DISSERTATION

FRAGMENTATION AND SETTLEMENT PATTERN IN MAASAILAND – IMPLICATIONS FOR PASTORAL MOBILITY, DROUGHT VULNERABILITY, AND WILDLIFE CONSERVATION IN AN EAST AFRICAN SAVANNA

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JEFFREY S. WORDEN ENTITLED FRAGMENTATION AND SETTLEMENT PATTERN IN MAASAILAND – IMPLICATIONS FOR PASTORAL MOBILITY, DROUGHT VULNERABILITY, AND WILDLIFE CONSERVATION IN AN EAST AFRICAN SAVANNA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF THESIS

SETTLEMENT PATTERN AND FRAGMENTATION IN MAASAILAND – IMPLICATIONS FOR PASTORAL MOBILITY, DROUGHT VULNERABILITY, AND WILDLIFE CONSERVATION IN AN EAST AFRICAN SAVANNA

Fragmentation through land privatization and sedentarization impacts the conservation and management of grazing systems around the world. In this study I examine how rangeland fragmentation and the loss of key resource areas impact the structure and function of the pastoral grazing system and the implications for large wild herbivore (wildlife) distribution and abundance. I used a land tenure and sedentarization gradient in the Greater Amboseli Ecosystem (GAE) of Kajiado District, Kenya to quantify the effects of fragmentation on patterns of pastoral settlement, livestock mobility and drought vulnerability at multiple spatial and temporal scales. I developed a new high resolution aerial counting technique to examine both broad and fine scale responses of wildlife to fragmentation and pastoral settlements, and the loss of key resource areas to agriculture and conservation.

Fragmentation has led to a fundamental transformation of pastoral settlement and grazing patterns in the GAE. Formerly flexible settlement systems have been replaced with dispersed and clustered patterns of settlement in privatized and collectively managed areas respectively. Seasonal grazing patterns have moved from a wet to a dry season dispersal system as forage availability replaced water distribution as a fundamental constraint. Livestock in highly fragmented areas moved less under normal rainfall conditions, but appeared to move earlier, and farther than their less fragmented neighbors under drought conditions. Analyses of broad scale livestock movement over a two year period (1999 – 2000) revealed that livestock were not maximizing their access to green forage biomass as indicated by NDVI.

Increasing pastoral land-use intensity reduced wildlife biomass and differentially altered wildlife distribution patterns in relation to pastoral settlements depending on body size and feeding strategy. Similarly, increasing agricultural development in key resource areas reduced wildlife biomass and altered distributions relative to permanent water. Protection increased wildlife biomass and provided an important refuge for certain species, but some species were locally absent due to habitat changes associated with elephant compression. This study illustrates the importance of fragmentation in altering patterns of pastoral production and exacerbating vulnerability to extreme climatic events, and highlights the cascading effects these changes may have for wildlife conservation inside and outside protected areas.

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CHAPTER 1

INTRODUCTION

Revealing the role of land use change in shaping earth's environment is fundamentally important to understanding human impacts on ecosystems (Ojima et al. 1994). This is particularly true in the savannas of East Africa where land privatization and sedentarization have altered pastoral land-use patterns and led to the fragmentation of arid and semi-arid rangelands (Hobbs et al. in press). Fragmentation and land-use change have, in turn, led to changes in disturbance regimes associated with pastoral production and the loss of key resource areas. These changes have important implications for the vulnerability of pastoral people and the structure and function of the savanna ecosystems they inhabit. The goal of this research was to quantify the effects of fragmentation and land-use change on 1) pastoral settlement patterns, 2) livestock mobility, forage access, and drought vulnerability, 3) wildlife distributions, abundance, and community structure, and 4) large herbivore utilization of key resource areas in the swamps of Greater Amboseli Ecosystem (GAE).

CHAPTER 2 - EFFECTS OF FRAGMENTATION ON SETTLEMENT PATTERNS

Changing land tenure regimes have had important impacts on pastoral societies all over the world. In particular, the move from communal resource management to private, individualized land tenure systems and the parallel process of sedentarization has lead to increased vulnerability to extreme climatic events and poverty (Galaty 1992, Galaty 1994a, Galvin et al. in press), increased landlessness and resource alienation (Galaty 1992, Rutten 1992), greater economic diversification (Little et al. 2001), compromised health and nutrition (Nestel 1986, Shell-Duncan and Obiero 2000, Fratkin et al. 2004), reduced mobility and declining access to heterogeneity (Scoones 1999, Coughenour in press). In Africa, increases in the rate of land-use change (Ojima et al. 1994, Lambin and Ehrlich 1997, Linderman et al. 2005) and policies aimed at "rationalizing" pastoral production (Talbot 1972, Rutten 1992, Galaty 1994b), have resulted in the loss of important rangeland resources to agricultural encroachment (Campbell 1999, Campbell et al. 2000) and conservation (Western 1982a), and the widespread dissection of remaining range through development interventions (Talbot 1972), sedentarization (Fratkin 2001), and the privatization of land tenure (Galaty 1994a, Homewood 1995, Kimani and Pickard 1998, BurnSilver et al. in press, Reid et al. in press). The combined effects of privatized land tenure and sedentarization result in a decline in the spatial scale of ecological and social interactions (Hobbs et al. in press). This decline in scale, or reduction in spatial extent (Hobbs et al. in press), has important implications for pastoral movement (Worden 2007, BurnSilver and Worden in press) livestock population dynamics (Boone et al. 2005, Worden 2007), vegetation patterns (Stokes et al. 2006) and wildlife populations (de Leeuw et al. 2001, Reid et al. in press). Similarly, changes in tenure and land-use impact human-environment interactions through the spatial distribution of settlements (Theobald et al. 1997). Although it is clear that settlements play an important role in structuring the interactions of humans and ecosystems (Western and Dunne 1979), this relationship between land tenure and settlement pattern has been poorly studied in Africa.

Settlements are the integrator of human-environment interactions in pastoral systems. The spatial and temporal patterns of settlement determine how people and their livestock access and impact grazing resources (Western and Dunne 1979, Schwartz et al. 1995, Coppolillo 2000, Coppolillo 2001). Among the Maasai of East Africa, settlements link people together in complex social networks at multiple scales (Grandin 1985), and are the central point from which livestock travel for forage and water on a daily basis (Western 1973, Western and Dunne 1979). Settlements influence the composition and abundance of woody and herbaceous plant species (Western and Dunne 1979, Jensen 1983 unpublished, Reid 1992, Reid and Ellis 1995, Muchiru et al. in press-a), landscape level patterns of nutrient redistribution and concentration (Blackmore et al. 1990, Turner 1998a, b, Augustine 2003) and patterns of wildlife utilization (Muchiru 1992, Reid et al. 2001, Muchiru et al. in press-b). These patterns influence the productivity and sustainability of pastoral systems through their feed backs on the spatial and temporal availability of forage resources (Coughenour 1991).

In Chapter 2 I consider how land privatization and sedentarization impact the spatial and temporal patterns of pastoral settlement in an East African semi-arid savanna ecosystem. The objective was to understand how increasing constraints on movement and resource access through sedentarization and land subdivision impact settlement and land-use at multiple scales. I examined current and historical patterns of pastoral settlement and land-use across a land tenure gradient in the Greater Amboseli Ecosystem in Kajiado District, Kenya. To assess the impacts of land subdivision and sedentarization I considered settlement patterns at regional, landscape, and settlement scales.

CHAPTER 3 - IMPLICATIONS FOR PASTORAL MOBILITY AND DROUGHT VULNERABILITY

Increasingly, human-induced habitat fragmentation are constraining the movement of pastoralists, livestock, and native ungulates. The effects of fragmentation and habitat loss are particularly acute in African rangelands where expanding settlement and agriculture (Homewood et al. 2001, Serneels and Lambin 2001a, Serneels and Lambin 2001b, Serneels et al. 2001, Lamprey and Reid 2004), and fencing (Reid et al. in press) harm migratory ungulates. Although the impacts of fragmentation on populations of wildlife have been well studied, less attention has focused on the effects of habitat fragmentation on pastoralists (but see Galvin et al. in press). Mobility is an essential strategy for pastoralists in variable environments (McCabe 1994, Swallow et al. 1994, Swift et al. 1996, Niamir-Fuller 1999, Niamir-Fuller and Turner 1999, Coppolillo 2000, 2001, Boone et al. 2005). When coupled with other coping mechanisms, such as herd splitting (Coughenour et al. 1985, Coppock et al. 1986, Swift et al. 1996) and herd diversification (Little et al. 2001, Desta and Coppock 2004), mobility provides a means to enhance the stability of livestock production and survival in the face of marked temporal variability in forage resources, variability that characterizes arid and semi-arid ecosystems (Coughenour 1991). Managing movements of herds across a range of spatial scales enables pastoralists to maintain higher stocking densities than would be possible without movement (Scoones 1992, Scoones 1993) and it facilitates rapid herd recovery after drought. These benefits occur because managed movements enhance access to areas with ephemeral high quality forage resources, areas of low utilization, and spatially and temporally heterogeneous resources. Furthermore, movement distributes livestock impacts in space, reducing the likelihood of localized degradation (Sinclair and Fryxell 1985, Coughenour 1991).

In Chapter 3 I examine how mobility is evolving in an African pastoral ecosystem in the face of increasing constraints on movement and access to resources, and the implications of these changing movement patterns for the stability of semi-arid grazing systems. Using a land-use intensity gradient in the Greater Amboseli Ecosystem (GAE) I focus on the question of how land privatization and sedentarization influence pastoral herd sizes, opportunistic access to forage resources, vulnerability to drought, and thus pastoral well-being.

CHAPTER 4 - FRAGMENTATION AND WILDLIFE IN PASTORAL RANGELANDS

Human actions during the last 30 years have caused unprecedented declines in African wildlife (Ottichilo et al. 2000, Ottichilo et al. 2001, Serneels and Lambin 2001, Kiss 2004, Georgiadis et al. 2007). In the semi-arid and arid savannas of East Africa habitat conversion (Serneels et al. 2001), fragmentation (Reid et al. 2004, Hobbs et al. 2007, Hobbs et al. in press, Reid et al. in press), and legal harvesting and poaching (Campbell and Hofer 1995) have all contributed to wildlife declines that have exceeded 40% in the last 30 years (Norton-Griffiths 1998). Apart from high profile declines in elephant and rhino, most of these wildlife losses are associated with agricultural conversion and human population increases in higher rainfall areas such as the Masai

Mara (Ottichilo et al. 2000) leaving much of the remaining wildlife resource in the drier pastoral regions. However, as competition for resources in these areas increases people and agriculture begin to spill over into the drier more marginal areas. As land-use change continues to cascade down the rainfall gradient there is increasing pressure to reduce the scale of pastoralism through privatization and sedentarization. Understanding how wildlife respond to this subtle transformation in the patterns of pastoral land-use is one of the most pressing challenges for wildlife conservation in Africa. The spatial distribution of pastoral impacts that emerges from settlement patterns (through their direct and indirect effects) has potentially important implications for the distribution and abundance of large herbivores at multiple spatial and temporal scales.

In Chapter 4 I quantify the effects of increasing pastoral land-use intensity, represented by the degree of land privatization and settlement dispersion, on the distribution, abundance, and community structure of large herbivores in the Greater Amboseli Ecosystem. I used a high-resolution aerial counting technique to enumerate the dry and wet season distributions of large herbivores in three areas representing a gradient of pastoral land-use. To assess the effects of pastoral disturbance at different spatial and temporal scales I quantified the responses of individual species and functional groups based on body size and feeding strategy at both the landscape and settlement level.

CHAPTER 5 - LARGE HERBIVORE RESPONSES TO THE LOSS OF KEY RESOURCE AREAS

Land-use change and human environmental impacts are widely recognized as fundamentally important forces shaping the structure and function of ecosystems worldwide (Vitousek et al. 1997, Western 2001). Increasing human populations and accelerated land-use change are threatening arid systems across Africa (Ellis and Galvin 1994), as rapid transformation of arable land has resulted in increased pressure on less productive areas. Although this pressure comes from a variety of different sources and manifests itself in myriad ways, the most intense change has focused on key resource areas. Key resource areas for large herbivores are areas of semiarid and arid landscapes that provide forage and water during dry seasons and droughts, thus constituting the resource that ultimately limits herbivore populations (Illius and O'Connor 2000). Consequently, key resource areas are fundamental components of spatially and temporally variable arid and semi-arid ecosystems and important determinants of ecological patterns and processes. They have disproportionate impacts on herbivore and ecosystem vulnerabilities relative to their areas. Land-use change, and especially changes in key resource areas, can have important implications for the structure and function of ecosystems at multiple spatial scales. In the savannas of East Africa, where humans have lived for millennia as important components of the ecosystem (Western 1982b), changes in human land-use in key resource areas could have far reaching implications for entire ecosystems.

Herbivores are key components of East African savannas because they impact the ecosystem by modifying habitat structure and composition (Laws 1970, Western 2006 (online)), by changing nutrient cycling (McNaughton et al. 1988, Muchiru et al. in press-a, Pastor et al. 2006, Hobbs 1996), and altering disturbance regimes, particularly interactions with fire frequency and intensity (Hobbs et al. 1991, Hobbs 1996, van Langevelde et al. 2003). Similarly, herbivore impacts have cascading effects on biodiversity (Cumming et al. 1997, Pringle et al. 2007). The susceptibility of herbivore populations to changes in human land-use has lead to the widespread decline of these important components of savanna ecosystems across East Africa (Norton-Griffiths 1996, Ottichilo et al. 2000, Serneels and Lambin 2001a).

In Chapter 5 I examine the effects of changes in human land-use in the wetlands of the Greater Amboseli Ecosystem on the composition and distribution of large herbivores. I used high-resolution aerial count data to quantify the impacts of protection and agricultural conversion along a gradient of pastoral land-use intensity for large herbivore abundance and diversity at local and landscape levels. In particular I consider how land-use change affects the spatial structure of savanna large herbivore communities in relation to surface water.

CHAPTER 6 – SUMMARY

In the final Chapter I summarize the major findings and implications of this research and suggest management and policy options that may help reduce pastoral vulnerability and maintain dynamic ecosystem patterns and processes in the face of increasing rangeland fragmentation in the Greater Amboseli Ecosystem.

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CHAPTER 2

SUBDIVISION, SEDENTARIZATION, AND SETTLEMENT PATTERNS – FRAGMENTING THE RANGELANDS IN THE GREATER AMBOSELI ECOSYSTEM, KENYA

INTRODUCTION

Changing regimes of land tenure have had important impacts on pastoral societies all over the world. In particular, the trend from communal resource management to private individualized land tenure systems and the parallel process of sedentarization has lead to increased vulnerability to climatic fluctuations and exacerbated poverty (Galaty 1992, Galaty 1994a, Galvin et al. in press). Changes in land tenure and sedentarization have also resulted in increased landlessness and resource alienation (Galaty 1992, Rutten 1992), greater economic diversification (Little et al. 2001), compromised health and nutrition (Nestel 1986, Shell-Duncan and Obiero 2000, Fratkin et al. 2004), reduced mobility and declining access to heterogeneity (Scoones 1999, Coughenour in press). In Africa, increases in the rate of land-use change (Ojima et al. 1994, Lambin and Ehrlich 1997, Linderman et al. 2005) and policies aimed at "rationalizing" pastoral production (Talbot 1972, Rutten 1992, Galaty 1994b), have resulted in the loss of important rangeland resources to agricultural encroachment (Campbell 1999, Campbell et al. 2000) and conservation (Western 1982), and the widespread dissection of remaining range through development interventions (Talbot 1972), sedentarization (Fratkin 2001), and the privatization of land tenure (Galaty 1994a, Homewood 1995, Kimani and Pickard 1998, BurnSilver and Worden in press, Reid et al. in press). The combined effects of privatized land tenure and sedentarization result in a decline in the spatial scale of ecological and social interactions (Hobbs et al. in press). This decline in spatial extent (Hobbs et al. in press) has important implications for pastoral movement (Worden 2007a, BurnSilver and Worden in press) livestock population dynamics (Boone et al. 2005, Worden 2007a), vegetation patterns (Stokes et al. 2006) and wildlife populations (de Leeuw et al. 2001, Reid et al. in press). Similarly, changes in tenure and land-use impact human-environment interactions through the spatial distribution of settlements (Theobald et al. 1997). Although it is clear that settlements play an important role in structuring the interactions of humans and ecosystems (Western and Dunne 1979), this relationship between land tenure and settlement pattern has been poorly studied in Africa.

Settlements are the integrator of human-environment interactions in pastoral systems. The spatial and temporal patterns of settlement determine how people and their livestock access and impact grazing resources (Western and Dunne 1979, Schwartz et al. 1995, Coppolillo 2000, Coppolillo 2001). Among the Maasai of East Africa, settlements link people together in complex social networks that extend across multiple scales (Grandin 1985). Moreover, settlements are the central point from which livestock travel daily in search of forage and water (Western 1973, Western and Dunne 1979). Settlements influence the composition and abundance of woody and herbaceous plant species (Western and Dunne 1979, Jensen 1983 unpublished, Reid 1992, Reid and Ellis 1995, Muchiru et al. in press-a), landscape level patterns of nutrient redistribution and concentration (Blackmore et al. 1990, Turner 1998b, a, Augustine 2003) and patterns of wildlife utilization (Muchiru 1992, Reid et al. 2001, Muchiru et al. in press-b). In turn these patterns influence the productivity and sustainability of pastoral systems through their feed backs on the spatial and temporal availability of forage resources (Coughenour 1991).

Here I consider the effects of subdivision and sedentarization on the spatial and temporal patterns of pastoral settlement in an East African semi-arid savanna ecosystem. My objective is to understand how increasing constraints on movement and resource access through sedentarization and land subdivision impact settlement and land-use at multiple scales. To answer this question I examine current and historical patterns of pastoral settlement and land-use across a land tenure gradient in the Greater Amboseli Ecosystem in Kajiado District, Kenya. To assess the impacts of land subdivision and sedentarization I consider settlement patterns at three spatial scales, 1) regional scale, 2) landscape scale, and 3) the settlement scale (Fig. 1).

Historical Context

Human-Environment Interactions and Pastoral Settlements

At the broad scale, individual Maasai settlements traditionally acted as nodes in complex and dynamic social and spatial networks linking people and resources, and dispersing impacts, across landscapes. At finer spatial and temporal scales, the daily movement of livestock from settlements in search of forage results in a central place foraging system with the settlement as its focus. As the core unit of pastoral production and resource management systems, settlements and their distribution in space and time ultimately constrain potential livestock production strategies and the environmental impacts of pastoral activities. This does not mean that livestock distributions and impacts are necessarily clustered around settlements (Turner and Hiernaux 2002), but rather that settlement position defines the potential livestock utilization universe. This potential resource access and impact zone is not limited to individual settlements, however. Individual settlements are linked together in vast networks that enable pastoralists to access ephemeral resources in heterogeneous environments. The multi-scale nature of settlements and settlement patterns as an integrator of both access to and impact on rangeland resources is what makes their distribution in space and time so important to the stability of pastoral systems and the ecosystems they depend on.

Settlement distributions and limiting resources –forage and water

The distributions of forage and water resources are the primary determinants of spatial and temporal patterns of livestock utilization in pastoral societies (Western 1973, Western and Dunne 1979, Western and Finch 1986, Coughenour 1991). As in other semiarid regions, the Maasai pastoral system in Amboseli is ultimately limited by forage and water. Although livestock frequently succumb to disease, predation, and flooding, by far the largest losses of livestock are due to starvation and drought (Rainy and Worden 2003). Typically, livestock mortality during a drought results even though animals may have access to water. What they lack is access to forage sufficient in quantity and quality to prevent starvation. Drought affects pastoral livestock through lack of forage, which in turn is an outcome of low forage production and livestock utilization (Western and Nightingale 2003).

The forage resource has two primary components – quality and quantity. Forage quality is affected by fire and grazing, which maintain intermediate levels of forage biomass in early phenological states with higher nutrient contents (McNaughton 1984, McNaughton 1986, 1990, Wilsey 1996, Archibald and Bond 2004, Archibald et al. 2005). However, quality is ultimately controlled by underlying edaphic and precipitation gradients and plant species composition (Coughenour in press). In contrast, forage quantity, while also a function of environmental gradients, is more susceptible to temporal and spatial patterns of livestock grazing. Both of these components of the forage resource are susceptible to changes in patterns of pastoral land-use, and as we shall see below, their relative importance in limiting livestock production in the Greater Amboseli Ecosystem has changed through time. Indeed, although forage has been and continues to be the ultimate limiting factor for livestock in Amboseli, the Maasai have seen a gradual change in the proximate limitations of pastoral productivity.

Historically, while human and livestock populations were in the early phases of recovery from the "Great Disaster" (Mutai) associated with the spread of rhinderpest, smallpox, and famine during the late 1800s (Waller 1978, 1985), there were large seasonally unoccupied areas on the landscape. Animals still suffered from drought during this period, but the proximate limit on livestock production was water, not forage. In the Amboseli study area, surface water was highly heterogeneous in its distribution and traditional permanent water sources were limited to the swamps, rivers, and springs at the foot of Mt. Kilimanjaro in the south, and hand dug wells in dry river beds near Eselenkei in the north. During the dry season, the distribution of water limited the movements of both wild and domestic animals (Western 1975). The concentration of wild and domestic animals around water points, coupled with the functional limits on daily ranging distances (Western 1973, Western and Finch 1986) resulted in the gradual depletion of accessible forage resources around water points through out the dry season (Western 1975, Georgiadis and McNaughton 1990). With the arrival of the rains, water was no longer limiting due to water in plant tissues and ephemeral surface water sources, and both domestic and wild herbivores immediately dispersed across the landscape to take advantage of previously inaccessible forage resources, and the new high quality flush of green vegetation associated with the onset of the rains (Western 1973, 1975).

In response to this seasonal variability in the distribution of water across the landscape the Maasai in Amboseli developed a wet season dispersal system that sought to maximize access to high quality forage by mimicking the movements of wild herbivores (Western 1973, Western and Dunne 1979). During the dry season, as seasonal water sources began to dry out, the Maasai and their livestock would retreat to their settlements near the perennial swamps of Amboseli. The swamps provided both water and forage, and while the forage was of significantly poorer quality (Western 1973), it was sufficient for maintaining livestock and wildlife under normal dry season conditions. During periods of severe drought, a number of escape mobility (Oba and Lusigi 1987) strategies would be employed, including movement to higher well-watered pastures in the foothills of Mt. Kilimanjaro as well as long distance movements to areas of localized rainfall and forage reserves (Western 1975).

The Maasai dispersal system in Amboseli was based upon a series of settlements that were maintained by households or collections of households over a number of years (Western and Dunne 1979). The dry season settlement, located near the perennial water of the Amboseli swamps, was the permanent or core settlement. With the onset of the first rains, the main herds would disperse to the wet season settlements to take advantage of the new green flush of forage and the standing pools of water in seasonal stream beds and natural sumps (Western 1973). Ideally, a household's settlement network would provide a reasonable degree of flexibility and spatial coverage that allowed herders to access different areas depending on the spatial distribution of rainfall in any given year. This physical network of settlements was augmented with a social network of stock relationships that further enhanced Maasai access to spatially and temporally heterogeneous resources, and helped to reduce risk and dampen the effects of variability (Grandin 1985). Maasai herders and their livestock were not limited to existing settlements or kinship networks, but also utilized temporary settlements to access remote grazing resources either within their own local grazing areas or in more distant areas under the control of other Maasai sections or different cultures all together (Jacobs 1975, Berntsen 1976, Grandin 1985, Waller 1985, Rutten 1992).

Interviews with local informants and a survey of abandoned settlement sites in the Eselenkei and Osilalei areas north of Amboseli suggest that a similar wet season dispersal system existed there as well. In Eselenkei and Osilalei, dry season settlements were positioned within a few kilometers of the perennial hand-dug wells of the seasonal Selenkei river. From these dry season areas pastoral herds would disperse with the rains and return to the core settlement as the seasonal pools and forage resource gradually dried up (see Chapter 3 for more detailed description of daily and seasonal grazing patterns). Although this system was limited by the production needs of Maasai pastoralists and the constraints of a central place foraging system discussed above, it enabled Maasai to take advantage of the inherent benefits of migration in a spatially and temporally heterogeneous environment (Western 1973, Fryxell et al. 1988). It also created a system of de facto grazing controls with water being the primary limiting resource. This wet season dispersal system provided the foundation for local systems of resource use and control (Grandin 1985), and through the distribution of settlements provided the key to balancing access to heterogeneous resources within the constraints of a dynamic settlement network.

History of rangeland fragmentation in Kajiado

Historically, Maasai and related Maa speaking pastoralists have addressed the issue of resource competition through conquest and expansion (Talbot 1972, Waller 1985). However, with the advent of colonial rule, the imposition of national and district boundaries constrained the traditional pattern of broad scale movement as local resources were depleted. Not only was expansion limited, but new colonial constraints on movement such as the initial division of Maasailand into British and German controlled territories, policies of closed districts, quarantines and pass laws all worked to erode the flexible and adaptive nature of Maasai pastoralism (Kerven 1992). These limits to movement and the restriction of Maasai identity were compounded by the forced removal and resettlement of Maasai and their livestock from the Northern to the Southern Maasai Reserve in 1905 and 1911 (Waller 1985, Hughes 2005, 2006). These initial constraints on the broad scale movement of Maasai and their livestock, which began at the end of the 19th Century, were the first steps on the long and convoluted path of rangeland fragmentation seen today in Maasailand.

As this process of rangeland constriction continued to limit broad scale movements, a parallel and interlinked effort was initiated to enhance livestock production through carefully controlled grazing programs and the implementation of development interventions designed to reduce limitations on productivity (e.g. water development, cattle dips, disease eradication programs) (Talbot 1972). Market integration and the "rationalization" of pastoral production became the development goal for arid and semi-arid rangelands with little or no appreciation for the complexities of indigenous production systems and ecological realities. Although these programs were effective in increasing the numbers of both pastoralist and their livestock (Talbot 1986), primarily through the provision of water and expanded access to forage resources, they have lead to the localized degradation of forage resources around water points (Talbot 1986), and the elimination of areas far from water that historically acted as grazing reserves (Newton 1990, Coughenour in press, Western 1975).

The systematic excision of key resource areas through agricultural development and conservation occurred concurrently with these policies of restriction, "rationalization", and enhanced rangeland productivity. During the colonial period vast areas of Maasailand were carved out for European settlement (Waller 1985, Hughes 2006). The creation of the white highlands, and the development of commercial ranching in Laikipia displaced thousands of people and removed valuable dry season grazing reserves (Hughes 2006). Similarly, other key resources were lost to conservation beginning with Nairobi National Park in 1942 and culminating with the creation of Amboseli National Park in 1974. Further losses occurred with the creation of forest reserves in Oldonyo Orok, Chyulu, and Kilimanjaro. Finally, increasing pressure on arable land in other parts of the country has lead to the immigration of agriculturalists into the wetter regions of Maasailand (Campbell 1999, Campbell et al. 2003). The net result of these excisions is more than just the loss of large tracks of Maasailand, as these losses are concentrated in the high potential areas and are therefore disproportionately important as key resource areas and drought refuges.

In keeping with calls for the "rationalization" of pastoral production, national government policy in Kenya called for a gradual transition to private land ownership through a process of first group and finally individual subdivision (Rutten 1992, Galaty 1994a, Kimani and Pickard 1998). To control movement and limit livestock numbers the Government of Kenya initiated a program of group ranch formation in the early 1960s (Olang 1982). These areas were to be owned and managed collectively as a means to encourage investment, development, and responsible resource management (Galaty 1980, Rutten 1992). A number of these group ranches still exist in Kajiado District but most have been divided into individual parcels (Kimani and Pickard 1998) as expanding human and livestock populations have lead to a push for subdivision and private ownership of land.

METHODS

Study Area

The Greater Amboseli Ecosystem (GAE) is approximately 8,500 km^2 (Western 1973)[1] and encompasses Amboseli National Park and the surrounding rangelands utilized

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[1] More detailed social and ecological descriptions of the Greater Amboseli Ecosystem can be found in Chapter 1, Rutten (1992) and Western (1973)

seasonally by dispersing wildlife. This study focused on the semi-arid pastoral rangelands north of Amboseli National Park in Kajiado District, Kenya (Fig. 2). The three focal areas: Olgulului/Lolarashi (147,050 ha), Eselenkei (74,794 ha), and Osilalei (38,629 ha)[2] represent a land tenure and sedentarization gradient. Osilalei was subdivided in 1990 (BurnSilver and Worden in press), and Eselenkei and Olgulului/Lolarashi still operate as communally owned and managed group ranches. Olgulului/Lolarashi has subdivided two high potential areas, Emurutot and Namelok swamp, and allocated the parcels to individuals for rain-fed and irrigated agriculture respectively. Although these allocations have had important implications for the diversification of economic strategies on Olgulului/Lolarashi (BurnSilver in prep, in press) the drier rangelands under consideration in this study are still largely intact and continue to be managed communally by the group ranch members as a whole[3].

Much of the land-use planning and decision making is conducted at the group ranch level; however, the communal nature of resource management in the Ilkisongo group ranches (Eselenkei and Olgulului) means that group ranch boundaries do not stop the flow of people and livestock across the landscape. As a result, these are inappropriate boundaries for studying patterns of settlement and resource use. For this reason, and for the purposes of this study, I separated the three group ranches into four study areas (Fig. 2 and Table 1) based on existing settlement and management systems (Emeshenani = 45,193 ha, Lenkisim= 51,983 ha, Eselenkei = 24,673 ha, and Osilalei = 17,539 ha[4]).

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[2] Group Ranch sizes as reported in Rutten (1992).

[3] Since the time of the study the membership of both Eselenkei and Olgulului/Lolarashi have voted in favor of the complete subdivision of the group ranch.

[4] Study zone sizes from GIS

The four study zones were selected to represent a land tenure and sedentarization gradient ranging from highly mobile in Meshenani to sedentary and subdivided in Osilalei, with Lenkesim and Eselenkei falling in between these two extremes. I chose these sites because they were similar in vegetation, soils, and land use history. The four study zones are located on rolling Commiphora/Acacia dominated savannas of basement complex soils with low topographic heterogeneity intersected with seasonal rivers and fluvial deposits (Touber 1983). There is a shallow gradient in rainfall ranging from approximately 350 mm/year at Meshenani to approximately 400 mm/year in the hills of Osilalei. Discussions with local elders and long-term observations (D. Western, personal communication) confirm that pastoral families used these four zones in the same way in the past. Field observations suggest that rainfall differences may be sufficiently significant to encourage attempts at rain-fed agriculture in Eselenkei and Osilalei[5], but recent failures in both normal and dry years highlight that this may be perception rather than ecological reality (Ellis and Galvin 1994).

Data Collection

To establish settlement patterns and herder movements, I conducted two separate surveys of current and historical settlements and informal individual and group discussions with key local informants. Two Maa speaking field assistants, Sauna Lemiruni and Jacob Loorimirim, and I used 1:50,000 topographic map sheets and the help of local informants to locate all currently occupied permanent (emparnat) and seasonal (enakaron) settlements within the study area in 2000. The UTM coordinates at

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[5] Small scale rain fed agriculture first expanded in Eselenkei and Osilalei during the very wet El Nino year of 1998.

the center of each settlement were recorded with a Garmin 12 GPS. All of the houses in the settlement were counted and each was allocated to a roofing material category as an indicator of degree of permanence (skin, dung, grass, or tin). The total number of elders in each settlement, the family name, the number of houses associated with each, and the year the settlement was built were recorded from discussions with occupants.

A second survey of all known abandoned settlements (murua) was conducted in 2001. Earlier studies in other areas of the Amboseli Ecosystem and my preliminary work on abandoned settlements suggest that Maasai have an excellent understanding of local environmental history and a particularly good knowledge of past patterns of settlement (Western and Dunne 1979, Muchiru 1992). To take advantage of this expert local knowledge local informants assisted in locating and describing all abandoned settlements in a subset of the Eselenkei area, hereafter referred to as the Eselenkei Murua Survey area (Fig. 2). The survey was conducted on foot and with bicycles to achieve complete coverage of the area (79 km^2). Survey intensity was guided by local knowledge, and key informants from the area were essential in identifying, locating and providing historical information about the settlements, their occupants and how long they stayed. I was especially interested in the perspective of older members of the community and information was cross-checked with them and other community members when possible.

Data Processing and Analysis

To assess changes in water distribution over the past 50 years I created two separate maps of permanent water - one for the early 1950s and one for 2000. The map of permanent water availability in 2000 was created using field data and interviews. All known sources of permanent water in the study area, including piped water, wells, boreholes, and swamps (the extent of the swamps was mapped using an ultra-light aircraft (Worden 2007b)), were mapped with a Garmin 12 GPS. The historical distribution of water presented here is based on the literature and interviews of local Maasai and is by necessity an approximation of the actual distribution. The water points in the north along the Selenkei river are hand-dug wells that are abandoned and rebuilt over time, and I used the current distribution of these wells to indicate the general position and extent of historical water availability in this seasonal riverbed.

Similarly, I have used the current distribution of surface water and hand dug wells in the south as an indicator of the approximate distribution of water in the early 1950s. This is a conservative estimate of surface water availability in the southern end of the study area (i.e. there was likely to be less water available than shown here) as the extent of the swamps in Amboseli National Park has increased dramatically since the 1950s (Western and van Praet 1973, Lovett-Smith 1997, Western 2006). The distribution of water on this landscape has varied between 1950 and 2000 as boreholes were established and abandoned. I did not attempted to document all of these changes through time, but rather used these two periods to illustrate the dramatic shift in water availability in the ecosystem. I reconstructed current patterns of seasonal settlement and grazing using the current and historical settlement surveys (above), and informant interviews. Historical patterns of seasonal movement were reconstructed based upon movements described in the literature (Western 1973, Western and Dunne 1979).

Settlement and movement patterns in the study area integrate traditional scales of resource access and control (Grandin 1985) within contemporary land tenure boundaries.

For example, at the broadest scale, cultural boundaries between Maasai sections (*oloshon*) apply except under severe drought conditions (Galaty 1994b, Worden 2007a, BurnSilver and Worden in press). In Eselekei and Olgului/Lolarashi , resources such as grazing areas (*donko nkishu*), water points, and grazing reserves (*olopololi*), appeared to be managed collectively across group ranch boundaries. In Osilalei, in contrast, these resources were increasingly managed at the former group ranch or individual plot level. To capture this reality I divided the study area into four zones representing landscape level units of resource access and management. I created four zones with Thiessen polygons centered on the three settlement clusters (Eselenkei, Lenkesim, and Meshenani) and the group ranch boundary for Osilalei (Fig. 2). Thiessen polygons were created to equalize the distances between settlements in the different areas, and were suggestive of the relative grazing area available per settlement. The exact boundaries of these zones are not officially recognized or delineated, but they generally represent de facto resource management units due to the existence of close social and familial ties across group ranch boundaries and their proximity to shared resources.

To compare the degree of clustering and dispersion of settlement distributions across the study areas I conducted a nearest neighbor analysis in ArcView 3.2a using the Spatial Statistics v 1.0 extension. To illustrate the stark differences in the degree of contagion in settlement patterns across the land tenure gradient I created four polygons of equal area (100 km^2) and overlaid these on each study zone to identify a representative subset of settlements. Only permanent settlements were selected with the polygon overlay and used for the analysis. Because nearest neighbor analyses are sensitive to area, I used these polygons and the representative settlements for statistical analysis. The selected areas were enlarged and rotated for visual comparison.

I calculated the relative distance to settlement across the study area. The point density of permanent settlement, in which each 50 m x 50 m grid cell represents the total number of settlements within a circle of 5km radius divided by the area of that circle, was calculated in ArcGIS 9.1 (ESRI, Redlands, California).

To evaluate the position of settlements relative to water in each study zone, I calculated the number of settlements in bands around water sources 1 km wide. Mean distance to water was calculated by study area for both permanent and seasonal settlements. I used historical settlement patterns for the area from Western (1973) and the abandoned settlement sites recorded in the Eselenkei Murua Survey for analyzing regional and landscape level changes in settlement pattern over time. Here I present the data as they were collect from informants, but it is worth noting that human recall, especially over 50 years, has its limits and that while this is the best data available, some of the start and end times may have varied. I do not think that there was an inherent bias, however, and I believe that the overall patterns are correct. The total number of settlements in the survey area was calculated as the total number of occupied permanent settlements in each year. Settlement occupancy was more dynamic in the past (unpublished data), so I only included permanent settlements (*emparnat*) as indicated by key informants. Decadal maps were constructed to depict all the permanent settlements that were occupied during each time period. The decadal interval captures the extent of the human "footprint" associated with settlements as it depicts the cumulative distribution of settlements, including those that were created and abandoned during each ten year period. All maps were created with ESRI's ArcGIS 9.1 and Kruskal-Wallis tests for differences between study zones were conducted in the R software package (R Development Core Team 2006).

RESULTS

Regional Scale

An analysis of current and historical water distributions in the study area (Fig. 3) indicates that the reduction of water as a limiting resource has had important implications for pastoral settlement and land-use at the regional scale. Water development has enabled Maasai to expand permanent settlement into formerly wet season grazing areas (Fig. 4). In turn, the presence of permanent settlement in the wet season grazing area has forced local Maasai to abandoned historically variable long distance wet season dispersal patterns (Fig. 4a) in favor of a series of prescribed finer scale dry season movements (Fig. 4b).

Interviews with informants and observations of abandoned settlement distributions corroborated previous research (Western 1973) indicating that dry season settlements in the study area were historically limited to areas within relatively easy access of permanent surface water – the swamps in the south and the wells in the north (e.g. the shaded areas in Figure 4a that represent areas within 8km of water). With the rains livestock from each of these settlement concentration areas would disperse into the flood plains of the Ol Kejuado river in search of fresh green forage (Fig. 4a) (Western 1973). The development of boreholes in the wet season dispersal area during the 1950s, meant water no longer constrained settlement distributions and Maasai began locating permanent settlements in the Lenkesim area (Fig. 4b). The year round presence of settlement in these previously inaccessible areas lead to forage availability constraints as what were once wet season grazing areas were no longer rested. At the same time, constraints on access to the Amboseli swamps, culminating in the formation of the park in 1974, effectively removed an essential dry season forage reserve.

Interview data indicated that local patterns of settlement and movement shifted from a wet season (Fig. 4a) to a dry season dispersal system (Fig. 4b) to preserve dwindling forage reserves in the face of reduced access to key resources and increasing rangeland congestion. Field observations and interviews indicated that in both Olgulului/Lolorashi and Eselenkei group ranches these new movements consisted of a series of ordered stages with clearly defined grazing areas and zones for settlement (Worden 2007a, BurnSilver and Worden in press). During the rains all herd owners are required to move their livestock back to the permanent settlement area (Stage 1). As the dry season progresses elders from each neighborhood decide on when the next stage of settlement (*enkaron*) will be opened (Stage 2). When resources are depleted in the local grazing areas associated with Stage 2 the next *enkaron* area is opened. Subsequent stages are opened up for settlement and grazing as the dry season continues until the rains come again and all herds move back to stage one to allow the dry season grazing areas to regenerate (Fig. 4b). Under extreme circumstances all local resources are exhausted and able herders negotiate access to other resources in neighboring areas (Worden 2007a). In the subdivided area of Osilalei, these movements are even further constrained. Discussions with local Maasai and abandoned settlement patterns (data not presented) indicated that settlement and grazing patterns were similar to those found in Eselenkei and Ogulului/Lolorashi, but the recent subdivision of the group ranch into individual plots has increasingly resulted in the limitation of settlement and daily movements to individual land holdings (Worden 2007a, BurnSilver and Worden in press).

