses, with six conducted before 1985 and six after 1985.

8.3.2 Changes in spatial distribution of species

There were significant changes in the wild ungulate population trends in the Mara ($\ln(Y) = 12.60 \pm 0.92 - 0.055x \pm 0.01$, $r^2 = 0.63$, $P < 0.001$, $n = 15$), Loita ($\ln(Y) = 12.45 \pm 1.11 - 0.055x \pm 0.13$, $r^2 = 0.58$, $P < 0.001$, $n = 15$) and Siana ($\ln(Y) = 9.77 \pm 0.99 - 0.038x \pm 0.02$, $r^2 = 0.46$, $P < 0.005$, $n = 15$) during the wet season. In the dry season there were no changes in trends in the Mara and Loita, but the Siana ($\ln(Y) = 11.52 \pm 1.80 - 0.058x \pm 0.02$, $r^2 =$

0.44, P < 0.02, n = 15) showed a decline in ungulate population (Figure 8.4). The spatial analyses of individual species trends for the wet and dry seasons for the three range units are summarized in Table 8.3. Thomson's gazelle and topi are the only species that showed declining populations in all three range units. The resident wildebeest trend shows declines in the Loita and Siana. The distribution patterns of giraffe, kongoni, waterbuck and buffalo showed that significant declines occurred in the Mara range unit, while declines in the zebra and warthog populations were observed in both the Mara and the Loita range units. The wildebeest and impala revealed localized declines in the Loita and Siana range unit respectively. The change in trends of livestock occurred in the Mara, where donkey as well as sheep and goats showed a declining population. Cattle and sheep and goats remained constant in both the Loita and Siana range units.

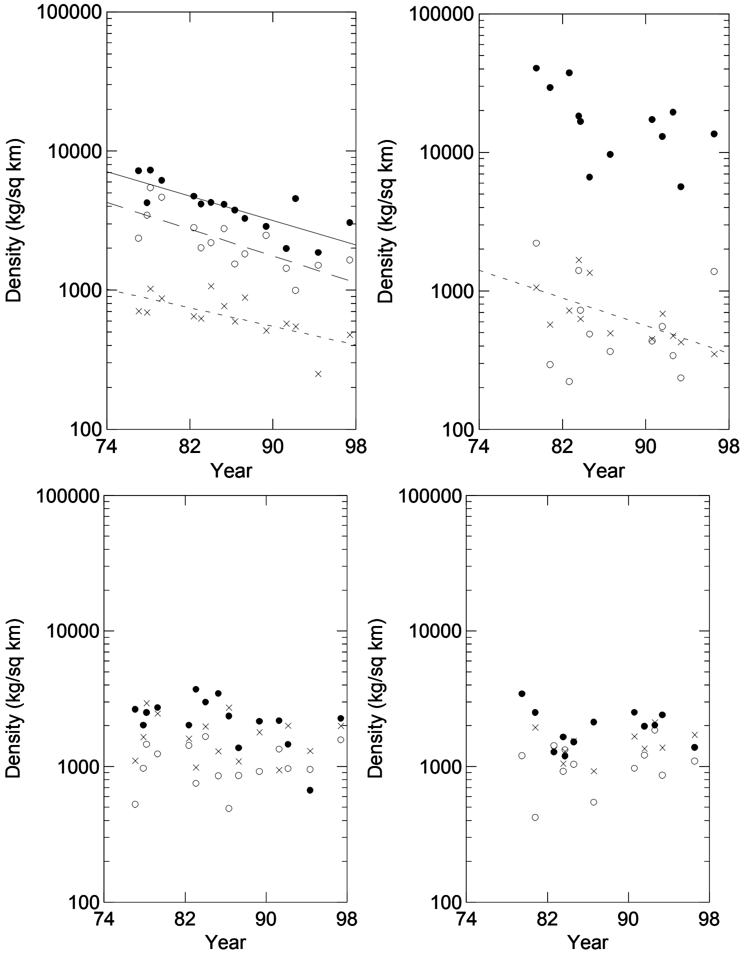

Figure 8.4: Changes in wildlife (top) and livestock (bottom) populations in the Mara (●), Loita (○) and Siana (x) range units for the wet season (left) and dry season (right).

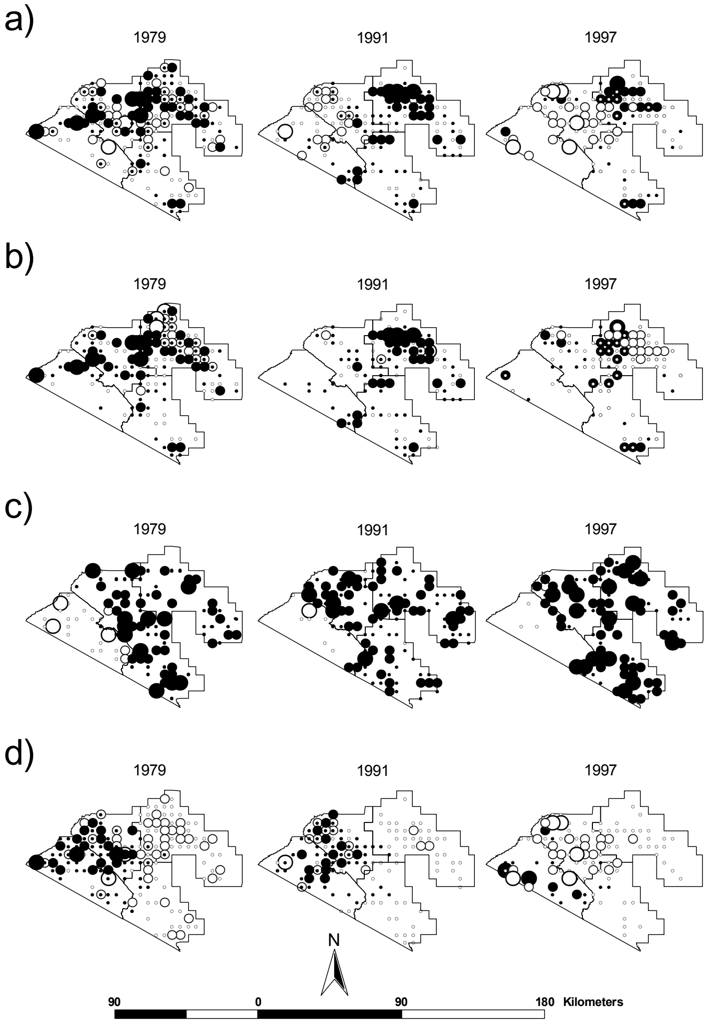

Figure 8.5a: Distribution of species during the dry or migratory season. Species patterns show changes in both distributions and densities over the years. The distributions of the species are as follows: a) Thomson's gazelle (○) and zebra (●); b) wildebeest (○) and zebra (●); c) buffalo (○) and livestock (●); and d) impala (○) and topi (●). 1979 represents the peak herbivore biomass, 1991 represents a drought year, and 1997 was a year that had similar rainfall to that of 1979.

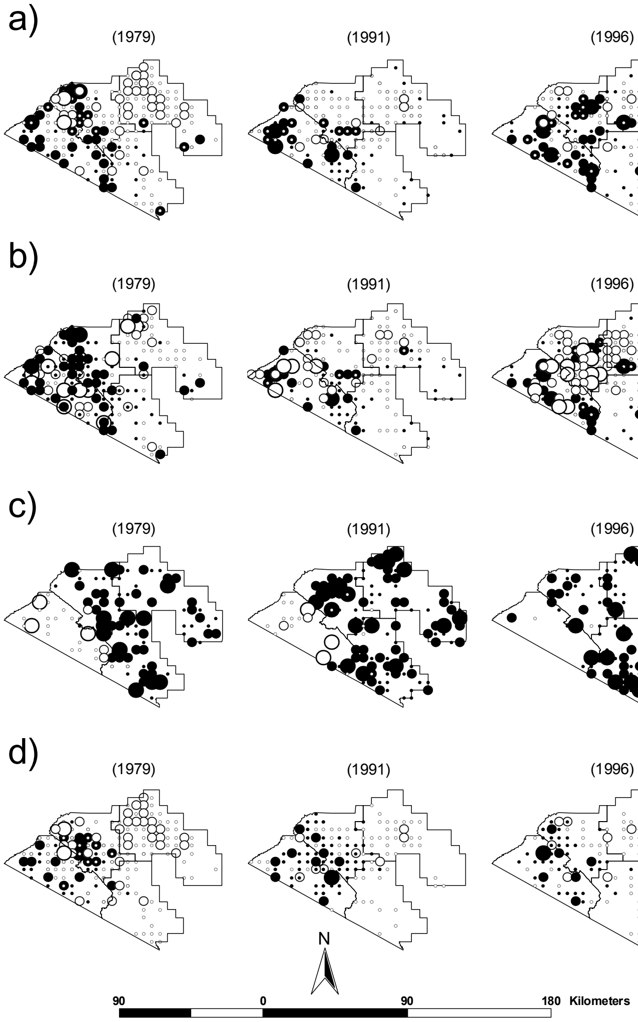

Figure 8.5b: Distribution of species during the wet or non-migratory season. Species patterns show changes in both distributions and densities over the years. The distributions of species are as follows: a) Thomson's gazelle (○) and zebra (●); b) wildebeest (○) and zebra (●); c) buffalo (○) and livestock (●); and d) impala (○) and topi (●). 1979 represents the peak herbivore biomass, 1991 represents a drought year, and 1996 was a year that had similar rainfall to that of 1979.

Table 8.3: Regression equation describing the best-fitting model between herbivore species and time. The formulas for the regressions are indicated if the models are significant at $P \leq 0.05$. The trend analysis was conducted for the entire Masai Mara (MM) and the three range units (Mara, Loita and Siana).