Landscape Scale

Within the broader context of regional scale shifts in settlement associated with broad scale constraints on movement and water development, patterns of settlement at the landscape scale were also in a state of transition. Changes in land tenure and sedentarization have created divergent patterns of settlement and associated human impacts. These changes have altered reserve grazing areas, local settlement densities, and the interaction of settlements and water. Similarly, the longitudinal study of settlement patterns over six decades revealed how occupancy patterns have changed.

The processes of subdivision and sedentarization led to significant changes in the spatial distribution of settlements (Fig. 5). The changes were especially clear in representative areas of equal size from each study area (10 x 10 km boxes in Fig. 5). The subdivided area of Osilalei had a widely dispersed pattern of settlement (Fig. 5). In contrast, the communally managed areas of Eselenkei, Lenkesim, and Meshenani, had much more contagious distributions of settlement. This visual interpretation was supported by nearest neighbor analyses (Table 2) that indicated that the subdivided distribution was not significantly different from complete spatial randomness ($Z = -0.887$, $p < 0.05$). The dispersed settlement distribution in the subdivided area is compounded by increases in the numbers of settlements (Table 2 and Table 3) associated with the effects of fragmentation at the settlement level.

Osilalei's dispersed pattern of settlement has lead to a nearly uniform distribution of human disturbance with very few areas on the landscape that are far from settlements (Fig. 6a). The communally managed group ranches, in contrast, have maintained areas that are far from settlement, which serve as important dry season grazing refuges (Worden 2007a). The combined effects of settlement pattern (Fig. 6a) and the density of settlements (Fig. 6b) have resulted in divergent disturbance patterns at the landscape scale. Similarly, changes in land tenure and sedentarization have also altered the distribution of settlements relative to permanent water (Fig. 6c). The number of settlements at different distances from water varies considerably among zones (Fig. 7). In the subdivided area settlement numbers are relatively high as far as eight kilometers from water. The majority of settlements in the communally managed areas are within three kilometers of water, while settlements in the subdivided area are relatively evenly dispersed up to six kilometers from water. An important consequence of subdivision then, is that human impacts are more uniformly distributed across the landscape. Thus, subdivision acts to homogenize forage gradients associated with distance from settlement and distance from water.

A detailed consideration of settlement in the Eselenkei area over the past 50 years indicates that sedentarization has had important effects on the spatial and temporal patterns of settlement. The spatial distribution of all previously occupied settlements in the Eselenkei study area reveals a marked difference between the current distribution of settlements and settlement patterns prior to the 1980s. Decadal intervals of settlement distributions (Fig. 8) indicate that the current concentrated pattern of settlement emerged in the 1970s, when two broad zones of settlement began to take shape. This was followed by a fairly rapid transition in the 1980s[6]. By the 1980s the settlements in the southwest zone were disappearing while settlements appeared to be coalescing in the northeast. Northeastern zone settlements became increasingly aggregated through the 1990s and into 2000 until there were four clearly defined neighborhoods, as they exist today.

Occupancy patterns of settlements (ratio of abandoned to total occupied) are also useful indicators of sedentarization. There was a high degree of temporal variability in the numbers of permanent settlements in the Eselenkei Murua study area (Fig. 9). Pre-1980s settlement appears to be dominated by two periods of relatively high numbers of settlement (1950 - 1957 and 1964 – 1976) interspersed with two periods of low settlement centered around 1962 and 1977 corresponding to periods of below average rainfall and widespread droughts in the area. This dynamic pattern of settlement begins to erode in the early 1980s as the number of abandoned settlement sites gradually declined and the number of currently occupied permanent settlements increased for a few years before leveling off around 20.

Settlement Scale

One of the most important impacts of changes in land tenure and sedentarization at the settlement level is the reduction in the spatial extent of pastoral networks, thereby comnpressing the social scale of pastoralism. There were significant differences in the mean number of elders (heads of household), houses per settlement, and mean number of

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[6] Note that these maps record the position of all the settlements that were occupied during that decade so while they accurately portray the spatial distribution of settlements they are not an accurate depiction of the change in the total number of settlements through time (see Figure 9). For example, the maximum number of settlements occupied in this area during any given year was 35 in 1952. Similarly, the mean annual number of settlements for the 1950s was 24.1 while the map for the 1950s (1950-1959) shows a total number of 46 settlements suggesting that some of these were abandoned and others created throughout this period.

houses per elder (Table 3) across the study zones. In particular, the subdivided area of Osilalei had significantly fewer elders per settlement than both Eselenkei and Lenkesim ($p < 0.05$). Similarly, Osilalei also had fewer houses per settlement, and houses per elder (the latter difference is significant for Eselenkei only). In contrast, there was no significant difference between Osilalei and Meshenani for any of these indicators of changing pastoral land use and tenure patterns.

Another potentially useful indicator of the degree of sedentarization is settlement age. When combined with the seasonal patterns of occupancy, age can be an important integrator of pastoral impacts at the local level. Settlement age, or the length of time that a settlement has been occupied, is similar across all the study zones with only Osilalei and Lenkesim areas showing significant differences. The mean ages of settlements for each of the study zones (Table 3), and the overall mean of age of 6.4 years, contrasts sharply with the mean age of 3.7 years observed by Western and Dunne (1979). Settlement structure, or the types of the houses used in the settlement, is also a good indicator of relative permanence (Western and Nightingale, 2003). Although Osilalei had twice or more as many grass and tin roofed houses as the other communally managed areas, generally there was little evidence of investment in permanent housing. Indeed the high proportion of dung houses in all areas (Osilalei = 0.965, Eselenkei = 0.992, Lenkesim = 0.961, Meshanani = 0.947) suggests that this region is still in transition. The spatial distributions of settlement structural characteristics are summarized in Figure 10.

DISCUSSION

Regional Scale

Changes in the patterns of sedentarization and land tenure have profoundly altered settlement and land-use in the Greater Amboseli Ecosystem. At the regional scale, the excision of key resource areas, and the development of water resources for livestock in previously inaccessible areas have fundamentally modified the distribution, number and permanency of settlements. Settlement and land-use patterns have changed radically as the pastoral system has moved from being limited by water to one limited by forage. As water development has made more land available for year round grazing, livestock production is less constrained by access to forage resources due to the limited distribution of water and more constrained by the amount of forage available during periods of stress as grazing reserves far from water have disappeared.

The initial effect of this shift in limiting resources has been the transformation of the grazing system from one based upon wet season dispersal and dry season concentration (Fig. 4a) to a system of finer-scale dry season dispersals (Fig. 4b). Until recently, pastoralists and their livestock congregated at permanent water during the dry season and dispersed to wet season grazing areas with the rains in an effort to maximize access to high quality forage. This pattern has been increasingly replaced by pastoralists managing livestock grazing patterns to stabilize access to forage biomass through the year. The shift of emphasis from maximizing forage quality in the wet season, to maximizing forage quantity year around constitutes a significant change in the pastoral grazing system in response to sedentarization and the associated constraints on resource accessibility and elevated livestock densities across the landscape.

Landscape Scale

Landscape scale settlement patterns have important implications for the accessibility and availability of resources (Western and Dunne 1979). One of the key factors determining patterns of mobility in pastoral societies is the spatial relationship of settlements to water and forage resources (Coppolillo 2001, Worden 2007a). Subdivision and sedentarization have had clear effects on the distributions of settlement at the landscape scale. Interviews with local informants suggest that the widely dispersed pattern of settlement in Osilalei is a direct response to the privatization of land tenure. There was an initial lag following subdivision where most people maintained their settlements in a traditional configuration, but during the extended and substantial rains in the 1997 El Nino, many people decided to move to their individual parcels of land (BurnSilver and Worden in press). With subdivision, controls on settlement distribution collapsed and human impacts dispersed across the landscape. This dispersed pattern of settlement (Fig. 5, and Table 2) has affected grazing management and mobility (Worden 2007a), social relations and settlement structure (see below), and the availability and management of grazing reserves.

In contrast, in the non-subdivided areas, a controlled settlement and grazing system has developed in response to broader scale constraints on movement and access. This has resulted in a highly clustered distribution of settlements. Consensus among elders and local management units has lead to the identification of strict settlement areas. In response to the broad scale shift from a wet season to a dry season dispersal system, certain areas have been reserved for clusters of permanent (*emparnat*) settlements, which are supplemented by more widely dispersed temporary settlements (*enkaron*) in predetermined areas. This system has the potential to reduce conflict and help to equalize access to resources for wealthy and poor pastoralists alike. Most importantly, this system concentrates human impact in certain areas to reduce forage losses due to trampling and human disturbance. Indeed, the *emparnat – enkaron* system, which was established in response to the loss of reserve grazing areas far from water and permanent settlement, has been quite successful in maintaining access to forage resources through flexibility and mobility.

These patterns of dispersion and aggregation have important implications for the spatial patterns and densities of settlement across the study zones (Fig. 6a and 6b). The relative proportion of the landscape at different distances from settlement (Fig. 6a) indicates the distribution of human impacts and the potential for maintaining grazing reserves. This is also clear in the point density of settlement across the study area (Fig. 6b) which shows high levels of cumulative human impact associated with concentrated settlement in Osilalei, and intermediate levels of disturbance concentrated around settlement areas in the communally managed areas. One potential implication of these patterns is a divergence of landscape level disturbance patterns. The relatively even distributions of settlement in Osilalei will inevitably lead to a homogenizing effect of human disturbance, ultimately leading to a reduction in spatial heterogeneity and complexity. Alternatively, in the communally managed areas the pattern of concentrated settlements within a larger matrix of less utilized areas results in a reduction in finer scale heterogeneity through the imposition of a broader scale pattern of polarization.

In both scenarios, the collapse of the former system of opportunistic movement, the dynamic disturbance regime associated with seasonal grazing impacts, the periodic creation and abandonment of settlements and the resulting redistributions of grazing impacts - reduce the complexity, and the sustainability of these rangeland systems (Coughenour 1991). Sustainability is potentially reduced for two reasons. One is that grazing impacts are imposed on a more sustained basis with fewer periods of rangeland rest and recover. The other is that there are fewer opportunities for opportunistic movement in response to drought.

Similarly, subdivision and sedentarization have encouraged a dramatic shift in settlement distributions relative to water compared to those observed by Western and Dunne in 1979 (Fig. 6c and Fig. 7). The divergent patterns observed in the subdivided and communally managed areas have potentially important implications for the creation and maintenance of forage availability gradients, grazing reserves, and heterogeneity. As with the regional scale, dispersed settlement homogenizes forage availability gradients associated with water points at the landscape scale.

Temporal changes in settlement patterns illustrate the cascading effects of land tenure change and sedentarization in the rangelands of the Greater Amboseli Ecosystem. The shift to the dry season dispersal system following the installation of boreholes along the Ol Kejuado river bed during the 1950s (Fig. 3) appears to have caused a gradual retraction of settlements into designated settlement zones over three decades, culminating with the creation of the *emparnat* - *enkaron* system following group ranch adjudication in 1982 (Fig. 8). The balanced use of *emparnat* settlements over a large spatial scale that characterized the original grazing systems of the Maasai in this area (Western 1973, Western and Dunne 1979) has been gradually replaced with fixed areas for permanent wet season settlement (*emparnat*) and temporary dry season settlement (*enkaron*).

The periodicity and age structure of settlement indicates that the temporal dynamics of settlement in the study area have changed significantly over time. The number of settlements in the Eselenkei *murua* study area appears to have fluctuated greatly prior to 1982 (Fig. 9). Whether this was due to social dynamics, rainfall and forage abundance, or both is not clear, but the fluctuations suggest a high degree of mobility. Periods of low settlement density appear to correspond generally to times of below average rainfall and recorded drought (Fig. 9). Whether pastoralists were responding to resource scarcity by leaving the system or collapsing back on to a few core settlements, the dynamic nature of settlement occupancy over this period suggests a high degree of flexibility.

With the formation of group ranches in the early 1980s, however, there was a substantial shift in the temporal patterns of settlement. The periodic fluctuations of settlement numbers have dampened and disappeared. More importantly, settlements are no longer being abandoned. Although the mean age of 9.3 years for settlements in the Eselenkei area suggests some degree of sedentarization, when considered in light of the trend suggested by changes in the periodicity of settlement (Fig. 9), it is obvious that the region is in a transitional phase, with settlement ages gradually increasing. The nature of pastoral settlements requires periodic movements, to clean-out the settled area, to reduce build up of urine and risk of disease, and to allow for the recovery of vegetation and forage resources (Western and Dunne 1979). However, these results suggest that fragmentation and the sedentarization of Maasai in the Greater Amboseli Ecosystem are delaying the frequency of these settlement moves to well beyond the historical periods of seven to eight years (Western and Dunne 1979) with numerous implications for both rangeland and livestock condition .

Settlement Scale

One of the most important effects of sedentarization and land privatization at the settlement level is social fragmentation. The reduced number of elders and number of houses, in both communal and subdivided areas suggest that while land-privatization may encourage individuality and reduce cooperation, sedentarization alone can also quickly and radically alter social networks. Within the communally managed zones, the relatively low number of houses and houses per elder in the Meshenani area is the result of a household splitting strategy that enables households to maintain a presence in the subdivided irrigated agricultural areas of the former Namelok swamp adjacent to Amboseli National Park (BurnSilver in prep). Although interview data suggested that some elders in Eselenkei and Lenkesim have split their households to take advantage of opportunities for rainfed or irrigated agriculture in the Kilimanjaro foothills and swamp systems to the south, this was less common in these areas relative to Meshenani (unpublished data). In Osilalei, where very little spatial splitting of households was found, the low number of houses per elder was indicative of a trend towards smaller individual family units that is occurring across the ecosystem. This is also supported by declines in the mean number of houses per settlement and the mean number of houses per elder.

The structure and age of settlements are also potentially useful indicators of the degree of sedentarization in a pastoral system. As pastoral mobility declines, settlements are used for longer periods and more continuously. Settlements are being used for nearly twice as long as they were in the 1970s and before (Western, 1973). Although there were longer occupancy periods in Lenkesim than in Meshenani, there was a decline in settlement age in both Eselenkei and Osilalei, contrary to predictions. This pattern is likely the result of relatively recent land-use changes in the Eselenkei and Osilalei areas. The heavy rains of El Nino (1997-1998) inspired many people in Eselenkei to move their settlements to take advantage of rain fed agriculture, while in Osilalei we see the creation of a vast number of new settlements as individuals move to their own parcels (Fig. 10d). Each of these processes would lower the overall mean age of settlements and mask the underlying trend towards sedentarization that both moves represent. Indeed, the highly variable nature of settlement ages in this landscape suggest that these communities are in a transitional period with different areas and different individuals at different points along the sedentarization continuum.

One interesting comparison that stands out is the relative proportion of different house types in each of the study zones. House type, or roofing material, reflects the degree of sedentarization (Western and Nightingale 2003) with traditional mud houses indicative of periodic movement, and grass and tin roofs suggesting increased investment and decreased mobility. Initially, I predicted that the subdivided area would have a higher proportion of improved houses but there were no clear differences between zones (Osilalei = 0.03, Eselenkei = 0.02, Lenkesim = 0.04, Meshenani = 0.05). The high number of tin houses in Eselenkei and the use of grass in some areas of Meshenani suggests that sedentarization and subdivision have similar effects on investment in housing. The self-reinforcing process of sedentarization and increasing investment in semi-permanent housing has important implications for household economies, production systems, and movement (BurnSilver and Worden in press).

The spatial distribution of patterns of settlement structure are illustrative of how the process of sedentarization moves across the landscape. For example, in Fig. 10a and 10c the spread of small settlements with one to four houses and one to two elders in the subdivided area of Osilalei is indicative of uniform drivers of change such as subdivision. In contrast, the localized nature of investment in relatively permanent grass and tin roofed houses is apparent in Meshenani, Lenkesim, and Eselenkei, suggesting the importance of infrastructure and individual preference and inclination in the sedentarization process. As with settlement size, the distribution of grass and tin houses in Osilalei, in contrast to other areas, suggests that subdivision has encouraged investment in semi-permanent structures in areas far from both water and infrastructure (Fig. 10b).

CONCLUSIONS

An appreciation of the patterns and processes of changing pastoral settlement is fundamental to our understanding of the evolving nature of the interaction between humans and the environment in the world's arid and semi-arid lands. The spatial and temporal dynamics of settlement have important implications for the management and conservation of grazing lands through their impacts on woody vegetation cover and plant species composition (Jensen 1983 unpublished, Reid and Ellis 1995, Young et al. 1995, Lamprey and Reid 2004, Muchiru et al. in press-a), nutrient flows (Blackmore et al.

1990, Augustine 2003), wildlife utilization (Young et al. 1995, Muchiru et al. in press-b), and pastoral mobility, resource access and drought vulnerability (Worden 2007a).

In the Greater Amboseli Ecosystem fragmentation has played an important role in shaping the contemporary structure of pastoral interactions with the environment through its impacts on the scale of ecological and social interactions. The interaction of fragmentation and settlement patterns at multiple scales has had cascading effects on the spatial and temporal dynamics of Maasai land-use. Through the opportunities and constraints associated with a central place foraging system, these new settlement patterns have important implications for the structure and function of savannas, the creation and maintenance of grazing reserves, and the vulnerability of pastoralists and their livestock to drought (Worden 2007a).

At the regional scale national and international constraints on movement and expansion, the excision of key resource areas, land tenure change, and the development of water resources for livestock in previously inaccessible areas initiated a process of rangeland fragmentation and an associated decline in inter and intra-cultural connectivity. Subsequent increases in human and livestock population densities and shifts in broad scale settlement patterns have resulted in emergence of forage availability, as opposed to forage access as a function of water distribution, as the proximate constraint on livestock production. This in turn promoted a shift from the traditional wet season to a dry season dispersal system, and a corresponding emphasis on preserving dry forage biomass as opposed to maximizing access to ephemeral high quality forage resources.

Within this larger regional context, fragmentation at the landscape level has been exacerbated by further reduction in the scale of land tenure (group ranch adjudication and subdivision) and sedentarization. Changes in the disturbance pattern associated with the creation and abandonment of settlements has important implications for the mosaic of grassland patches in savanna ecosystems. In subdivided areas settlements were widely dispersed across the landscape resulting in a relatively homogeneous distribution of human impacts. In contrast, the communally managed areas took an alternative trajectory in which sedentarization in the context of increasing forage constraints lead to a highly clustered pattern of settlement with distinct grazing stages and seasonal movements. Clustered distributions have concentrated human disturbance at intermediate distances from water thereby conserving grazing reserves and balancing access to forage and water. Although this may enhance control over the spatial and temporal distribution of grazing, it also results in a collapse of the dynamic shifting mosaic of abandoned settlements and promotes a polarization of the landscape into over and under utilized areas. The loss of flexibility and dynamism in both scenarios may have important implications for the stability of plant herbivore systems as heterogeneity declines and the shifting mosaic of patches in different states of recovery from settlement and grazing collapses (Coughenour 1991). A longitudinal analysis of settlement patterns in the Eselenkei area indicated that this shift in the spatial patterning of settlements was accompanied by a parallel decline in settlement turnover rates.

At the local level, fragmentation has altered the physical and social structure of settlements. Subdivision and the associated individualization of production has resulted in more numerous smaller settlements with reduced internal social networks. Although settlement ages were found to be generally younger, increasing investments in permanent housing suggests that this is primarily a result of recent subdivision and allocation and that over time settlement ages will increase significantly. In the communally managed areas we see that even though settlements are being occupied for increasingly longer periods, they continue to act as hubs for linking people and landscapes. These larger multi-family settlements prevent the complete collapse of traditional multi-scale social networks that once linked cultures, sections, landscapes, settlements, and households.

Fragmentation in the Greater Amboseli Ecosystem has impacted Maasai pastoralism at multiple scales. Unfortunately, policies that are often designed to enhance and stabilize pastoral production in variable environments have created a system that is more constrained and less flexible. Ironically, the underlying unpredictability of these systems, the very characteristic that managers seek to control and to limit, may have enhanced their stabilities by increasing spatial heterogeneity, flexible and opportunistic movement, and a diversity of functions on the landscape (Coughenour 1991). As managers seek to reduce unpredictability and variation through restrictions on mobility, disease prevention, and water provision, pastoralists have had to seek new ways to compensate for the loss of dynamism and movement. This has been achieved through two divergent strategies, the one involving forage resources conservation and a focus on quantity rather than quality, and the other individualization and privatization. Both strategies have potentially far reaching implications for pastoral vulnerability and ecosystem stability. Ultimately, policy and development interventions in pastoral systems need to embrace heterogeneity and work within the context of fragmentation to enhance the availability of forage in space and time.

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TABLES

Table 1. Table of general site characteristics. The area of private land tenure is indicated in grey

	Osilalei	**Eselenkei**	**Lenkesim**	**Meshanani**	**Total**
Total Area (km^2)	175	247	520	452	1394
Total number of bomas	137	57	50	54	298
Total Num Houses	546	480	475	396	1897
Total Elders	276	189	183	184	832
Boma Density (#/km)	0.781	0.231	0.096	0.119	0.214
House Density (#/km)	3.113	1.945	0.914	0.876	1.361
Elder Density (#/km)	1.574	0.766	0.352	0.407	0.597

Table 2. Nearest Neighbor Analysis of permanent settlements in 10 x10 km blocks (Fig. 5). The area of private land tenure is indicated in grey. Accept or Reject refers to the null hypothesis of Complete Spatial Randomness (CSR).

	Osilalei	**Eselenkei**	**Lenkesim**	**Meshenani**
Area (km^2)	100	100	100	100
No. of Settlements	86	27	26	16
NN R	0.95	0.366	0.377	0.44
NN Z	-0.887	-6.307	-6.082	-4.282
Null - CSR	Accept	Reject	Reject	Reject
Mean of NN dist (m)	512.22	351.731	369.203	550.579
SE of NN dist	27.219	52.59	62.186	147.484

Table 3. Settlement Structure Characteristics by Study Area. The grey column indicates the area of private land tenure. Means are displayed with standard deviations in parentheses. Means with the same superscript are not significantly different at $p< 0.05$ (Kruskal-Wallis multiple comparison test, R). Different sample sizes due to missing data are indicated.

	Osilalei	**Eselenkei**	**Lenkesim**	**Meshanani**
Elders per boma (mean (SD)) *	2.01 (1.1)^{a}	3.32 (1.92)^{b}	3.71 (2.12)^{c}	3.41 (1.86)^{abc}
Houses per boma (mean (SD)) *	3.99 (1.84)^{a}	8.42 (5.08)^{b}	9.69 (6.54)^{c}	7.33 (4)^{abc}
Houses per elder (mean (SD)) **	2.27 (1.05)^{a}	2.71 (1.05)^{b}	2.69 (1.66)^{ab}	2.37 (1.08)^{ab}
Boma Age - years (mean (SD)) ***	6.04 (5.06)^{a}	9.3 (7.91)^{ab}	10.98 (10.47)^{b}	6.63 (5.18)^{ab}
Number of Dung houses	527	476	421	375
Number of Grass houses	1		11	19
Number of Tin houses	18	9	4	2
Number of Skin houses	0	0	2	0
Number of bomas with houses of Dung	136	57	45	53
Number of bomas with houses of Grass	1	0	5	5
Number of bomas with houses of Tin	13	6	3	1
Number of bomas with houses of Grass or Tin	0	0	0	1
Total Bomas with good house composition data	137	57	45	54
Total houses with good composition data	546	480	438	396

Some settlements were missing data in different categories resulting in the following sample sizes

* Sample sizes Osilalei = 137, Eselenkei = 57, Lenkesim = 49, Meshenani = 54

** Sample sizes Osilalei = 136, Eselenkei = 57, Lenkesim = 49, Meshenani = 54

*** Sample sizes Osilalei = 135, Eselenkei = 57, Lenkesim = 46, Meshenani = 54

FIGURES

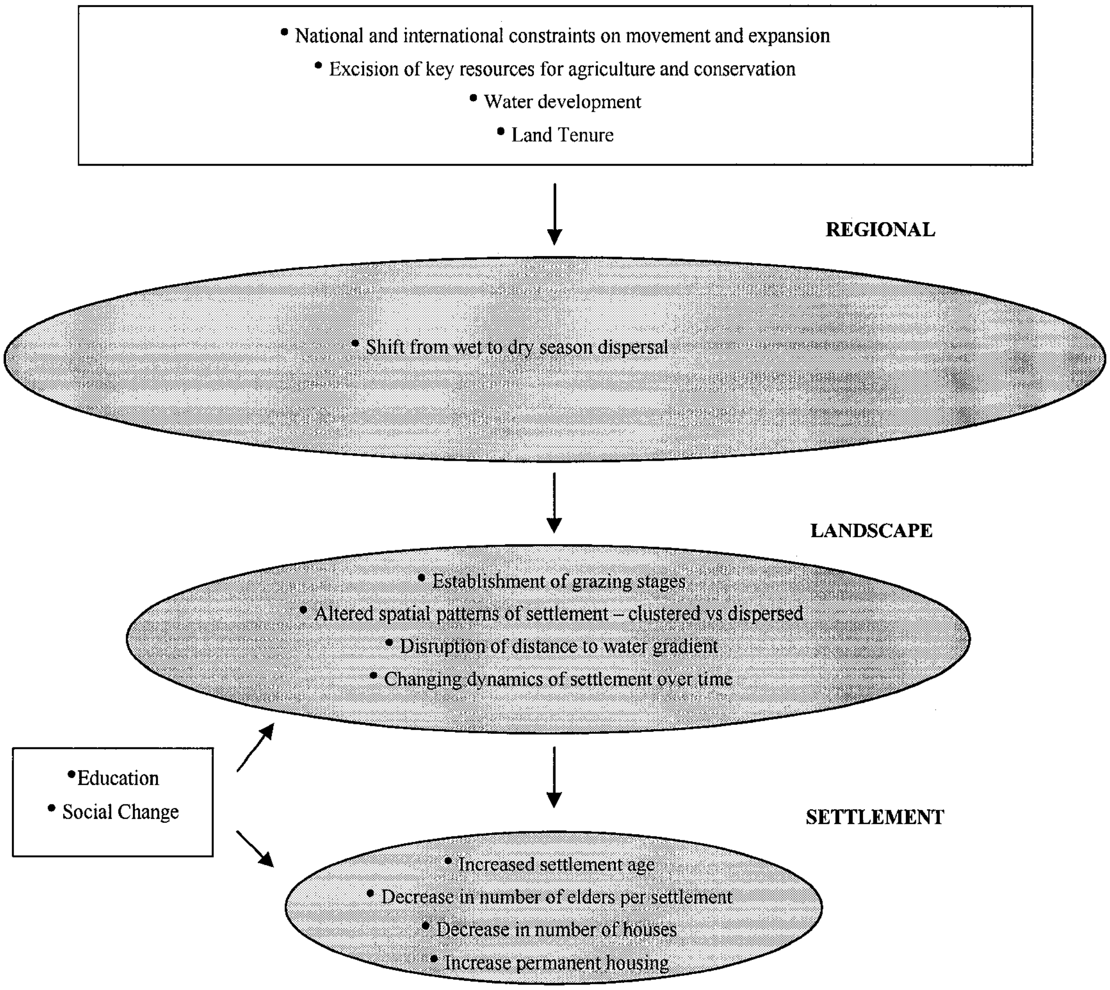

Figure 1. Changing patterns of settlement at multiple scales in the Greater Amboseli Ecosystem. Boxes indicate primary drivers and grey circles indicate patterns of change.

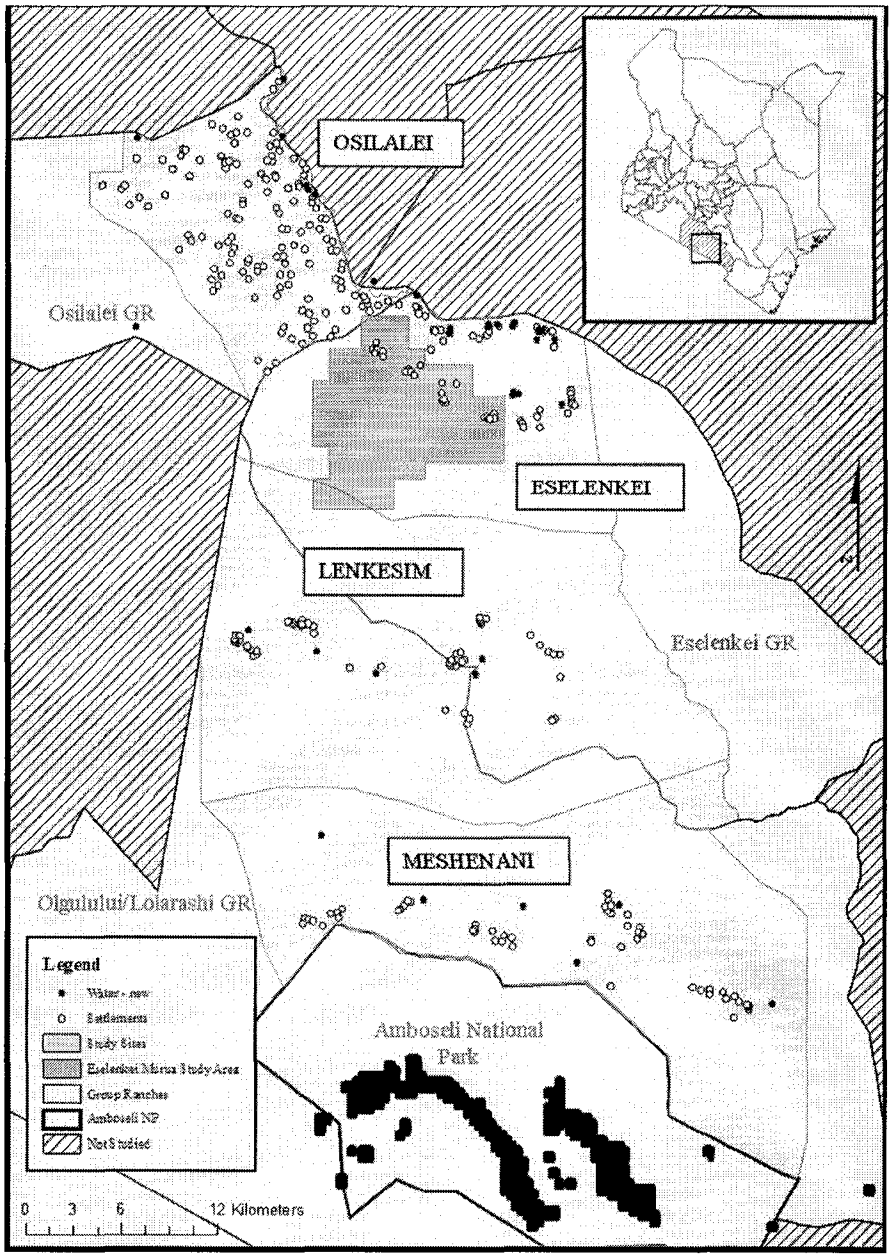

Figure 2. Map of study area showing the four study zones. Grey boundary lines delineate group ranches (light) and Amboseli National Park (dark). Shaded polygons define study zones – Osilalei, Eselenkei, Lenkesim, and Meshenani; and open circles indicate permanent settlements. The Eselenkei Murua Study Area is indicated as a grey polygon in the center of the map. Group ranches not considered in this study have grey cross hatching.

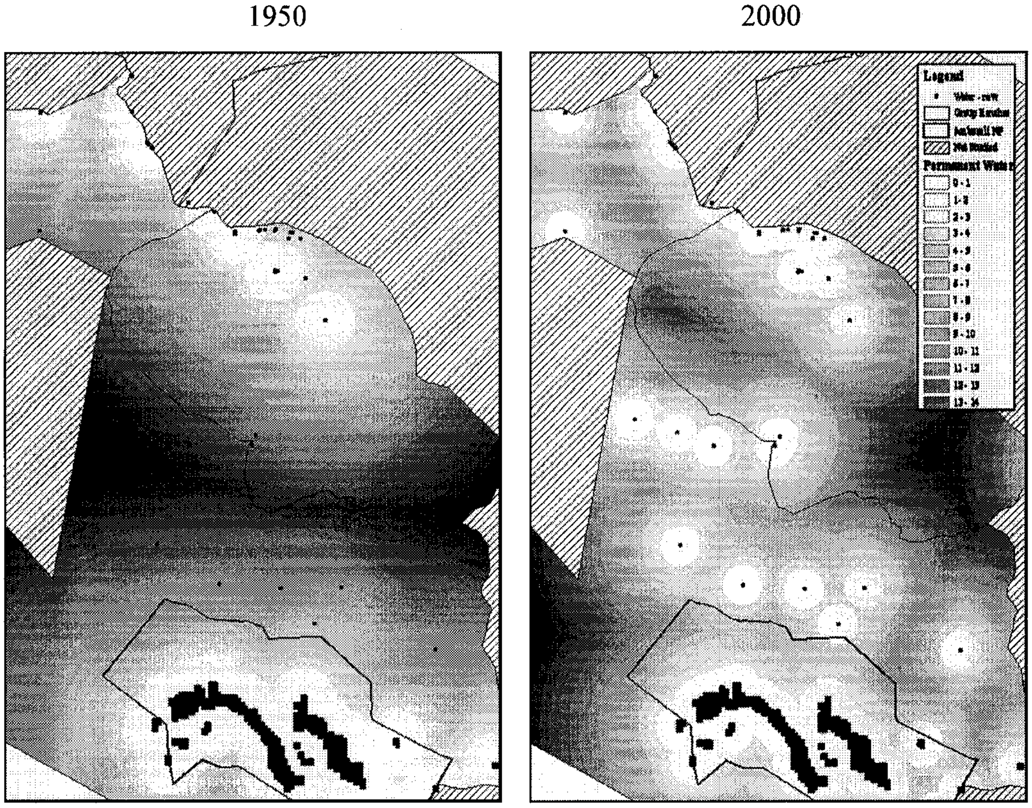

Figure 3. The approximate distribution of permanent water in 1950 and 2000. Permanent water includes all sources available to livestock in the dry season – e.g., swamps, springs, hand dug wells, and boreholes.

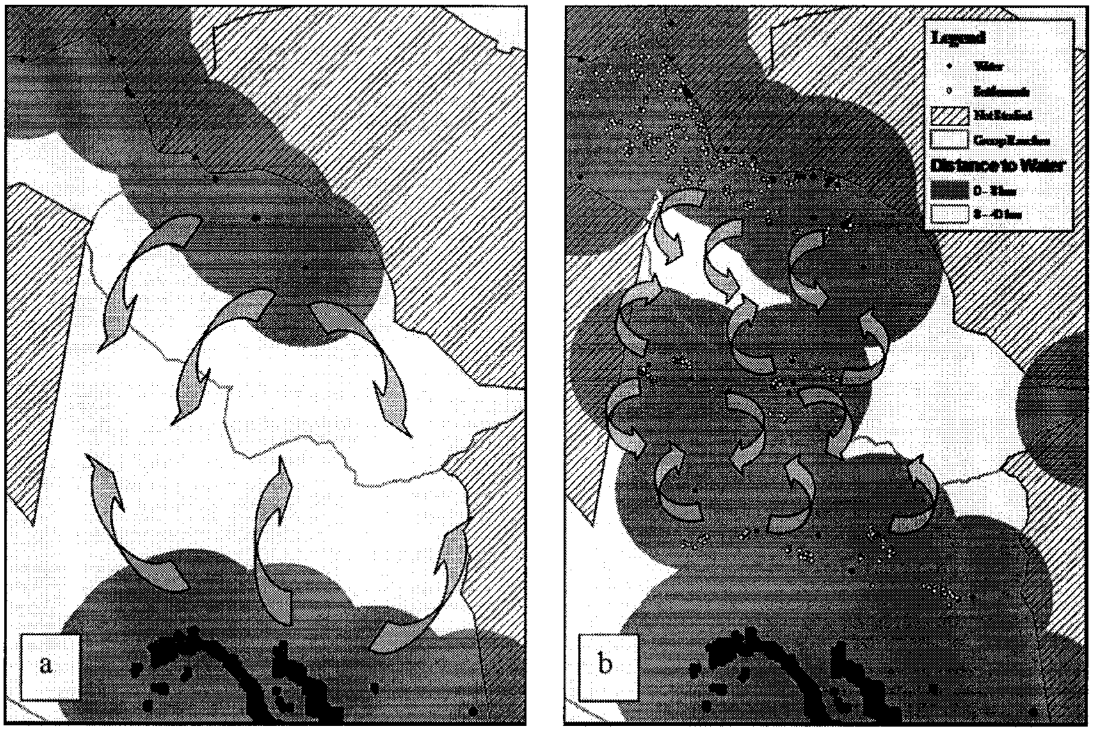

Figure 4. Historical (wet season) versus current (dry season) dispersal patterns. Arrows indicate general dispersal areas in the past (a) and currently (b). Arrows indicate direction and magnitude of dispersal. Precise locations of settlements in the past are not known so they are not included in (a).

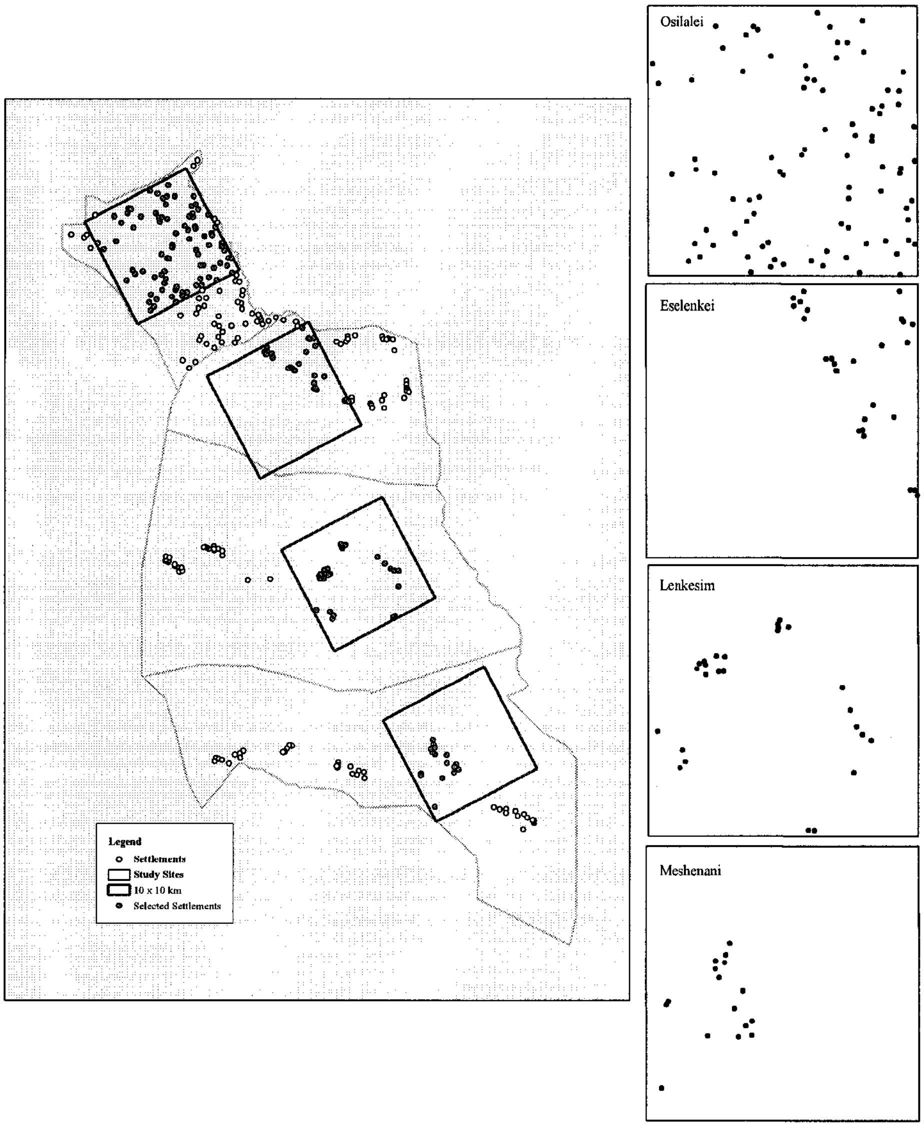

Figure 5. Patterns of aggregation and dispersion. The left hand map shows the placement of 10 km by 10km blocks that were selected to illustrate the differences in the spatial distribution of settlements across the study area. These boxes are enlarged and arranged vertically at right to enhance comparisons across sites. Both selected (grey circles) and non-selected (open circles) permanent settlements are shown.

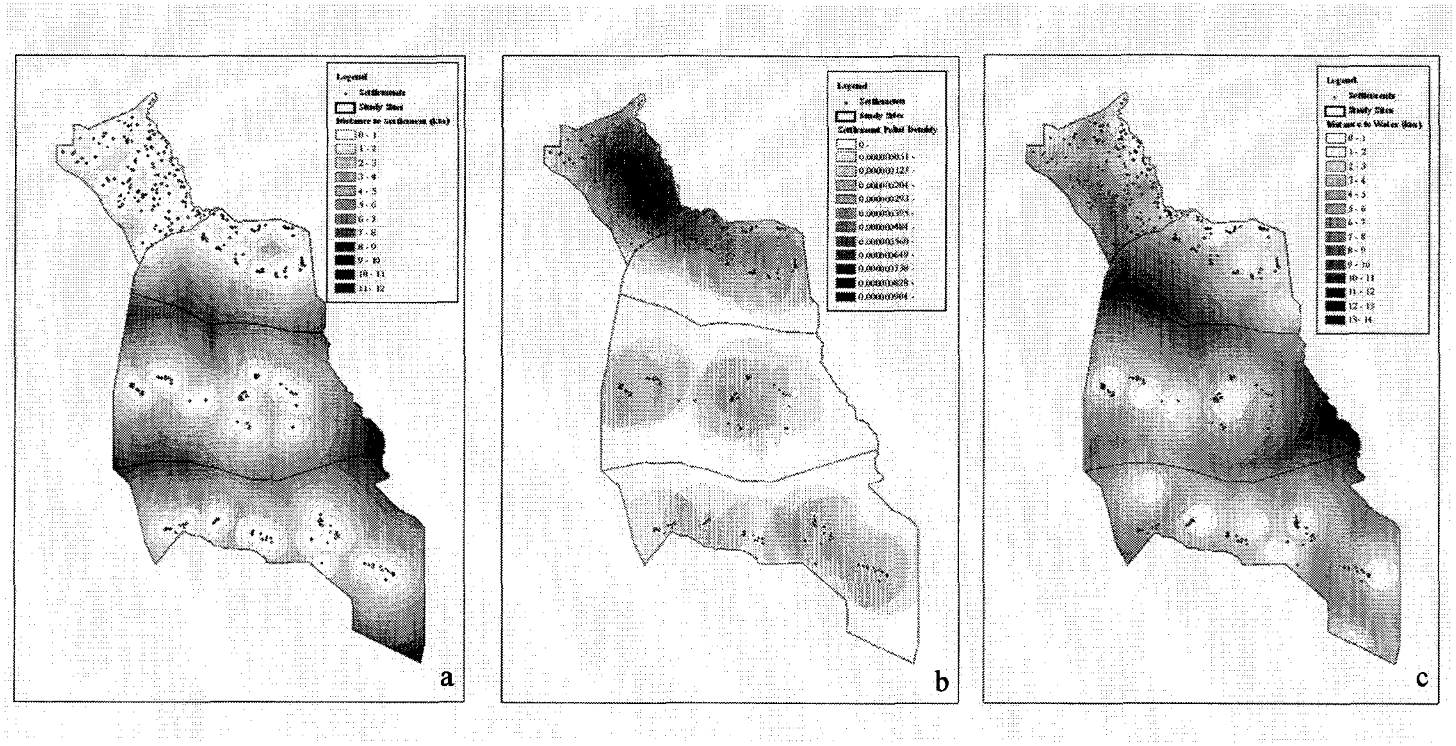

Figure 6 Distance to settlement (a). Bands represent 1 km distances from settlement. Black polygons delineate study zones, and open circles represent settlements. Settlement point density for a 5 km radius (b). White represents areas of lowest density and dark areas represent the highest settlement point density. Point density was calculated as the density of settlement within a 5 km radius of a given point. Distance to water (c). The current distribution of settlements in relation to permanent water points as indicated with 1 km distance bands. Permanent settlements are displayed as open circles.

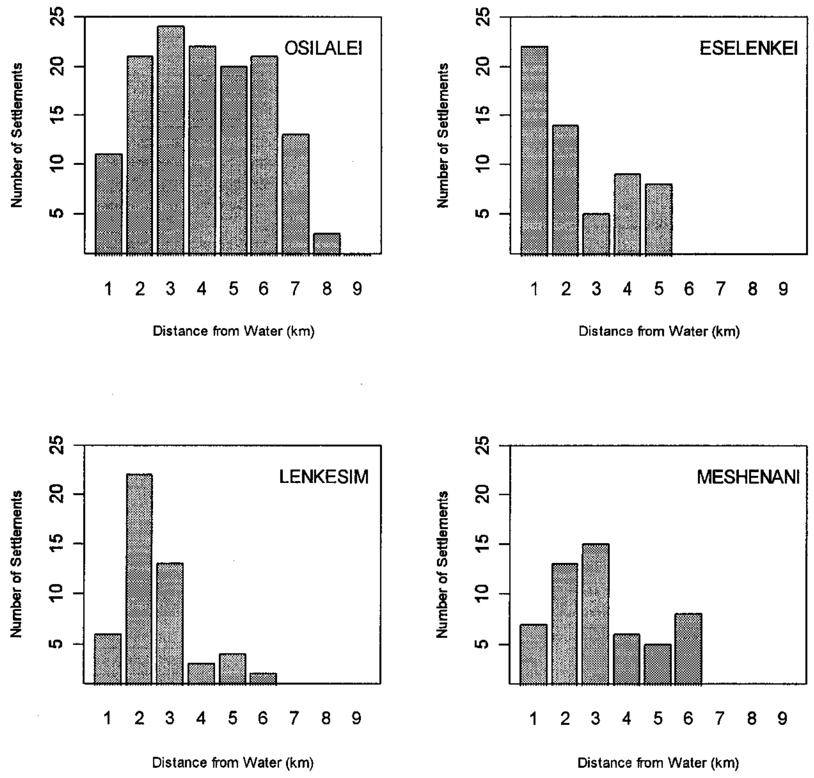

Figure 7. Total number of settlements at different distances to water by LUA (1 km bands). Each panel indicates the total number of settlements in 1 km distance bands from water.

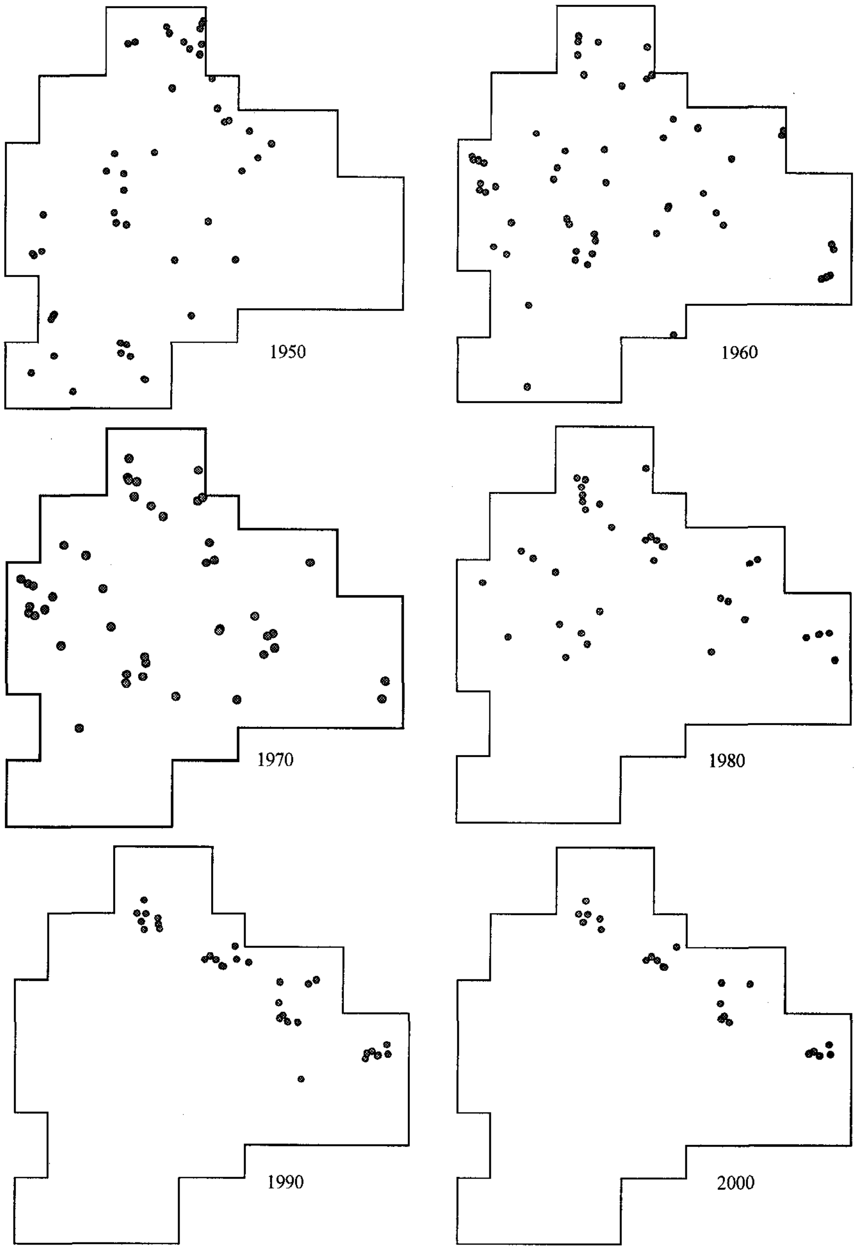

Figure 8. Settlement distributions through time for Eselenkei Murua Study area 1950 to 2000. Each panel in this figure represents a decade (e.g., 1950 covers the period 1950 to 1959). Occupied permanent settlements are indicated as grey circles. Each decadal map includes all permanent settlements that were occupied, including those that were started or abandoned during that period.

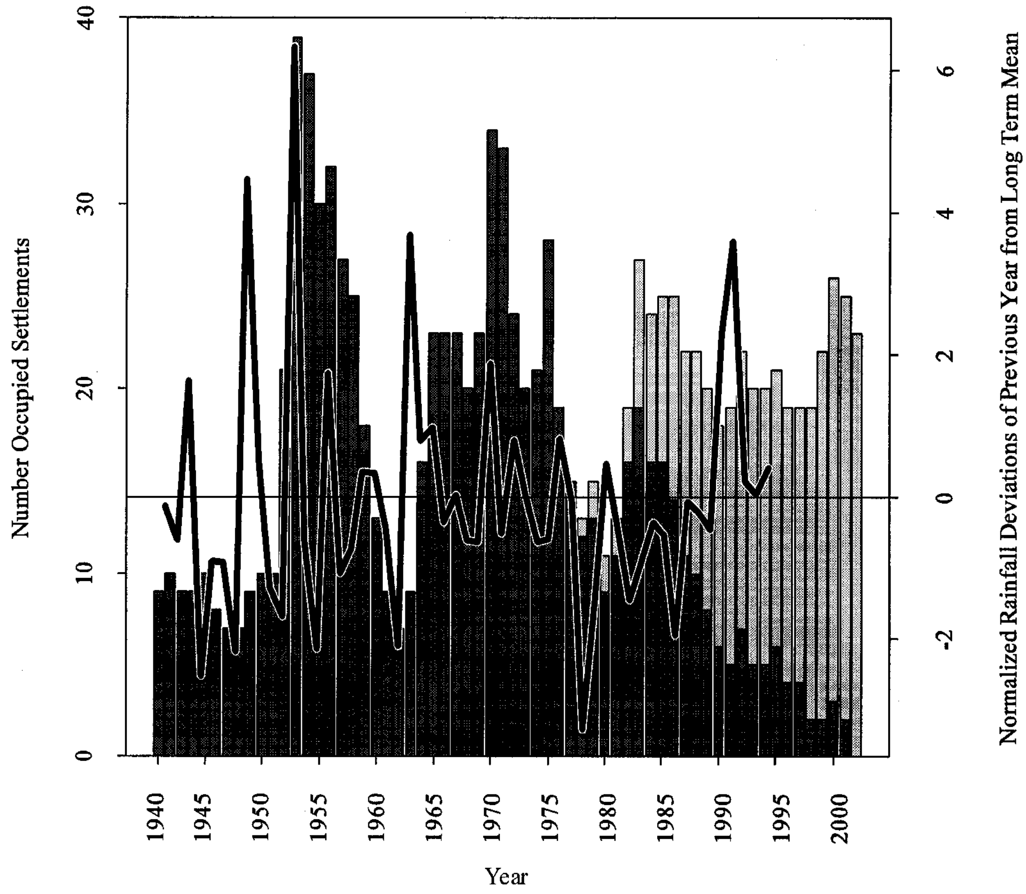

Figure 9. Frequency plot of number of occupied settlements in Eselenkei Murua Study area. All abandoned permanent settlements (dark grey) and currently occupied settlements (light grey) are shown. Pre 1950 data should be considered with caution because of limits of human memory. The lack of known settlements prior to 1940 is not necessarily an indicator of no settlement, but more likely represents the limits of human knowledge and the tendency for pastoralists to re-use previously occupied sites. Normalized rainfall deviations are indicated with the black line.

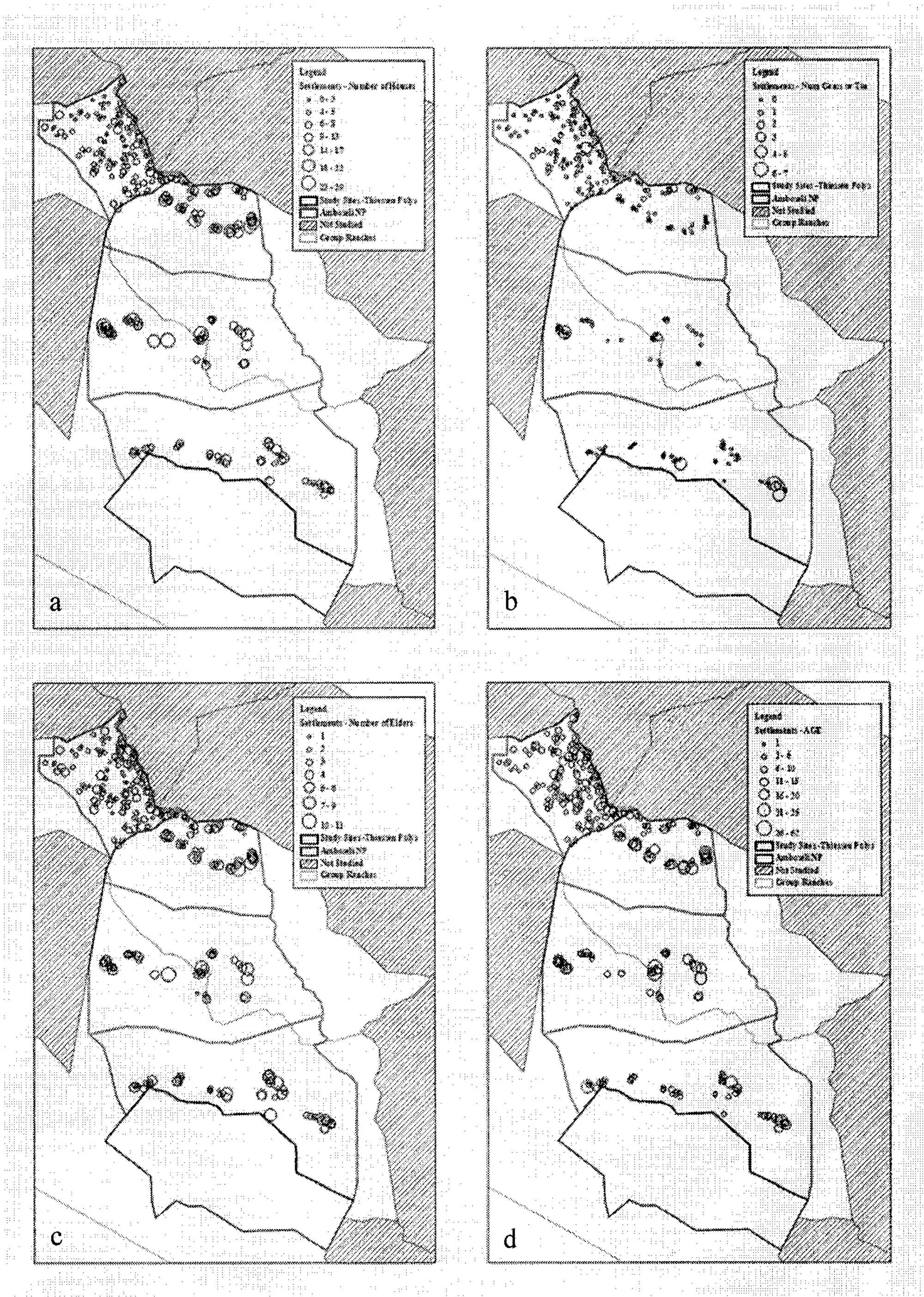

Figure 10. Map of structural characteristics by study area. Maps refer to number of houses per settlement (a), the proportion of houses in a settlement which have grass or tin roofs (b), number of elders per settlement (c), and settlement ages (d). The settlement sampling area boundaries (study zones) are shown in grey. Group ranch, national park, and not studied areas are represented as in Figure 2.

CHAPTER 3

RANGELAND FRAGMENTATION IN AN EAST AFRICAN SAVANNA – IMPLICATIONS FOR PASTORAL MOVEMENT AND DROUGHT VULNERABILITY

> "...it is no longer useful to speak of a continuum between mobile and sedentary systems, since mobility is not merely variable but multi-dimensional. No society is sedentary, not even our own industrial one-people simply move in different ways. The dimensions of movement need to be disentangled and studied independently so that we can understand how factors altering one component affect other areas..." (Kelly, 1992, p. 60)

INTRODUCTION

Human-induced dissection of habitats into spatially isolated parts and conversion of habitat to render it unsuitable for grazing animals are disrupting patterns of movement by pastoral peoples and native ungulates worldwide. The effects of fragmentation and habitat loss are particularly acute in African rangelands where expanding settlement and agriculture (Homewood et al. 2001, Serneels and Lambin 2001a, Serneels and Lambin 2001b, Serneels et al. 2001, Lamprey and Reid 2004) and fencing (Reid et al. in press) have negative impacts on migratory ungulates. Although the impacts of fragmentation on wildlife populations have been well studied, less attention has been given to the effects of habitat fragmentation on pastoralists (but see Galvin et al. in press). Mobility is an essential strategy for pastoralists in variable environments (McCabe 1994, Swallow et al. 1994, Swift et al. 1996, Niamir-Fuller 1999, Niamir-Fuller and Turner 1999, Coppolillo

2000, 2001, Boone et al. 2005). When coupled with other coping mechanisms, such as herd splitting (Coughenour et al. 1985, Coppock et al. 1986, Swift et al. 1996) and herd diversification (Little et al. 2001, Desta and Coppock 2004), mobility provides a means to stabilize the spatial and temporal variability in forage resources in arid and semi-arid ecosystems (Coughenour 1991). Managing movements of herds at multiple scales enables pastoralists to maintain higher stocking densities (Scoones 1992, Scoones 1993) and facilitates rapid herd recovery after drought, by enhancing access to areas with ephemeral high quality forage resources, areas of low utilization, and spatially and temporally heterogeneous resources. Furthermore, movement distributes the impacts of livestock in space, reducing the likelihood of localized degradation (Sinclair and Fryxell 1985, Coughenour 1991). Mobility or migration as a mechanism for stabilizing populations and managing heterogeneous resources is not limited to pastoralists and their livestock, but is also an important aspect of native large herbivore populations in Africa (Talbot and Talbot 1963, Western 1973, 1975, Sinclair 1979, Fryxell et al. 1988, Fryxell and Sinclair 1988) and elsewhere (Berger 2004, Ito et al. 2006).

Pastoral mobility opportunistically enhances access to variable forage resources, thus reducing fluctuations in forage availability due to spatial and temporal variations in rainfall (Ellis and Swift 1988, Coughenour 1991). Empirical evidence from studies of mobility in southern Africa (Scoones 1993, Baker and Hoffman 2006), East Africa (McCabe 1990, Boone et al. 2005, BurnSilver and Worden in press), and West Africa (Adriansen and Nielsen 2002, Turner and Hiernaux 2002) as well as Asia (Fernandez-Gimenez 1999) and Australia (Stokes et al. 2006) suggest that increased mobility and an increase in the spatial extent of movement enhances and stabilizes the resource base of pastoral livestock. Similarly, simulation models suggest that the ability of pastoralists to utilize larger areas through movement results in increased access to heterogeneity with important implications for livestock carrying capacity (Boone et al. 2005, Illius and O'Connor 2000, Fryxell et al. 2005, Owen-Smith 2004) and livestock impacts on rangelands (Boone 2005).

Movement is the mechanism that enables wild and domestic herbivores to access forage resources and integrate heterogeneity at multiple spatial and temporal scales (Hobbs et al. in press, Senft et al. 1987, Bailey et al. 1996). At the finer spatial scales outlined in Figure 1, such as bite, feeding station, and patch, domestic and wild herbivores use similar criteria for allocating foraging effort. As spatial and temporal scale increases, however, foraging patterns of domestic herbivores in traditional central place pastoral systems are increasingly constrained by human production needs and limitations. At broader spatial and temporal scales exogenous and endogenous factors transform historical patterns of movement and utilization in pastoral societies (Fig.1) with important implications for the stability of both human and ecological systems in variable environments.

Although mobility is recognized as an important adaptive strategy of pastoral societies in variable environments (Swallow et al. 1994, Swift et al. 1996, Niamir-Fuller 1999, Fernandez-Gimenez and Le Febre 2006), this has not been the prevailing view among policy makers. Indeed, through much of the colonial and post colonial history of East Africa, movement and mobility were seen as disruptive to development and "progress". Pastoral populations were encouraged to settle so that they could be integrated into the social and economic fabric of emerging nations (Campbell 1993). In southern Kenya, this sedentarization process had two primary components – infrastructure development such as dips, dams, boreholes, and schools (Talbot 1972), and the evolution of land tenure systems from communal to private management and control (Rutten 1992, Worden 2007). The effects of these direct initiatives were compounded by indirect effects associated with population growth and the excision of key resource areas for agriculture and conservation (Western 1982, Campbell 1984, 1999, Campbell et al. 2000, Worden 2007). The net result has been a gradual trend towards the sedentarization of pastoral communities in the Greater Amboseli Ecosystem and throughout East Africa (Galaty 1992, Rutten 1992, Galaty 1994a, Homewood 1995, Fratkin 1997, 2001, McCabe 2003, Worden 2007).

Here, I examine how mobility is evolving in an African pastoral ecosystem in the face of increasing constraints on movement and access to resources, and the implications of these changing movement patterns for the stability of semi-arid grazing systems. Using a land-use intensity gradient in the Greater Amboseli Ecosystem (GAE) I focus on the question of how land privatization and sedentarization influence pastoral herd sizes, opportunistic access to forage resources, vulnerability to drought, and thus pastoral well-being. Specifically, I test the following three hypotheses:

1) Land privatization and sedentarization result in decreased pastoral mobility, reduced herd sizes, and decreased human well-being.

2) Movement provides an increased range of opportunities for pastoralists to cope with spatio-temporal variations in forage abundance.

3) Mobility reduces livestock losses during droughts.

METHODS

Study Area - The Greater Amboseli Ecosystem

The Greater Amboseli Ecosystem (GAE) includes approximately 8,500 km^2 (Western 1973) within Amboseli National Park and the surrounding rangelands. The ecosystem is used seasonally by dispersing wildlife (for detailed ecological and social descriptions see Western 1973 and Rutten 1992). This study focuses on the semi-arid pastoral rangelands north of Amboseli National Park in Kajiado District, Kenya (Fig. 2). I present data from daily and monthly herd movements (Fig. 3) of Maasai pastoral households on three focal group ranches: Olgulului/Lolarashi (147,050 ha), Eselenkei (74,794 ha), and Osilalei (38,629 ha) (Rutten 1992).

Across the GAE, the gradual erosion of inter-cultural connectivity, the excision of key resource areas, and the development of water resources for livestock in previously inaccessible areas initiated a process of de facto rangeland fragmentation through the restriction of pastoral movement and access. Subsequent increases in human and livestock population densities and shifts in broad scale settlement patterns necessitated a shift from the traditional wet season dispersal system to a dry season dispersal system, with a corresponding emphasis on preserving dry forage biomass rather than to maximizing access to ephemeral high quality forage resources (Worden 2007).

Within this larger regional context, de facto fragmentation at the landscape level has been exacerbated by changes in land tenure and sedentarization. To encourage investment and "rational" resource management in Kenya's rangelands following widespread livestock losses in pastoral areas due to drought, the Government of Kenya initiated a program of group ranch formation in the 1960s (Galaty 1980, Olang 1982, Galaty 1992, Rutten 1992, Galaty 1994b). Group ranches were to be run collectively in recognition of traditional Maasai systems of resource management. However, mismanagement and unequal resource appropriation, combined with an increasing desire for autonomy among the members of the group ranch has lead to the gradual subdivision of many of these group ranches into individual parcels across Kajiado District (Galaty 1994a, Kimani and Pickard 1998).

This process of rangeland fragmentation has constrained movement and led to two divergent patterns of settlement in the study area (Chapter 2). In the subdivided area of Osilalei settlements are widely dispersed across the landscape resulting in a relatively homogeneous distribution of human impacts and the collapse of grazing and drought reserves. In contrast, the communally managed areas of Eselenkei and Olgulului/Lolarashi took an alternative trajectory. In these areas sedentarization in the context of increasing forage constraints has led to a highly clustered pattern of settlement with distinct grazing stages and seasonal movements. Clustered distributions, while polarizing the landscape into areas of high and low disturbance, concentrate human disturbance at intermediate distances from water thereby conserving grazing reserves and balancing access to forage and water (Worden 2007).

I separated the three group ranches into four Land Use Areas (LUAs) (Fig. 2) based on existing settlement and management systems (Meshenani = 45,193 ha, Lenkesim= 51,983 ha, Eselenkei = 24,673 ha, and Osilalei = 17,539 ha) to document the patterns of pastoral resource access and management on the ground. The four LUAs were selected to represent a land tenure and sedentarization gradient ranging from highly mobile in Meshenani to sedentary and subdivided in Osilalei (subdivided in 1990), with

Lenkesim and Eselenkei falling in between these two extremes (Worden 2007). The broad scale similarities in vegetation, soils, and land use history between these zones provided an ideal setting to assess the effects of subdivision and sedentarization on pastoral mobility at landscape spatial scales.

The four Land Use Areas are rolling Commiphora/Acacia dominated savannas of basement complex soils with low topographic heterogeneity intersected with seasonal rivers and fluvial deposits (Touber 1983). A shallow rainfall gradient extends northward from Meshenani, where annual rainfall averages 350 mm to the hills of Osilalei where annual rainfall is approximately 400 mm. Even at the highest end of the rainfall gradient, the distribution of total precipitation over two wet seasons (April – May, and Nov – Dec) precludes rain-fed agriculture in all but the wettest years (Ellis and Galvin 1994, Kristjanson et al. 2002). Discussions with local elders and long term observations (D. Western, personal communication) confirm that pastoral families have employed similar land use strategies historically.

Data Collection

Patterns of Movement

Herds from across the study area (n=71) were followed to establish the effects of subdivision and sedentarization on daily movement patterns. The herd following data was collected in two phases. In the first phase, five households in each study zone were selected from a complete census of all permanent settlements in the study area using a stratified random sampling technique. Households were stratified by location (n=4) and wealth category – rich, medium, poor (Grandin 1988, BurnSilver in prep). The main cattle herds of each of these households were followed once in the dry and once in the wet season to quantify the grazing orbit in different seasons and areas. The unusually dry conditions of 2000 prevented the collection of a complete set of all wet-dry pairs for each zone. The second phase of sampling involved following individual cattle herds over a five day period. Seven households in the Eselenkei and Lenkesim areas were selected to determine the variability of herd movement over consecutive days. Herd locations, general behavior, and dominant herbaceous and woody species were recorded at 30 minute intervals using a Garmin 12 GPS for both the single and multi-day orbits (only location data is presented here).

Intra- and inter-annual herd movements (n=78) were reconstructed from household interviews. Respondents were randomly selected from three wealth strata in each study zone (see BurnSilver and Worden in press for further details on wealth ranking). The location of the main cattle herd at monthly intervals from January 1999 through December 2000 (24 months total) was recorded using known settlement and place names. Contrasting rainfall patterns in 1999 and 2000 provided the context for a natural experiment for comparing normal seasonal and drought induced movements across the study area (Fig. 4). Local informants confirmed that 1999 was an "average" year with representative herd movements occurring in all zones. The year 2000, however, was a year of intense drought stress across the region. I compare movement patterns between zones in 1999 to characterize and contrast "typical" intra-annual movements, and differences between zones and years to assess the impacts of changing land-use and tenure regimes on drought induced mobility.

Livestock Losses

I used estimates of livestock (cattle) mortality during drought as an indicator of drought vulnerability. Data on herd sizes, age and sex structure and breed composition for cattle and sheep and goats were collected from interviews of Maasai pastoralists across the study area (see monthly movement data above). Herd sizes at the beginning of 2001 were used as the year 2000 final herd size. Respondents were also asked what the sizes of their herds were at the end of 1999 as well as what all the additions and subtractions from their herd were through sales, theft, slaughter, gifts, births and mortality throughout the year. The cause of livestock mortality was indicated as being the result of predation, starvation, loss, theft, disease, hypothermia (following rains) or other.

Data Processing

Patterns of Movement

Maximum distances from the settlement of origin were calculated from the UTM coordinates of all herd locations using the bearing and distance tools extension in ArcView 3.2a (ESRI 2002). Results from both single and multi-day grazing orbits were combined. Because of the lack of independence in the multi-day orbits, I used the mean of all the consecutive daily orbits for each household for calculations of mean herd sizes and mean maximum distance from water, the difference between permanent and seasonal settlements, and seasonal differences. For comparisons between watering and non-watering (grazing) days I subsetted the multi-day orbit data into grazing and watering days before taking the means (graze n=6 and water n=7).

One of the strategies employed by pastoralists in the GAE to increase their access to limited dry season forage is a system of alternating grazing and watering days (Western 1973, Worden 2007). To visualize how daily grazing patterns vary by season relative to forage and water I plotted all the grazing orbits on a standardized grid. The X and Y coordinates of all grazing orbit observations were transformed to a standard grid with the settlement of origin at its center and the direction of permanent water at the top. Only directions to permanent water were standardized and all observations were plotted using 0 to 180 degrees – i.e. observations that were either side of the settlement – water axis were all plotted on one side to facilitate comparisons. Distances were not scaled and all observations were plotted on a 1km grid. In this way orbits that may have differed in their cardinal directions can be overlain to facilitate comparison of daily movements relative to settlement and water (Coppolillo 2001). All the grazing orbit point locations were transformed into the standard coordinate system using the Distance and Azimuth extension in ArcView 3.2a (http://www.jennessent.com/). I then separated all the standardized orbit points by season and water dependence. Water dependent (watering day) points were data from days in which the herd traveled for water, or in the wet season when water was not limiting and herds drank at various points along their grazing route. Water independent, or non-watering, points are from days when herds did not water at all and were grazing only.

As with other central place resources such as water points (Andrew 1988, Pickup and Chewings 1994, Thrash and Derry 1999), livestock utilization around pastoral settlements creates a gradient of forage availability. Across this gradient forage biomass generally increases as a function of distance from settlement. The presence of this underlying gradient implies that under conditions where forage is limiting pastoralists should graze their herds farther from settlements in an effort to maximize forage intake. To quantify how the Maasai strategy of alternating grazing and watering days affects the amount of time a herd spends in the potentially high forage biomass areas far from the settlement I plotted the frequency distribution of all grazing orbit points (30 minute intervals) as a function of distance from the settlement of origin, all permanent settlements, and water, for both the wet and dry season and grazing and watering days. To facilitate comparison all distributions were smoothed using a 500 m bandwidth and plotted together.

Distances from the core settlement to permanent water and to the nearest settlement were calculated for each respondent in ArcView 3.2a. Metrics for seasonal and drought induced movements were calculated to characterize patterns of distance, location, and timing of movement in each study zone.

Forage Resources and NDVI

Characterizing forage availability at broad spatial scales offers one of the central challenges for understanding plant-herbivore systems worldwide. Remotely sensed data, while by definition a surrogate for direct measurements of forage quality and quantity has proven to be a useful indicator of vegetation characteristics at broad scales (Kerr and Ostrovsky 2003, Pettorelli et al. 2005). In particular, the Normalized Difference Vegetation Index (NDVI) is correlated with primary production (Paruelo and Lauenroth 1995) and regional livestock densities (Oesterheld et al. 1998), and has been widely used as an indicator of green forage biomass in rangelands (Wylie et al. 1995, Boone and

Hobbs 2004, Musiega and Kazadi 2004, Kawamura et al. 2005, Boone et al. 2006). NDVI takes advantage of the unique spectral properties of green vegetation that has a particularly high reflectance in the near infrared (NIR) band and low reflectance in the Red band and is calculated as:

$$NDVI = (NIR - Red)/(NIR + Red)$$

NDVI data were from the SPOT VEGETATION censor and represent 10 day decadal composite images with raw values ranging from 0 to 255 (Boone and Hobbs, 2004). Higher NDVI values indicate more green vegetation biomass. To reduce errors and interference from excessive cloud cover I used pre-processed images with NDVI values representing the maximum value observed within the 1km grid cell over the 10 day period. A total of 72 images from January 1999 to December 2000 were used. Movement location data from the interviews and the location of each settlement were recorded at monthly time steps. To calculate each herd's access to forage biomass throughout the two years of monthly movement data mean NDVI values were calculated for each herd location for an area spanning a typical maximum daily grazing radius ($NDVI_{herd}$). To capture the potential forage available at each site a 10 km grazing radius was used for all analyses. This radius was a good indicator of potential forage availability as it is consistent with the maximum recorded radius (8,077 m) and published accounts for the area (Western 1973). Cumulative NDVI values for each herd were used as a greenness index to represent the total green forage available to the herd over the year. To assess the effects of movement on forage availability across study zones, and control for the underlying differences between zones I calculated a "NDVI mobility value" ($NDVI_{mv}$) by subtracting the cumulative NDVI value for a theoretical sedentary herd that spent the entire year at the permanent settlement ($NDVI_s$) from the actual cumulative NDVI value for the herd ($NDVI_m$).

$$NDVI_{mv} = NDVI_m - NDVI_s$$

To assess the NDVI perturbation that might have initiated movements, I calculated a normalized deviation in NDVI as

$$NDVI_{dev} = (NDVI_{t-1} - NDVI_{avg})/SE$$

Where $NDVI_{t-1}$ is NDVI in the month before the move and $NDVI_{avg}$ is the mean NDVI and SE is the standard error of the NDVI for all observations in the study area. To quantify the difference between mean NDVI accessed ($NDVI_{herd}$) and mean NDVI available I calculated the following NDVI difference:

$$NDVI_{dif} = NDVI_{herd} - NDVI_{avail}$$

Where $NDVI_{herd}$ is the observed NDVI value at a given time step and $NDVI_{avail}$ is the mean NDVI for the entire Land Use Area at that same time.

Livestock Losses

Total herd sizes for 1999 and 2000 were extracted from the interview data and cross-checked with the more detailed herd structure data. Initial estimates of herd size given by informants were closely related to the totals calculated from the herd structure data but data containing numbers by age and sex proved to be more accurate and they were used here. Data on the total losses to drought and the timing of losses independently of the herd age/sex structure data was also collected. Similarly, the data on losses from the herd structure data appeared to be more precise so they were used here.

Statistical Analyses

Data were checked for normality and transformations were applied where appropriate. Transformations generally failed to achieve normality or substantially reduce skewness so non-parametric Kruskal-Wallis tests were used to assess differences in mean herd size, maximum daily distance traveled, mean NDVI values, and mean livestock losses among Land Use Areas. Seasonal and inter-annual differences were tested with the paired Wilcoxon rank sum test. To assess the relationship between movement and forage availability, and forage access and drought vulnerability I calculated Spearman's R correlations between movement metrics and NDVI, and NDVI and cattle losses. All statistical analyses were conducted in R (R Development Core Team 2006) and the PGIRMESS package (Giraudoux 2006) with significance level set at 0.05 except where stated otherwise.

RESULTS

Patterns of Movement

Herd Sizes and Daily Grazing Orbits

Herd size differed across the study area (Table 2, Kruskal-Wallis, df = 3, p = 0.024) with the largest differences occurring between zones at the extremes of the land tenure gradient in Osilalei and Meshenani (Kruskal – Wallis multiple comparison test, df = 3, p< 0.05) (Appendix 1 Table 1, Fig. 5). These differences were corroborated by data from household interviews that suggested that herd sizes in Osilalei households were significantly smaller than in Eselenkei and Meshenani, (see livestock losses below). When the data were subdivided by season and watering vs. grazing day, the trend in reduced herd sizes with land privatization and sedentarization persisted but the significance of the differences were diminished. Herd sizes were only significantly different among zones on watering days (Appendix Table 1, Fig 6). Despite this lack of significance it is important to note that herd sizes in Meshenani were highly variable and generally larger than all the other zones. In particular, herds in Meshenani were largest during the dry season on grazing days from seasonal settlements. In contrast, herd sizes in Osilalei were by far the smallest and least variable. Zero values for Osilalei reflect the fact that pastoralists have abandoned the seasonally occupied *enkaron* settlement system. Logistical constraints resulted in missing data for the dry season in Osilalei. Maximum daily distance traveled and herd size were positively correlated, although the strength of the correlation was low (R= 0.376, df = 69, p = 0.001). Daily distances traveled by herds of less than 200 animals were highly variable, but herds of greater than 350 animals (n = 3) appeared to travel longer distances (> 7 km).