Species	Unit	Wet Season	r^2	P		Dry Season	r^2	P
Buffalo	MM	15.715 – 0.121x	0.80	0.001	Buffalo	16.272 – 0.132x	0.35	0.044
	Mara	16.913 – 0.119	0.78	0.001		18.039 – 0.136x	0.36	0.040
	Loita		0.81	0.099			0.09	0.629
	Siana		0.03	0.648			0.40	0.609
Eland	MM	10.690 – 0.085x	0.50	0.003	Eland		0.22	0.126
	Mara	11.496 - 0.088x	0.28	0.040			0.07	0.405
	Loita		0.15	0.155			0.10	0.496
	Siana	11.837 – 0.106x	0.42	0.012			0.18	0.220
Elephant	MM		0.11	0.229	Elephant		0.01	0.806
	Mara						0.01	0.860
	Loita							
	Siana						0.89	0.213
Giraffe	MM	10.645 – 0.076x	0.87	0.001	Giraffe	7.904 – 0.046x	0.61	0.003
	Mara	11.682 – 0.076x	0.56	0.001		9.530 – 0.055x	0.70	0.001
	Loita		0.16	0134			0.05	0.488
	Siana		0.18	0.113			0.24	0.107
Grant’s gazelle	MM	7.765 – 0.049x	0.51	0.003	Grant’s gazelle		0.25	0.096
	Mara		0.29	0.057			0.17	0.181
	Loita		0.47	0.005			0.21	0.135
	Siana		0.14	0.174			0.18	0.168
Impala	MM		0.16	0.145	Imapla		0.13	0.251
	Mara		0.02	0.589			0.03	0.575
	Loita		0.02	0.671			0.00	0.954
	Siana	8.313 – 0.038x	0.47	0.005		9.184 – 0.050x	0.36	0.039
Kongoni	MM	7.470 – 0.051x	0.39	0.014	Kongoni	0.144 – 0.041x	0.37	0.036
	Mara	9.288 – 0.060x	0.38	0.014		8.940 – 0.060	0.50	0.010
	Loita		0.01	0.857			0.01	0.398
	Siana		0.26	0.055			0.08	0.437
Thomson’s gazelle	MM	8.080 – 0.039x	0.46	0.006	Thomson’s	10.639 – 0.074x	0.78	0.001
	Mara		0.25	0.057		11.704 – 0.069x	0.83	0.001
	Loita	10.017 – 0.064x	0.47	0.005			0.44	0.072
	Siana	9.775 – 0.072	0.44	0.007		12.087 – 0.106x	0.40	0.027
Topi	MM	8.762 – 0.049x	0.48	0.004	Topi	10.189 – 0.013x	0.73	0.001
	Mara	10.414 – 0.051x	0.52	0.003		11.704 – 0.069x	0.71	0.001
	Loita	9.932 – 0.094x	0.47	0.005		8.037 – 0.077x	0.39	0.042
	Siana		0.17	0.165		12.054 – 0.115x	0.45	0.024
Waterbuck	MM	7.786 – 0.069x	0.37	0.016	Waterbuck		0.05	0.489
	Mara	9.926 – 0.081x	0.35	0.021			0.09	0.364
	Loita							
	Siana		0.04	0.570				
Warthog	MM	10.774 – 0.097x	0.77	0.001	Warthog	8.357 – 0.074x	0.40	0.026
	Mara	12.425 – 0.101x	0.73	0.001		10.372 – 0.084x	0.35	0.041
	Loita		0.13	0.308			0.00	0.975
	Siana		0.55	0.002		9.644 – 0.096x	0.56	0.020
Wildebeest	MM	12.623 – 0.076x	0.75	0.001	Wildebeest	13.944 – 0.068x	0.32	0.057
	Mara		0.06	0.401			0.30	0.064
	Loita		0.74	0.001			0.01	0.730
	Siana		0.40	0.011			0.21	0.131
Burchell’s zebra	MM	7.455 – 0.017x	0.15	0.154	Burchell’s zebra		0.00	0.986
	Mara	12.541 – 0.073x	0.38	0.015			0.00	0.938
	Loita		0.06	0.385			0.07	0.389
	Siana		0.01	0.703		11.189 – 0.073x	0.57	0.005
Cattle	MM		0.02	0.663	Cattle		0.00	0.989
	Mara		0.18	0.117			0.01	0.838
	Loita		0.16	0.140			0.04	0.535
	Siana		0.10	0.721			0.07	0.431
Donkey	MM	8.011 –0.055x	0.44	0.007	Donkey	8.193 - 0.061x	0.48	0.013
	Mara	9.688 –0.071x	0.33	0.024		11.073 – 0.087x	0.54	0.007
	Loita		0.13	0.183			0.23	0.113
	Siana		0.12	0.213			0.03	0.580
Sheep and goata	MM		0.16	0.137	Sheep and goats	3.138 + 0.020x	0.36	0.040
	Mara	8.932 – 0.041x	0.42	0.009		8.932 – 0.041x	0.42	0.009
	Loita		0.19	0.104			0.13	0.258
	Siana		0.04	0.500			0.27	0.085

8.4 DISCUSSION

The results reveal a decline in 10 out of 13 wild ungulate species during non-migratory period and 6 out 13 species during the migratory period, with significant changes occurring in the period after 1985. Five species (Thomson's gazelle, topi, buffalo, kongoni, giraffe) show significant declines after 1985, and two species (wildebeest and giraffe) before 1985. We assume that if only food supply limits ungulate populations, then more ungulate species would have declined between 1977 and 1985 (a low rainfall period) and increased between 1986 and 1997 (a high rainfall period). However, it seems that the loss of the wet season range may have created an environment for resource competition. Resource competition takes place when there is a high degree of habitat and diet overlap between species (see Hansen *et al.*, 1985; Voeten and Prins, 1999; Illius and O'Connor, 2000; Prins, 2000) and food supply is limited. And it can be demonstrated to occur when an increase in the population of one of two animal species causes a reduction in the population of the other (Sinclair *et al.*, 1985; de Boer and Prins, 1990; Mduma *et al.*, 1999). However, apart from the diet overlaps, other factors such as the long-lasting cohabitation strategy of wild herbivores of partitioning resources among the different species that is linked to vegetation preferences, and digestive and feeding styles also counts on the success of a species out competing the other (Gwynne and Bell, 1968; Jarman and Sinclair, 1979; Hansen *et al.*, 1985; Illius and Gordon, 1991; Murray and Brown, 1993; Murray and Illius, 2000). Three broad patterns that impact on species trends are identified in this study: populations of species may either be (i) regulated by intraspecific competition for food; (ii) regulated by interspecific competition; or (iii) no signs that they are regulated by either of the above processes.

The wildebeest and the buffalo fall into the category of species whose populations may be regulated through intraspecific competition for food (Sinclair, 1979b; Sinclair, 1983; Sinclair *et al.*, 1985; Prins, 1996; Mduma *et al.*, 1999). Previous studies in the SE indicated that dry season rainfall was the most important extrinsic determinant of food supply for the wildebeest and buffalo (Sinclair, 1979b; Sinclair *et al.*, 1985; Mduma *et al.*, 1999). In contrast, a recent study in the MM showed that the wet and dry seasons are both important factors in determining the resident wildebeest population (Serneels and Lambin, 2001). The decline in wildebeest in the MM occurred between 1977-85. In this period both the wet and dry season rainfall declined, and there were high numbers of wildebeest migrating from the SE to the MM during the dry season (Ottichilo, 2000; Serneels and Lambin, 2001). The combination of sub-optimal conditions during the wet season and increased competition during the dry season in the MM probably led to high wildebeest and buffalo mortality during the period 1977-85. But the severe drought of 1993 sharply affected the buffalo and contributed to a significant crash in the population in the MM (Figure 8.6a; also refer to Dublin, 1994). However, prior to the sharp decline there seems to have been heavy pressure on the buffalo wet season population and this might be related to increased densities of elephant in the MM. Almost 500 elephants moved from the SE to the MM in the early 1980s due to poaching in the SE (Dublin and Douglas-Hamilton, 1987). Drent and Prins (1987) and de Boer and Prins (1990) observed forage competition between elephant and buffalo in the Lake Manyara National Park. In the MM the elephant population has remained constant and this may well affect the densities of buffalo in terms of competition for forage during periods of limited food supply.

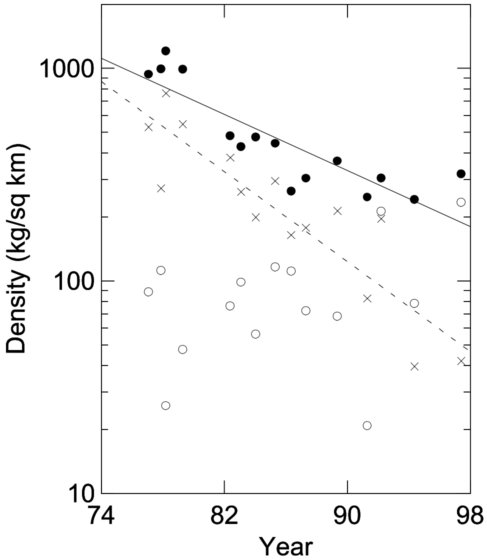

Figure 8.6a: The trends of both wildebeest (●) and buffalo (x) show declines over time during the wet or the non-migratory period, while the elephant (○) population has remained constant throughout the study period. The wildebeest population during the wet season is predominately located in the Loita and has little interaction with buffalo, while both the elephant and the buffalo are located mainly in the Mara range unit both during the wet and dry seasons (refer to the distribution of these two species - Figure 6a and b).

The rapid decline in Thomson's gazelle, topi, kongoni and warthog coincided with the levelling out of the wildebeest, zebra and elephant populations (Figure 8.6b). The dominance of both zebra in the Loita (declining trends in the Mara – high productive areas) and wildebeest in the Mara (declining trends in the Loita and Siana – low productive areas) seems to have had an impact on a number of species. Hansen *et al.* (1985) found the highest diet similarities among the buffalo, kongoni, wildebeest, topi and Thomson's gazelle in the MM. In addition, Murray and Illius (2000) observed that herbivory by one species can modify the vegetation in a way that makes it less profitable for competing species. The situation seems to be much more severe during the migratory season, when the wildebeest and zebra dominate natural pastures and can preclude utilization of the resource by other selective ruminant species – especially if the grazing areas decrease as demonstrated in this study. The declines in Thomson's gazelle and topi were higher in the dry season than in the wet season, particularly in the period 1986-97. And there further declines of buffalo, kongoni and warthog even during a period of high forage availability. This would support the hypothesis of interspecific competition between species.

Among the wild ungulates the zebra, elephant and impala populations remained constant over time within the entire MM. However, the spatial based on range unit analysis show the distribution of the resident zebra population in the MM changed with local declines in the Mara range unit and dominance in the Loita over other species. The dominance of non-ruminant zebra in the Loita is partly explained by its tolerance of poor-quality diets – a tolerance higher than that of hindgut ruminant species such as the wildebeest (Demment and Van Soest, 1985; Prins and Olff, 1998; Voeten and Prins, 1999). The overall trend of impala shows a stable population and this may be attributed to its high trophic diversity – its great choice of plants (both monocots and dicots) depending on the season (see Jarman and Sinclair, 1979; Hansen *et al.*, 1985). However, the spatial analysis based on range units also showed localized declines in impala in the Siana, the area that had had an increase in livestock (especially sheep and goats). Several studies have indicated dietary overlaps between impala and sheep, which may have caused resource competition between the species. Habitat overlap between wildlife and livestock is likely to be high in areas where they co-occur, thus outside protected areas (Prins, 2000; Voeten and Prins 1999).

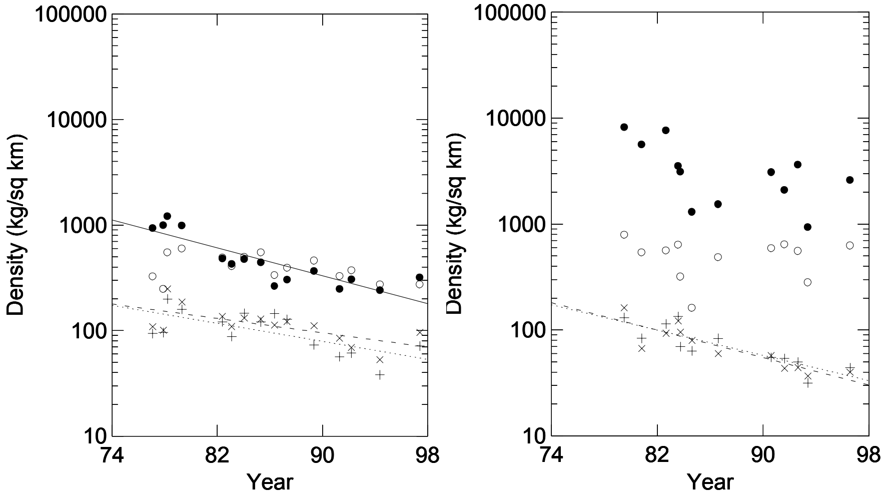

Figure 8.6b: The trends of wet (left) and dry season populations of wildebeest (●), zebra (○), Thomson's gazelle (x) and topi (+). The decline in Thomson's gazelle and topi occurred as the populations of both wildebeest and zebra stabilized during the wet season in 1986-97 and the migratory populations of wildebeest and zebra slightly increased during the dry season in 1986-97.

In conclusion this study shows that in general competition appears an important process affecting large ungulates. The study has shown that when common resource (food supply) and key habitats are intact, climate changes (decline in rainfall) had a moderate affect of wildlife population, except during severe and prolonged drought. However, as resources become scarce through habitat modification (especially loss of critical habitats), competition for resources between species become evident - as reflected by the declines in a number of species (both during the dry and wet seasons), and especially after the large land use changes after 1985. This paper analysed on two possible regulatory processes governing ungulate population (rainfall and land use changes), diseases and predation are other factors that also regulate ungulate population but was not dealt in this paper.

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Chapter 9

Synthesis

Multiscale perspectives of species richness in East Africa – patterns and processes

9.1 INTRODUCTION

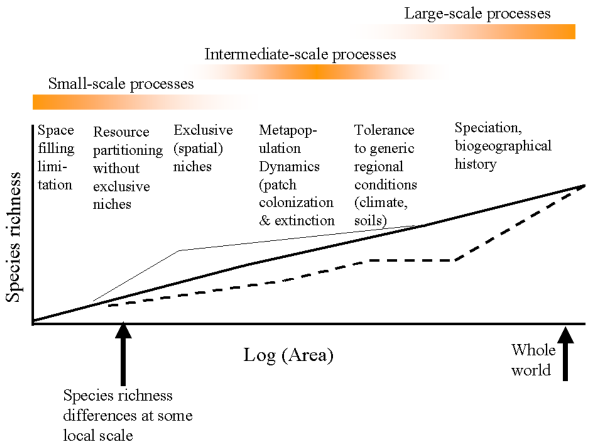
Studies on species diversity have been conducted at various scales. Several authors have suggested that species diversity patterns are scale-dependent (Schimda and Wilson, 1985; Ricklefs, 1987; Wiens, 1989; Levin, 1992; Caley and Schluter, 1997; Gaston and Blackburn, 1999). Also it has been argued that biodiversity could be determined by processes that replace one another across scale (Turner, 1989; Christensen *et al.*, 1996), implying that processes important at one scale may not be at another scale (Turner, 1989; Levin, 1992; Huston, 1999). Levin (1992) proposed that the key to prediction and understanding lay in the elucidation of mechanisms underlying observed patterns. Levin (1992) and Meentemeyer and Box (1987) suggested that these mechanisms responsible for a pattern typically operated at scales different from those at which the patterns are observed. In some cases, the patterns must be understood as emerging from collective behaviours of large ensembles of smaller-scale units.

There have been suggestions that further work on ecology should incorporate observations at various scales of space and time (Turner, 1989; Christensen *et al.,* 1996; Levin 1992; Weins, 1989). Further Ricklefs (1987), Myers and Giller (1988), Ricklefs and Schluter (1993) all advocated that historical events and ecological processes should be part of any complete explanation of patterns of species diversity. Moreover, Brown (1999) proposed that the challenge for the future would be to build and evaluate mechanistic models that could explain macroecological patterns in terms of established physical and biological principles. The aim of this study is directed towards developing a framework for analyzing the ungulate dynamics from a multiscale perspective. The study analyzes the long-term outcomes of historical and recent changes in demography and land use practices (and policies) with respect to wildlife and livestock. These tasks are accomplished by integrating climatic, land cover and land use data (gathered by remote sensing), as well as human demographics, with meta-analysis and in-depth trend analysis of existing long-term data sets on wildlife and livestock.

9.2 CONCEPTUAL FRAMEWORK

Whittaker (1977) segmented the scale continuum of species richness into four levels of representation: regional (epsilon – incorporates more than one landscape), landscape (gamma – describes the number of species in a landscape containing more than one community), community (alpha – measure of richness within a homogenous community) and microhabitat (point – species differences due to microhabitat differences). In GIS and remote sensing, however, the cartographic definition of scale is mostly used (Goodchild and Quattrochi, 1996). The three most important elements are metric scale (defined as a ratio between distance on the map and distance on the ground – large-scale maps have more detail than small-scale maps), geographical extent, resolution (grain) and time (temporal scale). These are some of the definitions that will be used in the context of this study.

Species composition within some spatial extent can always be viewed as a subset of the species composition at some larger spatial extent with different structuring ecological processes (Olff and Ritchie, 2002a). At the large scale, species diversity is controlled by factors such as climate (Fischer, 1960; Connell and Orias, 1964), availability of energy (Hutchinson, 1959; Wright, 1983; Currie and Fritz, 1993; Olff *et al.*, 2002b) and area (MacArthur and Wilson, 1967; Terborgh, 1973; Brown and Lomolino, 2000). Processes leading to change in species diversity include migration, isolation, speciation and extinction (MacArthur and Wilson, 1967; MacArthur and Levins, 1967), past climate history and geographical position of dispersal barriers and corridors (Ricklefs, 1987). At the intermediate scale, natural and anthropogenic disturbance can reduce the availability of resources to be subdivided among species or species groups (such as livestock versus wild ungulates).



Adapted from Olff and Ritchie (2002a)

Figure 9.1a: Species-area curve showing how ecological processes at different scales may structure species diversity. The thin sold line represents situations where species richness is higher because of exclusive spatial niches, while the thick bold line indicates less species at a local scale because there are fewer exclusive spatial niches. The dashed line indicates less species because of the processes at intermediate spatial scale, such as regional conditions (climate and soils), and because metapopulation dynamics constrains the diversity.

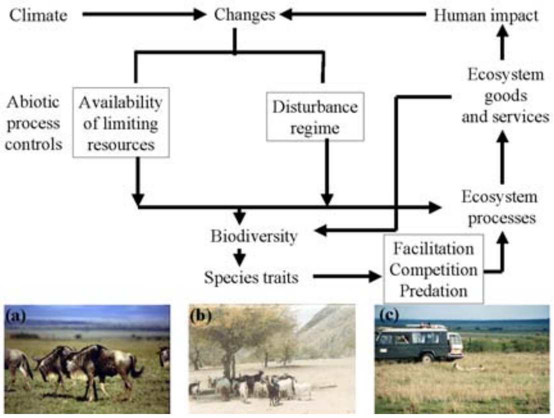


Figure 9.1b: Conceptual model of factors determining herbivore distribution at various spatial scales. The past ungulate diversity patterns were based on the evolutionary process and depended on climatic stability and productivity. The species traits are adaptations to environmental changes (a – eruption and migration of the wildebeest in the Serengeti Mara ecosystem). At landscape level disturbance is related to climate and resource availability limits species diversity through competition (b – livestock around water hole with low herbaceous cover) that takes place at local level. All these have an effect on the ecosystem processes, which in turn have a bearing on the ecosystem goods and services (c – tourism can help the local economy).