Livestock grazing orbits in Amboseli were generally elliptical on non-watering days, and were more complex on watering days. Maximum distances and total distances traveled in the multi-day grazing orbits were positively and strongly correlated (Pearson's $R = 0.725$). Mean maximum distances from settlement for all the grazing orbits were significantly different among LUAs (Kruskal-Wallis, $df= 3$, $p < 0.05$). Maximum distance traveled was lower in Osilalei than in Lenkesim, but there were no significant differences between Eselenkei, Lenkesim, and Meshenani (Fig. 6, Appendix 1 Table 1). Significant differences between zones were not apparent at the levels of settlement types, seasons, or watering vs. grazing days (Fig 6 and Appendix 1 Table 1). When comparing orbits by settlement type and season, Osilalei and the neighboring communally managed Eselenkei had remarkably similar mean maximum distances for herds at permanent settlements and during the wet season, suggesting that sedentarization has the potential to constrain fine scale movement regardless of land tenure.

To assess the effects of alternate grazing and watering days on seasonal patterns of forage access I plotted all daily grazing orbit observations in a standard space (Fig. 7). In the standardized space the settlement of origin forms a vertical settlement-water axis with the direction to water at the top of the plot. All water independent orbits were plot to the left of this axis and all orbits in which livestock drank water (dependent) were plotted on the right. Therefore, a point that is located one grid cell directly left of the central point on the central axis represents a water independent herd observation that was one kilometer away from the settlement, but neither towards nor away from water. In turn, an observation in a similar position on the right of the central axis would represent a water dependent observation. A point on the central axis one grid cell up from the settlement represents an observation that is one kilometer from settlement in the direction of water, while a similar observation on the axis in the opposite direction (i.e. down from the central settlement) indicates movement away from water.

In the wet season, when forage and water were not limiting, herds spent the majority of their time (67.2 %) on watering days between the settlement and the water source with 82.0 % of those observations occurring within a 1 km band between the settlement and water (right hand side of Fig. 7a). In contrast, during the dry season, forage appeared to be much more limiting with 56.1% of the orbit observations occurring in the opposite direction from water. Similarly, for those observations nearer to water only 62.5 % of them occurred within a 1 km band between water and the settlement (right hand side of Fig. 7b). Grazing-only days enabled herders to concentrate their foraging efforts in areas of higher forage biomass farther from both settlement and water. In the wet season, on grazing-only days, 100% of the observations were in the opposite direction from water (left hand side of Fig. 7a). Similarly, in the dry season the only non-watering orbits that were not in the opposite direction from water were those of herds that were using alternative water sources (left hand side of Fig. 7b).

In both seasons, non-watering days enabled herds to spend more time away from sacrifice zones near water and permanent settlements and concentrate their foraging effort farther afield. Frequency distributions of grazing orbit observations as a function of distance from settlement of origin, permanent settlements, and water (Fig. 8) highlight how this strategy allows herds to graze areas that could not be utilized on watering days due to time constraints. In relation to the settlement of origin, the peak frequency of watering day orbits in both the dry and the wet season occurred within two kilometers of the settlement (Fig. 8a). The peak frequency of points on non–watering days, in contrast, was closer to four kilometers away from the settlement. The frequency distribution of grazing orbit observations in relation to permanent settlements was similar, but on watering days there was a higher concentration of points near permanent settlements (Fig. 8b). Herd distributions during grazing days, in contrast, were more evenly distributed between three and eight kilometers of permanent settlements. Similar distributions relative to water were found, with peak watering day frequencies between three and four kilometers, and peak grazing day frequencies between seven and eight kilometers (Fig. 8c). Thus, this grazing strategy enhanced the ability of pastoral livestock to access areas farther from settlements and water.

Movement patterns in drought vs. non-drought years

In the non-drought year of 1999, the proportion of households that moved was significantly different among zones with Osilalei having by far the least number of households that moved (Fig. 9a, Table 1a). Very few of the respondents in any zone moved off their respective group ranches in 1999 (Fig. 9b, Table 1a). There were only two respondents who moved in Osilalei in 1999 and they tended to move to fewer places, spent fewer months away from their permanent settlements, and moved earlier and over shorter distances than the herders in the other areas. Both the total distance traveled and the maximum distance from the permanent settlement reached over the course of the year were shorter in the subdivided area of Osilalei than Eselenkei and Meshenani. A similar pattern held for the mean distance traveled per move and the mean distance traveled per month away from the group ranch. A notable exception to the significant differences mentioned above was the contrast between Osilalei and Lenkesim. Although mean values for distance metrics between these two areas were substantially different there was no significance difference between these two LUAs due to the large variability in distances moved in Lenkesim (Table 1a).

In contrast, during the drought of 2000, patterns of movement were very similar among Land Use Areas. The proportion of herds that moved varied little between LUAs (Fig. 9a). Although there were some significant differences in the number of places visited by herders and the number of months away from the permanent settlement between the LUAs (Table 1a) there were no significant differences in any metrics associated with movement off the group ranches or in distances traveled over the year. However, there were differences in trends among LUAs. Generally, herds from Osilalei moved to fewer places and spent less time away from home. Contrary to initial predictions, however, herds from the subdivided Osilalei area moved earlier within their own group ranch and later to other group ranches. A high proportion of Osilalei herders left their group ranch in 2000 (Fig. 9b), and once they left, they tended to stay on other group ranches longer (Table 1a). Similarly, Osilalei herds traveled substantially farther during the year, with higher mean distances per move and per month away from the group ranch (Table 1a).

Differences in movement metrics between 1999 and 2000 within a LUA reflected the impacts of, and responses to drought (Table 1b). All of the metrics for Osilalei herds were significantly different ($p < 0.05$) among years. In Eselenkei 90% of the metrics were different between years, while Lenkesim there were significant differences between years in 60% of metrics. In contrast to the other three study LUAs, movement patterns in

Meshenani differed very little between years. The only significant differences between years were in the numbers of places, months away, and timing of the initial move (30% of metrics). In 2000 herds in Meshenani tended to move to more places, spend more time away from their permanent settlement, and initiate their first move nearly one month sooner on average (end of June in 2000 vs end of July in 1999). The differences in significance levels between years suggested very different levels of drought vulnerability among LUAs. In Osilalei, the drought of 2000 completely altered their usual patterns of movement while herders in Meshenani changed their strategies only slightly. Generally, herders across the study area responded to the drought by moving earlier, moving more, and for longer periods of time. The drought caused a higher proportion of herders to move off their group ranch in 2000, and those that did move did so later and stayed off longer. In all cases, herders that moved in 2000 moved farther with larger mean distances traveled per move and per month away from the group ranch.

Spatial and Temporal Variation in Forage Availability

Spatial and Temporal Patterns of Forage across the Study Area

Spatial and temporal patterns of variability in NDVI differed across the region (Fig. 10). The range of NDVI values at each decadal time step, calculated as the mean NDVI value for a 1 km radius around each pixel through time, indicated the degree of spatial heterogeneity of green vegetation within each LUA. Note that the wide range of NDVI values in Meshenani indicated a high degree of variability in forage biomass. In contrast, the relatively narrow range of values in Osilalei indicated that green forage densities were more uniform. Mean NDVI values and the spatial CV of NDVI also differed among LUAs (Fig. 11), however, the temporal dynamics of green forage were generally similar. Most of the differences in NDVI values between LUAs occurred during the wet season. The mean NDVI values during the long dry period (Aug – Oct, 1999 and Aug – Nov, 2000) were very similar among LUAs. As we shall see below, it is during these dry season forage bottlenecks in the Greater Amboseli Ecosystem that mobility, heterogeneity, and reserve grazing areas become important. Spatial CV values in Osilalei, Eselenkei, and Lenkesim were similar, while the spatial CV in Meshenani was considerably higher.

Annual differences (1999 vs. 2000) are more difficult to interpret, but four points regarding the drought in 2000 warrant consideration here. First, precipitation data suggest that 2000 was one of the lowest rainfall years in the last 40 (Fig. 4). Second, while the initial vegetation response (NDVI) in early 2000 appeared to be quite strong, the NDVI patterns in April and May 2000 peaked later and decreased more rapidly than in 1999. Similarly, the long dry period was both longer and more acute in 2000. Finally, the spatial CV values indicated that there was less spatial heterogeneity in dry season forage resources in 2000 than in 1999. These patterns suggest that for pastoral systems that are on the edge the timing and persistence of vegetative response to rainfall may ultimately be more important than the absolute magnitude of that response.

Movement and NDVI

Multiple lines of evidence indicated that fragmentation may constrain access to green forage (NDVI) through reduced mobility and that seasonal and drought response strategies that incorporate mobility may be more focused on accessing standing dry biomass rather than green forage as represented by NDVI. Temporal profiles of mean NDVI within a 10 km radius of herd locations ($NDVI_{herd}$) revealed each herd's access to forage throughout 1999 and 2000 (examples from each LUA in Fig. 12). Vertical lines indicating the timing of moves and a horizontal line representing the overall mean NDVI for all observations in the LUA are included for reference. The monthly mean of these temporal profiles ($NDVI_{herd}$) and thus access to green forage were similar among LUAs (Fig. 13a). There were minor differences in the relative magnitude of observed NDVI accumulation, with Osilalei slightly higher than the other LUAs, but this difference was primarily limited to April and May of both years. Temporal profiles of $NDVI_{mv}$ for each LUA indicate how movement affected NDVI experienced by livestock over time relative to what was available at their permanent settlement (Fig. 13b). Herds in Meshenani exhibit a steady decline in $NDVI_{mv}$ through 1999 and 2000. In Eselenkei and Lenkesim movement had little effect on the NDVI experienced by the herd except in the final months of 2000 where movement appeared to have increased the NDVI experienced. Similarly, $NDVI_{mv}$ oscillated near zero in 1999 for herds in Osilalei. In contrast to the other LUAs, $NDVI_{mv}$ in Osilalei dipped sharply in mid 2000 as herds moved to areas with lower mean NDVI values than were available at home (Fig. 13b).

Cumulative values of $NDVI_{herd}$ over time, essentially time integrals of NDVI, measured total forage access throughout the year (Fig.14a and Appendix 1 Table 2a). Cumulative $NDVI_{herd}$ values differed significantly between LUAs in both 1999 and 2000 (Kruskal- Wallis, df = 3, $P < 0.001$ for both 1999 and 2000). In 1999 there was no significant difference between Osilalei and Eselenkei however, suggesting similar forage accumulation patterns in both areas. A slightly different pattern emerged in the $NDVI_{mv}$, however. Significant differences between sites persisted ($p < .0001$) in 1999, but the pattern was reversed with the highest $NDVI_{mv}$ values occurring in Meshenani and Lenkesim, and the lowest in Osilalei and Eselenkei. Interestingly, in the drought year of 2000, while there were no significant differences in $NDVI_{mv}$ between LUAs, the subdivided area of Osilalei had by far lowest values (Fig.14a and Appendix 1 Table 2a).

Cumulative $NDVI_{herd}$ was significantly higher in 2000 than in 1999 ($p < 0.0001$) for all LUAs except Meshenani. However there were no significant differences between years in $NDVI_{mv}$ ($p > 0.05$) except in Eselenkei where $NDVI_{mv}$ was higher in 2000 than in 1999 (Appendix 1 Table 2b). Although not significant, $NDVI_{herd}$ and $NDVI_{mv}$ declined between 1999 and 2000 in Meshenani, and both Meshenani, and Osilalei respectively. Dividing the herds from each of these LUAs into groups based on whether they moved (mobile) or did not move (sedentary) in both 1999 and 2000 provided additional insights (Fig. 15 and Appendix 1 Table 3). All of the herds in Meshenani and Lenkesim were mobile in 1999 and 2000 respectively. Although there were some significant differences in $NDVI_{herd}$ between LUAs in both 1999 and 2000 for mobile and sedentary herds there were no significant differences between LUAs for $NDVI_{mv}$. Differences in $NDVI_{herd}$ values between 1999 and 2000 were significant for mobile herds in Eselenkei and Lenkesim, and for sedentary herds in Osilalei (Fig. 15 and Appendix 1 Table 3). Interestingly, there were no significant differences in $NDVI_{herd}$ between mobile and sedentary herds between 1999 and 2000(Appendix 1 Table 3).

The complexities of movement were also apparent in the $NDVI_{mv}$ values (Fig. 16). Over 50% of all $NDVI_{mv}$ values in both 1999 and 2000 for herds in Eselenkei, Lenkesim, and Meshenani were negative, thus herds experienced lower NDVIs than they would have had they moved back to their permanent settlement. In Osilalei, however, approximately 60% of all time spent away from the permanent settlement resulted in increased access to forage. Interestingly, the proportion of movements resulting in a negative $\mathrm{NDVI}_{\mathrm{mv}}$ increased during the drought of 2000. In both years, Osilalei had the lowest proportion of negative differences suggesting a grazing strategy that may be fundamentally different from that found in the other LUAs.

A series of movement metrics representing the key components of movement – distance, location, and timing (Table 1 and Appendix 2 Table 1), showed that in 1999 total distance traveled was positively related to $\mathrm{NDVI}_{\mathrm{mv}}$ for all herds combined . This was also true for the number of months spent away from home, but the number of places visited showed no significant trend for $\mathrm{NDVI}_{\mathrm{mv}}$ in 1999. In 2000, however, none of these metrics were significant, and there was weak evidence that total distance moved, although not significant, may have been negatively related to $\mathrm{NDVI}_{\mathrm{herd}}$. The lack of clear relationships between these movement metrics and $\mathrm{NDVI}_{\mathrm{herd}}$ in 2000 provides further support for the suggestion that standing dead biomass in dry season grazing reserves is currently the key to drought survival in the Greater Amboseli Ecosystem. Correlations between different metrics and $\mathrm{NDVI}_{\mathrm{mv}}$ by LUA suggested that in 1999 distance was particularly important in Meshenani alone (Appendix 2 Table 1). In 2000, the distance traveled per month away and the month of first move were important in Meshenani, while the total distance traveled, and number of moves and months off group ranch were important in Lenkesim and Osilalei, respectively.

The relationship between movement and NDVI was more complicated than initially predicted. The relationship between the number of moves and the $\mathrm{NDVI}_{\mathrm{dev}}$

indicated that a decrease in $NDVI_{herd}$ may have encouraged herders to move their animals the following month (Fig. 17a). There was a pattern of increased movement across the study area during periods of low, or negative, $NDVI_{dev}$ (Fig. 17b). A similar pattern held when considering the proportion of households that moved in each month by LUA. There were clear temporal patterns of movement in each of the four LUAs (Fig. 18). In all LUAs there appeared to be an association between low $NDVI_{herd}$ values and the proportion of households that moved. Interestingly, there was a low proportion of households that moved in Osilalei in 1999 despite the low $NDVI_{herd}$ values.

Temporal profiles of the $NDVI_{dif}$ indicated that herders in Osilalei and Meshenani experienced consistently lower NDVI values than expected for their areas (Fig. 19). In contrast, NDVI values for herders in Eselenkei and Lenkesim were frequently higher than expected. The temporal variations in $NDVI_{dif}$ values in the wet season (when most herds are still at their permanent settlements) indicated that herders were not maximizing intake of potentially available green forage during the wet season (Fig. 19). The convergence of $NDVI_{dif}$ values experienced by the herds and average NDVIs ($NDVI_{avail}$) across the landscape in the dry season (i.e.. $NDVI_{dif} = 0$) suggested that herders were employing a grazing strategy designed to efficiently utilize dwindling dry season forage resources.

This pattern of not necessarily accessing the "best" available forage resources at the "best" time was evident in an example of the temporal profiles of $NDVI_{dif}$ for all the locations visited by a herd in 1999 and 2000 (Fig. 20). This example highlights two important points about patterns of NDVI access. First, there was very little difference in $NDVI_{dif}$ values in each of the three potential locations defined by the universe of observed movements over the two year period at the time the herd moved in both 1999 and 2000 (Fig. 20, hatched area). Secondly, $NDVI_{dif}$ values were negative, indicating that areas they were moving to had lower $NDVI_{herd}$ than the average NDVI for the area ($NDVI_{avail}$). These patterns indicate that while herders may have been generally interested in maximizing access to high quality green forage, the shift from water to forage limitation (Worden 2007) has constrained movement and resulted in a shift to a grazing system that strives to maintain forage quantity in the dry season.

Livestock Losses and Drought Vulnerability

I consider the combined effects of constraints on movement and access to resources across spatial and temporal scales on livestock vulnerability to drought. The 2000 drought resulted in the death of large numbers of cattle across Kajiado District (David Nkedianye, personal communication). Over 80 % of the respondents in the study area lost cattle to drought in 2000. Large herds are recognized as an important drought survival technique in a number of pastoral societies, and the strong correlation between cattle herd size in 1999 and 2000 (Fig. 21a - b) suggests that this may be true in Amboseli as well. It appears that herds of intermediate size sustained the highest number of losses with the number of animals lost to starvation gradually increasing up to herd sizes of about 500 (Fig. 22c - d). This pattern is confirmed with a consideration of the proportion of the herd lost (Fig. 22e - f) which suggests that larger herds lost a smaller proportion of their animals with a potential threshold at a herd size of approximately 150 animals. Furthermore, the total number of cattle that died from all causes was strongly correlated with the total number of cattle that were lost to drought (Osilalei $R = 0.897$, Eselenkei $R = 0.830$, Lenkesim $R = 0.919$, Meshenani $R = 0.907$).

The proportion of herders who lost livestock in 2000 was significantly different between LUAs ($\chi^2 = 9.664$, df = 3, p-value = 0.022). In Lenkesim and Meshenani only one herder in each area did not lose any cattle. As expected, there were significant differences in the initial herd sizes between areas (Kruskal-Wallis, df=3, $p = 0.003$) with the most important difference occurring between Osilalei and Meshenani (Table 2). Post drought herd sizes followed a similar pattern with mean LUA losses ranging from 15% to 25%. Only Meshenani showed a significant decrease in herd size between 1999 and 2000 (Kruskal-Wallis multiple comparison test, $p < 0.05$). Contrary to initial expectations, there were no significant differences between the numbers of animals lost overall (Fig. 22a) or when data were subdivided into mobile and sedentary households (move vs no move, Table 2). The only marginal differences in the numbers lost by LUA were in those herders who did not travel off their group ranch (Kruskal-Wallis, df=3, $p = 0.036$).

Considering the variation in initial herd sizes in this study, the proportion of the total herd that was lost to drought is another useful indicator of relative drought impact across the study area. Lenkesim and Osilalei lost the highest proportions of their herds (Fig. 22a, Table 3). Similarly, although differences were not significant, sedentary herds in Osilalei and Meshenani lost the highest proportion overall, but the relative lack of sedentarism in the communal areas in contrast to Osilalei meant that their impact was greater in the subdivided area (Table 3, Fig. 2b). Similarly, there were no significant differences between years for mobile and sedentary herds, and both mobile and sedentary herds lost a similar proportion of animals in both years (Table 3). The mean proportions of the herd lost to drought were poorly correlated with any of the movement metrics

(Appendix 3). The only correlations that were significant ($p < 0.05$) were the positive relationships between $NDVI_{herd}$ and $NDVI_{mv}$ and drought losses in Osilalei and Meshenani respectively.

DISCUSSION

In the Greater Amboseli Ecosystem, land privatization and sedentarization have fragmented the pastoral system through altered settlement patterns (Worden 2007) and changes in the timing, location and extent of movement across spatial and temporal scales. I evaluated patterns of movement, forage access and drought vulnerability in four adjacent pastoral areas representing a land-use gradient ranging from communal access and management to small (approximately 25 hectares) individual land holdings. At the scale of daily grazing orbits the data indicated that land tenure and sedentarization have resulted in reductions in the sizes of cattle herds and possibly a decline in the overall daily distance traveled. Similarly, at the seasonal scale, privatization reduced intra annual movement.

During drought, however, there was evidence that the individualization of land tenure and livestock production may not reduce broad scale drought avoidance movements. Indeed, it appeared that changes in patterns of settlement and daily and seasonal grazing associated with subdivision may push herders in these areas to move their animals to communal areas with established drought reserves sooner and over longer distances during periods of extreme climatic stress. Contrary to initial predictions, there were no substantial differences in the ability of herders in different areas to access forage as indicated by cumulative annual NDVI scores. Data on the location and timing of moves indicated that most herds in the study area moved out into the reserved grazing areas as the dry season progressed and then back to the permanent settlement with the arrival of the rains. This controlled grazing pattern appears to be driven by the push of declining green forage biomass rather than the pull of higher greenness elsewhere. This tendency to use areas of below average NDVI ($NDVI_{dif}$) suggested that pastoralists employ a grazing strategy that aims to preserve standing biomass for dry season and drought utilization (Worden 2007). This strategy was corroborated in discussions with local Maasai, and appears to contrast markedly with the historical strategy that focused on maximizing access to high quality green forage (Western 1973). Drought vulnerability, as measured by livestock losses, was variable across all Land Use Areas with evidence suggesting that large herd sizes and mobility may provide a potential buffer to climatic perturbations.

Pastoral Mobility at Multiple Scales

Data from daily grazing orbits suggested that land privatization and sedentarization have led to smaller herd sizes, decreased grazing radii, and reduced access to grass banks far from permanent settlement and water. Differences in herd size were not significant between LUAs in this relatively small grazing orbit sample (n= 29). In the much larger sample of households from the monthly movement survey (n = 78), however, there were clear differences between LUAs with the subdivided area of Osilalei having the smallest mean herd size (Table 2). The length of the grazing radii, or maximum distance traveled, was only loosely correlated with herd size across the study area, and while there appears to be a trend towards reduced grazing radii in the subdivided and more sedentary areas of Osilalei and Eselenkei the differences between LUAs were variable (Appendix 1 Table 1). This lack of clear differentiation in grazing radii between the sites may reflect a real similarity in daily grazing patterns, or it may be the result of limited data. In particular, the small sample sizes, the lack of dry season grazing orbits for Osilalei when the largest differentiation between sites would be expected, and the relatively recent subdivision and settlement redistribution in Osilalei (Worden 2007) might all limit the detection of real differences. This last point is particularly important, and warrants further study, as there may be significant time lags in the effects of subdivision on daily patterns of movement. Although these results lend some support to my initial prediction that subdivision and sedentarization would result in reduced grazing radii, it appears that the current levels of subdivision and sedentarization observed in the study area have only a limited effect on cattle foraging at the daily time scale.

One clearly important characteristic of the daily grazing patterns in the Greater Amboseli Ecosystem is the strategy of alternating grazing and watering days. In contrast to other pastoral grazing systems reviewed in Coppolillo (2001), the Maasai in the GAE have long maintained a flexible grazing system in which herders may opt to graze their animals for between two and three days without taking water (this grazing period may be increased under extreme conditions when the only remaining forage is far from water). This strategy enables pastoralists to concentrate their herd's grazing effort away from the heavily utilized areas near water (Fig. 7). In contrast to the grazing patterns observed by Coppolillo (2000, 2001), herds in Amboseli commonly traveled farther than the distance to water with normal grazing radii extending up to nearly 9000m from the settlement of origin. The effectiveness of this system depends on the relative position of grazing resources in relation to water and the maintenance of grazing reserves and resource gradients through controls on settlement distribution and grazing patterns (Worden 2007). Although alternate grazing and watering days were still practiced in Osilalei, the widespread distribution of settlements across the landscape (Worden 2007) and the associated homogenization of resource gradients may be the reason that it is far less common than in neighboring areas.

At the seasonal level, an important shift in grazing patterns emerged with the collapse of the dry season *enkaron* settlement system under land privatization (Worden 2007). This is clearly evident in the data of seasonal, or intra- annual movements, with only eight percent of herds moving under normal circumstances in Osilalei. This contrasts markedly with the other three LUAs where over 80 % of all herds combined moved away from their permanent settlement in 1999. Across all areas, movement during normal conditions appears to peak during the dry season and coincides with periods of low green biomass (Figs. 17 and 18). The abandonment of this system of dry season movement to semi-permanent seasonal settlements was the core of a major shift in patterns of forage resource utilization in the Greater Amboseli Ecosystem.

Pastoral movements in the GAE historically mirrored those of wildlife – dispersing into waterless areas with the rains to take advantage of ephemeral high quality forage resources (Western 1973). This pattern has been observed in other pastoral livestock (Coppolillo 2001) and wild herbivore systems (Western 1975, Sinclair 1979, Fryxell and Sinclair 1988), and appears to be an effective strategy for ungulates in ecosystems where the distribution of water in dry seasons and droughts is localized rather than dispersed. As with the well known example of Kruger National Park (Owen-Smith 1996) the development of more widely dispersed water sources (Talbot 1972) and the subsequent changes in settlement patterns in the previously waterless areas of the GAE has resulted in a shift from a water limited to a forage limited pastoral system (Worden 2007). To dampen the effects of seasonality through the maintenance of gradients in forage availability, pastoralists in the group ranches north of Amboseli National Park developed a grazing system based on dry season dispersal. The dispersal of settlements across the landscape during 1997 in Osilalei appears to have disrupted this new system of forage gradients and dry season grazing reserves with implications for both intra and inter – annual movement patterns.

Drought induced movement in 2000 was highly variable across the study area. The fact that over 85 % of all respondents in the study area moved in 2000 suggests that the pastoral system in Greater Amboseli has retained a good deal of flexibility. What is less clear, however, is whether this level of movement is the result of a dynamic pastoral system where movement is preferred, or increasing constraints on movement caused by resource alienation, fragmentation, and sedentarization. As suggested above, in the communally managed areas of Eselenkei, Lenkesim, and Meshenani, mobility, although significantly different from previous generations, is still an established strategy for maintaining and accessing heterogeneous resources. In Osilalei, however, it appears that intra – annual mobility is no longer a core strategy. This difference between the subdivided and communal areas is even stronger when considered in the context of the drought induced mobility of 2000. Summaries of movement metrics indicate substantial differences between years for most metrics in all LUAs except Meshenani (Table 1b) with the most extreme differences occurring in Osilalei. Even more telling than the metrics is the difference in the total number of respondents who moved in each year. Although the number of herds that moved in Eselenkei and Lenkesim increased by 5 % and 100 % respectively, and Meshenani experienced a decline of 4 %, there was an eightfold increase in the number of herds that moved in Osilalei. This clear contrast between movement patterns for Osilalei in 1999 and 2000, when combined with evidence for decreasing herd sizes and increasing individualization of production, social fragmentation, and a reduction in the size and an increase in the dispersal of settlements (Worden 2007), indicates that movement and the ability to move are in gradual decline. Furthermore, these data suggest, and local informants confirm, that movement is always easier from private to communal land. As key resource areas continue to be privatized and alienated for agriculture and conservation, broad scale drought induced mobility will become increasingly difficult. Increasing constraints on access to heterogeneous forage resources at large spatial scales will require pastoralists to develop strategies, like the *enkaron* system, that create and maintain local heterogeneity and resource gradients and the ability to access them through movement.

Mobility and Access to Forage Resources

In this study, as in numerous other studies (Musiega and Kazadi 2004, Kawamura et al. 2005, Boone et al. 2006) green forage biomass was indexed using NDVI. The temporal and spatial continuity of remotely sensed data such as NDVI makes it an ideal tool for landscape scale studies (Kerr and Ostrovsky 2003). NDVI does have its limitations, however. For example, NDVI is designed to detect green vegetation and currently has limited utility in quantifying standing dry biomass (Marsett et al. 2006). There is also the potential for interference from woody vegetation and complications associated with soil reflectance (Pettorelli et al. 2005). Recognizing these potential limitations I selected study zones with similar levels of woody vegetation cover and soils (Touber 1983), amalgamated dekadal NDVI values to match monthly movement data when appropriate, and limited my inferences to green forage biomass. Using NDVI as a surrogate for green forage availability in this context has clear advantages as it facilitates the evaluation of movement at multiple spatial and temporal scales and helps move us towards a truly effective linkage between ground based ecological and social data and remote sensing.

Temporal patterns of forage availability as represented by mean NDVI greenness profiles (Fig. 11a) were similar across all LUAs. Differences in the magnitude and variability of NDVI values between LUAs at each time step were likely the result of underlying differences in landscape structure, but they may be exacerbated by differences in area and the scale of heterogeneity as larger areas may encompass more heterogeneity (Boone and Hobbs 2004). These background differences in the spatial and temporal patterns of forage availability, while relatively small, are evident in the differences in observed mean NDVI profiles for the different LUAs (Fig. 13a). The metric $NDVI_{mv}$ was developed to partly correct for differences in mean NDVI among LUAs, however, as it assessed NDVI experienced by the herds relative to the average NDVI at each herd's permanent settlement.(Fig. 13b). Thus, differences between LUAs in $NDVI_{mv}$ were primarily consequences of differences in movement. Another possible explanation for low $NDVI_{mv}$ values is that the simulated sedentary scenario described here may result in unnaturally high NDVI values as vegetation would have been grazed down more had the herd remained at the permanent settlement throughout.

Contrary to initial predictions, patterns of mean NDVI accumulation were highly variable across the study area (Fig. 14 and Appendix 1 Table 2a). Interestingly, three of the four LUAs had significant increases in mean NDVI values from 1999 to 2000. The lack of significant differences in $\mathrm{NDVI}_{\mathrm{mv}}$, however, suggest that while the observed increase in $\mathrm{NDVI}_{\mathrm{herd}}$ in 2000 is surprising in light of the drought conditions in 2000 this may be a function of background conditions rather than pastoralists ability to increase access to green forage through movement These patterns suggest that for pastoral systems on the edge the timing and persistence of the vegetative response to rainfall may ultimately be more important than the absolute magnitude of that response. There were significant differences in standardized mean $\mathrm{NDVI}_{\mathrm{mv}}$ between LUAs for 1999 but not for 2000. Differences among LUAs in $\mathrm{NDVI}_{\mathrm{herd}}$ of mobile and sedentary herds were both highly variable. There were no significant differences among LUAs for mobile herds in either 1999 or 2000. More importantly there were essentially no differences between sedentary and mobile herds for $\mathrm{NDVI}_{\mathrm{herd}}$ in either year (Appendix 1 Table 3b). Thus, my prediction that land privatization and sedentarization would reduce herder's access to green forage resources as indicated by NDVI has little support in the data. Under normal conditions (1999) the subdivided area of Osilalei had intermediate $\mathrm{NDVI}_{\mathrm{mv}}$ values. There was some evidence that Osilalei herders had the lowest $\mathrm{NDVI}_{\mathrm{mv}}$ values in 2000 but the differences were not significant. Mobile herds in Osilalei also appear to have the lowest $\mathrm{NDVI}_{\mathrm{mv}}$ values but again the differences between LUAs were not significant.

I predicted that movement would enhance access to green forage resources as indicated by NDVI. In general, movement metrics were not correlated with NDVI (Appendix 2 Table 1). Although there were exceptions to this pattern, the overall lack of significance in correlations between movement metrics and $\mathrm{NDVI}_{\mathrm{herd}}$ and $\mathrm{NDVI}_{\mathrm{mv}}$ indicates that the relationship between movement and forage resources is more complex than initially predicted. Indeed, in all areas except Osilalei, the majority of the $\mathrm{NDVI}_{\mathrm{herd}}$ values for herds that had moved away from their permanent settlements were lower than what they would have achieved if they had not moved (Fig. 16). It appears that pastoralists in the Greater Amboseli Ecosystem were not moving to access areas of high NDVI per se, but rather were pushed to the next grazing stage by local declines in green forage biomass. Low monthly NDVI values were correlated with an increased number of moves the following month (Fig. 17 and 18) and it appears that in some instances herders were not taking advantage of the areas of highest greenness within their universe of potential moves (Fig. 19 and 20)

In contrast to the wet season dispersal system previously recorded for pastoralists in the Amboseli Ecosystem (Western, 1973), the Maasai in the group ranches north of Amboseli National Park have developed a new dry season dispersal system that appears to depend upon maximizing access to gradients of standing dry forage rather than ephemeral high quality wet season forage. Land privatization appears to be undermining this system of dry season grazing reserves in Osilalei through declines in intra-annual mobility and shifts in settlement patterns (Chapter 2), with the result that off-ranch resources are increasingly important for the survival of cattle herds during drought. These data suggest that movement continues to be an important mechanism for drought avoidance across the study area, but changes in the timing of movement and the resulting NDVI accumulation patterns indicate that there has been a fundamental shift in the nature of movement. It is also clear that while there is still a high degree of flexibility within the study area, pastoralists have become more aware of the limitations of movement in an increasingly fragmented and constrained ecosystem and are managing their resources in the communal areas accordingly. Movement in the privately owned area was clearly based on necessity and was fundamentally dependent on the protection and maintenance of dry season grazing reserves in non-fragmented communal areas.

Livestock Losses and Drought Vulnerability

Patterns of cattle losses, like those of NDVI accumulation, were highly variable across the study area. As with other studies, drought or lack of forage was the most frequent cause of death in livestock in the study area (Rainy and Worden 2003). It is important to recognize, however, that drought related stress may increase mortality from different causes as well. For instance, drought stress increases an animal's susceptibility to disease and movement to new areas to access forage often exposes livestock to new diseases, insecurity, and enhanced predation pressure. Interestingly, the relationship between herd size and drought losses was non-linear with larger herds experiencing lower than expected losses. This observation provides an explanation for why pastoralists desire larger herds. Similarly, it highlights the difficulties facing pastoralists with average herd sizes in an increasingly constrained ecosystem. Contrary to predictions there were no significant differences in mean values of total cattle lost or proportion of herd lost between LUAs (Table 3). Although the results were not significant, the subdivided area of Osilalei lost a relatively high proportion of their herds with sedentary herders getting hit particularly hard. Initially small herd sizes combined with the relatively high proportion of sedentary herds and the higher losses associated with those herds means that pastoralists in Osilalei were disproportionately impacted by the drought. Few of the correlations between movement metrics and drought losses were significant, but the ones that were suggested that drought losses may have actually increased with increasing access to NDVI. Mobility is clearly an important strategy for avoiding drought in the Greater Amboseli Ecosystem but broad scale mobility is also costly. A grazing system that can maintain forage reserves through controls on settlement and utilize regular fine scale proactive rather than broad scale reactive movements will be at a distinct advantage in the increasingly fragmented rangelands of southern Kenya.

An important consideration when evaluating the effect of drought on pastoral populations through changes in herd size is the relationship between total number lost and the proportion of animals lost, and the implications for drought recovery. Discussions with local Maasai suggest that pastoralists don't evaluate the impact of the drought by the total number of animals lost but rather on the amount that remain. In this scenario, a herder with 200 who lost 50 is much better off than a herder who started with 50 and lost 10. The lack of emphasis on the total numbers lost indicates that the value of livestock is still widely perceived in the context of subsistence and potential production rather than as a commodity. This discrepancy between the market value and perceived value of livestock lost to drought has potentially important implications for managing stocking rates in Africa. Although these attitudes are likely to change as herds become smaller, production becomes increasingly individualized, pastoralists are further integrated into the market economy, and rangelands are increasingly constrained, the current system appears to favor large herd sizes which tend to increase pressure on limited resources and exacerbate resource access inequalities in the absence of strict grazing controls.

Mobility and Changing Land Tenure, the future of pastoralism in EA

Historically, Maasai in the GAE exhibited two types of movement as described by Oba and Lusigi (1987) – 1) resource exploitation mobility and 2) escape mobility. These results demonstrate that extreme range congestion and fragmentation has resulted in the collapse of resource exploitation mobility. The shift from a wet to a dry season dispersal system (Worden 2007) has meant that livestock are no longer accessing ephemeral wet season forage resources at the time of peak quality, but rather are concentrating in former dry season areas of poorer quality and often degraded forage resources. Data presented here suggest that pastoralists in the Greater Amboseli Ecosystem are no longer moving to the areas of highest forage quality within their annual range and that intra-annual, or seasonal, mobility has shifted in focus and been reduced in scale. Although pastoralists in the study area may still search out ephemeral high quality forage resources within their daily grazing orbits, grazing patterns at the seasonal scale focus on enhancing the conservation of forage quantity through the lean dry season.

Inter-annual, or drought induced mobility (what Oba and Lusigi, 1987 refer to as escape mobility) is constrained in its spatial extent through fragmentation and the loss of key resources to cultivation, conservation, and privatization, and it is possibly less achievable for certain members of the community due to the disintegration of social relationships and the individualization of production (BurnSilver in prep, in press). Yet, it is still practiced in the Greater Amboseli Ecosystem and elsewhere in Kajiado District. Where daily grazing orbits and intra-annual movements have become increasingly constrained with the fragmentation of the rangelands, escape mobility continues to be practiced over broad scales. Indeed, fragmentation and congestion may in fact require more frequent and longer range drought induced mobility among pastoralists in the study area as local grazing reserves disappear and sedentarization prevents the dynamic shifting mosaic of grazing disturbance necessary for the sustainability of plant-herbivore interactions (Coughenour 1991).

Historically, movement was something that people did to take advantage of high quality ephemeral resources to maximize production. Now with increasing constraints movement is something that is done to minimize losses in the face of diminishing resources and range congestion. Increasingly, movement appears to be something that pastoralists "have" to do rather than "want" to do. As we explore the possibility that sedentarization under certain circumstances may not reduce mobility we must consider how it affects the different facets of mobility and how it might alter patterns of movement at different levels and scales (Kelly 1992). For instance, we need to differentiate between planned moves, such as the seasonal enkaron system maintained in some areas of the Greater Amboseli Ecosystem, and moves of last resort. The former, while clearly constrained by increasingly fragmented rangelands, is an indicator of a proactive pastoral system that recognizes the importance of grazing reserves. The latter, such as we see in the subdivided area of Osilalei, suggests a system in transition that is losing the ability to maintain reserve grazing areas. The increasing sedentarization we see reflected in the lack of seasonal movement in Osilalei contrasts sharply with the broad scale movements employed during the 2000 drought and highlights the limitations of a dispersed settlement system and the individualization of production associated with subdivision, and the dependence of these herders on grazing reserves in communally managed areas during times of stress.

CONCLUSIONS

Mobility is complex and multidimensional (Kelly 1992). This study demonstrates that subdivision and sedentarization reduce mobility at the daily to seasonal time scales, but have unanticipated consequences for inter-annual or drought-induced mobility. Similarly, although there is some evidence that movement increases herder's access to green forage, this was less than expected suggesting that there may be fundamental changes in the nature of mobility in the increasingly constrained rangelands of East Africa. Finally, although there are clear differences in the herd sizes supported under normal conditions in the privately and communally managed systems, the persistence of open access areas and drought mobility in the face of, or possibly because of, subdivision and sedentarization resulted in little difference in the overall number of cattle and proportion of the herd lost to drought, indicating that drought-induced mobility continues to be an important strategy for stabilizing pastoral livestock populations despite increasing fragmentation. Ultimately, while these analyses are intended to help to enhance our understanding of the evolving patterns and processes of mobility in contemporary pastoral societies and its importance in the management and conservation of these increasingly threatened rangeland ecosystems, there is still much work to be done. Indeed, it is only through long-term and widespread monitoring that we can understand the changing and multifaceted nature of mobility in contemporary pastoral society and its implications for the sustainability and conservation of the world's arid and semi-arid ecosystems.

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TABLES

Table 1a. Differences between Land Use Areas (LUAs) and years for movement variables. Means with standard error in parentheses. Different superscript letters indicate significant differences between LUA means (Kruskal- Wallis multiple comparison test, $p < 0.05$). Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

Table 1a.

	1999				2000			
	Osilalei	Eselenkei	Lenkesim	Meshenani	Osilalei	Eselenkei	Lenkesim	Meshenani
Number of Households	24	23	18	23	24	23	18	23
Number of Households Moved	2	20	9	23	16	21	18	22
Househlds Moved in 99 & 00	–	–	–	–	2	20	9	22
Number of Places	0.08 (0.05)^{a}	1.04 (0.13)^{ab}	0.61 (0.16)^{a}	1.04 (0.04)^{b}	0.79 (0.13)^{a}	2 (0.2)^{b}	2.05 (0.22)^{b}	1.39 (0.13)^{a}
Number of Months Away	0.25 (0.17)^{ad}	2.65 (0.38)^{bc}	1.44 (0.43)^{bd}	3.39 (0.25)^{c}	3.33 (0.56)^{a}	4.43 (0.38)^{ab}	5.33 (0.42)^{b}	5.17 (0.46)^{ac}
Month of First Move	0.66 (0.46)^{a}	7.6 (0.67)^{abc}	4.44 (1.11)^{b}	7.6 (0.46)^{c}	4.25 (0.68)^{a}	6.52 (0.47)^{a}	6.5 (0.35)^{a}	6.82 (0.39)^{a}
Number of Moves off GR	0 (0)^{a}	0.04 (0.04)^{a}	0.16 (0.12)^{a}	0 (0)^{a}	0.5 (0.12)^{a}	0.39 (0.16)^{a}	0.55 (0.21)^{a}	0.13 (0.09)^{a}
Number of Months off GR	0 (0)^{a}	0.04 (0.04)^{a}	0.22 (0.15)^{a}	0.17 (0.17)^{a}	1.87 (0.43)^{a}	0.56 (0.21)^{a}	1.27 (0.47)^{a}	0.26 (0.19)^{a}
Month of First Move off GR	0 (0)^{a}	0.47 (0.47)^{a}	1.16 (0.8)^{a}	0.04 (0.04)^{a}	3.2 (0.73)^{a}	2.56 (0.92)^{a}	2.72 (0.94)^{a}	0.52 (0.38)^{a}
Total Distance Traveled	1290 (892)^{a}	9114 (2663)^{bc}	9823 (4335)^{a}	12728 (2179)^{b}	50607 (12865)^{a}	37325 (7933)^{a}	38681 (7871)^{a}	18141 (5034)^{a}
Max Distance Traveled	645 (446)^{a}	4717 (1330)^{bc}	5954 (2744)^{a}	7942 (1479)^{b}	25239 (6336)^{a}	17598 (3676)^{a}	16746 (3597)^{a}	8441 (2091)^{a}
Mean Distance per Move	645 (446)^{a}	4419 (1316)^{bc}	4696 (2138)^{a}	6718 (1039)^{b}	23340 (5859)^{a}	11227 (1955)^{a}	12446 (2093)^{a}	8377 (1670)^{a}
Mean Distance per Month Away	430 (297)^{a}	4980 (2680)^{bc}	4695 (2181)^{a}	3951 (582)^{b}	11411 (3070)^{a}	8082 (1774)^{a}	7389 (1399)^{a}	4572 (1389)^{a}

Table 1b P Values for the differences between 1999 and 2000 for movement variables by Land Use Area (LUA). Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

	Osilalei	Eselenkei	Lenkesim	Meshenani
Number of Places	< 0.001	< 0.001	< 0.001	0.017
Number of Months Away	< 0.001	< 0.001	< 0.001	0.002
Month of First Move	< 0.001	0.002	0.413	0.013
Number of Moves off GR	< 0.001	0.041	0.117	0.162
Number of Months off GR	< 0.001	0.036	0.078	0.590
Month of First Move off GR	< 0.001	0.055	0.192	0.538
Total Distance Traveled	< 0.001	< 0.001	< 0.001	0.560
Max Distance Traveled	< 0.001	< 0.001	< 0.001	0.709
Mean Distance per Move	< 0.001	< 0.001	< 0.001	0.496
Mean Distance per Month Away	< 0.001	0.006	0.005	0.231

Table 2. Summary of cattle herd characteristics by Land Use Area (LUA). Means with SE in parentheses. Different superscript letters indicate significant differences between LUA means (Kruskal- Wallis multiple comparison test, $p < 0.05$). Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

	Osilalei	Eselenkei	Lenkesim	Meshenani
Sample size	24	23	18	23
Prop of obs that lost cattle in 2000	0.79	0.65	0.94	0.96
Herd Size - 1999	44 (10.4)^{a}	77.5 (22)^{ab}	74.4 (24.6)^{ab}	138 (47.7)^{b}
Herd Size - 2000	33.4 (8.8)^{a}	65.2 (18.1)^{ab}	59.1 (20.4)^{ab}	115.4 (45.4)^{b}
Total died	7.6 (1.7)^{a}	10.3 (3.7)^{a}	13.4 (4)^{a}	10.6 (1.8)^{a}
Total starved	7.3 (1.8)^{a}	9.8 (3.7)^{a}	13.2 (4.1)^{a}	10 (1.7)^{a}
Total starved - move	7.1 (1.4)^{a}	10.7 (3.8)^{a}	13.2 (4.1)^{a}	9.8 (1.7)^{a}
Total starved - no move	7.9 (2.4)^{a}	0 (0)^{a}	–	14 (*)^{a}
Total starved - off GR	8.5 (1.7)^{a}	17.8 (6.3)^{a}	7.8 (1.8)^{a}	4 (0.3)^{a}
Total starved - no off GR	6.4 (1.9)^{a}	6.9 (2.2)^{a}	15.9 (4.8)^{a}	10.5 (1.7)^{a}

* single observation

Table 3. Mobile versus sedentary contrast of percent herd lost to drought. Land Use Area (LUA) differences are means and standard errors (parentheses) by mobility category, year and LUA. Different superscript letters indicate significant differences between study zone means (Kruskal- Wallis multiple comparison test, $p < 0.05$). Annual differences are p values for differences between 1999 and 2000 between mobility categories within LUAs. Mobility differences are p values for differences in the proportion of the herd lost to drought in 2000 for mobility categories in 1999 and 2000 within LUAs. Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

			Osilalei	Eselenkei	Lenkesim	Meshenani
Zonal Differences	Mobile	1999	0.114(0.022)^{ab}	0.084(0.021)^{a}	0.199(0.021)^{b}	0.111(0.013)^{ab}
		2000	0.155(0.025)^{ab}	0.103(0.028)^{a}	0.195(0.028)^{b}	0.107(0.012)^{ab}
	Sedentary	1999	0.178(0.031)^{a}	0.167(0.06)^{a}	0.191(0.036)^{a}	--
		2000	0.208(0.039)^{a}	0(0)^{a}	--	0.215(*)^{a}
Annual Differences	Mobile		0.944	0.802	0.738	0.829
	Sedentary		0.758	0.683	--	--
Mobility Differences		1999	0.753	0.709	0.536	--
		2000	0.580	0.095	--	0.132

Appendix 1

Table 1. Mean number of cattle per herd and mean maximum distance the herd traveled from settlement by Land Use Area (SE in parentheses). Total orbits include all single day orbits and the mean values for multiday orbits. The subsequent sections of the table use the same data separated into different categories – Emparnat (permanent settlements) and Enkaron (seasonal settlements), Wet and Dry seasons, and Watering and Grazing (non-watering) orbits. The number of orbits for the Single and Multi – day records and their distribution over the sample households is presented in the first two rows (read 5 / 5 as 5 orbits from 5 households). Different superscript letters indicate significant differences between study zone means (Kruskal- Wallis multiple comparison test, $p < 0.05$). Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

Appendix 1. Table 1.

		Osilalei	Eselenkei	Lenkesim	Meshenani
Number of Orbits	Single	5/5	11 / 5 *	9 / 5 **	13 / 7 ***
	Muli-day		4 / 1 and 6 / 1	20 / 4 and 4 / 1	
Herd Size	All Combined	29.6(4.32) ^{a}	95.77(15.05)^{abc}	101.82(11.82)^{b}	194.08(63.39)^{c}
	Empart	29.6(4.32) ^{a}	81.43(23.68) ^{a}	100.81(17.35) ^{a}	143.78(52.2) ^{a}
	Enkaron	—	112.5(16.99)	103.17(16.87)	307.25(172.4)
	Wet Season	29.6(4.32) ^{a}	90.67(25.79) ^{a}	86.5(18.36) ^{a}	128.67(61.89) ^{a}
	Dry Season	—	100.14(18.95)	113.31(15.14)	250.14(105.14)
	Water Dependent	29.6(4.32) ^{a}	78.63(19.36)^{ab}	91.3(14.78)^{b}	111.75(46.7) ^{a}
	Water Independent	—	116.33(17.92)	104.89(16.46)	325.8(134.87)
Max Distance Traveled	All Combined	2361 (171) ^{a}	3886 (194)^{ab}	4833 (152)^{b}	4778 (161)^{ab}
	Empart	2361 (171)^{a}	2872 (220) ^{a}	4505 (177) ^{a}	4959 (185) ^{a}
	Enkaron	—	5070 (83)	5272 (111)	4369 (149)
	Wet Season	2361 (171) ^{a}	2868 (229) ^{a}	4457 (225) ^{a}	4192 (189) ^{a}
	Dry Season	—	4759 (115)	5116 (94)	5280 (150)
	Water Dependent	2361 (171) ^{a}	3352 (261)^{ab}	4942 (199)^{b}	3960 (183)^{ab}
	Water Independent	—	5019 (84)	4860 (100)	6086 (125)

* one extra dry season orbit recorded for one household

** one dry season and no wet season recorded for one household

*** two extra households were added with a single dry season orbit only recorded for one

Table 2a. $NDVI_{herd}$ and $NDVI_{mv}$ values for herd movements by LUA and year. Means with SE in parentheses. Different superscript letters indicate significant differences between LUA means (Kruskal- Wallis multiple comparison test, $p < 0.05$). Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

Appendix 1. Table 2a.

		Osilalei	Eselenkei	Lenkesim	Meshenani
$NDVI_{herd}$	1999	$3797.52(38.43)^{a}$	$3220.45(12.53)^{abc}$	$3181.8(11.8)^{b}$	$3089.91(39.36)^{c}$
	2000	$4013.73(17.06)^{a}$	$3653.94(15.91)^{ab}$	$3278.82(15.43)^{b}$	$3018.08(41.01)^{c}$
$NDVI_{mv}$	1999	$0.69(1.46)^{a}$	$0.4(1.87)^{bc}$	$-6.87(8.01)^{ac}$	$40.06(15.88)^{bc}$
	2000	$-9.66(11.31)^{a}$	$10.28(3.64)^{a}$	$15.14(11.16)^{a}$	$12.04(8.08)^{a}$

Table 2b. P values for the differences in $NDVI_{herd}$ and $NDVI_{mv}$ values between years (1999 and 2000) for each LUA. Different superscript letters indicate significant differences between LUA means (Kruskal- Wallis multiple comparison test, $p < 0.05$). Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

Appendix 1. Table 2b.

	Osilalei	Eselenkei	Lenkesim	Meshenani
$NDVI_{herd}$	< 0.001	< 0.001	< 0.001	0.455
$NDVI_{mv}$	0.644	0.016	0.072	0.468

Table 3a. $NDVI_{herd}$ and $NDVI_{mv}$ values for herd movements, and by mobility, LUA, and year. Means with SE in parentheses. Different superscript letters indicate significant differences between LUA means (Kruskal- Wallis multiple comparison test, $p < 0.05$). Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

Apendix1. Table 3a.

			Osilalei	Eselenkei	Lenkesim	Meshenani
Mobile	$NDVI_{herd}$	1999	3801.1(23.6)^{a}	3217.5(13.2)^{ab}	3173.5(15.7)^{a}	3089.9(39.4)^{b}
		2000	4024.4(14.4)^{a}	3652.5(16.4)^{a}	3278.8(15.4)^{b}	3010.8(41.3)^{b}
	$NDVI_{mv}$	1999	8.3(6.6)^{a}	0.5(2)^{a}	-13.7(11.4)^{a}	40.1(15.9)^{a}
		2000	-14.5(13.9)^{a}	11.3(3.8)^{a}	15.1(11.2)^{a}	12.6(8.3)^{a}
Sedentary	$NDVI_{herd}$	1999	3797.2(39.9)^{a}	3240(6.6)^{ab}	3190.1(6.4)^{b}	--
		2000	3992.4(21.9)^{a}	3669.4(14.2)^{a}	--	3177.5(*)^{a}
	$NDVI_{mv}$	1999	NA	NA	NA	NA
		2000	NA	NA	NA	NA

Table 3b. P values for differences between years for mobile and sedentary herders in each LUA. P values for differences between mobile and sedentary herders in each LUA by year. Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

Appendix 1. Table3b.

		Osilalei	Eselenkei	Lenkesim	Meshenani
$NDVI_{herd}$	Mobile	0.013	< 0.001	< 0.001	0.395
	Sedentary	0.026	0.2	NA	NA
$NDVI_{mv}$	Mobile	0.837	0.009	0.131	0.563
	Sedentary	NA	NA	NA	NA
1999	NDVI	0.754	0.235	0.825	NA
2000	NDVI	0.245	0.445	NA	0.132

Appendix 2

Table 1. Spearman's R correlations and p values for the relationship between movement variables and mean NDVI$_{herd}$ and NDVI$_{mv}$ values by year and LUA. Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey

Appendix 2. Table 1.

		1999								2000							
		Osilalei	Osil_p	Eselenkei	Esel_p	Lenkesim	Lenk_p	Meshenani	Mesh_p	Osilalei	Osil_p	Eselenkei	Esel_p	Lenkesim	Lenk_p	Meshenani	Mesh_p
NDVI$_{herd}$	NDVI$_{herd}$	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0
	NDVI$_{mv}$	-0.125	0.56	0.107	0.626	0.577	0.012	0.252	0.247	-0.079	0.713	0.763	<0.001	0.73	0.001	0.024	0.913
	Total Distance Traveled	-0.06	0.781	-0.212	0.332	-0.014	0.955	0.563	0.005	-0.068	0.753	-0.326	0.129	0.631	0.006	0.257	0.237
	Max Distance Traveled	-0.06	0.781	-0.222	0.309	-0.052	0.838	0.516	0.012	-0.047	0.829	-0.383	0.072	0.542	0.022	0.273	0.207
	Mean Distance per Move	-0.06	0.781	-0.2	0.36	-0.014	0.955	0.521	0.011	-0.013	0.952	-0.377	0.076	0.562	0.017	0.183	0.402
	Mean Dist per Month Away	-0.06	0.781	-0.224	0.304	0.012	0.962	0.61	0.002	0.006	0.979	-0.233	0.285	0.395	0.105	0.327	0.128
	Number of Moves	-0.065	0.762	-0.191	0.383	-0.076	0.766	0.311	0.148	0.017	0.936	-0.302	0.161	0.403	0.097	0.25	0.25
	Number of Places	-0.065	0.762	-0.166	0.449	-0.159	0.529	0.354	0.098	0.065	0.761	-0.404	0.056	0.399	0.101	0.16	0.465
	Number of Months Away	-0.065	0.762	-0.246	0.257	-0.165	0.514	0.098	0.655	0.075	0.729	-0.489	0.018	0.359	0.144	-0.552	0.006
	Month of First Move	-0.065	0.762	-0.152	0.489	0.004	0.986	-0.26	0.231	0.308	0.143	0.34	0.113	-0.391	0.108	0.271	0.212
	Number of Moves off GR	—	—	-0.129	0.559	-0.032	0.899	—	—	-0.172	0.422	-0.128	0.559	0.041	0.873	-0.024	0.913
	Number of Months off GR	—	—	-0.129	0.559	0	1	0.289	0.181	-0.249	0.24	-0.12	0.584	0.049	0.846	-0.024	0.913
	Month First Move off GR	—	—	-0.129	0.559	-0.032	0.899	0.289	0.181	-0.106	0.623	-0.174	0.426	-0.005	0.984	-0.024	0.913
NDVI$_{mv}$	NDVI$_{herd}$	-0.125	0.56	0.107	0.626	0.577	0.012	0.252	0.247	-0.079	0.713	0.763	<0.001	0.73	0.001	0.024	0.913
	NDVI$_{mv}$	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0
	Total Distance Traveled	-0.043	0.84	-0.136	0.537	0.15	0.554	0.586	0.003	0.106	0.623	-0.106	0.629	0.457	0.058	-0.284	0.189
	Max Distance Traveled	-0.043	0.84	-0.107	0.627	0.11	0.665	0.653	0.001	0.028	0.897	-0.161	0.464	0.377	0.123	-0.3	0.164
	Mean Distance per Move	-0.043	0.84	-0.05	0.822	0.15	0.554	0.652	0.001	0.073	0.734	-0.146	0.507	0.385	0.115	-0.236	0.279
	Mean Dist per Month Away	-0.043	0.84	0.007	0.973	0.114	0.652	0.459	0.028	0.125	0.559	-0.028	0.898	0.296	0.23	-0.425	0.043
	Number of Moves	0	1	-0.118	0.592	0.179	0.478	0.104	0.637	0.188	0.38	-0.038	0.865	0.358	0.145	-0.401	0.058
	Number of Places	0	1	-0.247	0.256	0.077	0.762	0.354	0.098	0.15	0.484	-0.131	0.55	0.345	0.161	-0.108	0.623
	Number of Months Away	0	1	-0.23	0.292	0.149	0.556	0.457	0.028	0.084	0.696	-0.113	0.608	0.255	0.308	0.319	0.138
	Month of First Move	0	1	0.149	0.496	-0.018	0.944	-0.452	0.031	0.211	0.322	0.42	0.046	-0.258	0.301	-0.493	0.017
	Number of Moves off GR	—	—	0.354	0.097	-0.034	0.892	—	—	0.197	0.357	-0.012	0.958	-0.078	0.759	-0.489	0.018
	Number of Months off GR	—	—	0.354	0.097	0	1	0.321	0.135	0.197	0.356	-0.008	0.97	-0.093	0.715	-0.489	0.018
	Month First Move off GR	—	—	0.354	0.097	-0.034	0.892	0.321	0.135	0.405	0.049	-0.08	0.716	-0.174	0.49	-0.489	0.018

Appendix 3

Table 1. Spearman's R correlations and p values for the relationship between NDVI and movement variables, and the proportion of the cattle herd that died from drought. Osilalei, the LUA that has been subdivided into individual land holdings, is shaded in grey.

Appendix 3. Table 1

	Osilalei	Osil_p	Eselenkei	Esel_p	Lenkesim	Lenk_p	Meshenani	Mesh_p
$NDVI_{herd}$	0.453	0.026	0.042	0.848	0.126	0.618	0.262	0.226
$NDVI_{mv}$	-0.078	0.718	0.217	0.320	0.085	0.738	0.471	0.023
CV $NDVI_{herd}$ (mean)	-0.261	0.218	0.059	0.790	0.049	0.848	0.319	0.138
CV $NDVI_{mv}$ (mean)	-0.048	0.825	-0.101	0.646	-0.342	0.165	0.149	0.498
Total Distance Traveled	-0.185	0.388	0.199	0.363	0.171	0.496	-0.276	0.202
Max Distance Traveled	-0.138	0.519	0.206	0.346	0.191	0.448	-0.332	0.122
Mean Distance per Move	-0.103	0.633	0.251	0.248	0.152	0.548	-0.272	0.209
Mean Distance per Month Away	-0.075	0.727	0.159	0.470	0.106	0.674	-0.193	0.377
Number of Moves	-0.199	0.350	0.181	0.410	0.112	0.658	-0.327	0.127
Number of Places	-0.221	0.300	0.040	0.856	0.067	0.791	-0.305	0.157
Number of Months at Home	0.328	0.118	-0.060	0.787	0.076	0.764	0.214	0.327
Number of Months Away	-0.328	0.118	0.060	0.787	-0.076	0.764	-0.214	0.327
Month of First Move	0.109	0.612	0.163	0.458	-0.009	0.972	-0.256	0.238
Number of Moves off GR	-0.082	0.705	0.085	0.700	-0.232	0.354	-0.305	0.157
Number of Months off GR	-0.198	0.355	0.102	0.644	-0.263	0.292	-0.305	0.157
Month of First Move off GR	0.060	0.782	0.109	0.620	-0.315	0.203	-0.305	0.157

FIGURES

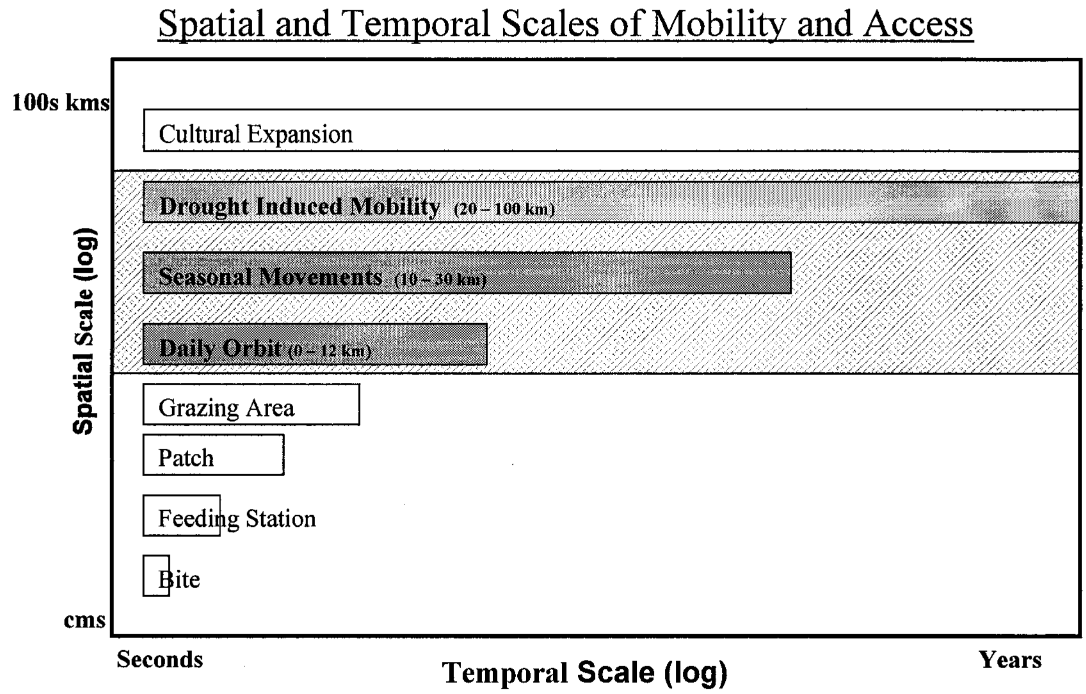


Figure 1. Describes the different spatial and temporal scales of mobility and access for wild and domestic herbivores. This study focuses on the intermediate and broad scale patterns highlighted in the shaded box – daily orbits, seasonal movements, and drought induced mobility (adapted from Senft *et al*, 1987 and Bailey *et al*, 1996).

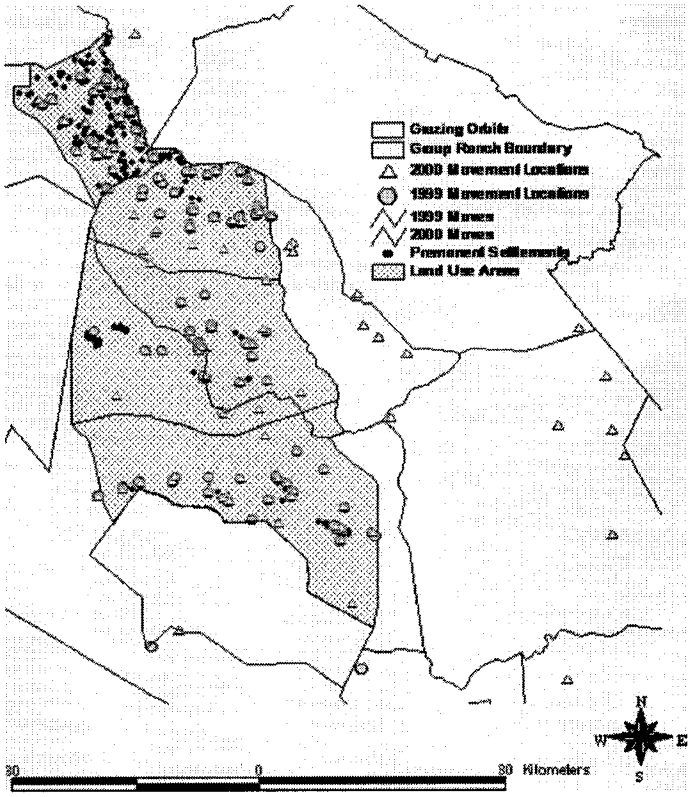


Figure 2. Map of the study area including all the locations recorded in the informant interviews, the settlement census area (LUAs) and current settlement distribution (black dots), and group ranch boundaries.

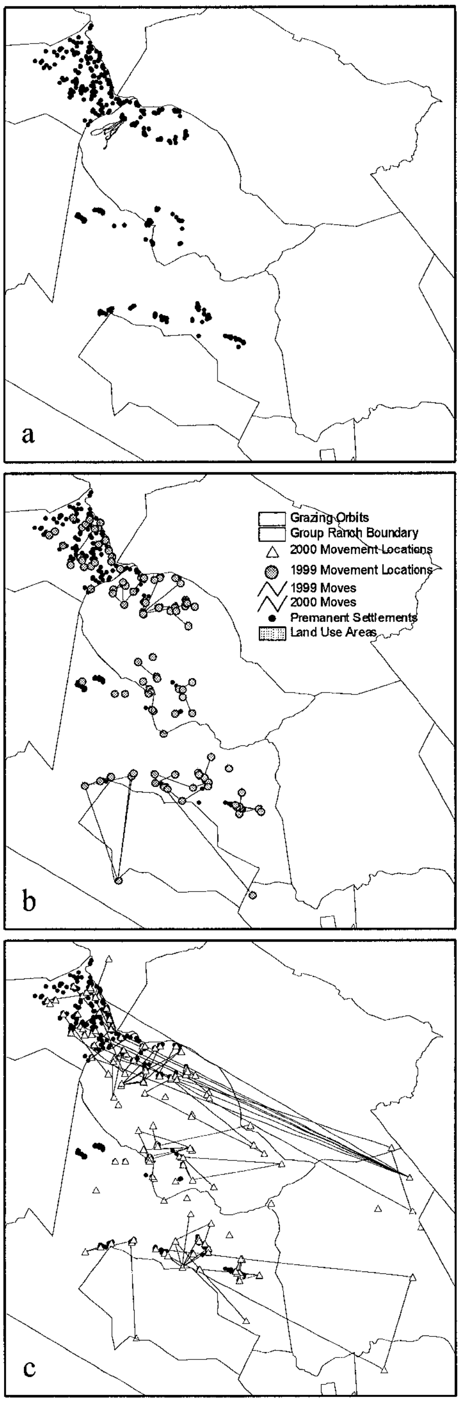


Figure 3. Examples of the 3 different scales and types of movement under consideration in this chapter – daily orbits (a), seasonal movements between permanent and dry season settlements (b), and long distance drought induced movements (c). Only a subset of movements are shown for clarity.

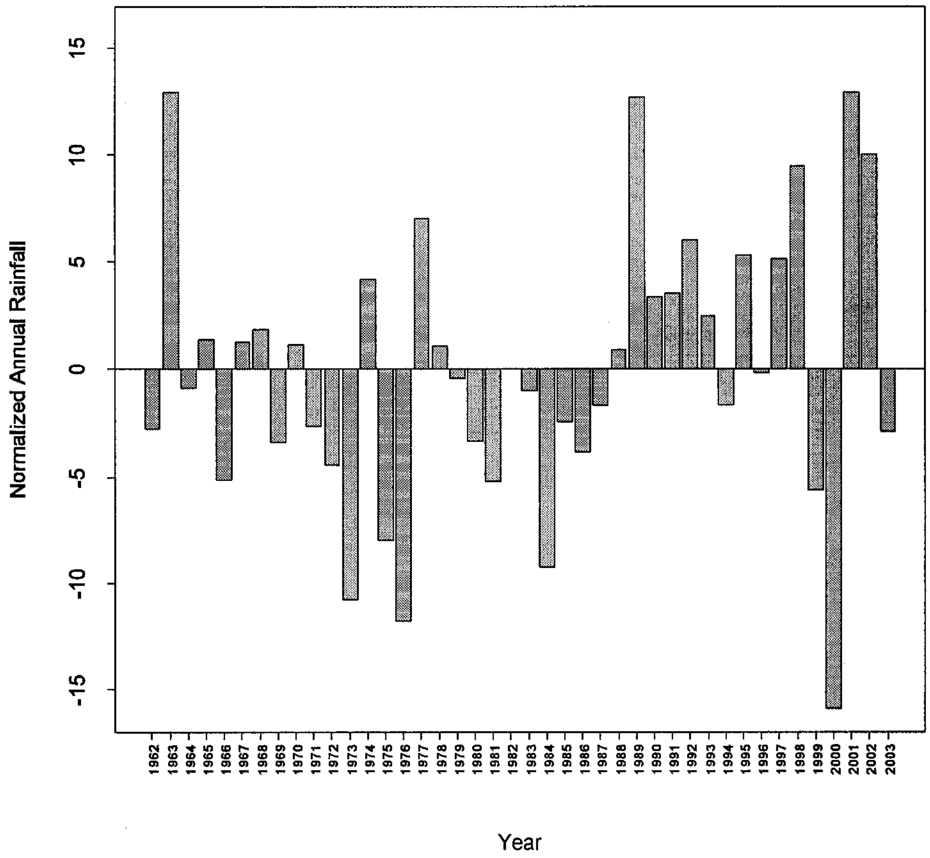


Figure 4. Normalized rainfall deviations from the long term mean. Rainfall data from the Kenya Meteorological Department – Maasai Technical Training Centre, Kajiado Kenya.

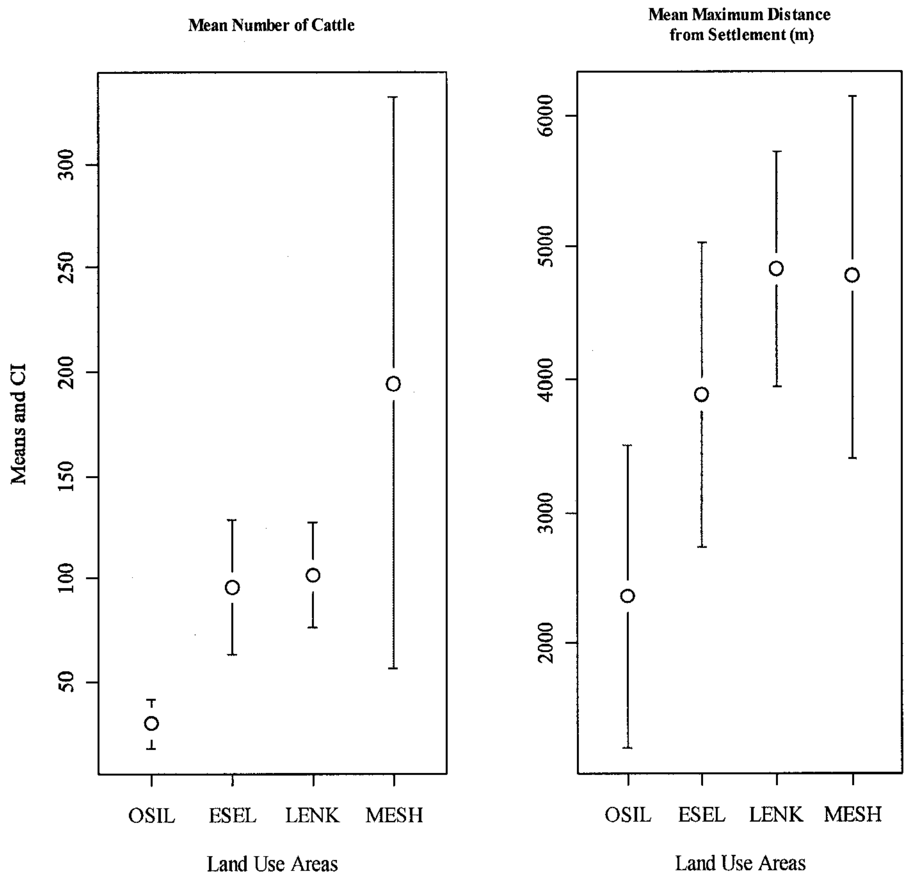


Figure 5. The mean number of cattle per herd and the mean maximum distance from the settlement of origin that each herd travelled during grazing orbits by LUA.

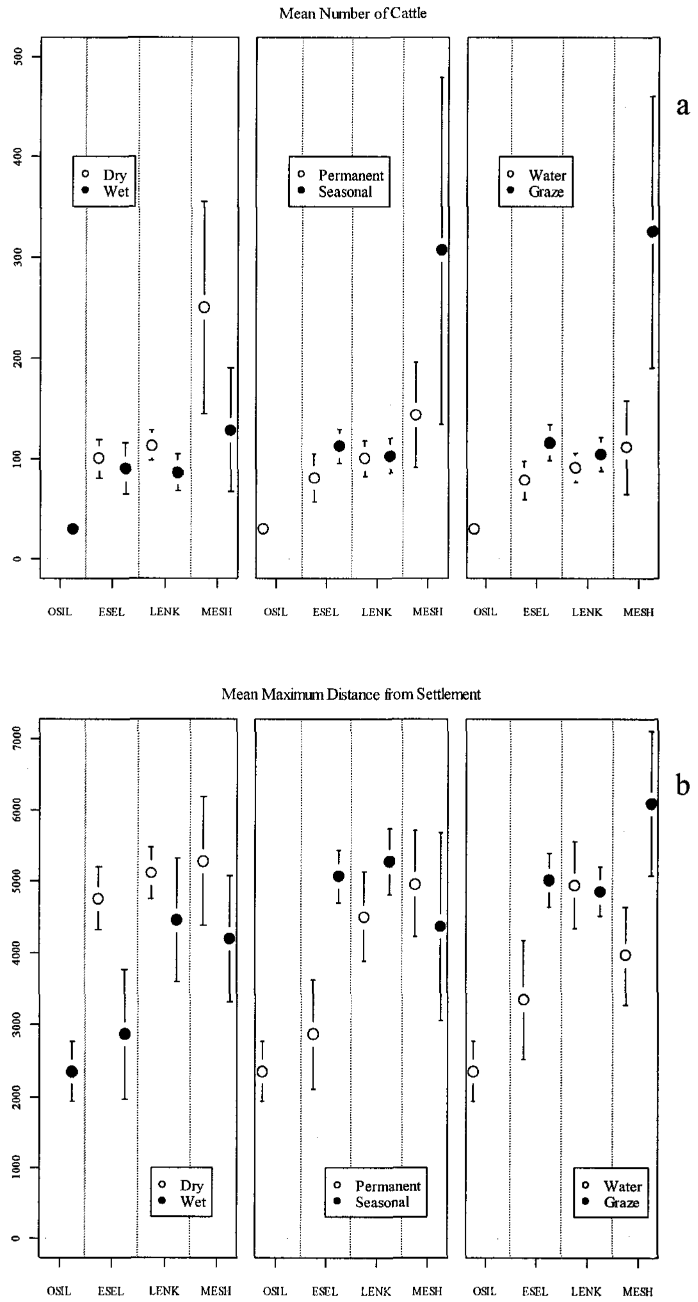


Figure 6. The mean number of cattle (a) and mean maximum distance from settlement travelled (b) for each LUA by season (panel 1), settlement type (panel 2) and grazing days (panel 3). These plots use the same data as Figure 5 but with further differentiation for clarity. See text for description of classifications in each category.

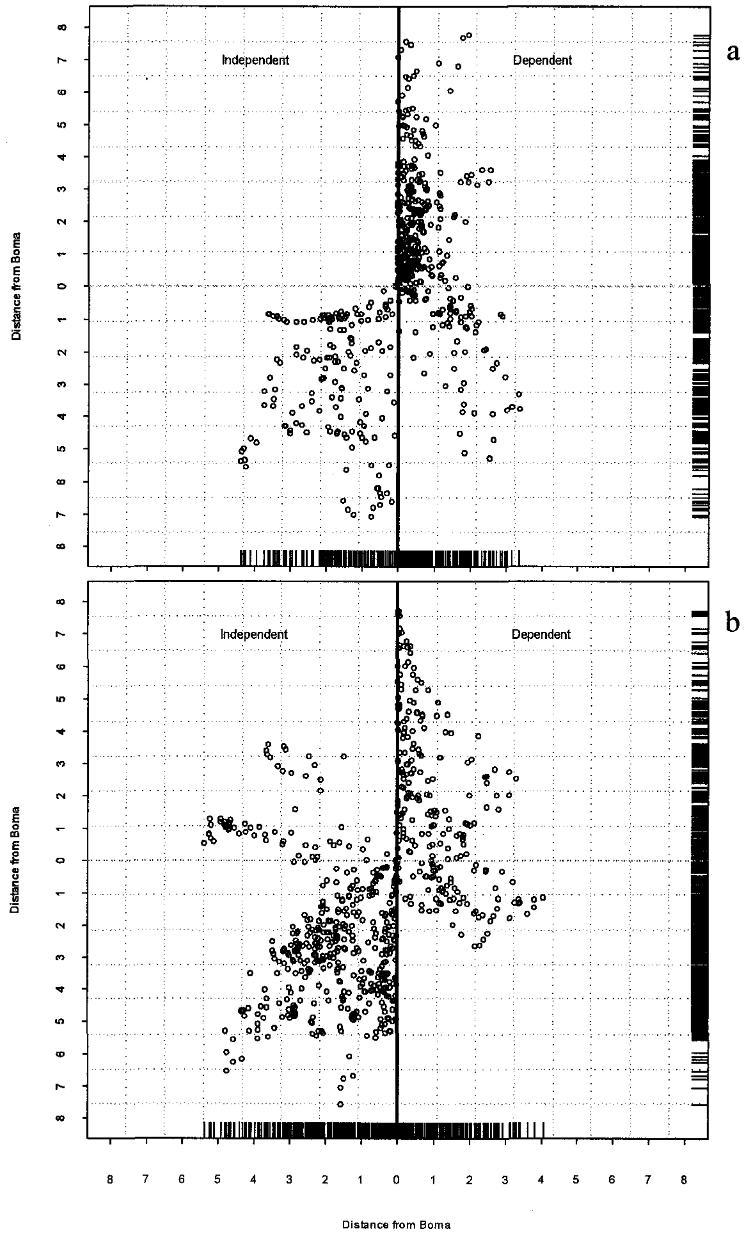


Figure 7. Standardized plots of each grazing orbit observation (30 min intervals) for all single and multi-day orbits. Points were standardized to a universal coordinate system with permanent water at the top centre and the settlement of origin in the centre of each plot. Grazing orbit observations were further separated into WET (a) and DRY (b) season observations and divided into orbits where cattle drank water (dependent) and orbits where cattle were grazing only, i.e. not taking water (independent).