Any changes in the physical characteristics of environments will impact on the interspecific interactions among species at local level. Predation, facilitation and competition are some of the important interaction processes (Sinclair and Norton-Griffiths, 1982; Murray, 1993; Prins and Olff, 1998; Mduma *et al.*, 1999; Murray and Illius, 2000) that determine the dynamics changes in ungulate species diversity at this level (Figure 9.1b). The framework of this relationship will be used as a guide to link the ecological processes and the scale of observation conducted in this study.

9.3 DIVERSITY OF UNGULATES ACROSS THE SCALE

I. Determinates of ungulate diversity in East Africa

We examined the proposition that productivity at regional level is a useful predictor of regional patterns of ungulate species richness (Sp_{rich}). The ungulate species richness maps were gathered from species distribution maps of the African Mammalian Database (Boitani *et al.*, 1999), and the maximum species richness was extracted for each of the 1.5° by 1.5°

quadrats. Climatic descriptors (rainfall, potential evapotranspiration, temperature, solar radiation) and elevation were determined for each quadrat, and statistical relationships among the variables were then sought through regression analysis (see methodology in Currie, 1991). Rainfall (P) and potential evapotranspiration (PET) explained a significant proportion of the variance in the species richness ($r^2 = 0.76$, $P < 0.0001$, $n = 69$). The hump-shaped curve of the species richness–productivity relationship appears to be composed of at least two phases: the positive (Kenya) and negative slopes (Tanzania and Uganda) that make up the two sides of the hump-shaped curve, with maximum species richness occurring at the intermediate level (falls between Kenya and Tanzania; see Figure 9.2a and 9.2b).

Contrary to expectations that high productivity areas would have high species richness (energy limitation theory; see Wright, 1983), ungulates were highest at the intermediate productivity level. Recent studies have indicated that the species diversity of ungulates varies across gradients of plant abundance and quality (McNaughton, 1985; Prins and Olff, 1998; Baird, 2001; Oindo and Skidmore, 2002; Olff *et al.*, 2002b). Olff *et al.* (2002b) suggested that herbivore species must encounter plants of both sufficient abundance and quality to persist, and therefore may be constrained to persist only under certain conditions of plant-available moisture and nutrients. The highest herbivore density is thus expected in locations of intermediate biomass and nutrient concentration (Olff *et al.*, 2002b). The dry and infertile habitats have low population abundance – raising extinction rates, which may limit species diversity (Rosenzweig and Abramsky, 1993; this study), while the low biomass of herbivore communities in moist savannas may reflect the limitation imposed by vegetation quality rather than quantity (Bell, 1982; Olff *et al.*, 2002b).

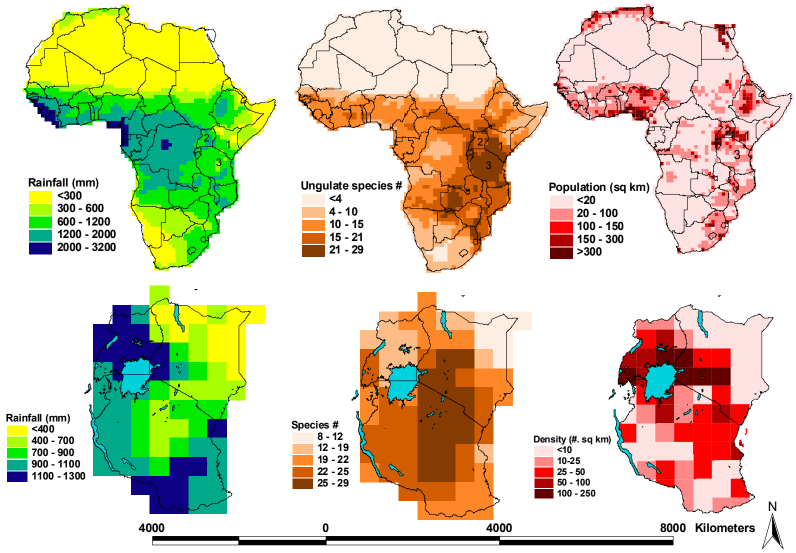


Figure 9.2a: Distribution of ungulates, rainfall and human population at continental (Africa) and regional (East Africa) levels. The focus of the study is the regional level comprising the East African countries of Kenya (1), Uganda (2) and Tanzania (3).

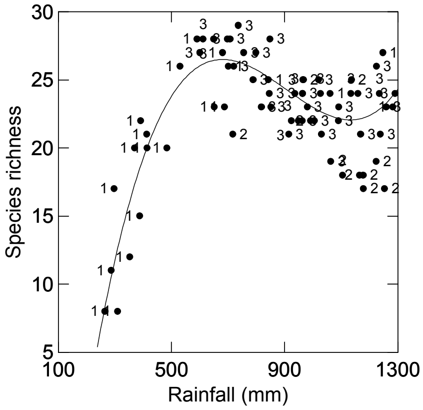


Figure 9.2b: Relationship between ungulate species richness and productivity in East Africa and within the individual countries of Kenya (1), Uganda (2) and Tanzania (3).

We further analyzed how the historical pattern relates to the human population density (P_{dens}) in East Africa. Rainfall alone explained 23% of the observed variations. When we analyzed for Kenya we found that human populations are consistently dense in areas of high primary productivity ($InP_{dens} = -2.829 + 0.011P - 0.00000379P^2$, $r^2 = 0.84$, $P < 0.0001$, $n = 24$), which is a pattern similar to that exhibited by ungulate species richness ($Sp_{rich} = -2.16 + 0.064P - 0.00003462P^2$, $r^2 = 0.67$, $P < 0.0001$, $n = 24$). The correlations between species richness (Sp_{rich}) and human density (P_{dens}) exhibit marked congruence ($r_{s\ corr} = 0.75$, $n = 24$).

The direction and course of such a relationship are difficult to analyze using species range information alone, and the inclusion of trends (time component) and the comparison of different landscapes (space component) should provide additional information on the dynamics of these changes. We developed a quantitative method (**meta-analysis**) for analyzing changes in wildlife and livestock, compared resources use in different landscapes (**spatio-temporal analysis**), and later related landscape patterns to **ecological function**.

II. Identifying trends and course of conservation conflicts

There are two contrasting perceptions with respect to the coexistence of pastoralism and wildlife in Africa: those claiming that people and wildlife continue to coexist, and others who question the sustainability of this coexistence, arguing that an increase in human and livestock populations would displace wildlife. Meta-analysis was used to assess the trends in wildlife and livestock. The method allows many data sets to be analyzed simultaneously and thereby improves confidence in the result. The results of the meta-analysis showed a significant trend towards the decline in both wildlife (correlation coefficient of –0.71) and livestock (correlation coefficient of –0.23) in the rangelands. The rate of decline in wildlife (2.5% per annum) was much higher than in livestock (0.6% per annum). Next, we established the relations between people, wildlife and livestock among the districts by extending and modifying (introducing spatio-temporal changes) the ‘road to extinction’ model of Prins (1992) and are summarised in Figure 9.3.

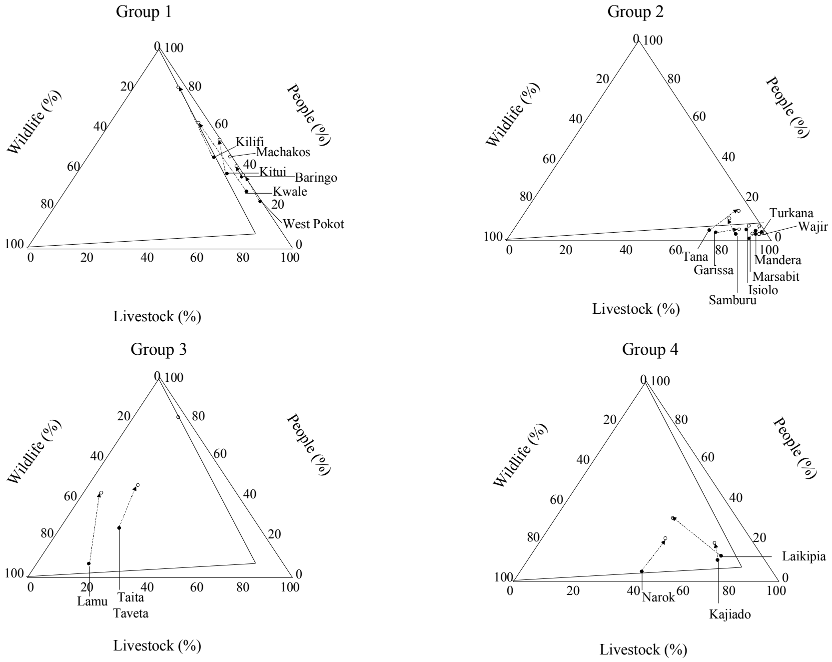


Figure 9.3: The relation between people, wildlife and livestock in the Kenyan rangelands between 1978 (●) and 1994 (○). The three axes express the relative contribution (%) of people, wildlife and livestock to the total combined metabolic densities of the three categories. The four broad patterns of the relation between people, wildlife and livestock in the Kenyan rangelands are highlighted in the above figure. Group 1 consists of districts with moist climatic conditions; here agriculture and urbanization are rapidly replacing pastoralism and wildlife, hence the movement of these districts along the right-hand side of the triangle. Group 2 consists of the arid to semi-arid districts with low population; these are increasingly moving towards the lower right corner, indicating more livestock. The two districts (Tana River and Samburu) with slight potential for agriculture show a slightly higher human population density. Group 3 shows districts (with large tracts of parks) that were once dominated by wildlife; these have suffered heavy poaching, and later resettlement programmes have increased the population in these districts. Group 4 consists of districts combining both high wildlife and livestock with potential for agriculture. The pattern here is mixed, with Narok experiencing a high decline in wildlife, Laikipia experiencing an increase in wildlife and decline in livestock, and Kajiado having stable populations of both wildlife and livestock. All three districts continue to have an increasing human population.