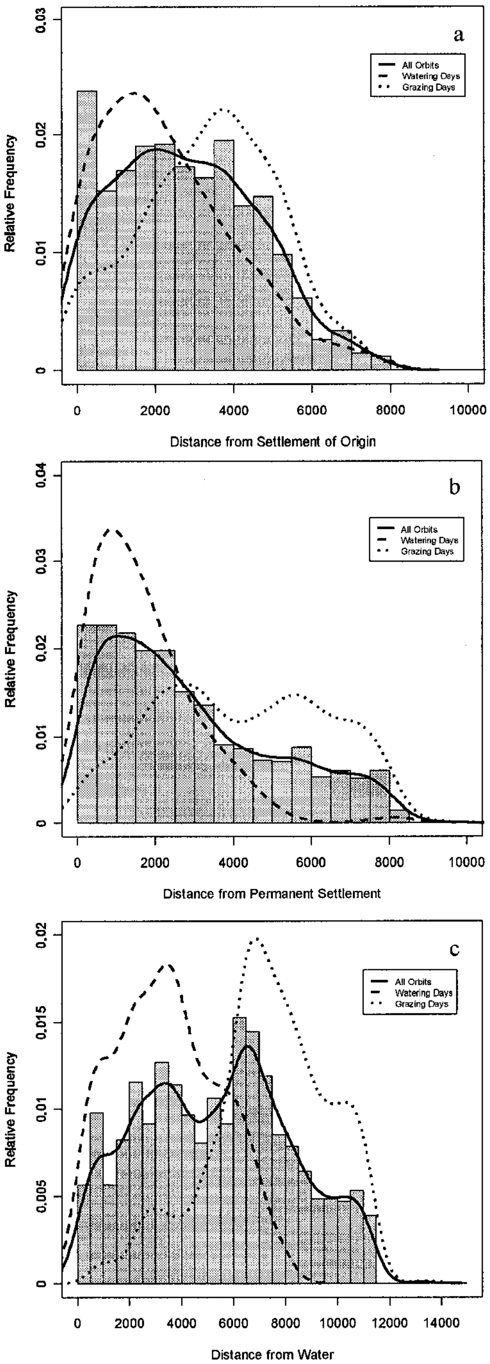


Figure 8. Histograms and density lines (500m bandwidth) for the frequency distribution of grazing orbit observations (30 minute intervals, excluding distance = 0) as a function of distance from settlement of origin (a), any permanent settlement (b), and permanent water (c). The magnitude and breadth of the peaks in the density of points for all orbits (solid lines), grazing days (dotted), and watering days (dashed) illustrate the importance of independent grazing and watering days for accessing forage resources far from settlements and water.

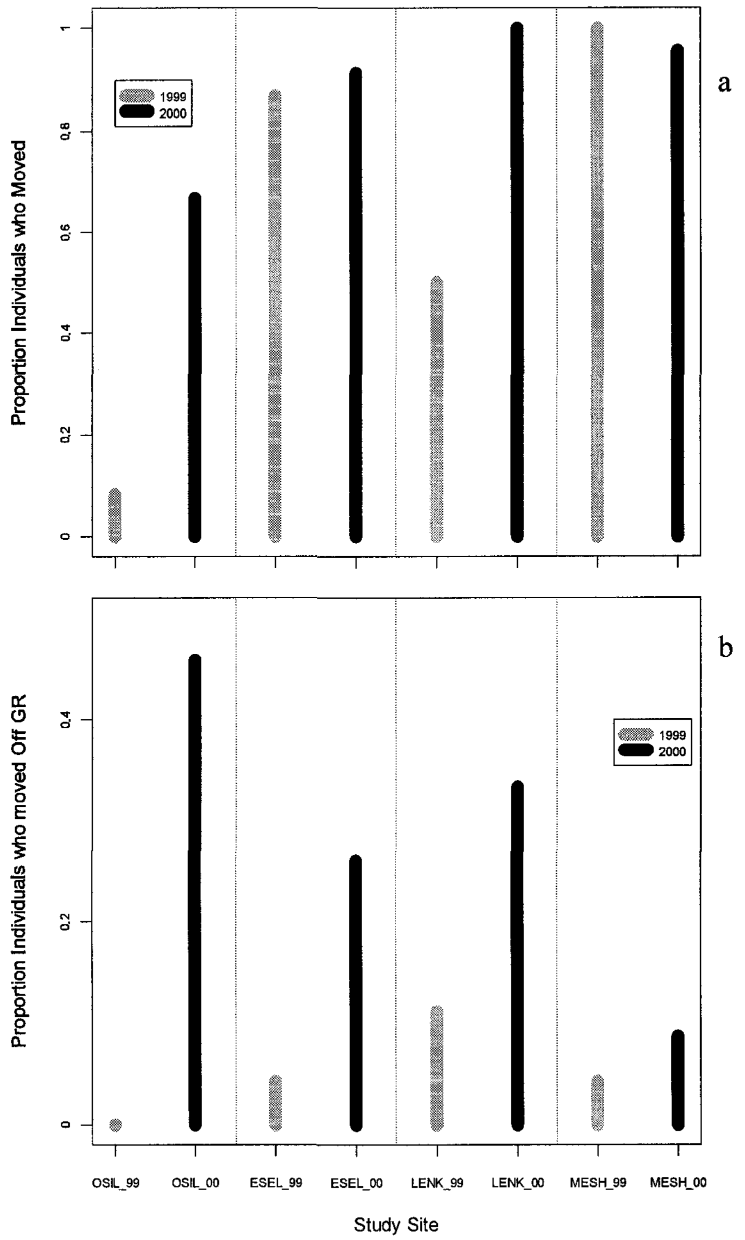


Figure 9. Proportion of households that moved (a) and the proportion of households that moved off the group ranch (b) in 1999 (grey) and 2000 (black).

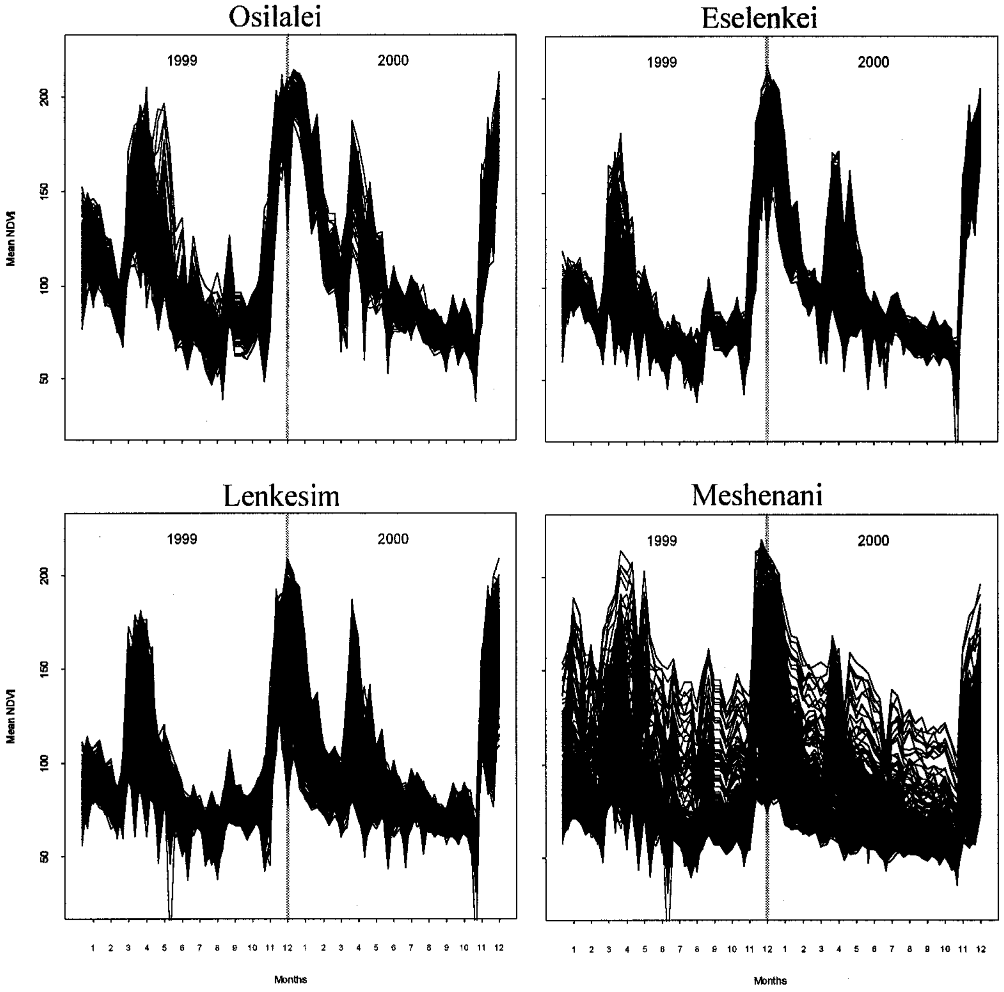
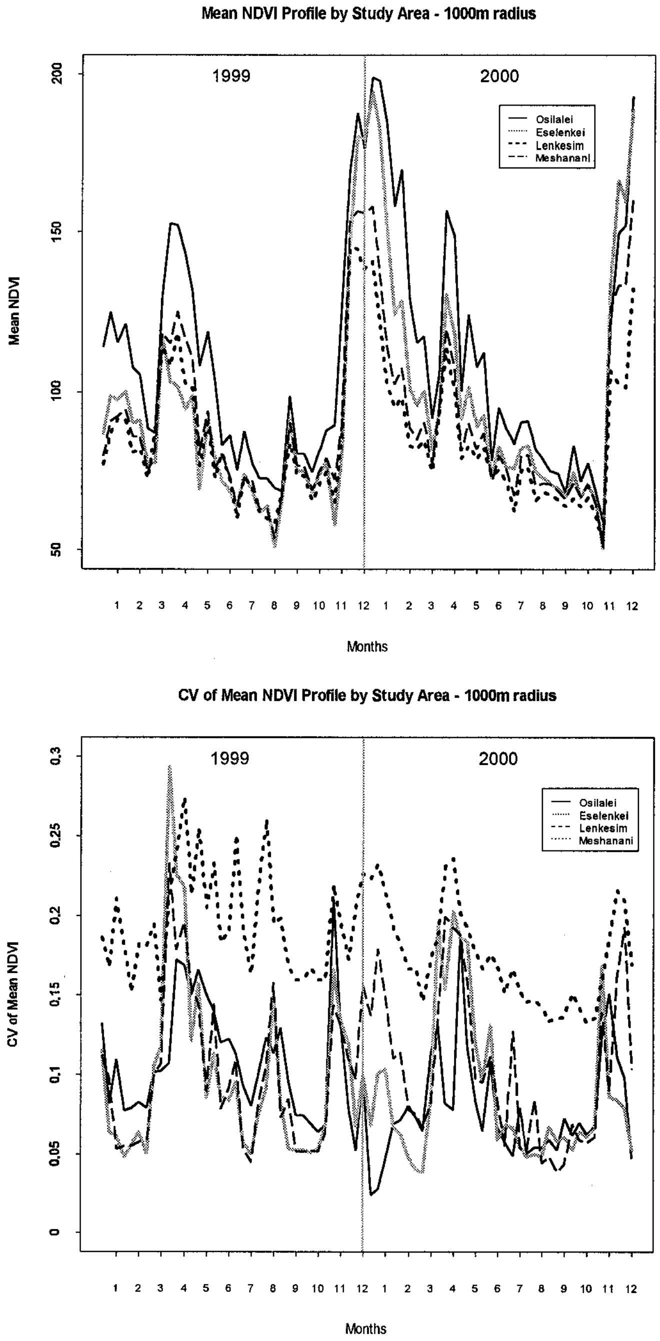


Figure 10. NDVI profiles for each study zone. Each black line traces the mean NDVI for each cell in a 1 km grid of each LUA from January 1999 to December 2000. Means were calculated using a 1 km radius from each cell centre. The overall magnitude of the lines indicates the general greenness of each area and the difference between the highest and the lowest line in each plot is an indicator of the spatial variability in each zone at each decadal time step.


Mean NDVI Profile by Study Area - 1000m radius

CV of Mean NDVI Profile by Study Area - 1000m radius

Figure 11. Mean $NDVI_{herd}$ and CV of the $NDVI_{herd}$ of all pixels in each study area. Each profile line indicates the mean available green biomass (NDVI) and the spatial variability of available green biomass (CV) in the LUA. Note that temporal patterns are generally similar across all LUAs for NDVI and CV.

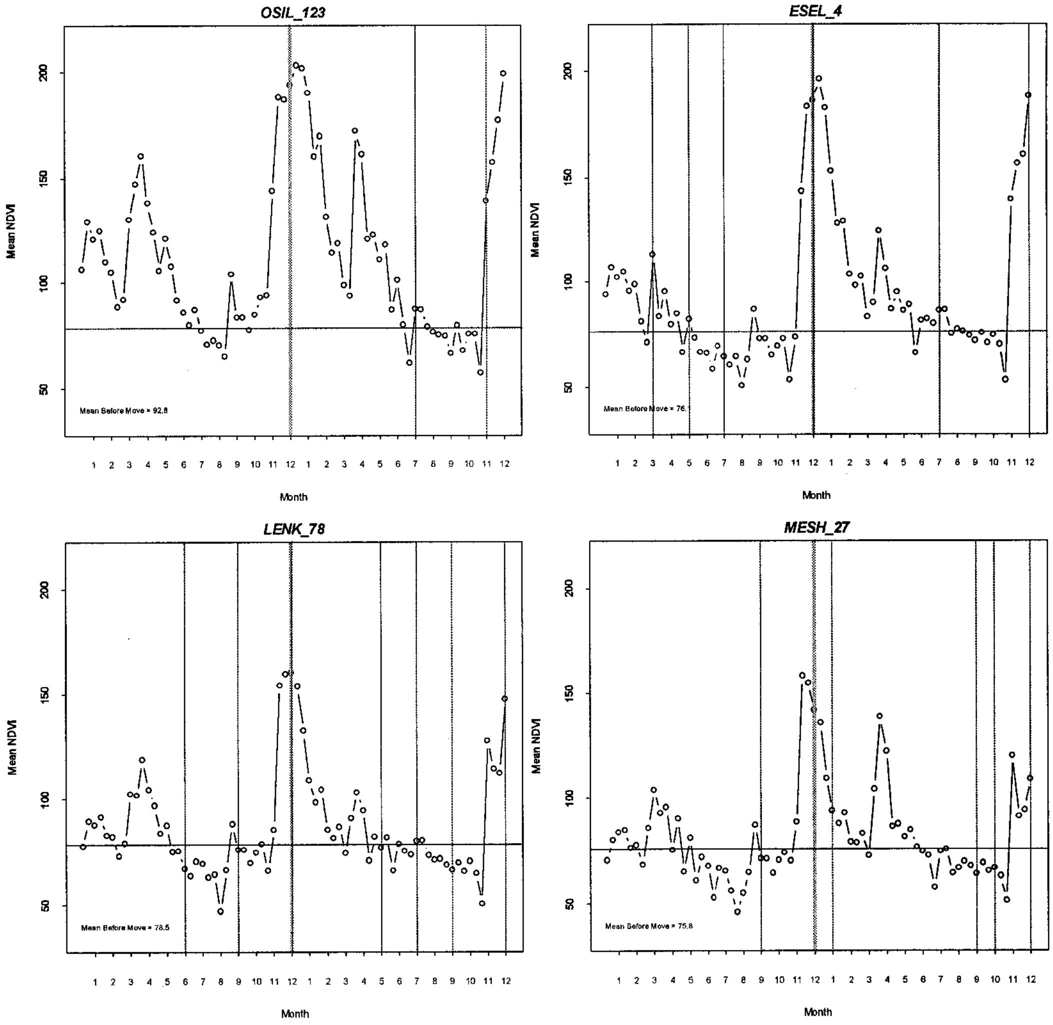


Figure 12. Samples of individual $\mathrm{NDVI}_{\mathrm{herd}}$ profiles using 10 km radius. Vertical light grey lines indicate months where the herd was moved. Vertical dark grey line separates 1999 and 2000. Black horizontal line indicates the overall mean NDVI for the observations in the LUA the month before the move.

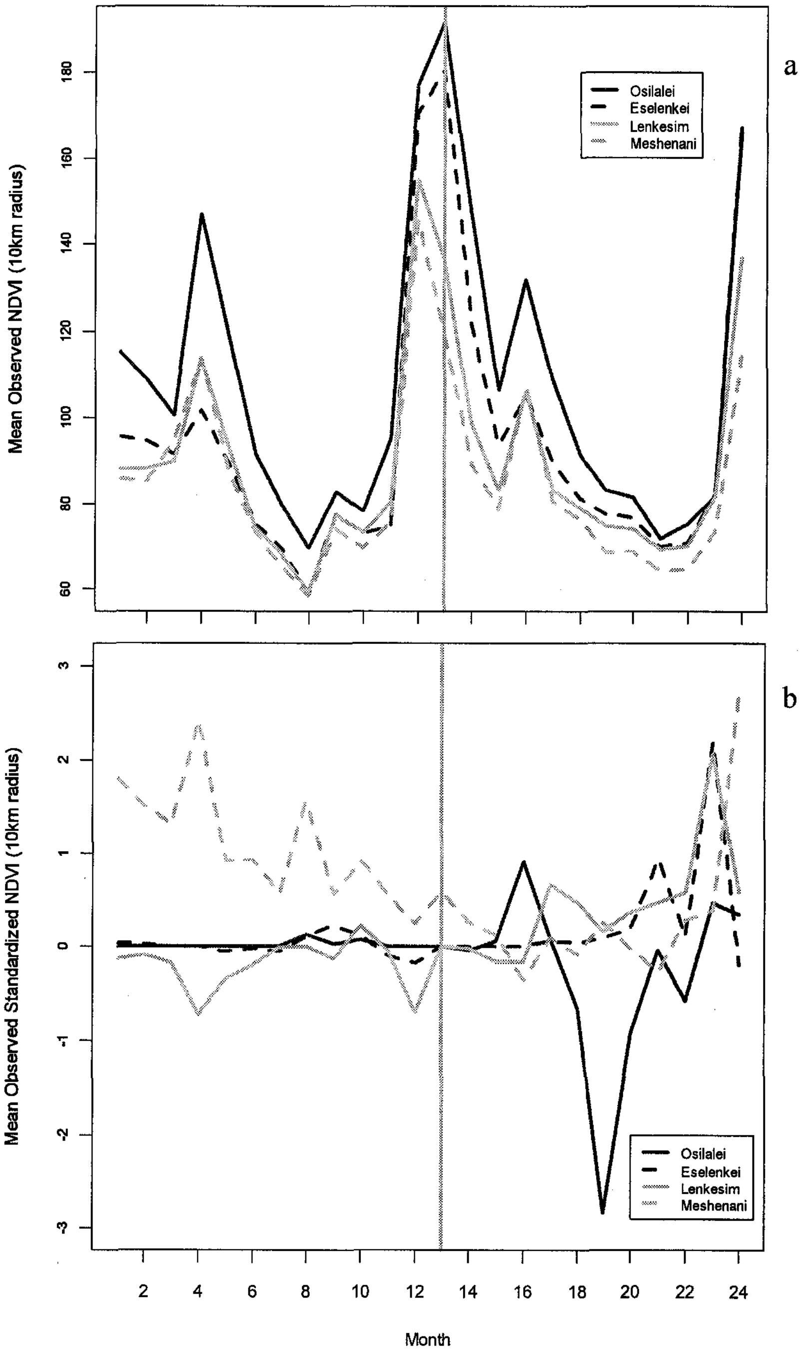


Figure 13. Mean $NDVI_{herd}$ and $NDVI_{mv}$ profiles for each LUA. Each zonal profile represents the mean of all observed monthly mean NDVI values. $NDVI_{herd}$ (a) and $NDVI_{mv}$, or the difference between observed and simulated sedentary scenarios (b), are presented.

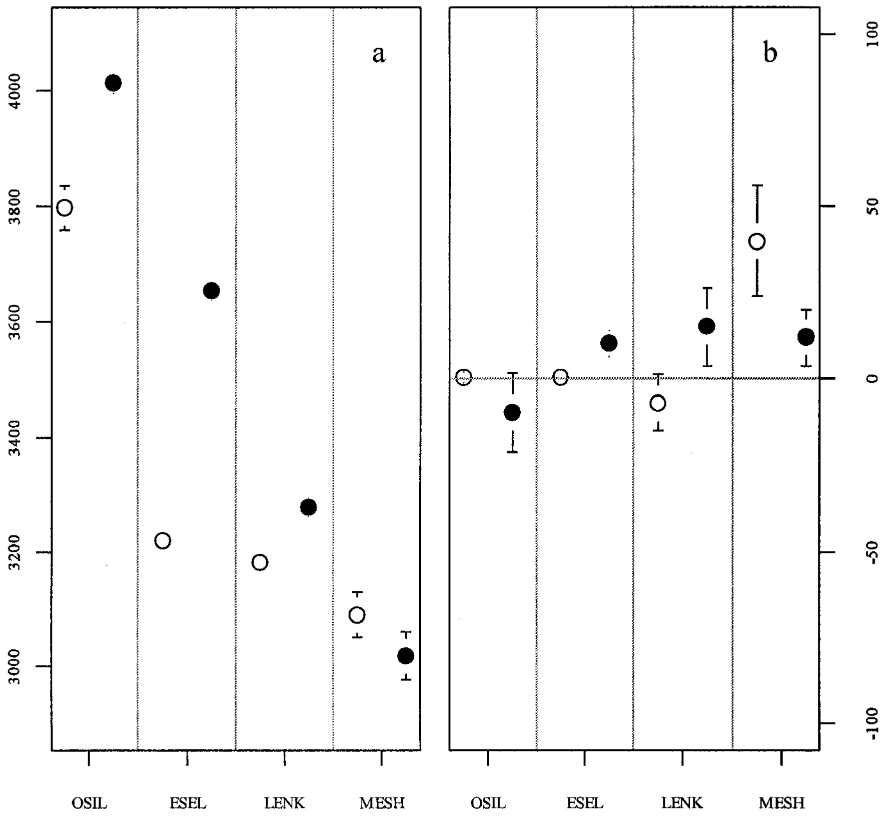


Figure 14. Cumulative mean with SE of $\mathrm{NDVI}_{\mathrm{herd}}$ (a) and $\mathrm{NDVI}_{\mathrm{mv}}$ (b) for each LUA by year. Open circles represent data from a normal year (1999) and shaded circles represent data from a drought year (2000).

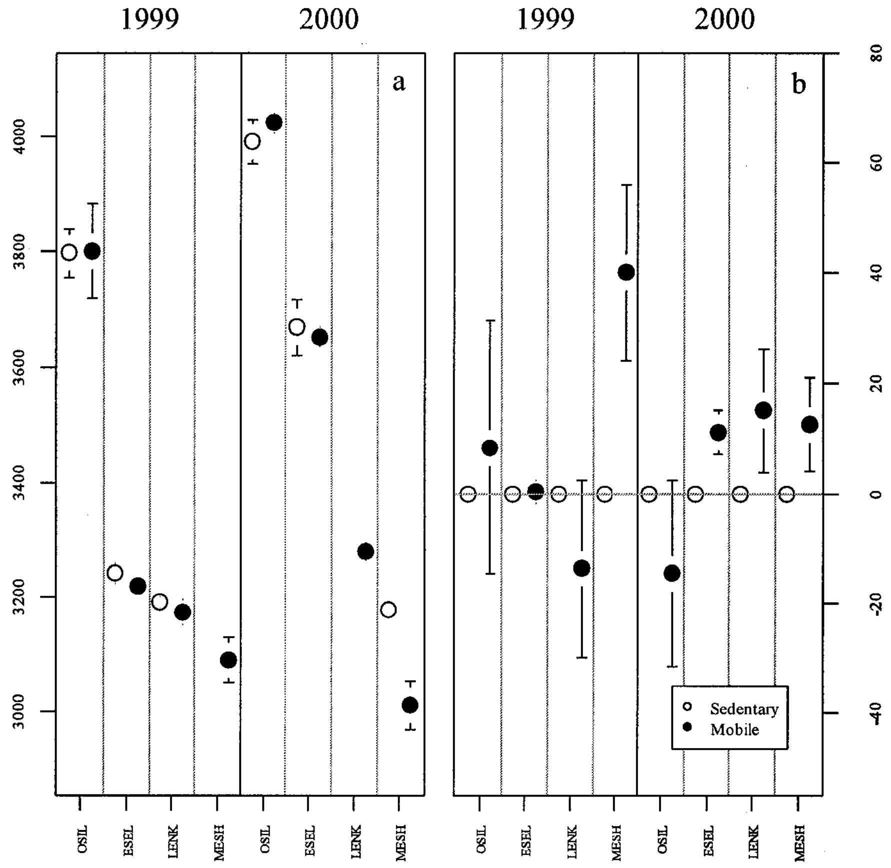


Figure 15. Cumulative mean and SE of $\mathrm{NDVI}_{\mathrm{herd}}$ (a) and $\mathrm{NDVI}_{\mathrm{mv}}$ (b) for each LUA by year and mobility category (mobile vs sedentary). Open and shaded circles represent data for sedentary and mobile groups respectively).

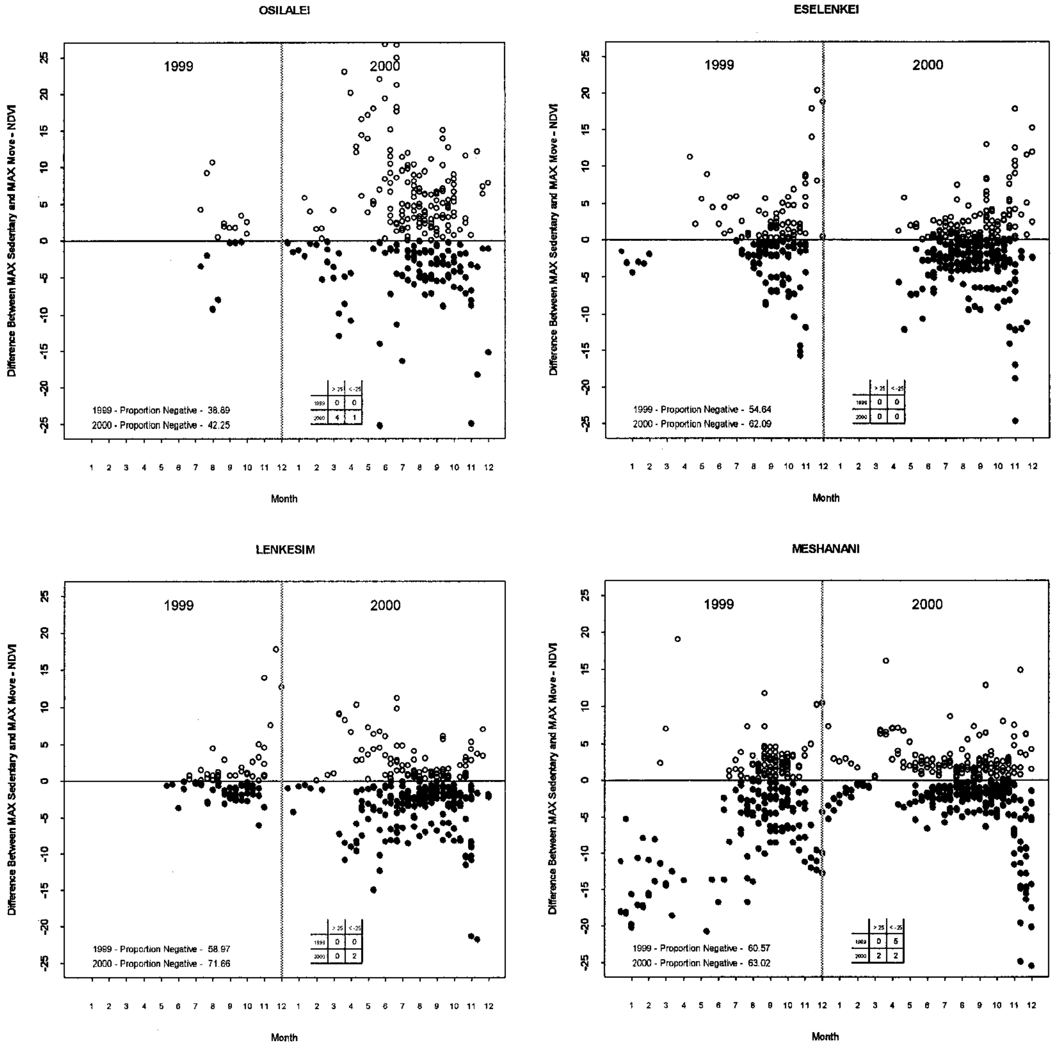


Figure 16. Difference between mean NDVI$_{mv}$ values for observed movements and simulated sedentary scenarios by LUAs. Open and closed circles indicate positive and negative differences between observed and simulated values respectively. The proportion of total observed mean NDVI$_{mv}$ values that were negative (i.e. observed mean NDVI was less than simulated mean NDVI) for both years is presented by LUA. The total number of extreme data points and their approximate values are given by year and LUA.

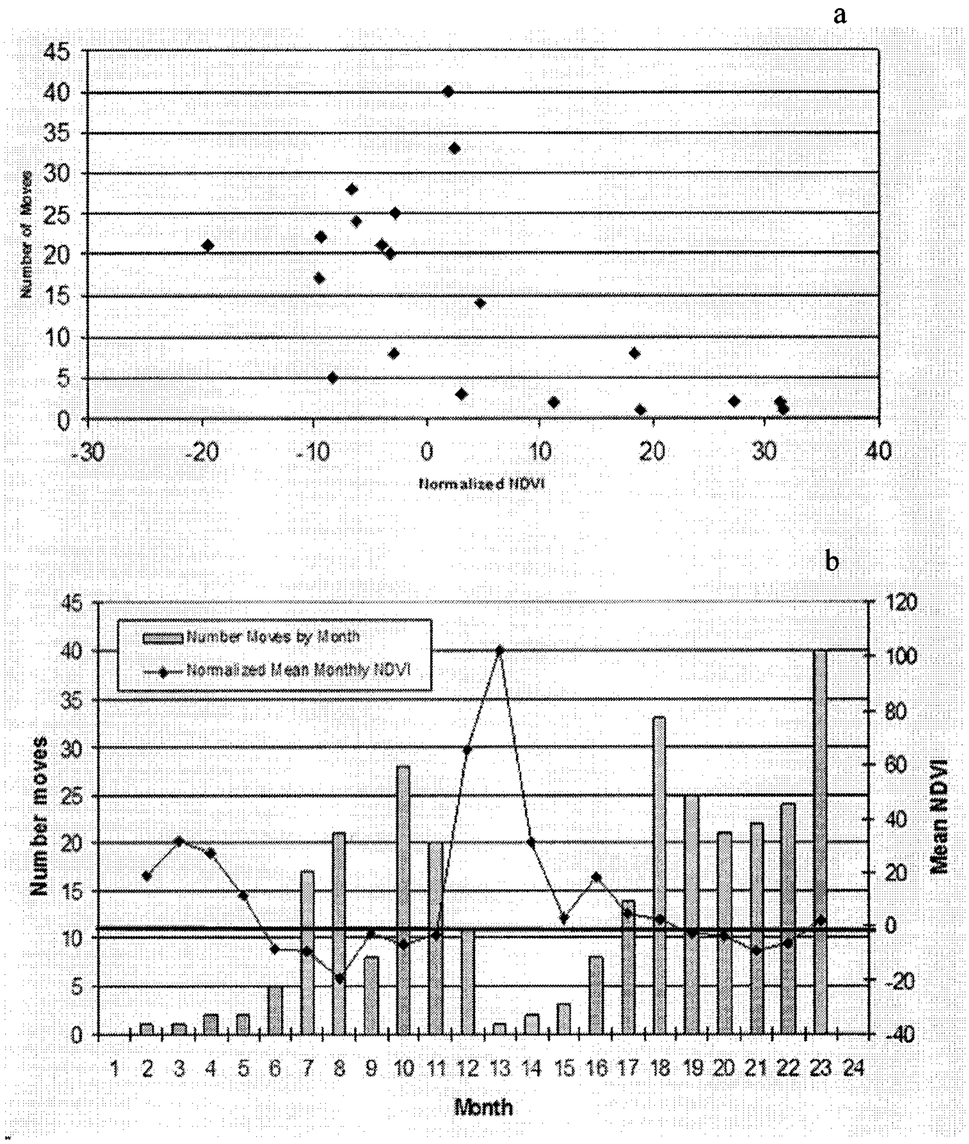


Figure 17. Normalized monthly $NDVI_{dev}$ (calculated by subtracting the overall mean and dividing by the overall SE) for the previous month and the number of moves during that month for the entire study area (a). Sub figure (b) is a temporal representation of the normalized mean monthly NDVI and the number of moves in all study areas by month.

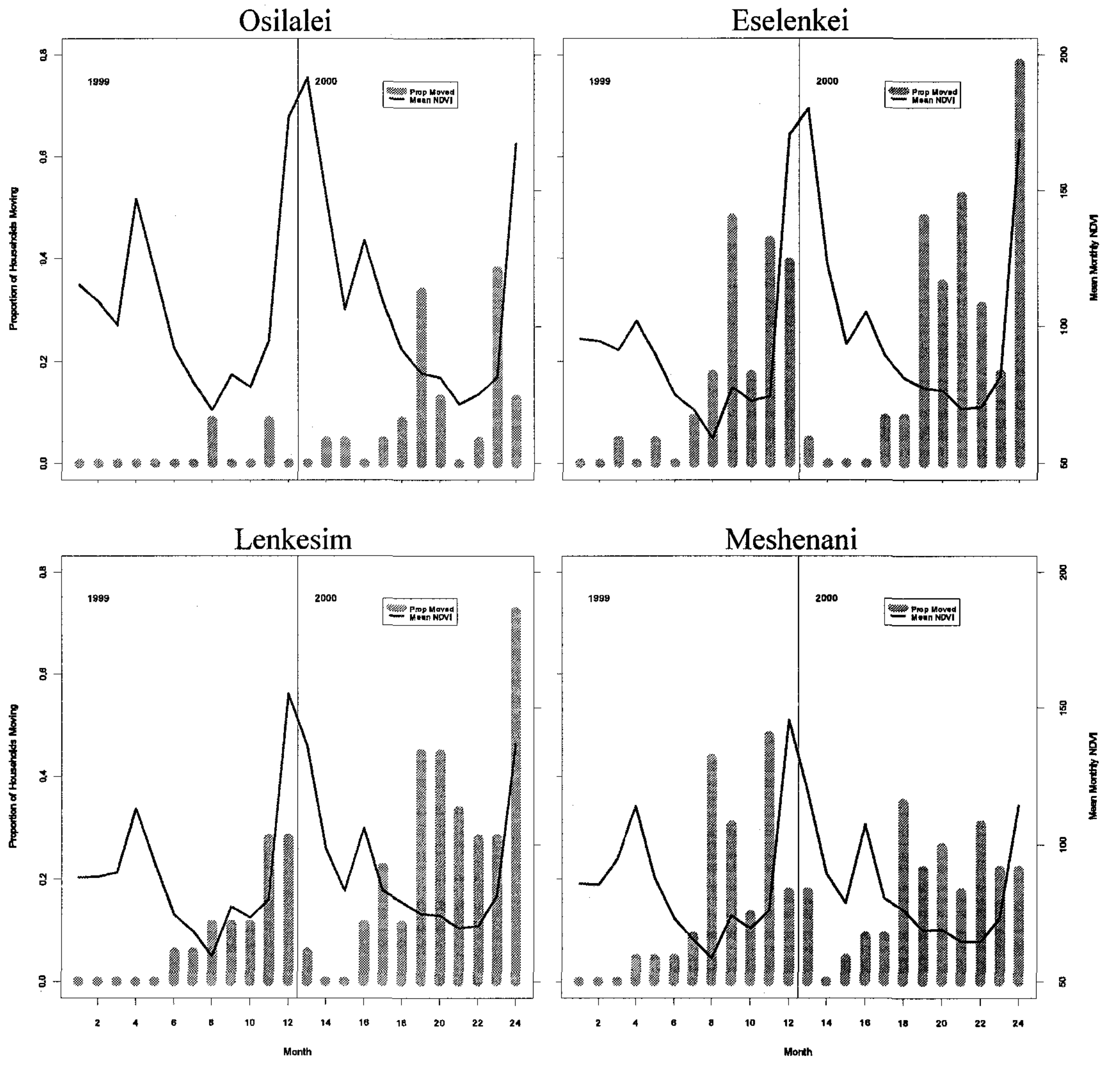


Figure 18. The proportion of sampled households that moved in each month by Land Use Area (bars), and the overall observed $\mathrm{NDVI}_{\mathrm{herd}}$ for each LUA (black line).

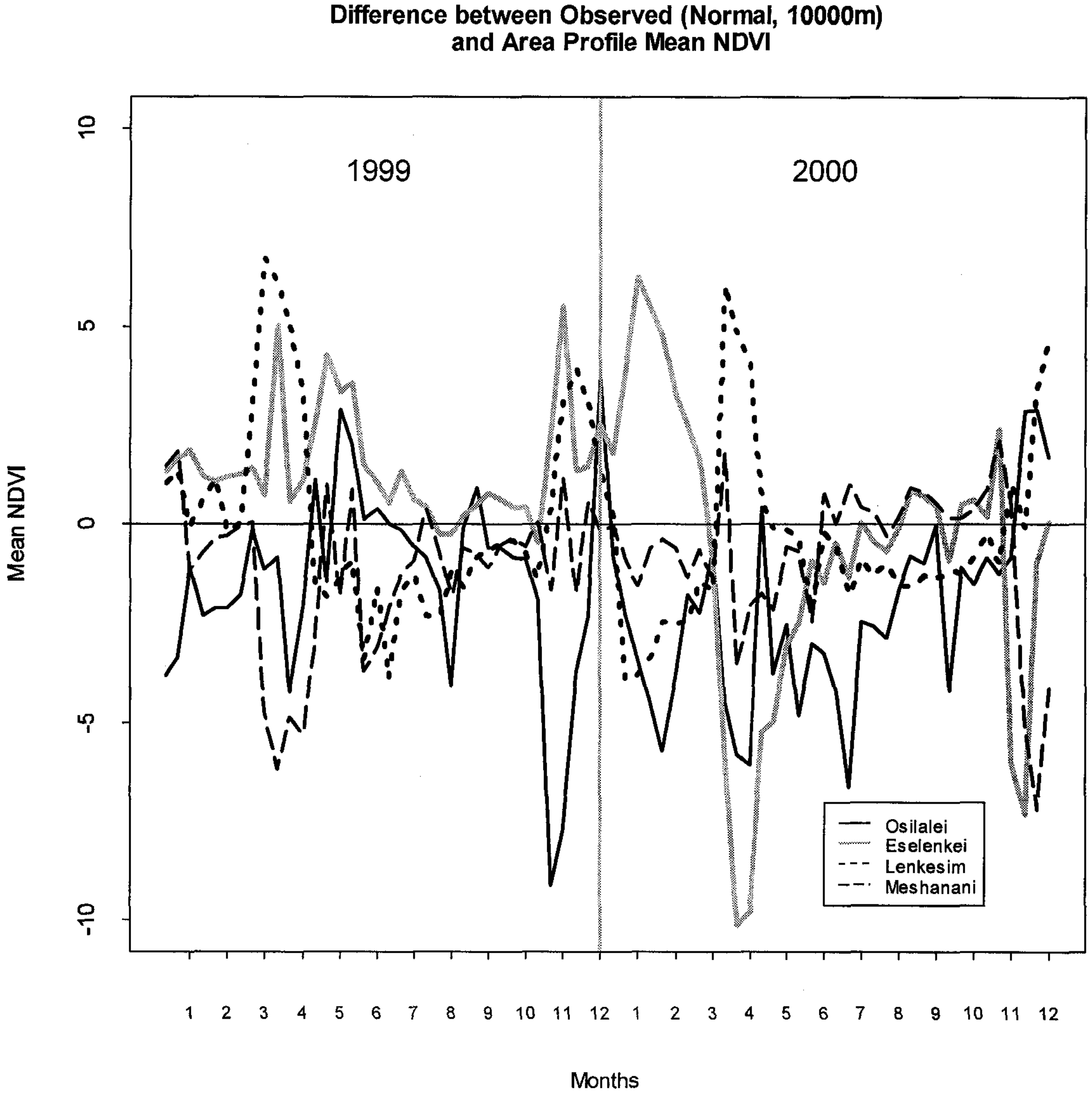


Figure 19. Mean $\mathrm{NDVI}_{\mathrm{dif}}$ by LUA. Note the relatively large number of observed mean NDVI values that are lower than expected given overall mean values in each LUA.