The results of this study indicate that the perception of the harmonious coexistence of pastoralism and wildlife is questionable. The coexistence of people and wildlife that once existed may well be the result of low human population, tribal warfare, diseases (rinderpest, cholera and smallpox), famine and droughts rather than a reflection of harmony (see Ochieng', 1980; Lamprey, 1984; Waller, 1990; Homewood and Rodgers, 1991; Prins, 1996). A similar pattern is exhibited at continental level, where there have been marked changes in human population, livestock and wildlife (Osemeobo, 1988; Bowen-Jones and Pendry, 1999; Brashares *et al.*, 2001). It has been observed that many parks are rapidly becoming habitat islands as a result of human settlement, agriculture and the elimination of wildlife (Osemeobo, 1988; Newmark, 1996; Brashares *et al.*, 2001). Loss of wildlife and livestock habitat will continue in most of these countries as human population increases. Immediate action is needed to address the conflict if we are to ensure the coexistence of people, wildlife and livestock in the arid and semi-arid ecosystems in Africa.

III. Ecological functions – interaction between species at landscape level

The analysis reported so far was undertaken at sub-continental or national level. An interesting question is how do the changes in human population and livestock influence the ecosystem and its species diversity patterns at landscape level. We undertook a study that focused on the impacts of water development on wildlife assemblages in the six arid and semi-arid districts of Turkana, Samburu, Marsabit, Isiolo, Wajir and Mandera (districts that formed the second group with increased progression towards more livestock keeping – see Figure 9.4a). The development of drinking water resources for people and livestock forms one of the main development interventions in the arid and semi arid lands (ASAL). The study was based on comparing the distribution (presence or absence) of either wildlife or livestock, or both, from a source of water, the distance range increasing from 0 to 10 km, to 10 to 15 km, to more than 15 km. The animal data were derived from an aerial census conducted in the early 1990s and the water points were derived from the Kenyan German technical cooperation (GTZ) ASAL programme.

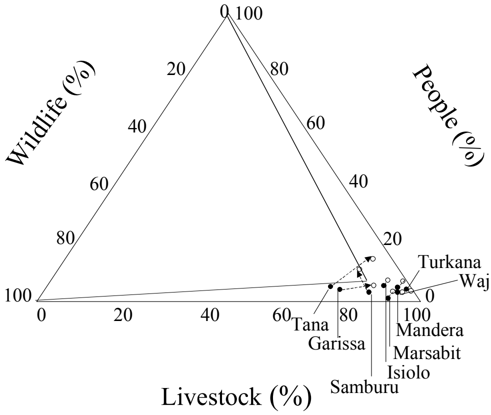


Figure 9.4a: The relation between people, wildlife and livestock in the arid and semi-arid districts at an ecosystem level, showing a movement towards pastoralism. The Samburu and Tana River districts have a slightly higher population as the districts have the potential to support limited agriculture.

The results of the landscape patterns revealed that most of the wildlife in the northern rangelands resided outside the protected areas, where the mean density of livestock was 33 times higher than the mean density of wildlife (refer to Figure 9.4b). Livestock were more clustered near water points in the northwestern parts of the study area, as compared with the northeastern areas. Wildlife avoided areas within 10 km of water but were attracted to areas 10 to 15 km away from water, as shown in Table 9.1.

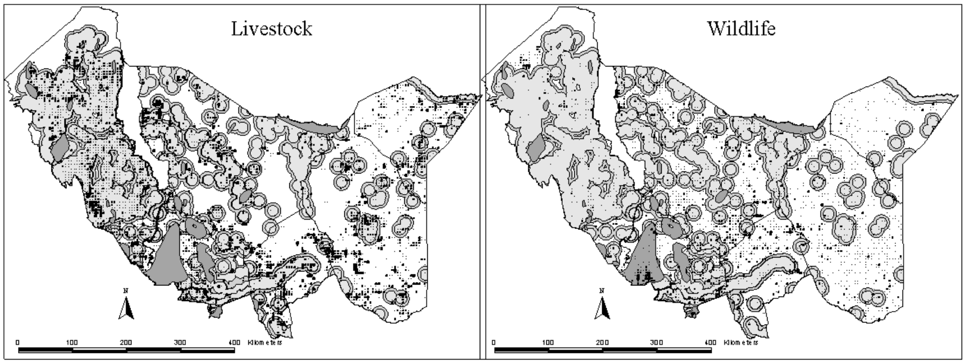


Figure 9.4b: Maps of northern Kenya displaying the density and distribution in 1990 of (top) livestock and (bottom) wildlife in relation to the distance to permanent water sources as recorded in the late 1980s. Dark gray represents the semi-arid zone, which was excluded from further analysis. White, medium and light gray represent areas at distances from permanent water sources of more than 15 km, 10 to 15 km, and less than 10 km respectively. Dot sizes represent the following animal densities / km^2: livestock: small = > 0-50, medium = > 50-250, large = > 250; wildlife: small = > 0-5, medium = > 5-25, large = > 25.

Table 9.1: Distribution of wildlife in relation to distance to permanent water (km) and the presence /absence of livestock*.

Species	Livestock present			Livestock absent			Ratio		
	0-10 km	10-15 km	>15 km	0-10 km	10-15 km	>15 km	0-10 km	10-15 km	>15 km
Grevy's zebra	0.60	0.97	0.47	0.64	0.71	0.31	1.06^{ns}	0.73^{ns}	0.66^{ns}
Burchell's zebra	0.66	0.00	0.09	0.21	0.09	0.03	0.32^{*}	∞^{ns}	0.33^{ns}
Giraffe	1.27	1.35	2.75	3.32	4.25	5.46	2.61^{***}	3.15^{**}	1.99^{***}
Warthog	0.48	0.97	1.42	0.75	0.80	1.00	1.56^{ns}	0.82^{ns}	0.70^{ns}
Oryx	0.48	3.48	2.37	3.43	5.40	4.77	7.15^{***}	1.55^{ns}	2.01^{***}
Ostrich	1.03	3.48	2.28	2.09	4.52	4.15	2.03^{*}	1.30^{ns}	1.82^{**}
Lesser kudu	0.54	0.00	1.14	1.61	1.24	1.59	2.98^{**}	∞^{*}	1.39^{ns}
Impala	0.12	0.19	0.19	0.48	0.18	0.25	3.98^{ns}	0.92^{ns}	1.31^{ns}
Gerenuk	2.05	2.71	3.98	4.45	5.76	5.52	2.17^{***}	2.13^{**}	1.39^{*}
Grant's gazelle	9.35	11.99	6.92	11.41	13.55	11.07	1.22^{*}	1.13^{ns}	1.60^{***}

*Each value shows the percentage of the aerial census sub-units where the species was observed. The ratio was calculated and statistically tested; values > 1 indicate a negative association between livestock and wildlife; ns = not significant; *P < 0.05; **P < 0.01; ***P < 0.001.

The interaction between livestock and wildlife species varied, with only Burchell's zebra being more frequent in the presence of livestock. Six species, namely giraffe, oryx, ostrich, lesser kudu, gerenuk and Grant's gazelle, were significantly reduced in the presence of livestock. Giraffe, gerenuk, oryx and ostrich (aridity-tolerant species that are less dependent on drinking water) tend to be observed more frequently away from water. Burchell’s zebra, Grevy’s zebra and warthog distributions reveal a positive or no relation to distance to water. These results show that livestock and human activities related to water points negatively affect the distribution of wildlife. They also highlight the dilemma of trying to improve one sector of the economy (livestock) while not considering the impacts on biodiversity (wildlife).

IV. Ecological functions – what factors or processes are important at the local level in determining ungulate species diversity?

At the local level resource exploitation, resource supply and interaction with wildlife species are the most ecosystem-important processes that govern species diversity, yet they are still poorly understood (Sinclair and Norton-Griffiths, 1982; Sinclair *et al.*, 1985; Prins and Douglas-Hamilton, 1990; Fritz and Duncan, 1993; Prins and Olff, 1998; Du Toit and Cumming, 1999; Voeten and Prins, 1999; Murray and Illius, 2000; Baird, 2001). Long-term studies are useful for exposing the full range of interactions, and therefore in helping to clarify ecosystem processes. Studies of ungulates in the Serengeti-Mara ecosystem (SME) have provided one of the longest time series of population data for East Africa. However, changes in populations of several species over the last 30 years suggest several hypotheses for the regulation of ungulates. These include interspecific competition, facilitation, density-dependent mortality, predation and diseases (Sinclair, 1973; Sinclair and Norton-Griffiths, 1982; Sinclair *et al.*, 1985; Borner *et al.*, 1987; Dublin *et al.*, 1990; Mduma *et al.*, 1999). Recent studies in the SME show a sharp decline in the ungulate population of the Masai Mara (MM) compared with what was observed in the Serengeti ecosystem (SE) (Broten and Said, 1995; Homewood *et al.*, 2001; Ottichilo *et al.*, 2001a; this study, refer to Figure 9.5a).

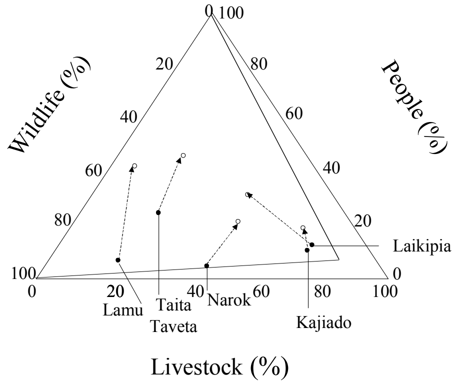


Figure 9.5a: Relationship between people, wildlife and livestock in semi-arid districts (with moist climatic conditions). The pattern is varied, with Lamu and Taita Taveta showing sharp declines (effects of poaching); Narok (the focus of this case study) shows moderate declines in wildlife but a high increase in human population; in Kajiado the wildlife and livestock populations have remained constant and in Laikipia, although there has been an increase in human population, wildlife has increased but most likely at the expense of livestock.

Analysis of rainfall in the SME shows a period of dry years (1977-85) and of wet (1986-97). A review of the land cover and climate established that the period 1975-1985 experienced less change in land cover. The period 1985-97 experienced a drastic change in land cover. Wheat farms occupied most of the wet season range for the wildebeest, zebra and smaller herbivore. We hypothesize that the wild ungulate population should show declining trends between 1977 and 1985 if food supply is the limiting factor. The period 1986-97 should show either an increasing or decreasing wildlife trend, depending on the effects and interaction between climate and land cover changes.

This study provides compelling evidence that habitat loss and fragmentation through land use change has a much wider effect than climatic variations on the dynamics of herbivores. Assuming that climate was the only factor affecting the wild herbivore in the SME, we would have expected similar trends relating to animals in both the MM and Serengeti. But the results reveal a decline in 10 out of 13 wild ungulates in the MM during the wet season (and 6 out 13 in the dry season), with most declines occurring after the 1985 period (Table 9.2 and also refer to Ottichilo *et al.*, 2001a).

Table 9.2: Wildlife ungulate and livestock population trends in the Masai Mara.

	Wet Season			Dry Season				
	Trends 1977-97 (n = 15)	Change in slope of linear trend before and after 1985		Trends 1977-97 (n = 12)	Change in slope of linear trend before and after 1985		Season	
Species	r^2 of model	Trends	r^2	r^2 of model	Trends	r^2	Season with a high population	P
Wildebeest	0.75***	B: decline	0.86***	0.31^{ns}	B: decline	0.65*	Dry	**
		A: no	0.01^{ns}		A: increase	0.03^{ns}		
Burchell's zebra	0.15^{ns}	B: no	0.22^{ns}	0.01^{ns}	B: decline	0.54^{ns}		ns
		A decline	0.45^{ns}		A: no	0.01^{ns}		
Thomson's gazelle	0.46**	B: no	0.03^{ns}	0.78***	B: no	0.13^{ns}	Wet	**
		A decline	0.36^{ns}		A: decline	0.69*		
Topi	0.48**	B: no	0.01^{ns}	0.73***	B: no	0.25^{ns}	Wet	*
		A: decline	0.53^{ns}		A: decline	0.63*		
Buffalo	0.80***	B: decline	0.44^{ns}	0.35*	B: decline	0.46^{ns}		ns
		A: decline	0.64*		A: no	0.17^{ns}		
Warthog	0.77***	B: decline	0.32^{ns}	0.40*	B: no	0.02^{ns}	Wet	**
		A: decline	0.47^{ns}		A: no	0.01^{ns}		
Grant's gazelle	0.51**	B: decline	0.16^{ns}	0.25^{ns}	B: no	0.11^{ns}		ns
		A decline	0.36^{ns}		A: no	0.05^{ns}		
Eland	0.50**	B: decline	0.42^{ns}	0.22^{ns}	B: decline	0.41^{ns}		ns
		A no	0.02^{ns}		A: increase	0.82*		
Giraffe	0.87***	B: decline	0.55*	0.61**	B: no	0.01^{ns}	Wet	*
		A decline	0.80**		A: decline	0.36^{ns}		
Waterbuck	0.37*	B: no	0.01^{ns}	0.07^{ns}	B: no	0.16^{ns}		ns
		A decline	0.29^{ns}		A: no	0.01^{ns}		
Elephant	0.11^{ns}	B: no	0.09^{ns}	0.01^{ns}	B: increase	0.41^{ns}		ns
		A no	0.12^{ns}		A: no	0.15^{ns}		
Impala	0.16^{ns}	B: no	0.16^{ns}	0.16^{ns}	B: no	0.01^{ns}		ns
		A: no	0.01^{ns}		A: no	0.03^{ns}		
Kongoni	0.38*	B: no	0.02^{ns}	0.37*	B: decline	0.42^{ns}	Wet	**
		A: decline	0.74*		A: no	0.24^{ns}		
Cattle	0.02^{ns}	B: no	0.23^{ns}	0.01^{ns}	B: decline	0.75*		ns
		A: no	0.03^{ns}		A: no	0.21^{ns}		
Sheep and goats	0.16^{ns}	B: decline	0.31^{ns}	0.36*	B: no	0.01^{ns}		ns
		A: no	0.02^{ns}		A: no	0.01^{ns}		
Donkey	0.44**	B: no	0.14^{ns}	0.48*	B: increase	0.51^{ns}		ns
		A: decline	0.47^{ns}		A: no	0.01^{ns}		

Note: Significance assessed by log-linear models (P values: *<0.05; **<0.01; ***<0.001; ns = not significant).
Notation B represents before and notation A after 1985.

- Declines in ungulates were generally higher in the wet season than in the dry season (Figure 9.5b). And this was reflected more in the sharp declines in the larger bodied ungulates than in the smaller bodied ones during the wet season (non migratory) as compared with the dry season (migratory).
- Earlier studies showed that the wildebeest and the buffalo are mainly regulated through intraspecific competition for food (Sinclair, 1979; Sinclair, 1983; Sinclair *et al.*, 1985; Prins, 1996; Mduma *et al.*, 1999; Ottichilo *et al.*, 2001b; Serneels and Lambin, 2001). The decline in wildebeest in the MM occurred between 1977 and 1985, and we assume the combination of sub-optimal conditions during the wet season and the increase in competition during the dry season in the MM may have led to high wildebeest and buffalo mortality during the period 1977-85. But the severe drought of 1993 seriously affected the buffalo and caused a crash in the population in the MM (Figure 9.5c and also refer to Dublin, 1994).
- However, prior to the heavy decline there seems to have been heavy pressure on the wet season buffalo population and it might be related to an increase in elephant densities in the MM. More than 500 elephants moved from the SE to the MM in the early 1980s due to heavy poaching in the SE (Dublin and Douglas-Hamilton, 1987). Drent and Prins (1987) and de Boer and Prins (1990) observed forage competition between elephant and buffalo in the Lake Manyara National Park, and most likely the two also compete for forage in the MM.

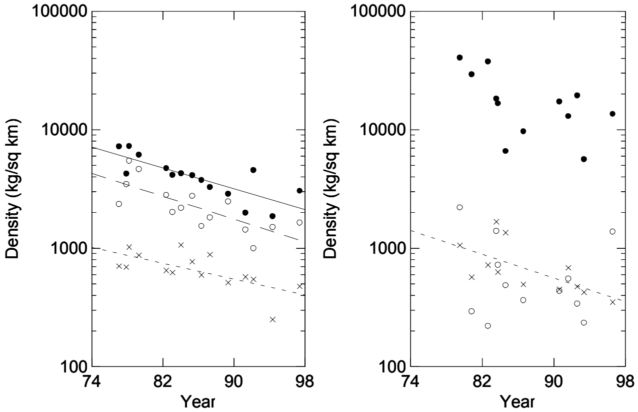


Figure 9.5b: Changes in wildlife trends in the Mara (●), Loita (○) and Siana (x) range units for the wet season or non-migratory population (left) and dry season or migratory population (right). The decline in wildlife in the dry season occurred only in the Siana range unit.

- The rapid decline in Thomson's gazelle and topi coincided with the levelling out of the wildebeest and zebra populations (Figure 9.5d). The dominance of both zebra in the Loita and wildebeest in the Mara seems to have had an impact on a number of species. Hansen *et al.* (1985) found the highest diet similarities were between the buffalo, kongoni, wildebeest, topi and Thomson's gazelle in the MM. Murray and Illius (2000) observed that herbivory by one species can modify the vegetation in a way that makes it less profitable to competing species. The situation seems to be very severe during the dry or migratory season, when the wildebeest and zebra dominate natural pastures and can preclude the utilization of the resource by other selective ruminant species, especially if the grazing areas decrease, as demonstrated in this study and the earlier studies of Sinclair *et al.* (1985) and de Boer and Prins (1990). (This is contrary to the facilitation processes – refer to Bell, 1971; Pennycuick, 1975; Maddock, 1979).

- The declines in Thomson's gazelle and topi were higher in the dry season than in the wet season and were particularly related to the period 1986-97 (of habitat loss). This would support the hypothesis of interspecific competition between species and this study reveals that competition becomes a strong factor under the condition of habitat loss. As regards the kongoni and warthog, the decline was higher in the wet season (sharp declines between the periods 1986-97), though also there significant declines in the dry season.

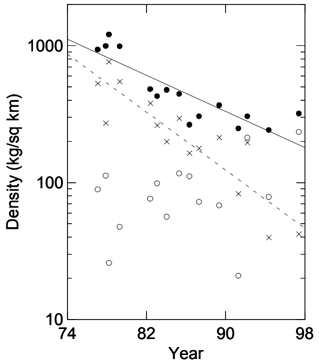


Figure 9.5c: The trends for both wildebeest (●) and buffalo (x) wet season population show declines over time; the elephant (○) population has remained constant throughout the study period. The wildebeest population is predominately located in the Loita and has little interaction with buffalo that is predominantly distributed in the Game Reserve – where the elephant density is highest.