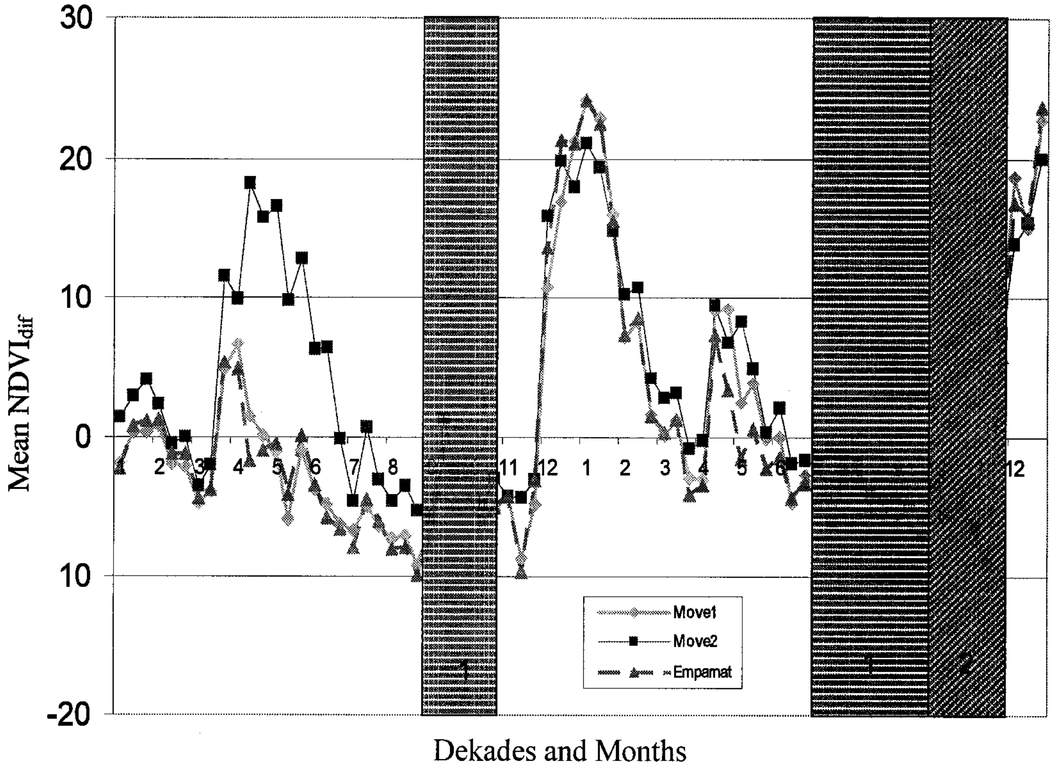


Figure 20. An individual example from Eselenkei showing the normalized mean NDVI profiles (NDVI$_{dif}$) for all locations to which the herd moved with vertical bars (hatched) indicating the time of the move and the period of occupancy in each area. Note that this individual did not move to the "best" resource at the "best" time but delayed his moves until all possible areas were similarly negative .

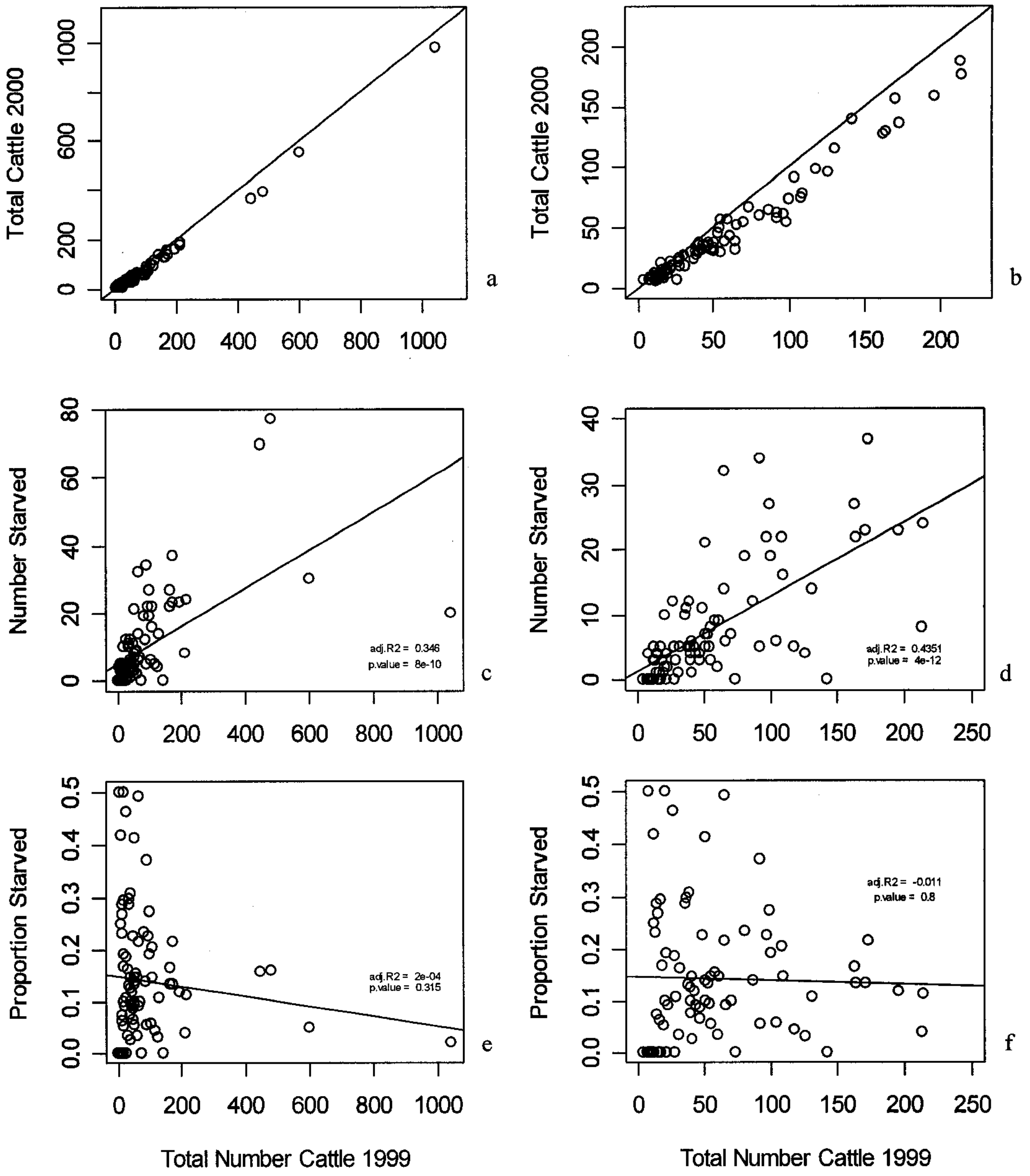


Figure 21. The total number of post drought (2000) cattle in relation to initial (1999) herd size (a-b), and the total number of cattle starved vs the initial number in 1999 (c-d), and the proportion starved vs the herd size in 1999 (e-f). In each instance, panel 2 highlights the relationship at smaller herd sizes for clarity (e.g. b,d,f). Note that almost all individuals lost cattle in 2000 irrespective of herd size, and that while total numbers of cattle lost to drought generally increased with increasing herd size there is evidence that larger herds may lose a smaller proportion of total animals than small herds.

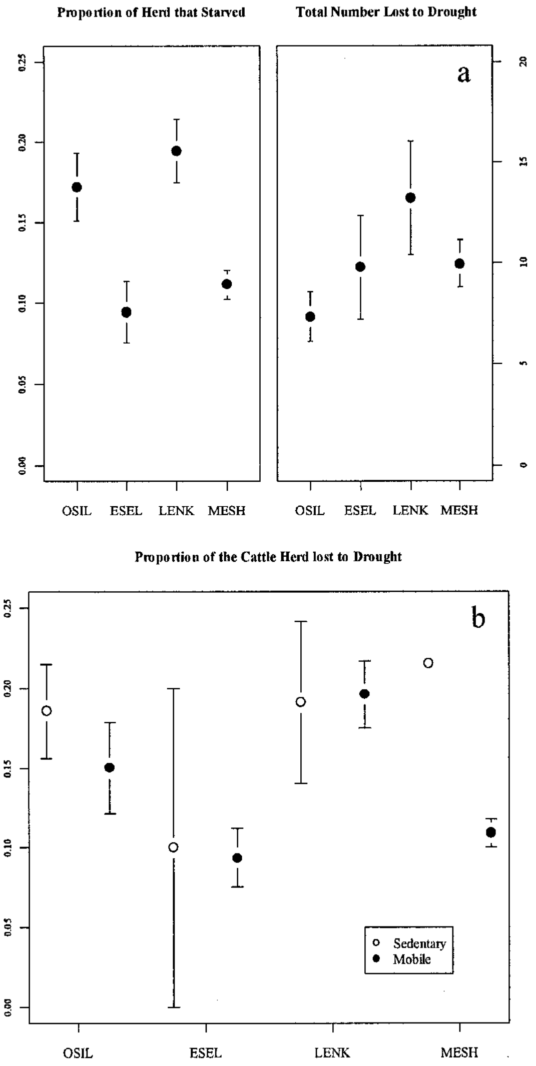


Figure 22. Proportion of herd and the total number of cattle lost to drought by LUA (a), and the proportion of the herd lost for sedentary and mobile groups within the study zones (b). All observations are pooled within a LUA for sub-plot (a) with sedentary herds indicated in white and mobile herds in grey in (b).

CHAPTER 4

LARGE HERBIVORE RESPONSES TO PASTORAL LAND-USE INTENSIFICATION AND SETTLEMENT PATTERN IN THE GREATER AMBOSELI ECOSYSTEM

INTRODUCTION

Human actions during the last 30 years have caused unprecedented declines in African wildlife (Ottichilo et al. 2000, Ottichilo et al. 2001, Serneels and Lambin 2001, Kiss 2004, Georgiadis et al. 2007). In the semi-arid and arid savannas of East Africa habitat conversion (Serneels et al. 2001), fragmentation (Reid et al. 2004, Hobbs et al. 2007, Hobbs et al. in press, Reid et al. in press), and legal harvesting and poaching (Campbell and Hofer 1995) have all contributed to wildlife declines that have exceeded 40% in the last 30 years (Norton-Griffiths 1998). Apart from dramatic declines in elephant and rhino, which were clearly caused by poaching, most of these wildlife losses have accrued coincident with agricultural conversion and human population increases in higher rainfall areas such as the Masai Mara (Ottichilo et al. 2000), leaving much of the remaining wildlife resource in the drier pastoral regions. The wetter and well watered rangelands are the first to be privatized and converted to crop production. However, as competition for resources in these areas increases people and agriculture begin to spill over into the drier more marginal areas. As land- use change continues to cascade down the rainfall gradient there is increasing pressure to reduce the scale of pastoralism through privatization and sedentarization. Understanding how wildlife respond to this subtle transformation in the patterns of pastoral land-use is one of the most pressing challenges for wildlife conservation in Africa. The spatial distribution of pastoral impacts that emerges from settlement patterns (through their direct and indirect effects) has potentially important implications for the distribution and abundance of large herbivores at multiple spatial and temporal scales.

Although pastoral interactions with wildlife are often considered benign historically (Little 1996), there is little doubt that pastoralists impact wildlife directly through harassment and hunting (Mol 1981) and indirectly through habitat modification associated with grazing and livestock production (Fritz et al. 1996, Williams 1998, Fritz et al. 2003), settlement construction (Western and Dunne 1979, Jensen 1983 unpublished-a, Muchiru et al. in press), and fuel wood harvesting (Jensen 1983 unpublished-b). East African pastoralists employ a central-place foraging system (Coppolillo 2000, Coppolillo 2001) in which livestock are herded daily to and from central settlements. Thus, settlements represent the focus of daily activity and the center of direct and indirect effects of pastoralists on wildlife. As with livestock impacts around water points (Georgiadis 1987, Andrew 1988, Georgiadis and McNaughton 1990, Thrash and Derry 1999) the intensity of these effects declines with increasing distance from settlement (Western and Dunne 1979, Reid et al. 2001, Muchiru et al. in press). The impact surface of pastoral effects that emerges from the spatial configuration of settlements (through their direct and indirect effects) has potentially important implications for the distribution and abundance of large herbivores at multiple spatial and temporal scales. In this paper I examine the effects of pastoralists and their livestock/pastoral settlement on wildlife populations and community structure across a gradient of pastoral intensification in an East African savanna.

Land privatization, or subdivision, and sedentarization are transforming pastoral systems in East Africa (Rutten 1992, Galaty 1994a, b, Homewood 1995, Fratkin 2001). The gradual conversion of key resources areas (Scoones 1989, 1995, Illius and O'Connor 1999) to agriculture (Campbell et al. 2005, Worden, 2007c), the expansion of conservation (Western 1982), and settlement (Lamprey and Reid 2004) combined with rangeland fragmentation through land tenure change and subsequent limits on access and movement (Rutten 1992, Galaty 1994a, b, Kimani and Pickard 1998, BurnSilver and Worden in press) has lead to a widespread decline in the spatial extent of pastoral systems throughout East Africa (Hobbs et al. in press) and beyond (Fernandez-Gimenez 1999, Ash et al. 2004, Fernandez-Gimenez and Le Febre 2006). This transformation is not limited to patterns of livestock movement and access, however. It also has important implications for settlement distributions in space and time and subsequent patterns of human disturbance, livestock utilization, and resource availability. Evolving settlement patterns lead to structural and functional changes in pastoral landscapes. The changing nature of pastoralism results in a change in the nature of pastoral wildlife interactions.

A multi-species approach is needed to determine the nature and degree of human impacts on wildlife because individual species and guilds respond differently to pastoral land-use (Fritz et al. 2003). These differential responses, in turn, have cascading effects on biodiversity across savanna ecosystems (Du Toit and Cumming 1999, McCauley et al. 2006, Pringle et al. 2007). Species level interactions, and the co-existence between domestic and wild grazers, are mitigated by differences in digestive systems (Demment and van Soest 1985, Van Soest 1994), feeding strategies (Hofmann 1973, 1989), body-size (Prins and Olff 1998, Olff et al. 2002), and migration patterns (Lamprey 1963, Prins 2000). Body size is a useful integrator of metabolic rate, gut size and morphology, feeding selectivity (Demment 1982, Demment and Soest 1985, Wilmshurst et al. 2000), movement and scale of perception (Fragoso 1999, Mech and Zollner 2002), hunting preference for human consumption, immunity to predation (Owen-Smith 1988, Sinclair et al. 2003) and perceived threats to humans. When coupled with feeding strategy, body size provides a framework for assessing the response of different species to pastoralism.

Here, I quantify species and functional group responses to pastoral land-use intensification at the landscape and settlement level as a function of body size and feeding strategy. I use the pattern of pastoral settlement and sedentarization as an indicator of pastoral land-use intensification. I develop species level hypotheses based on expected functional group responses to pastoral settlement pattern (landscape level), distance from settlement (settlement level), and season as indicators of spatial and temporal limitations in forage quantity and quality, habitat structure (relative proportion of grass and browse), and human disturbance.

Wild Herbivore Responses to Intensification of Pastoral Land- Use

Intensification of pastoral land-use is a multi-faceted, dynamic process (BurnSilver in prep, BurnSilver and Worden in press, BurnSilver in press). I define pastoral land-use intensification as a change in the spatial and temporal dynamics of pastoral settlement patterns and associated impacts. Historical patterns of settlement and mobility, in which pastoralists and their herds would move seasonally and relocate settlements frequently, have been altered as rangelands have become increasingly fragmented and congested (Worden 2007a, BurnSilver and Worden in press, Hobbs et al. in press). Fragmentation of the rangeland through land privatization has often lead to dispersal of settlements and associated impacts across the landscape as land owners move to their individual holdings (Worden 2007a). A parallel process of sedentarization means that these settlements move less often, resulting in an intensification of pastoral impacts in both space and time. In contrast, a clustered settlement pattern results in a lower pastoral land-use intensity because it typically maintains both spatial and temporal gradients of pastoral impact as herds continue to move seasonally between permanent settlements and grazing reserves.

Wildlife response to pastoral land-use intensification is expected to depend upon forage productivity (Fig. 1). In areas of relatively low forage productivity (curve 1 in Fig. 1) wildlife would be expected to decline as settlements become increasingly sedentary and dispersed across the landscape due to increased competition for forage from livestock. Low forage productivity intensifies this competition. Peak levels of wildlife abundance and diversity may occur at relatively high levels of settlement clustering and low levels of sedentarization. Pastoral land use patterns are characterized by mobile, temporary camps (bomas) that are clustered, but periodically moved. This creates a shifting mosaic of disturbance and nutrient enrichment associated with the creation and abandonment of livestock enclosures and dung deposition (Worden 2007a, Muchiru et al. in press)

As forage productivity and biomass density of large herbivores increases, other processes such as the construction of pastoral settlements, fire, and grazing begin to play a more important role in the creation and maintenance of broad scale vegetation heterogeneity. In areas of high productivity (e.g. rainfall > 800m), competition with livestock is reduced, and pastoral grazing and fire are more likely to improve grazing conditions for wildlife by converting tall low forage quality swards to short high quality swards or grazing lawns (McNaughton 1984). Thus, I expect that pastoralists and their livestock create and maintain a heterogeneous mosaic of low and high quality grazing environments and a diverse large herbivore community capable of exploiting different patch types (curve 3 in Fig. 1). Indeed, evidence from Kenya's Masai Mara area suggests that intermediate levels of pastoral land-use intensity may enhance the abundance and diversity of large wild herbivores (Reid et al. 2001). However at higher land use intensities, the positive effects are ultimately overcome by negative effects of overgrazing.

At intermediate levels of productivity I predict that pastoral land-use intensity will have little impact on wildlife until high levels of dispersion and sedentarization are attained (curve 2 in Fig.1). Productivity will not be high enough to support the positive effects of livestock grazing on wildlife. However, at high pastoral land use intensities, the negative effects of livestock overgrazing will negatively affect wildlife. These hypothetical responses to pastoral intensification are not only rainfall dependent, but also species specific. Based on the interaction of indirect pastoral effects on habitat and resource availability and feeding requirements suggested by body size and functional group classifications I expect species level responses at the landscape level as shown in Table 1.

Responses to Land-Use Intensity - Landscape Level

Generally, the wildlife response to increasing land-use intensity at the landscape level for a relatively low rainfall area such as the Greater Amboseli Ecosystem (GAE) would be one of gradual decline (curve 1 in Fig. 1). Although this may be true for the large herbivore community as a whole, I expect species and functional groups to exhibit individual responses. Similarly, the degree to which indirect and direct pastoral impacts alter wildlife abundance and community structure will vary by species, body size and feeding strategy. I expect grazers to be the most susceptible to competition with livestock and increasing pastoral land-use intensification. This will be particularly true for the larger bodied grazers as continuous and dispersed pastoral impacts reduce herbaceous forage availability. I expect mixed-feeders to respond negatively to increasing pastoral land-use intensification, but less so than grazers. Their adaptable feeding strategies may help to mitigate competition with livestock under intermediate and low levels of intensification as it enables them to utilize high quality herbaceous forage in the wet season while shifting to browse in the dry. Browsers are almost exclusively depended on woody vegetation and therefore should respond little to the direct effects of increasing pastoral land-use intensification. However, with extreme sedentarization woody vegetation may be eliminated from the immediate vicinity of settlements thus reducing browser habitat quality.

These patterns should hold across body sizes, but I expect the effects of forage competition to be particularly acute for intermediate and large bodied grazers (see species specific predictions in Table 1). Similarly, if the effects of altered settlement patterns on wildlife are primarily due to competition for forage resources with domestic animals, then I would expect to see a reduction in resource competition in the wet season across all functional groups and body sizes as forage quantity and quality becomes less limiting. Stasis in the composition and abundance of the large herbivore community between seasons would suggest that either the indirect effects of pastoralism have reached a degree that prevents a relaxation of competitive interactions during the wet season, or that there are some other direct effects, such as disturbance, inhibiting utilization of the area by wildlife.

Responses to Distance from Settlement - Settlement Level

Patterns of distribution and abundance as a function of distance from settlement provide further insight into species and functional group responses to gradients in pastoral land-use intensification. As with the landscape level comparison, I expect that as the effects of pastoralists and their livestock dissipate with distance from the settlement wildlife will generally increase. I also expect differential responses by species, functional feeding strategy and body size as pastoral impacts on herbaceous forage and woody vegetation as a function of distance from settlement mirror those at the landscape level. Areas near settlement represent high levels of pastoral land-use intensity while areas far from settlement are only intermittently impacted by pastoralists and their livestock. Probability of presence and abundance estimates are expected to be similar to each other unless otherwise indicated.

Domestic animals are expected to decline with increasing distance from settlement in both the wet and the dry season, but I would expect both the probability of a herd being present and the actual herd sizes to extend further from the settlement as forage becomes limiting in the dry season (curve 4 in Fig. 2). Similarly, I expect the presence and abundance of grazers to increase with distance from settlement during the dry season due to resource competition (curve 1 in Fig. 2). In contrast, I expect the distribution of mixed feeders and browsers to be relatively independent of settlement during the dry season (curve 2, Fig. 2). Both these groups may be slightly displaced from settlement as the construction and maintenance of houses and cattle enclosures leads to the localized removal of woody vegetation (Western and Dunne 1979, Muchiru et al. in press).

During the wet season increases in forage quantity and quality at intermediate distances from settlement will release grazers and mixed feeders from competition with livestock. The facilitative effects of livestock grazing on vegetation growth and quality (McNaughton 1979) will result in a hump shaped quadratic response with increasing distance from settlement (curve 3 in Fig. 2). The general form of the relationship for browsers should not change during the wet season (curve 2, Fig. 2). The curves for all species are expected to shift upward and closer to settlements (where appropriate) during the wet season as increased rainfall reduces the competition between livestock and wildlife.

In this study I quantify the effects of increasing pastoral land-use intensity, represented by the degree of land privatization and settlement dispersion, on the distribution, abundance, and community structure of large herbivores in the Greater Amboseli Ecosystem. I address the following questions:

1. Does pastoral land-use intensification influence the spatial distribution, density, and composition of the large wild herbivore community at the landscape level? Do these patterns differ by body size, functional group and season?

2. How do wildlife respond to pastoral settlements and do these responses vary across a gradient of pastoral land-use intensity and by season?

METHODS

Study Area and Sampling Design

This study was conducted in 2000 and 2001 in the Maasai pastoral areas north of Amboseli National Park in southern Kenya (Fig. 3). The Greater Amboseli Ecosystem is approximately 8,500 km^2 (Western 1973) and encompasses Amboseli National Park and the surrounding rangelands utilized seasonally by dispersing wildlife (for detailed ecological and social descriptions see Western 1973 and Rutten 1992). The study area is dominated by rolling Commiphora/Acacia dominated savannas of basement complex soils with low topographic heterogeneity intersected with seasonal rivers and fluvial deposits (Touber 1983). There is a shallow rainfall gradient extending from approximately 350 mm in the south to approximately 400 mm in the northern hills of Osilalei. Land-use in all three areas is predominantly pastoral with evidence of expeditionary (Campbell et al. 2005) agriculture in the northern areas (see BurnSilver, in prep for detailed description of socio-economic activities). However, even at the highest end of the rainfall gradient, the distribution of total precipitation over two wet seasons (April – May, and Nov – Dec) precludes rain fed agriculture in all but the wettest years (Ellis and Galvin 1994).

Historically, this area was used collectively by Maasai of the Ilkisongo and Matapato sections. Settlements were clustered in neighborhoods near permanent water – hand dug wells along the Eselenkei River in the north, and the springs and swamps in the Amboseli Basin in the south (Western 1973, Worden 2007a). As part of a national policy of land reform and privatization, communally managed Maasai lands were gradually adjudicated into individual plots and Group Ranches (large ranches owned and managed by a group of member families) in the 1970s and 1980s (Olang 1982, Rutten 1992, Galaty 1994a, b, Kimani and Pickard 1998). The combination of group ranch delineation and water development (beginning in the 1950s) lead to broad scale shifts in grazing and settlement patterns (Worden 2007a). As access to key resource areas and seasonal grazing reserves was reduced local Maasai gradually shifted from a wet season livestock dispersal system similar to the seasonal movements of wildlife (Western 1973), to a dry season dispersal system (Worden 2007a). This, in turn, led to the creation of a system of grazing stages with limited movement and permanent settlements restricted to defined areas. Osilalei was further subdivided into individual land holdings of approximately 25 – 70 hectares in 1994 (BurnSilver and Worden in press). Most individual landowners moved to their plots into the high rainfall zone in 1997. The subdivision of Osilalei and the collective management of Eselenkei and Meshenani have led to contrasting patterns of settlement and sedentarization (Figure 3 and Table 2) creating a gradient in pastoral land-use intensity.

I selected three counting areas to represent a gradient in pastoral land-use intensity based on the 1) status of land privatization (subdivision), 2) settlement distribution pattern, and 3) the degree of sedentarization (Table 2). Subdivision is the transformation of a communally managed group ranch to small individually owned parcels. Settlement pattern refers to the degree of clustering or dispersion of settlements across the landscape (Fig. 3). In the Greater Amboseli Ecosystem a clustered settlement pattern indicates a degree of collective management with certain areas designated for settlement and other areas for grazing. A dispersed settlement pattern, in contrast, suggests a transformation of management away from collective to individual decision making. Although dispersed settlement patterns are often associated with subdivision and individual land tenure, they are not limited to these areas. Indeed, areas in northern Eselenkei have intermediate settlement patterns as de facto subdivision becomes increasingly common. Sedentarization is the loss of mobility in a pastoral system with highly sedentarized populations moving less frequently. The degree of subdivision, settlement patterns, and sedentarization interact to form a gradient of human impact and disturbance. Pastoral areas with high dispersion and high sedentarization have a homogeneous pattern of continuous human impact. In contrast, areas of low dispersion (i.e. clustered) and low sedentarization (i.e. mobile) have more heterogeneous and dynamic patterns of human disturbance with areas of both high and low impact (see Worden 2007 Chapter 2 for a detailed analyses of land use and settlement patterns in each area). I classified the three counting areas as follows: Osilalei=HIGH, Eselenkei =INTERMEDIATE, and Meshenani=LOW (Table 2). The inherent restrictions associated with site selection in landscape scale studies precluded the identification of sites at equal distances from Amboseli National Park leading to a parallel distance from protected area gradient.

I delineated counting area boundaries to capture the dominant settlement pattern and associated grazing areas within each Land Use Area. To reduce the variance associated with differences in soil type, moisture availability, vegetation, and historical land-use legacies, I limited the counts to the older upland, granitically-derived red soils and avoided the alluvial flood plain of the Ol Kejuado River where possible. Dry and wet season counts were conducted in each area over four periods. I used a regular grid of north-south transects at one kilometer intervals, with a fixed width of 500m on either side of the aircraft, to attain a complete coverage of the counting areas.

Data Collection

Wildlife and livestock count data for both the landscape and settlement level analyses were collected using a high resolution aerial counting technique from an ultra-light aircraft. The counting team consisted of an observer and a pilot. The observer recorded the species, group sizes, and perpendicular and longitudinal distance of all wildlife and domestic animals within the one kilometer transect (Fig. 4). To quantify perpendicular distances from the transect line I allocated all observed groups into one of five distance bands using calibrated wing strut markings. The longitudinal position of the group along the transect line was recorded using a Garmin 12xl GPS at the point where the group center was perpendicular to the transect line. All waypoint and count data were recorded on a micro cassette. The open design of the ultra-light aircraft (Fig. 5) ensured that all animals on the transect line were observed in accordance with Distance sampling protocol (Buckland 2001). I counted all species independently except for sheep and goats which were aggregated as "shoats" due to the difficulty in differentiating them from the air.

To quantify settlement patterns I conducted a comprehensive ground survey in 2000 and 2001 for a subset of the total counting area (Fig. 3). The UTM coordinates, size, age, and type of all current permanent and seasonal settlements were recorded using a Garmin 12xl GPS.

Data Processing

All count data were transcribed from the microcassettes by the primary observer (JSW). Waypoint data were downloaded from the GPS and merged with the transcribed count data for GIS analyses. The data were checked for double counts and all observations beyond a 100 m buffer at the beginning and end of each transect were removed in ArcView 3.2a (ESRI). All mammals over 10 kg were counted in the original survey. In addition to the species listed in Table 1 I also recorded a single elephant on one occasion during the wet season in the LOW intensity area, and two groups of camels – one each in the wet and dry season in the INTERMEDIATE area. These observations, along with a single observation of hyena in the INTERMEDIATE area, were removed from subsequent analyses because of low sample size unless otherwise indicated. The species analyzed here were selected as they were relatively common within the Greater Amboseli Ecosystem and they represent a range of body sizes and feeding strategies.

I adjusted all counts at the species level based on detection functions calculated in DISTANCE 4.1 (Thomas 2004). The same transects were flown during each count and the 333 m grid design was maintained throughout. Perpendicular distance data were available for only a subset of the observations as the five distance bands were only added after preliminary analyses suggested the need for a detectability correction. Perpendicular distance classes were collected during the wet season count of the INTERMEDIATE and HIGH intensity areas. The limited number of groups observed for each species (Appendix 1 - Table 1) and the lack of repetition by season and area prevented the calculation of independent detection functions for all species, season, and area combinations. Using the best available data, detection functions were calculated for eight species (Appendix 3, Fig. 1). The best model was selected using AIC and appropriate detection functions and detection probabilities were calculated (Appendix 1 - Table 3). Model averaging was used when delta AIC values differed by less than 2 units (Burnham and Anderson 2001).

All observations (groups) of individual species were adjusted using the calculated detection probability where GS is group size and DP is the detection probability for species *i* ($GS_{NEWi} = GSOLD_i/DP_i$). Species for which no detection probability was calculated due to an insufficient number of groups were adjusted using the probability of detection for species of similar body size and coloration ($DP_{TM\,|\,IM} = DP_{GT}$ and $DP_{ED} = DP_{ZB}$) or the mean of similar species ($DP_{GK\,|\,LK\,|\,OX} = DP_{(GT+WT)/2)}$. For consistency total numbers and density estimates were calculated using adjusted group sizes as described above.

All observations (adjusted groups) were allocated to 333 m segments along the transect, and each segment was assigned an XY coordinated at its center point (Fig. 4). Multiple observations of individual groups of the same species were aggregated within each segment for a total number of individuals per species per segment. Count area totals were calculated as the sum of all segment totals for each species. The distance to permanent settlement was determined for each segment center point using ArcView 3.2a. Distance from settlement calculations and subsequent analyses included only count observations that fell within the area covered during the ground survey of current settlements (Fig. 3).

Each species was placed in one of three functional categories based on body mass, feeding ecology, and the degree of dependence on surface water for meeting daily water requirements (Table 1). Population unit weights from Western (1975) and Coe et al (1976) were used to allocate species into the following body size classes: SMALL (< 50 kg), MEDIUM (50-400 kg), and LARGE (> 400 kg). Species were allocated to three feeding strategy categories based upon the relative proportion of grass and browse in their diets across all seasons (Table 1). Feeding strategies between and within species may vary widely in space and time (Gwynne and Bell 1968, Fritz et al. 1996) within constraints associated with body size (Demment and Greenwood 1988) and gut morphology (Hofmann 1973). The degree of variability is not constant between species, however, and a visual inspection of a plot of estimates of the relative proportion of grass and browse and the degree of seasonal variation in these ratios reveals three broad categories in the Greater Amboseli large herbivore community – GRAZERS, BROWSERS, and MIXED feeders (Fig. 6 and Table 1). Aridity tolerance (after de Leeuw et al, 2001) represents a species' degree of dependence on surface water (i.e. drinking) to meet its daily moisture needs. I used Aridity Tolerance instead of the more common water dependent/independent classification (Western 1975) as it highlights that there is a gradient of daily water requirements within and between species, and avoids confusion between a species' biological requirements and its distribution (i.e. a flat or uniform distribution is "independent" of water). As with feeding guilds, there is a large seasonal variability in water requirements both within and between species depending on temperature, forage moisture content, and dew (Western and Finch 1986). Individual species were classified as HIGH, LOW or INTERMEDIATE (Table 1) based upon evidence from Western (1975) and de Leeuw et al (2001).

Domestic herbivore biomass density was calculated as the sum of the total biomass for all domestic animals (camels, cattle, shoats and donkeys) for each season divided by the area in square kilometers. Wild herbivore biomass density was calculated in a similar fashion for all the remaining (non-domestic) species – including elephant. Mean body mass represents the relative contribution of herbivores of different body size based upon their abundances. Mean body mass was calculated as the sum of the population weights for all individuals within a functional group within each counting area, divided by the total number of individuals in the area. Species richness is the number of all wild species observed in an area by season. To facilitate comparisons between counting areas of different size the total number of species was divided by the total km^2 for each counting area to get a species density, or number of species per km^2.

Statistical Analyses

Data were checked for normality and transformations were applied where appropriate. Transformations generally failed to achieve normality or substantially reduce skewness so Kruskal – Wallis tests were used to determine significant differences in species abundance, domestic and wild biomass density, and functional group biomass density between areas with different land use intensities and between seasons.

I used a two part conditional model and model-selection based upon information-theory (Burnham and Anderson 2002) to assess the nature of herbivore abundance as a function of distance from settlement. High resolution count data contain an excessive number of zero values and fail to meet the necessary assumptions of standard statistical analyses (Cunningham and Lindenmayer 2005). Two part conditional regression, or hurdle, models account for these excess zeros and have the added benefit of providing separate parameter estimates for presence/absence and abundance data (Cunningham and Lindenmayer 2005). First, a logistic model was fitted to the data to predict the probability of a transect segment containing one or more individuals of a given species. Then all zeroes were removed and a negative binomial count model was fit to the data to determine predicted values for the abundance of each species given presence. Based on the hypothesized relationships between herbivore presence and abundance and distance from settlement summarized in Figure 2 I considered the following three models: 1) constant, 2) linear, and 3) quadratic.

The following logistic regression model was used to determine the probability of a transect segment containing an individual of a particular species:

$$Pr = exp(z)/ 1 + exp(z)$$

where z is one of the following:

$$z = a$$

$$z = a + bX$$

$$z = a + bX + cX^2$$

and X is distance from settlement, and a, b, c being model parameters. Three zero truncated negative binomial models with similar terms were fitted to the abundance data.

The evidence for each model as the best fit for the data given the set of candidate models was determined using the Akaike information criterion (AIC) (Burnham and Anderson 2001). Similar models were used for the logistic and count steps in the two part conditional model and the best fit models were selected based on the lowest AIC values and their support in the data. R 2.4.0 was used for all statistical analyses (R Development Core Team 2006).

RESULTS

Responses to Land-Use Intensity - Landscape Level

Spatial patterns of domestic and wild biomass

The spatial patterns of domestic and wild herbivores differed markedly by season and degree of pastoral land-use intensity (Fig. 7 – 9). In the HIGH intensity domestic animals were evenly spread across the counting area with very little change in spatial distribution between seasons (Fig.7 – panel 1). In contrast, wildlife were more limited in their distribution with clear differences in seasonal distributions. In the dry season there was little overlap between the distribution of domestic animals and wildlife. During the wet season, however, wildlife appeared to move into the areas of high settlement and livestock concentrations (Fig. 7 – panel 2).

In the INTERMEDIATE intensity area there was more fluidity in the spatial distribution of domestics between seasons (Fig. 8 – panel 1). In the dry season, a few herds remained near settlement areas in the north and south, but many of the herds were concentrated in the centrally located dry season grazing reserves. During the wet season, in contrast, there was an influx of herds with the majority concentrated on the periphery near permanent settlement areas. A comparison between the wet and dry season distributions for domestic animals highlighted the organized grazing system employed in the collectively managed areas. Wildlife were more widely dispersed in the wet season with the highest concentrations occurring in the dry season grazing reserve areas away from settlement.

The spatial distribution of domestic animals in the LOW density area reflects the controlled herding strategy of that area as they were clustered in a line along the edge of the grazing area in the dry season. In the wet season the domestic animals were concentrated in the western half of the study area where they were widely distributed except for a high density cluster in the central settlement area of Nchakita. The dispersed distribution of livestock in the wet season suggested a widespread green flush in the west and a relaxation of the rules on the need to return to the permanent settlement area following the first rains. The wet season count was conducted at the end of a particularly intense drought in 2000 and this dispersed distribution reflected the flexibility inherent in the collective grazing management system which enabled herders to track green forage so that their herds could recover enough to return home. Wildlife in this area were in relatively small groups and widely distributed in the dry season. In the wet season wildlife were still found throughout the counting area, except in the vicinity of high livestock concentrations in the central area. However, their distribution was more clustered than in the dry season and there are large concentrations of wildlife in the western area with a high degree of overlap between domestics and wild.

Species and Functional Group Densities

Examination of the density of individual species by season and Land Use Area revealed a few key differences across the land-use intensity gradient. The only significant differences ($p < 0.05$, Table 3) between the sites in the dry season were for domestic animals with both shoats and cattle being highest in the HIGH intensity area (Table 3b). In the wet season, there were significant differences between all 3 areas for cattle and again for shoats between HIGH and the two lower intensity areas. There were also significant differences between the LOW and HIGH intensity areas for wildebeest and zebra in the wet season. The data suggests possible differences between sites for Grant's and shoats during the dry season, and eland, Grant's, Impala, Ostrich and Thomson's gazelle in the wet season, despite the lack of significant contrasts at the 0.05 level (Table 3b). Overall, mean wild herbivore density (combined dry and wet season) declined with increasing pastoral land-use intensity. The HIGH intensity area had a mean of 38 kg/km^2, while mean densities for the INTERMEDIATE and LOW intensity areas were 298 kg/km^2 and 528 kg/km^2 respectively. This pattern persisted when the dominant dispersing species (zebra and wildebeest) were excluded to control for the effects of distance from protected area. Mean density, excluding zebra and wildebeest, was 30 kg/km^2 in the HIGH intensity area, 246 kg/km^2 in INTERMEDIATE, and 267 kg/km^2 in LOW. Community structure was relatively stable across the seasons in all counting areas (Table 3c). Shoat density declined in the HIGH area and increased in the LOW area in the wet season. In contrast, cattle density did not change significantly in the HIGH area between seasons, but increased markedly in the INTERMEDIATE and LOW areas following the rains. Both Grant's gazelle and impala increased significantly during the wet season in the HIGH area. Similarly, giraffe, impala and wildebeest increased in the INTERMEDIATE area between seasons. Eland, giraffe, Thomson's gazelle, and wildebeest all increased significantly in the LOW intensity area. It is also important to note that some species were entirely absent under high pastoral land-use. For instance, eland, lesser kudu, oryx and wildebeest were absent from the HIGH intensity area in both seasons. In contrast, only Thomson's gazelle and lesser kudu were absent from the INTERMEDIATE and LOW intensity areas respectively. Elephant were only observed in the LOW intensity area, but observations of spoor and informant interviews confirm that they are occasionally in the INTERMEDIATE intensity area as well.