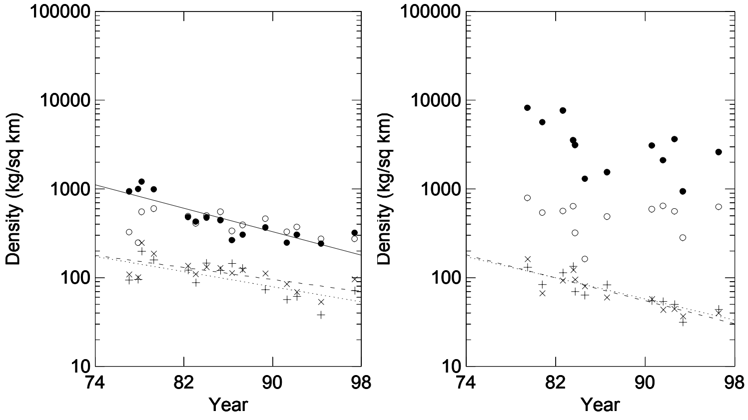


Figure 9.5d: The trends of wet (left) and (dry) season populations of wildebeest (●), zebra (○), Thomson's gazelle (x) and topi (+). The decline in Thomson's gazelle and topi occurred as the populations of both wildebeest and zebra stabilized during the wet period 1986-97, with a slight increase in migratory wildebeest and zebra populations during the dry season of 1986-97.

When one considers the question of which processes – interspecific competition, food supply or facilitation determine the ungulate population - this study reveals that when the resource and key habitats are intact a moderate change in climate does not drastically affect the wildlife species (unless the droughts are very prolonged, as experienced in 1984 and 1993; refer to Dublin, 1994; Mduma *et al.*, 1999). However, as resources become scarce through habitat modification (especially loss of critical habitats), competition sets in and this has an effect on species diversity as demonstrated in the decline of a number of species in the study area.

V. Ungulate diversity - relation between local processes and regional patterns

The role of regional and historical processes in determining local patterns of species diversity has recently regained prominence in ecological literature (see Ricklefs, 1987; Cornell and Lawton, 1992; Cornell, 1993; Ricklefs and Schluter, 1993; Westoby, 1993; Huston, 1999). In the search for patterns consistent with either local- or regional-scale processes, support has emerged for the dominance of regional processes (Huston, 1999). These processes, operating on large temporal and spatial scales, are likely to be important determinants of local patterns (refer to Figure 9.6a) of diversity because they will determine the characteristics of the species pools from which local communities can be assembled, and because they set the upper limit on local species richness (Caley and Schluter, 1997). Then it is important to ask whether variation in the number of species between regions should be considered to be the result of regional processes, or simply the result of local processes occurring under the environmental conditions of the region (refer to Figure 9.6a).

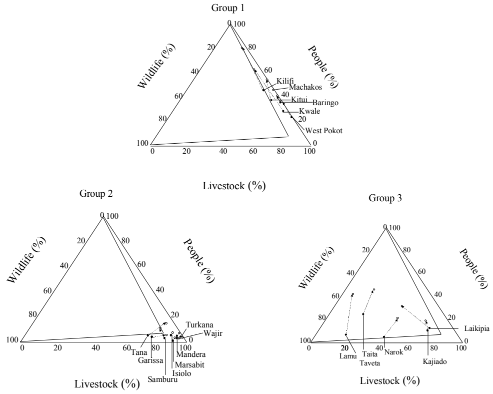


Figure 9.6a: The relation between people, wildlife and livestock in 19 Kenyan rangeland districts in 1978 (●) and 1994 (○) shows the local processes that are governed by environmental gradient. Group I with moist climatic conditions shows the demise of wildlife in the rangelands with most land being converted to agro-pastoral, agriculture or urban centers. These districts face rapid local extinction of species. Group II districts with arid climatic conditions the development is more predominant pastoralism and wildlife. Group III districts that have semi-humid to arid climate are districts with high wildlife, livestock and with increasingly pressure from agriculture.

The second part of study analysed the changes in species richness over time and at various spatial scales. The results shows at 20 by 20 km the variation in species richness in all agro-climatic zones was significant. At the intermediate scale of 50 by 50 km ACZ 4 (semi humid to arid), ACZ 5 (semi arid) and ACZ 6 (arid) showed variation in species richness, except for ACZ 7 (very arid). At the regional scale (100 by 100 km) the significance changes of species richness was reported in the semi humid to arid and arid areas. The implication of these findings is that there are significant declines in species richness in the semi-humid to semi arid (ACZ 4) and arid (ACZ 6) lands. The sub-humid to arid lands are areas that have been rapidly converted to agriculture. This process can be related to the regional patterns where a number of districts (Kilifi, Kwale, Kitui, Machakos, Baringo, West Pokot and Turkana) are facing local extinction of species (refer to Figure 9.6b) through conversions of their land from rangeland use to agriculture or urban use. The results highlights the relative contribution of regional properties and local processes vary along environmental gradient to produce-regulated pattern of species diversity.

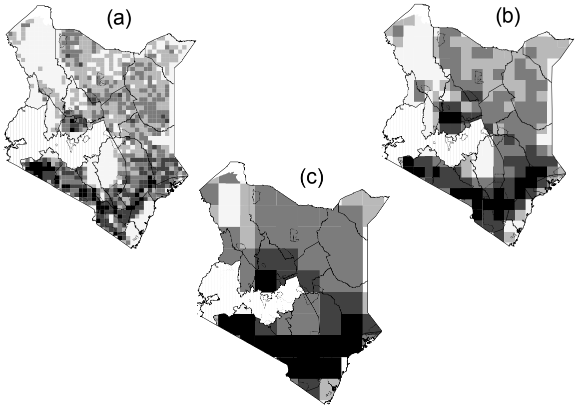


Figure 9.6b*:* Distribution of ungulate species in the arid and semi-arid districts of Kenya at three spatial scales. Picture (a) shows very clearly the low species diversity in northwestern, central and coastal districts. This is also highlighted at a regional scale (picture c), where the species pool in theses region is low. This demonstrates the link between local processes and regional patterns.

The impact of the local and regional processes in the arid and semi arid districts of Kenya is also reflected in regional individual species trends (based on meta-analysis analysis). The results revealed three patterns: (i) species that are declining sharply (such as Hirola, Grevy's zebra), (ii) species that are generally declining throughout the region (kongoni, wildebeest, topi, elephant) and (iii) species (Grant's gazelle, gerenuk, oryx, buffalo, lesser kudu, giraffe) that have mixed trends (increasing or decreasing in certain localities). The current status of the ungulate species in East Africa is out of 55 species, one is critically endangered, three are threatened and seven are near threatened, while the rest depend on the conservation status on where they are located. Therefore, concerted efforts are needed to manage and conserve the remaining species and their habitats. And there should be focus of both local and regional processes (across districts and across countries) if we are to conserve the species diversity in the region.

VI. Summary and conclusions

Multiscale perspectives of species richness in East Africa

This dissertation deals with multiscale perspectives of species richness in East Africa. The study demonstrated that species diversity patterns are scale-dependent, and that the patterns vary with spatial and temporal scales of observation and can be determined by multiple processes that function at various scales (**Multiscale perspectives**). Processes and parameters important at one scale may not be as important or predictive at another scale. However, most ecological studies are based on small-scale studies (take less time and involve small areas) or large-scale studies (depend mostly on observed pattern of distribution of species), while at the intermediate level (needs constant monitoring and involves large areas of contrasting landscape) there are fewer research efforts. This information gap is what may link ecologist to wildlife manager, and unless this information gap is filled we will not be able to manage our wildlife resources adequately and efficiently. The aim of this study is directed towards developing a framework for analyzing ungulate dynamics from a multiscale perspective (linking the three-scale level).

Four significant goals were achieved in undertaking this study that ranged from (i) linking data through spatial analysis, (ii) improvements in the statistical approach to analyzing multiple wildlife/livestock census data, (iii) integration of both low- and high-resolution remotely sensed data in analyzing land cover changes, (iv) synthesizing the relationship between pattern and processes across the scales (refer to Chapter 9).

1. The current study has demonstrated the usefulness of integrating scales in analyzing ungulate diversity patterns and trends. It has provided some useful insights in the mechanisms underlying past patterns and changes in ungulate species diversity in East Africa. The main observations on factors pertaining to these patterns and processes are:
    - The analysis of the relation between ungulate species richness and climatic and remotely sensed productivity indices revealed that the climatic model was more predictive than the remotely sensed NDVI data. The pattern is consistent with studies on variations in richness (plants and animals) as functions of productivity that show species richness reaches its maximum at intermediate productivity levels (see Grime, 1973; Huston, 1980; Tilman, 1982; Abramsky and Rosenzweig, 1984; Al-Mufti *et al.*, 1984; Owen, 1988; Rosenzweig and Abramsky, 1993; Prins and Olff, 1998; Huston, 1999; Balmford *et al.*, 2001; Olff *et al.*, 2002; Baird, 2001; Oindo and Skidmore, 2002). Additional pattern observed in this study is that geographical patterns in species richness were repeated among a number of taxonomic (order and family) and tended to converge towards the same level, particularly at the higher taxonomic level or faunal grouping.

- At the intermediate or national level the species diversity is influenced by both the human and livestock populations (not considered in many biodiversity studies). In this study we analyze the coexistence of pastoralism and wildlife and the results show that we are at a crossroads. The densely populated moist districts are continuing to lose their wildlife to agriculture, the very arid districts are intensifying livestock keeping, and in the semi-arid districts with dense wildlife (and potential for agriculture) the trends are mixed. The spatio-temporal extension of the 'road to extinction' model provided more insights into the resource use, areas of conflict and areas that need attention if pastoralism and wildlife are to coexist in harmony.
- At local or ecosystem level we have shown that, compared with the seasonal fluctuations of climate, land use change can have a drastic impact on the dynamics of wildlife population. The study conducted in the MM showed that wildebeest and buffalo population increases might be limited by the wet season food supply. Similar pattern was observed with the kongoni and warthog (the decline were a higher in the wet season than in the dry season). Thomson's gazelle and topi declined as the zebra and wildebeest populations levelled off. The decline was higher during the dry or migratory period than the wet or non-migratory (contradicting the facilitation process – but these pattern were observed under condition of land cover changes). But both Sinclair *et al.* (1985) and de Boer and Prins (1990) observed a similar outcome in situations where food resources were limited (in this study could have been caused by loss of wet season range).
- We further analyzed the role of regional and historical processes in determining local patterns of species diversity. The processes operating on large temporal and spatial scales (as shown in this study) have resulted in the turnover of species, especially in the very arid districts. This has led to the local extinction of species, especially in the northwestern parts of Kenya (Turkana, West Pokot and Baringo districts), the costal belt (Kilifi and Kwale) and in central (Kitui and Machakos) Kenya especially in Machakos and Kitui districts. This clearly demonstrates how regional species pools are an important determinant of local diversity patterns, because they will determine the characteristics of the species pools from which local communities can be assembled and because they set the upper limit on local species richness.

2. Methodological innovations: spatial analysis was conducted by integrating wildlife aerial census, climatic and remotely sensed images (physical dimension), and later human population (social dimension).
    - The use of remote sensing in quantifying land cover changes was based on combining both low-resolution (NOAA/AVHRR) and high-resolution satellite images (TM and Landsat). The development of the new change detection technique, combining a time contextual approach with a spatial contextual approach, further allowed us to detect small patches of vegetation change in a homogenous background independently of climate-driven changes in land cover. The coarse spatial resolution data allowed detection of

areas that were sensitive to inter-annual climate fluctuations, but were not subjected to land cover conversion. On the other hand, the fine spatial resolution data allowed land cover conversions or modifications of a more permanent character to be detected independently of climate-induced fluctuations in surface attributes.

- In order to develop policies at national, regional or international level information had to be aggregated to analyze trends and patterns. The debate that has ensued in wildlife forums is how reliable and consistent are these statistics for developing a unified policy (refer to debates of CITES meetings; East (1997); East (1999); Said *et al.*, (1995); McRae (1998) Norton-Griffiths (1996)). In this study we dealt with the issue by developing a methodology that summarized and analyzed multiple independent studies, our aim being to discover whether there are significant changes in regional trends (wildlife and livestock). Most of the statistical approaches are meant to deal with Type I errors and there is considerable concern as to how to treat Type II errors (where it is assumed no relationship exists when in fact it does). In conservation biology, failure to reject false null hypotheses can lead to detrimental policies that exploit natural resources or can change the course of management policies (as seen in many cases where there is no adequate information on the resource base or trends).

3. Has the problem been solved? The models developed in this study have been useful in identifying indices and indicators that provide a measure of the behaviour of a broad suite of properties (patterns and processes) at various scales or levels (**Multiscale perspectives**). However, the implication of this study for the policy and management of wildlife, in addition to other resources, shows that there should be much stronger proactive participation of resource managers, stakeholders and policy makers. The principles necessary to attain this are discussed in detail in 'Malawi Principles on Ecosystem Approach' (IUCN, 2000). This states that for sound ecosystem management we should include: (1) long-term sustainability as a fundamental value, (2) clear operational goals, (3) sound ecological models and understanding, (4) understanding of complexity and interconnectedness, (5) recognition of the dynamic character of ecosystems, (6) attention to context and scale, (7) acknowledgement of humans as ecosystem components, and (8) commitment to adaptability and accountability. This study has dealt with five of the eight goals set in this report. The three long-term goals of sustainability, clear operational goals, and commitment to adaptability and accountability are managerial functionalities, but they have to be linked to research work or findings.

4. Finally, for wildlife management to succeed we recommend that studies should deal with spatial and time scales that transcend the political, social or economic agenda, and that it incorporates long-term planning while recognizing the need to make short-term decisions. Management goals and strategies must be viewed as hypotheses to be tested by research and monitoring programmes that compare specific expectations with objective measures of results. To achieve the above objectives we need long-term monitoring programmes. This study clearly shows the benefits and potential value of

having long-term data on wildlife (this programme was partly supported by the World Bank, the Canadian International Development Agency and the Government of Kenya). Most of the wildlife monitoring programmes are either being suspended or have come to an end. One way to measure the success or efficacy of management strategy is by evaluating the status and course of change in species diversity through ecological monitoring programmes. This is the call of many conservation societies and wildlife stakeholders, yet many governments are unable to undertake the monitoring and evaluation process in order to employ effective policies.

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Samenvatting

Deze thesis beschrijft en analyseert de soortenrijkdom van herbivoren in oost Afrika vanuit een perspectief van meerdere schalen. Hiertoe bestudeerden wij patronen van diversiteit op sub-continentaal, nationaal en sub-nationaal niveau. De studie toonde aan dat diversiteits patronen schaal afhankelijk zijn. De patronen in diversiteit varieerden met de ruimtelijke en temporele schaal waarop waarnemingen werden gedaan. Processen die belangrijk waren op één schaal bleken op een andere schaal minder relevant ter zijn.

Herbivoor gemeenschapen bleken op subcontinentaal niveau een maximale diversiteit te vertonen bij een gemiddelde productiviteit van het ecosysteem. Deze bevinding komt overeen met de eerder beschreven relatie tussen productiviteit en diversiteit. Vergelijking van op klimaat respectievelijk remote sensing gebaseerde productiviteits indicatoren toonde aan dat klimaat een significant betere relatie met diversiteit opleverde. De geografische patronen in soort diversiteit bleek sterk vergelijkbaar te zijn tussen verschillende taxonomische dier groepen. De meeste taxa vertoonden eveneens een optimale diversiteit bij gemiddelde productiviteit.

We analyseerden de co-existentie van pastoralisme en wild op nationaal Kenyaans niveau. Een studie die zeventien aride en semi aride districten omvatte toonde een negatieve relatie aan tussen de biomassa van mensen, vee en wild. Een toename van de humane bevolkingsdichtheid werd begeleid door een significante afname van de dichtheid aan wild. Deze spatio-temporele uitbreiding van het “pastoral road to extinction” model vergrootte het inzicht in de antagonistische relatie tussen mensen vee en wild. Ook stelde het ons in staat conflict haarden te localiseren die speciale aandacht behoeven.

Een verdere studie naar de aride zone in Noord Kenya toonde aan dat de verspreding van wild negatief is gerelateerd aan de verspreiding van vee en drinkwaterpunten. Dit laatste suggereert dat deze op de veehouderij gerichte interventies een degraderende uitwerking hebben op de wildstand. Wij toonden verder aan dat locale processen (competitie en verstoring) een directe link vertonen naar regionale patronen. Er zijn aanwijzingen dat verschillende soorten wild lokaal zijn uitgestorven in noordwestelijk, centraal Kenya alsmede langs de kust.

In de laatste hoofdstukken werden studies uitgevoerd op sub nationaal niveau in het Masai Mara ecosysteem. We vonden tussen het eind van de 70er en de 90 er jaren een significante achteruitgang voor 10 van de 13 wildsoorten. Verdere analyse toonde aan dat deze achteruitgang toe te schrijven valt aan veranderingen in landgebruik en niet aan klimaatsfluctuaties. Dit suggereert dat de dynamiek van wildpopulaties in het Masai Mara ecosysteem onderworpen is aan processen die verschillen van die in het aansluitende Serengeti ecosystem in Tanzania.

Onze resultaten tonen aan dat rurale ontwikkeling en natuurbeheer in Kenya op een kruispunt zijn beland. Verdere ongebreidelde rurale ontwikkeling zal leiden tot een voortgaande degradatie van de wildstand. De uitdaging ligt in het integreren van rurale ontwikkeling en duurzaam wild beheer, waarbij de laaatste beperkingen oplegt aan de eerste. Dit vereist lange termijn planning van landgebruik, gebaseerd op een reele voorspelling van de interactie tussen wildbeheer en andere vormen van landgebruik op ruimtelijke en temporele schalen die voorbijgaan aan hetgeen volgens de politieke, economische en sociale agenda haalbaar lijkt.

Curriculum Vitae

Mohammed was born on 22nd of April 1960. He completed his undergraduate in 1984 with Bachelor of Science degree in Zoology and Botany. In 1985 joined the Department of Resource Surveys and Remote Sensing (DRSRS) as Biologist. He was involved in ecological monitoring work especially conducting aerial census of large mammals throughout the Kenya rangelands. Later in 1987 joined the Data Management section with additional responsibilities of coordinating the development of wildlife/livestock spatial database, but still involved in aerial census work and other ecological monitoring activities.

In 1989 he joined ITC for a postgraduate diploma for a period of 11 months. Later in 1992 joined Wageningen Agricultural University for an MSc course in application of GIS in Natural Resources Management. In 1994 was involved in the further development of GIS and updating the African Elephant Database, a joint program between African Elephant Specialist Group (AEfSG), United Nation Environmental Programme (UNEP) and International Union for Conservation of Nature (IUCN). In 1997 was conferred as the Head of the Data Management section at the Department of Resource Surveys and Remote Sensing. In same year he participated as a system analyst in the National Land Degradation-Mapping program jointly conducted by UNEP, DRSRS, Kenya Metrological Department, Nairobi University, Kenya Soil Surveys and ILRIC. He worked for more than a year as a World Bank consultant (GIS application specialist). In mid 1999 he started his PhD research at ITC and the last three and half years was spent on investigating the factors that influence species diversity of large herbivores at various spatial scales ranging from sub-continental to local level.

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