The mean number of individuals per transect segment, or the degree of aggregation, of different species varies across areas and seasons (Appendix 1 - Table2). Mean group size for cattle and shoats increased during the wet season in the INTERMEDIATE and LOW areas and declined in the HIGH intensity area. Similarly, giraffe group sizes declined in the HIGH area and increased in the INTERMEDIATE and LOW intensity areas. Wet season group sizes for Grant's gazelle and ostrich increased across all areas. In contrast, wet season group size in wildebeest decreased in the INTERMEDIATE and LOW intensity areas. Zebra group sizes were relatively stable across seasons and similar between sites except for LOW intensity wet season were groups were twice as large.

The composition of domestic stock appeared to influence the nature of livestock impacts on the environment and it reflected fundamental differences in pastoral land use in the three different land use intensity areas (Fig. 10a). For instance, the relatively low cattle to shoat ratio in HIGH is indicative of a pastoral society in transition from a subsistence to a market orientation and is consistent with other indicators of individualization and social fragmentation. Similarly, the temporal variability in the cattle:shoat ratio in INTERMEDIATE and LOW, in contrast to HIGH, suggests a higher degree of mobility with cattle leaving the system for reserve grazing areas during the dry season and returning to the core settlement and grazing areas during the wet season (Fig. 10a and Table 3).

Although the ratio of cattle to shoats is indicative of the changing nature of pastoral land-use, the ratio of domestic to wild biomass suggests the degree of human dominance in the system. For instance, the domestic:wild ratio declined with decreasing pastoral land-use intensity (Fig. 10b). Temporal differences in the ratio of domestic to wild biomass reflect the degree of interaction between each counting area and the dispersing wildlife populations from Amboseli National Park. The decline in the domestic:wild ratio in the HIGH intensity area, coupled with the fact that there was relatively little change in the domestic populations between seasons suggests that while livestock populations in Osilalei were relatively immobile (see also Fig. 7), wildlife continued to track resources at relatively broad spatial and temporal scales. In the INTERMEDIATE and LOW intensity areas there was little change in the ratio of domestic:wild biomass despite large changes in densities in both groups. The lack of seasonal differences suggests that while livestock and wildlife were increasingly dependent upon different dry season reserves (Chapter 3) both populations maintained a relatively high degree of flexibility in time and space.

Differences in domestic and wild densities become particularly clear when considered independently (Table 4). Overall, the biomass density of domestic and wild herbivores increased significantly in the wet season. As expected, pastoral land-use intensity was particularly important during the dry season with domestic and wild herbivore biomass density being inversely related. The effects of pastoral land-use are particularly clear in the dry season as dispersing wildlife are essentially constrained to the protected area and its immediate surroundings. During the wet season, domestic biomass densities in the HIGH and LOW intensity areas were significantly different, but there was evidence that the biomass density in the INTERMEDIATE area was the highest. Wet season wild biomass density was inversely related to pastoral land-use intensity with significant differences at the extreme ends of the gradient. This pattern also persisted when dispersing species were excluded. All areas had significantly higher biomass densities of both domestic and wild herbivores in the wet season (Table 4b).

The relative proportion of total biomass within the large herbivore community varied by season and area (Fig. 11 and Table 3). In both seasons domestic herbivores, and in particular cattle, comprised the largest proportion of total biomass density. In the HIGH intensity area cattle, shoats and donkeys were the most common species as indicated by biomass in both seasons. In contrast, during both seasons in the INTERMEDIATE and LOW intensity areas a relatively large proportion of the biomass was comprised of giraffe, and giraffe and zebra, respectively. The wet season increases in wildebeest and eland in the LOW intensity area were the most important seasonal shifts in relative biomass density.

Functional group biomass density varied significantly between Land Use Areas and seasons (Table 5a). The only exception was wild mixed feeders in the wet season, which did not differ significantly across areas. Although Kruskal-Wallis multiple comparison tests revealed no discernible differences in the biomass densities of wild grazers, mixed feeders, and browsers during the dry season, the LOW intensity area clearly had lower biomass values for grazers and browsers. Dry season wild biomass densities for grazers and browsers were highest in the LOW and INTERMEDIATE intensity areas respectively. As expected, domestic grazer and mixed feeder biomass was significantly higher in the HIGH intensity area. Wet season functional biomass density was slightly more variable with the highest domestic grazer and mixed feeder biomass occurring in the INTERMEDIATE and HIGH intensity areas respectively. Although individual area contrasts were not significant there were clearly more wild browsers in the INTERMEDIATE and LOW intensity areas during the wet season. Wet season wild grazer biomass was significantly higher in the LOW intensity area and mixed feeder biomass density was not significantly different across the gradient (Table 5b). As suggested by previous analyses, domestic grazer biomass density was significantly higher in the wet season in both the INTERMEDIATE and LOW areas. Wet season domestic mixed feeder biomass was slightly lower in the HIGH area, however. The only significant differences between seasons for wild functional group biomass were grazers and browsers in the LOW area, mixed feeders and browsers in the INTERMEDIATE area, and grazers in the HIGH intensity area.

To quantify the effects of pastoral land-use intensity on mean body weight for the entire herbivore community I compared mean biomass for all observed individuals of all species across Land Use Areas and seasons (Table 6a). HIGH and INTERMEDIATE mean dry season grazer body weights were significantly different. There were no differences in the wet season. The only significant differences for wild mean body weights were for wet season mixed feeders with the LOW intensity area having the highest mean body weight. Seasonally, domestic grazer mean body weight differed in both the HIGH and INTERMEDIATE intensity areas with the highest mean weights occurring in the dry and wet season respectively (Table 6b). For wildlife, grazer mean body weight was lower in the wet season in both the INTERMEDIATE and HIGH areas. Similarly, mixed feeder mean body weight in the HIGH area was lower in the wet season while mean body mass was higher for mixed feeders in the LOW area. There were no significant differences in the unique number of species encountered between Land Use Areas and seasons (Table 7). Although the large wild herbivore community was noticeably simpler in the HIGH intensity pastoral area there was little difference in the number of species per kilometer squared for both counts collectively or by season.

Responses to Distance from Settlement - Settlement Level

General Patterns

The species analyzed here exhibited diverse responses to human settlement (Fig. 12). For species with sufficiently high encounter rates (e.g. approximately 0.02 in Table

8) the two part conditional model provided insight into the potentially different processes underlying a species' presence/absence and the overall abundance of individuals when present (Cunningham and Lindenmayer 2005). At the level of the entire study area (all counting areas combined) the domestic animals – cattle and shoats – generally respond as expected. The probability of a grid cell/ transect segment containing cattle and shoats initially declined as a function of distance from permanent settlement in both the wet and the dry season (Fig. 12 – black line). Curiously, for cattle the probability increased again after approximately six kilometers in both seasons. In contrast, the probability of encountering shoats declined steeply within the first three kilometers from settlement. Wet season predicted intercepts were higher in both domestic species (Fig. 12 and Appendix 2 - Table 1).

The probability of encountering domestic animals generally declined with increasing distance from permanent settlement (but see cattle above). However, when domestic animals did occur their abundance was relatively independent of distance from settlement – i.e. abundance did not change as a function of distance from settlement (Fig. 12 – grey lines). There is some evidence that during the dry season that the number of shoats per block declined and cattle numbers increased with increasing distance from settlement. During the wet season both cattle and shoat herds increased slightly at farther distances.

As predicted, wildlife of different functional groups and body sizes responded differently to permanent settlement (Fig. 12). The probability of encountering zebra, a grazer of intermediate body size, gradually increased at farther distances from settlement during the dry season. As expected, zebra moved closer to settlements in the wet season exhibiting a hump shaped quadratic distribution. A small bodied mixed feeder, Grant's gazelle, was distributed evenly across the distance from settlement gradient in the dry season and declined with increasing distance from settlement in the wet season. The presence of giraffe, a large browser, increased slightly as a function of distance from settlement in the dry season and was unexpectedly hump shaped in the wet season.

In contrast to the predicted probability of encountering an individual, the abundance of zebra, Grant's gazelle and giraffe was independent of distance from settlement in the dry season (Fig 12 – grey lines). During the wet season, however, the modeled abundances of each species given presence were similar in form to the predicted distributions – both zebra and giraffe were uni-modal, and Grant's gazelle gradually declined with increasing distance from permanent settlement.

Species Responses to a pastoral land-use intensity gradient

The degree of pastoral land-use intensity had important implications for both the presence/absence and abundance of individual species (Fig. 13 and 14). The probability of encountering cattle and shoats generally declined across all counting areas and seasons. We would expect that domestic animals would be more evenly distributed in relation to settlement in the dry season as they search farther afield for dwindling forage resources. With the coming of the rains forage should become less limiting and domestic animals should concentrate closer to permanent settlement. These patterns were supported in the INTERMEDIATE and LOW intensity areas, but not in the HIGH intensity area.

The effects of pastoral land-use intensity on wildlife distributions in relation to settlement were highly variable. Relatively low numbers of observations for zebra, Grant's gazelle and giraffe in the HIGH intensity area in both the wet and dry seasons may limit the detection of clear patterns, but there was some evidence that all three species were distributed independently of settlement within the limited area between settlements. The one exception was Grant's gazelle in the wet season which possibly exhibited a uni-modal distribution (Fig. 13). In contrast, zebra were more likely to be found at farther distances from settlement during the dry season in both the INTERMEDIATE and LOW intensity areas, and they were uniformly and uni-modally distributed in the LOW and INTERMEDIATE areas respectively during the wet season. In the INTERMEDIATE intensity area Grant's gazelle were slightly more likely to occur far from settlement in the dry season and closer to settlement in the wet season. In the LOW area, contrary to expectations, their distribution was independent of settlement in the wet season and uni-modal in the dry. As predicted, giraffe presence was independent of distance from settlement in both seasons in the INTERMEDIATE area, and in the dry season in the LOW area. Unexpectedly, however, giraffe in the LOW area exhibited a uni-modal distribution in relation to permanent settlement during the wet season.

A similarly diverse set of responses to settlement emerges if we consider the abundance of a species in a 333 km^2 block given presence (Fig. 14). Cattle abundance was either independent of distance from settlement or positively related to distance from permanent settlement across the counting areas. Although there were seasonal differences in predicted cattle concentrations between areas, these data provide some support for the widely held pastoral view that large herds travel farther from settlement

(Informant interviews). Patterns for shoat abundance were similar to those for cattle in each of the areas and seasons except in the HIGH intensity area where shoats and cattle have contrasting distributions in the dry season. Abundance distributions for zebra, Grant's gazelle and giraffe were similar to those predicted for presence in most cases. Exceptions include the relatively independent distribution of zebra in the LOW area during the dry season, and the gradual decline in abundance of Grant's gazelle during the wet season in both the INTERMEDIATE and LOW intensity areas.

DISCUSSION

Responses to Land-Use Intensity - Landscape Level species and community patterns

Spatial Patterns

The spatial and temporal distribution of livestock biomass at the landscape level represents a fundamental indicator of changes in pastoral land-use intensity. The HIGH intensity area had a significantly higher density of livestock than the other areas (except for the INTERMEDIATE area in the wet season). More importantly, there was very little seasonal or spatial variation in domestic biomass distribution in the HIGH intensity area. The relatively homogeneous distribution of livestock across the landscape throughout the year was the direct result of the spatial limitations associated with central place foraging and a distributed settlement pattern. In contrast, the communal grazing and settlement system found in the INTERMEDIATE and LOW intensity areas resulted in a shifting and flexible pattern of resource utilization, with alternating areas of high and low pastoral impact and greater instantaneous utilization similar to that exhibited by migratory wild herbivores (Jarman and Sinclair 1979) and transhumant pastoralists (Worden 2007a). Although there were differences in domestic biomass densities among areas, the overall values for the HIGH and INTERMEDIATE intensity areas were relatively similar. The important difference between these two areas was not in their total livestock numbers, but in the composition and seasonal trends in those numbers. The HIGH intensity area had much lower cattle:shoat ratios as would be expected for a pastoral society in transition. Similarly, the overall ratio of domestic:wild biomass in the HIGH area was much higher with approximately 30 to 40 times more domestic than wild biomass in both seasons. The increase in relative herd sizes of domestic animals in the wet season, while contrary to predictions about herd size and dry season mobility (Worden 2007b, BurnSilver in prep), is consistent with idea that dry season resource limitation necessitates smaller groups to reduce intra-group competition (Fritz and Garine-Wichatitsky 1996). These differences suggest that an important structural shift in the large herbivore community occurs with pastoral intensification, with potentially cascading effects for biodiversity across the ecosystem (Cumming et al. 1997, Pringle et al. 2007).

Species and Functional Group Densities

The combined effects of high domestic biomass density and continuous utilization had important implications for the density, distribution, and composition of the wildlife community. Dry season wildlife biomass was inversely related to domestic biomass across all sites, with by far the lowest density occurring in the HIGH intensity area. A similar pattern existed in the wet season with wild biomass density increasing as we go down the pastoral land-use intensity gradient. As expected, all areas had higher densities of wild herbivores during the wet season, despite parallel increases in domestic biomass in the INTERMEDIATE and LOW intensity areas. In HIGH this increase was mainly the result of increases in mixed feeder biomass (especially Grant's and impala), while in the INTERMEDIATE area browsers (especially giraffe) increased the most. In the LOW intensity area, however, there were substantial increases in both grazers (wildebeest) and browsers (giraffe).

Historically, wildebeest, zebra, Thomson's gazelle and eland dispersed into the pastoral rangelands from swamps in protected areas in the wet season (Western 1973, Western and Nightingale 2003). As in other parts of the ecosystem, results here suggested that there has been very little seasonal changes in zebra populations in the pastoral rangelands north of Amboseli National Park. Nevertheless, the three-fold increase in zebra biomass in both the HIGH and LOW areas during the wet season suggests that limited seasonal movement may still be important for this species, especially in areas of intense pastoral utilization. Indeed, water development for livestock in the rangelands outside the National Park (Western and Nightingale 2003) and habitat changes over the past few decades inside the park (Western 2006) may have reduced the seasonal pull for zebras into the swamp. Patterns for Thomson's gazelle were unclear due to the low number of observations throughout the study area. Wildebeest continued to represent the majority of dispersing animals with significant population increases between seasons in the INTERMEDIATE and LOW intensity areas.

The LOW intensity area was clearly the most affected by dispersing populations from Amboseli National Park. This may be due to the low pastoral land-use intensity present there, but this was confounded with its closer proximity to the National Park. However, while distance may play a role, it should primarily be limited to the dry season. Key resource areas (mesic vegetation and watering points) are located within the Park. Consequently, animals are more likely to be within or near the park during the dry season. During the dry season animals move out of the park to access better foraging conditions on a daily basis (Worden 2007c). During the wet season, distance from the key resource areas in the National Park would be less important as forage and water are well distributed throughout the pastoral areas. Discussions with local informants suggest that dispersing species such as wildebeest reached the HIGH intensity area in the past and still do so occasionally. I also observed a herd of wildebeest during my flights that appeared to come to the boundary of the HIGH intensity area but did not enter.

Based upon our understanding of the effects of body size and feeding ecology on resource partitioning and competition (Jarman and Sinclair 1979, Prins and Olff 1998, Prins 2000) I expected wildlife to decline with increasing pastoral land-use intensity (Fig.1 curve 1). Furthermore, I expected that grazers would be most affected, followed by mixed feeders and finally browsers which would respond little to competitive interactions with livestock. Similarly, these relationships were expected to be most clear in the dry season when competition for forage resources is most acute. If alternative patterns were observed, it would suggest that other factors such as water availability and direct pastoral effects are also important in determining wildlife distribution and abundance. However, observations did support the prediction that wildlife biomass will decline as pastoral land-use intensity increases. In the dry season, the steep drop in wildlife biomass between the INTERMEDIATE and HIGH intensity areas suggested that the wildlife responses to livestock may be non-linear. When a threshold level of land-use intensity is reached, large declines in wildlife numbers occur. In the wet season, in contrast, the response was more linear, with the highest wildlife biomass in the LOW intensity area.

The general pattern of wildlife decline with increasing pastoral land-use intensity was primarily due to differences in grazer biomass. The observation that grazer biomass declined sharply with increasing pastoral land-use intensity is consistent with the hypothesis that competition between wild and domestic grazers will increasingly limit wild grazers as pastoral areas are subdivided and settlements become more widely distributed.

There was evidence that grazers decline along the land-use intensity gradient during the wet season. However, the primary comparison of interest is between the neighboring HIGH and INTERMEDIATE areas. The lack of a difference in wildlife biomass between these two areas suggests that at these levels of pastoral utilization, resource availability is not a constraint during the wet season. The second comparison of interest is the large differences in grazer biomass between these two more intensively utilized areas and the LOW area. This difference could be a function of pastoral land-use, or an effect of proximity to the National Park, as discussed above.

Contrary to initial predictions, the variation in browser biomass across the land-use intensity gradient was non-linear, with the highest mean density in the intermediate areas and the lowest mean densities in the high areas. Based upon feeding ecology I hypothesized that browser biomass would be independent of pastoral land-use as there would be little competition for forage with domestic livestock. The fact that none of the browsers in the Greater Amboseli Ecosystem are known to disperse during the wet season combined with their relatively high aridity tolerance means that their distributions should be independent of the key grazing resources in the protected area. It is important to note that browser biomass in these areas was dominated by giraffe. Although theory predicts that browser biomass should be independent of pastoral land-use (except under extreme circumstances where intensive utilization results in the elimination of woody vegetation), in this study browser biomass increased at intermediate pastoral land use, and decline dramatically at HIGH land use intensity. The initial increase could reflect increases in woody vegetation cover associated with minor increases in rainfall from south to north (Sankaran et al. 2005). If this were the case we would also expect the HIGH intensity area to have the greatest browser biomass due to its slightly higher rainfall (Touber 1983). However, the HIGH intensity area had the lowest browser biomass in both seasons suggesting that there are other limiting factors at work. This is corroborated by the unexpectedly large differences in wet season browser biomass, when resource limitation should be non-existent. Pastoral land-use may reach a threshold were impacts on woody vegetation have severe implications for browsing species, but in the current context the most likely explanation is related to body size and the differential susceptibility of large wild herbivores to direct human disturbance. Giraffe appear to be especially sensitive to direct disturbances such as domestic dogs, various human activities, and hunting in subdivided and homogeneously settled areas (Roque de Pinho, in prep.).

Mixed feeder biomass density was generally independent of increasing pastoral land-use intensity in both seasons, as predicted. There were significant increases in mixed feeder biomass in the HIGH and INTERMEDIATE areas during the wet season suggesting that competition for dry season resources may occur. The notable exception to this was eland, a large bodied mixed feeder which is well known for its flighty behavior and avoidance of humans (Estes 1991). Eland were not observed in any of the Land Use Areas during the dry season. During the wet season, however, they were found in the two lower intensity areas, but not the HIGH area. This may partly stem from the fact that they are seasonal dispersers from Amboseli NP, but their complete avoidance of the HIGH intensity area despite their occurrence in large numbers in similar habitat in other areas of the district (personal observation) suggests the importance of direct human impacts on their distribution. As with giraffe, eland are known to avoid settlement areas and are one of the few wildlife species that are widely recognized to be acceptable food in Maasailand (Roque de Pinho, in prep.). Wet season increases in Grant's gazelle and impala biomass densities in the INTERMEDIATE intensity area suggest the possibility of facilitation between livestock and mixed feeders, whereby habitat modification associated with intermediate levels of settlement and livestock grazing create beneficial foraging conditions for small bodied mixed feeders. Confirmation of this hypothesis will require further research across a variety of sites with differing rainfall, settlement and grazing regimes.

The examination of mean body masses of different functional groups was intended to detect shifts in body size within the herbivore community as a function of increasing pastoral land-use intensity. However, I found little evidence of major shifts in body sizes under different levels of pastoral utilization. The lack of differences across sites may be related to three factors. First, all of the sites are draw from the same relatively intact regional species pool. Second, it is possible that the extremes of land-use documented here, while sufficient to impact the relative abundance of different species, may not be severe enough to completely eliminate certain size classes. For instance, the loss of wildebeest would have much less of an impact on the overall grazer mean body weight than would the loss of buffalo or hippopotamus. Instead, data here suggest that while there has been a trend towards the elimination of large bodied wildlife under high pastoral land-use intensity (Prins and Olff 1998), these species have not been completely removed from the system. The one exception was the mixed feeders, where there was evidence of a decrease in mean body mass during the wet season with increasing land-use intensity. This difference is primarily the result of differences in the abundance of eland between sites and reflects the variability of body sizes within the mixed feeder functional group and the important absence of eland under intense pastoral land-use. Finally, although larger bodied animals comprised a relatively large proportion of the total herbivore biomass, they represent a small proportion of the total abundance.

One of the most important impacts of human activities globally is the effect of increasing intensification on species composition and community structure. Although there were no significant differences in the number of species per kilometer square between the land-use areas overall or by season in this study, these data suggest that there is a trend towards reduced species richness with increasing pastoral land-use intensification. Indeed, four of the primary wild species (excluding elephant) were not observed in either season in the HIGH intensity area – eland, lesser kudu, oryx, and wildebeest. In contrast, only lesser kudu and Thomson's gazelle were absent from both counts in the LOW and INTERMEDIATE areas respectively. As a grazer of intermediate body size, the absence of wildebeest in the HIGH area may be a result of periodic exclusion due to competition with cattle. Eland, lesser kudu and oryx represent a range of functional groups and body sizes, however, and their absence from the HIGH intensity area is likely the result of their relative rarity and susceptibility to direct human disturbance. Similarly, domestic species comprised an overwhelming majority of the large herbivore biomass in both the dry and wet seasons in the HIGH intensity area. In the INTERMEDIATE and LOW intensity areas cattle also made up the majority of the total biomass. However, the larger remainder consisted of seasonally dynamic associations of domestic and wild species. These shifts in species richness and community structure may have important implications for other taxonomic groups (Cumming et al. 1997, Pringle et al. 2007), and are indicative of the ever increasing pressure on less abundant species such as eland, lesser kudu, and oryx.

Responses to Distance from Settlement - Settlement Level

General Responses

Here, I consider how different species respond to the dominant feature of human land-use in the arid and semi-arid savannas of Africa – the pastoral settlement. By integrating the landscape and settlement level responses of different species and functional groups, first at the general level and then along a land-use gradient, the mechanisms underlying pastoral-wildlife interactions can be elucidated.

Due to the central place nature of pastoral herding strategies I predicted that the presence of cattle and shoats should decline as a function of distance from settlement in both seasons. However, the number of individuals in a transect segment given presence, should increase with increasing distance from settlement due to larger herd sizes at greater distances. Larger herds are expected at further distances from settlements, because large herds require denser forage resources. It is important to note that all of the following analyses are based upon distances from the core area of pastoral activity, the permanent settlement, irrespective of the location of temporary and seasonal settlements.

The probability of encountering, or presence of, a shoat within a transect segment declined as expected in both the wet and the dry season. In contrast, cattle presence unexpectedly followed a U-shaped or concave quadratic distribution with the highest probabilities both near and far from permanent settlement. This unexpected response likely reflects the high number of temporary settlements in the dry season grazing areas in INTERMEDIATE and LOW. Temporary settlements were placed far from the permanent settlement areas to maximize access to grazing reserves, and therefore cattle would be found farther from the permanent settlement than expected. This result emphasizes the importance of cattle movement and flexibility in these areas. The peak in cattle numbers far from settlement in the wet season suggests that a number of herders have opted to stay in the reserve grazing areas to take advantage of the green flush associated with initial rainfall. I do not have data to determine if this bi-polar pattern was sanctioned by the elders or was an example of "breaking" the rules, but during the wet season count I spoke with groups of warriors that were on their way to forcibly evict herds from the dry season grazing areas to give the vegetation an opportunity to recover. As expected, the abundance of cattle and shoats given presence, increased moderately with distance from settlement in all seasons, except for shoats in the dry season, which showed a slight decline in abundance with increasing distance.

As predicted, wildlife species exhibited differential responses to settlement that vary seasonally. The probability of encountering zebra matched perfectly the hypothesized distribution based on predictions from body size and feeding strategy. Abundance showed little change as a function of distance from settlement during the dry season, reflecting the discreet family units and limitations of intra-specific competition during periods of resource scarcity. During the wet season there is a slight increase in abundance at intermediate distances suggesting large concentrations and a localized increase in density associated with high quality foraging conditions. The combination of these probability and abundance curves suggests increasing density with distance in the dry season and a hump-shaped pattern of density in the wet season. Both of these patterns would be expected if the dominant processes determining the distribution and abundance of zebra were resource competition in the dry season and facilitation in the wet season.

The giraffe response to settlement was different from what was initially predicted based on feeding ecology alone. The slight increase in probability with increasing distance in the dry season and the hump-shaped quadratic response of both probability and abundance in the wet season, mirrored the results of giraffe biomass density to land use intensity. This suggests that the processes determining the distribution and abundance of giraffe at both the landscape and settlement level may be similar. The low density of giraffe close to settlement may be the result of direct human disturbance, or declines in the availability of woody vegetation due to utilization for settlement construction and fuel wood (Western and Dunne 1979, Jensen 1983 unpublished-b, a, Kiringe and Okello 2005). The peaked distribution in the wet season may be the result of these “push” factors (direct disturbance and declining woody vegetation), as well as “pull” factors possibly associated with increasing habitat complexity and a more diverse woody vegetation community at intermediate distances from settlement. The Grant’s gazelle responses to settlement were as predicted for the dry season with slight variations during the wet season. The uniform distribution of Grant’s gazelles as a function of distance from settlement in the dry season is consistent with what theory would predict if indirect competitive effects were the primary driver of distribution and abundance. In the wet season, however, while theory predicted a humped shaped distribution with the highest density at intermediate distances, observed probabilities and abundances were higher closer to settlement. The wet season distribution is consistent with a prediction of “facilitation”, but the strength of the positive interaction between pastoral settlements and Grant’s gazelle was unexpected. As with the giraffe, the seasonal responses to settlement are very similar to those observed at the landscape scale. At the settlement level Grant’s gazelle were relatively independent of pastoral land-use intensity during the dry season, in contrast to the declines observed with increasing intensity at the landscape level. During the wet season, there was evidence that Grant’s gazelle actually favored some level of pastoral land-use at both the settlement and landscape scale. This facilitative effect may stem from predator avoidance or enhanced forage resources associated with the effects of livestock utilization and habitat modification around human settlements. Possible correlation between water and settlement is unlikely to be important as all of these species are closer to settlements in the wet season when water is not limiting. Although determining the exact mechanism for the “facilitation” observed in the wet season for all three of these species requires continued research, the presence of this effect in all of these species suggests that the interaction of pastoralists and wildlife is more complex than the strictly benign or negative relationship that are so pervasive.

Species Level Responses to Pastoral Land-Use

To effectively integrate species level responses to pastoral land-use at different spatial and temporal scales we must also consider how a land-use intensity gradient modifies species' responses to pastoral settlement. Cattle distributions were highly variable across the Land Use Areas. In the LOW intensity area the probability of encountering cattle was independent of distance from settlement, with a slight increase in dry season abundance away from settlement. In the INTERMEDIATE area probability of occurrence and abundance were independent of distance in the dry season, but the wet season distribution revealed a contraction of herds around the settlement with only large herds grazing at farther distances. This wet season distribution reflected the dry season dispersal/wet season contraction grazing system that was created in response to increasing constraints associated with intensification (Worden 2007a). As predicted, probabilities of shoat occurrence declined with increasing distance from settlement in both seasons. At the extreme high intensity end of the gradient it appeared that herders were employing a different strategy to cope with the drastically reduced spatial scale of the system. In the HIGH area the probability of encountering both cattle and shoats declined as a function of distance from settlement while wet season patterns were independent of distance, suggesting that herders may be trying to maximize access to green forage during the wet season and are then falling back on individual reserve grazing areas during the dry season in the absence of a broad scale forage management strategy. The increase in dry season cattle abundance as a function of distance from settlement in the HIGH intensity area is consistent with this explanation as larger herds are forced to search more widely as constraints on forage availability increase. The dry and wet season abundances of cattle and shoats in the INTERMEDIATE and LOW intensity areas are highly variable with some herds increasing with distance and others declining. For cattle, abundance is either independent of distance or increasing with the largest herds having the need and/or the ability to access forage at farther distances. The seasonal variability in the response of domestic animals reflects the variability in local conditions and highlights the flexibility inherent in these communally managed systems.

In decomposing the responses of wildlife to pastoral settlement, two main trends emerge. First, the collapse of human impact gradients radiating from settlements due to their dispersion in the HIGH intensity area and the subsequent loss of habitat far from settlement is truly impressive. Second, as predicted (curve 1, Fig.1) most of the evidence for "facilitation" between pastoral settlements and wildlife in this low rainfall area occurs at the LOW intensity end of the pastoral land-use gradient. For example, the hump-shaped curves of probability and abundance versus distance from settlement in the wet season distributions of zebra and giraffe were only observed in the LOW intensity area. In contrast, however, the probability and abundance of Grant's gazelle declined with increasing distance from settlement suggesting a degree of "facilitation" at all levels of land-use intensity in the wet season. During the dry season there was some evidence for increased density of Grant's at intermediate distances suggesting that predator avoidance may be playing a role in structuring distributions of this small bodied mixed feeder so close to the National Park. In general, it appears that low or moderate use may "facilitate", or at least reduce competition between livestock and wildlife. Alternatively, wildlife may be drawn to settlements to avoid predation, especially in the LOW density area close to park. This is unlikely the dominant factor, however, as there are still many predators in the communally managed areas and the high profile killings of lions in the park in recent years means that predator densities may be higher outside of protected areas in this region (personal observation).

In summary, the data I present here indicate that increasing pastoral land-use intensity, as represented by land privatization and distributed settlement patterns, has important implications for the density, distribution, and structure of the wild large herbivore community. I have shown that species and functional group responses to pastoral land-use intensification at multiple spatial and temporal scales are generally predictable based on body size and feeding ecology. Grazers are most susceptible to competitive exclusion at high levels of pastoral land-use intensity while browsers appear to exhibit a threshold response to intensification at the landscape scale. Mixed feeders generally appear to be independent of intensification in keeping with the seasonal adaptability of their diet. Large bodied herbivores all but disappear under high levels of pastoral land-use. There are important exceptions however, and more in-depth research into the differential responses of large herbivores to direct and indirect pastoral impacts is required. At the settlement level, the spatial distributions of all three of the wild species analyzed here supported the idea that low intensity pastoral land-use may seasonally "facilitate" wildlife utilization of semi-arid savannas. Furthermore, this study demonstrates the importance of high resolution counting and detailed investigations of pastoral wildlife interactions for furthering our understanding of pastoral development and land-use change and its implications for the structure and function of East African savanna ecosystems.

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TABLES

Table 1. Species names, population weights and functional groups. Two species have been excluded (*Camelus dromedarius*) and Elephant (*Loxodonta africana* (Blumenbach)) because of low numbers of observations. Note the predicted responses of each species to increasing pastoral land-use intensity (Landscape Response) and increasing distance from settlement (Settlement Response) by season are listed. At the Landscape level a population response of increase, decrease and no change are indicated by +, - and 0 respectively. Numbers in the settlement level response columns refer to hypothesized curves in Figure 2.

Common Name	**Scientific Name**	**Species Code**	**Population Unit Weight (kg)***	**Body Size Class****	**Feeding Strategy*****	**Aridity Tolerance******	**Landscape Response**		**Settlement Response**	
							Dry	**Wet**	**Dry**	**Wet**
Cattle	*Bos indicus* (L.)	CT	180	Medium	Grazer	Intermediate	+	+	4	4
Donkey	*Equus asinus* (L.)	DK	130	Medium	Grazer	Low	0	0	4	4
Shoats	*Ovis aries* (L.) and *Capra hircus* (L.)	ST	18	Small	Mixed	Intermediate	+	+	4	4
Eland	*Taurotragus oryx* (Pallas)	ED	340	Medium	Mixed	High	-/0	0	1	3
Gerenuk	*Litocranius walleri*	GK	25	Small	Browser	High	0	0	2	2
Giraffe	*Giraffa cameleopardis* (L.)	GF	750	Large	Browser	High	0	0	2	2
Grant's Gazelle	*Gazella granti* (Brooke)	GT	40	Small	Mixed	High	-/0	0	1	3
Impala	*Aepyceros melampus* (Lichtenstein)	IM	40	Small	Mixed	Intermediate	-/0	0	1	3
Lesser Kudu	*Tragelaphus imberbis*	LK	70	Medium	Browser	High	0	0	2	2
Ostrich	*Struthio camelus*	OS	114	Medium	Mixed	High	-/0	0	1	3
Oryx	*Oryx beisa* (Pallas)	OX	150	Medium	Grazer	High	-	0	1	3
Thomson's Gazelle	*Gazella thomsonii* (Guntter)	TM	15	Small	Mixed	Low	-/0	0	1	3
Wildebeest	*Connochaetes taurinus* (Burchell)	WT	123	Medium	Grazer	Low	-	0	1	3
Zebra	*Equus burchelli* (Gray)	ZB	200	Medium	Grazer	Low	-	0	1	3

* all body weights from Western (1975) except for gerenuk, lesser kudu, waterbuck, warthog, and wildebeest which are from Coe, Cumming, and Phillipson (1976)

** body size classes as follows: Small (< 50 kg), Medium (50 to 400 kg), and Large (> 400 kg)

*** Grazer (G), Browser (B) or Mixed (M) feeder based on descriptions from Estes (1991)

**** the degree to which a species depends on surface water to meet its water requirements (after de Leeuw et al, 2001) - animals that need to drink daily have a low tolerance while those that can meet most of their requirements from moisture in vegetation have a high aridity tolerance - Western (1975) and de Leeuw et al (2001) differ on STs

Table 2. Table of counting area characteristics, count dates, and pastoral land-use intensity classifications.

	Osilalei	**Eselenkei**	**Meshenani**
Land-Use Intensity	HIGH	INTERMEDIATE	LOW
Land Tenure	Subdivided	Not subdivided	Not subdivided
Settlement Pattern	Dispersed	Clustered	Clustered
Degree of Sedentarization	High	Intermediate	Low
Count dates - Dry season	Oct 2001	Sept 2000	Sept 2000
Count dates - Wet season	Dec 2001	Dec 2001	Jan 2001
Area (km^2)	258	407	453
Area for Distance to Settlement Analyses (km^2)	154	403	397

Table 3a. (Table 3a) Densities (number/km^2) of domestic and wild animals by species, season and LUA. Panel one is the overall mean density for all count areas and seasons. Panels two and three include densities for the dry season and wet seasons respectively. All densities are adjusted using the detection probabilities calculated in DISTANCE 4.1 and summarized in Appendix 1 Table 3. Upper and lower confidence limits ($p < 0.05$) are based on the estimates of detection probabilities from DISTANCE 4.1.

Table. 3a.

			Overall Mean Density			
Species	HIGH	(lcl-ucl)	INTER	(lcl-ucl)	LOW	(lcl-ucl)
Camel	---	(--- - ---)	0.001	(0.001 - 0.002)	0.013	(0.011 - 0.015)
Cattle	26.88	(23.928 - 30.198)	26.082	(23.217 - 29.301)	15.49	(13.789 - 17.402)
Donkey	0.773	(0.603 - 0.992)	0.501	(0.391 - 0.642)	0.54	(0.421 - 0.693)
Eland	---	(--- - ---)	0.084	(0.084 - 0.084)	0.381	(0.381 - 0.381)
Elephant	---	(--- - ---)	---	(--- - ---)	0.001	(0.001 - 0.001)
Giraffe	0.073	(0.058 - 0.09)	0.773	(0.62 - 0.964)	0.604	(0.484 - 0.753)
Gerenuk	0.003	(0.002 - 0.004)	0.07	(0.055 - 0.089)	0.046	(0.036 - 0.058)
G. Gazelle	1.277	(1.091 - 1.494)	0.917	(0.784 - 1.073)	0.977	(0.835 - 1.143)
Impala	0.074	(0.063 - 0.087)	0.206	(0.176 - 0.241)	0.019	(0.017 - 0.023)
Lesser Kudu	---	(--- - ---)	0.008	(0.006 - 0.01)	---	(--- - ---)
Ostrich	0.179	(0.137 - 0.235)	0.117	(0.089 - 0.154)	0.223	(0.17 - 0.292)
Oryx	---	(--- - ---)	0.039	(0.031 - 0.049)	0.049	(0.038 - 0.062)
Shoats	50.928	(50.928 - 50.928)	15.826	(15.826 - 15.826)	6.359	(6.359 - 6.359)
T. Gazelle	0.049	(0.042 - 0.058)	---	(--- - ---)	0.081	(0.069 - 0.095)
Wildebeest	---	(--- - ---)	0.426	(0.31 - 0.586)	1.262	(0.917 - 1.735)
Zebra	0.167	(0.167 - 0.167)	0.459	(0.459 - 0.459)	2.447	(2.447 - 2.447)
			Dry Season Density			
Camel	---	(--- - ---)	---	(--- - ---)	---	(--- - ---)
Cattle	26.329	(23.437 - 29.579)	15.071	(13.416 - 16.931)	6.095	(5.425 - 6.847)
Donkey	0.56	(0.437 - 0.718)	0.503	(0.393 - 0.646)	0.429	(0.334 - 0.55)
Eland	---	(--- - ---)	---	(--- - ---)	---	(--- - ---)
Elephant	---	(--- - ---)	---	(--- - ---)	0.002	(0.002 - 0.002)
Giraffe	0.095	(0.076 - 0.118)	0.364	(0.292 - 0.454)	0.229	(0.183 - 0.285)
Gerenuk	0.006	(0.005 - 0.008)	0.062	(0.049 - 0.079)	0.049	(0.038 - 0.062)
G. Gazelle	0.229	(0.196 - 0.268)	0.462	(0.395 - 0.541)	0.785	(0.671 - 0.919)
Impala	---	(--- - ---)	0.008	(0.007 - 0.009)	0.039	(0.033 - 0.045)
Lesser Kudu	---	(--- - ---)	---	(--- - ---)	---	(--- - ---)
Ostrich	0.135	(0.103 - 0.177)	0.082	(0.062 - 0.108)	0.164	(0.125 - 0.215)
Oryx	---	(--- - ---)	---	(--- - ---)	0.046	(0.036 - 0.058)
Shoats	51.368	(51.368 - 51.368)	11.961	(11.961 - 11.961)	4.318	(4.318 - 4.318)
T. Gazelle	0.099	(0.085 - 0.116)	---	(--- - ---)	---	(--- - ---)
Wildebeest	---	(--- - ---)	0.217	(0.158 - 0.298)	0.077	(0.056 - 0.105)
Zebra	0.248	(0.248 - 0.248)	0.545	(0.545 - 0.545)	1.331	(1.331 - 1.331)
			Wet Season Density			
Camel	---	(--- - ---)	0.003	(0.003 - 0.003)	0.026	(0.023 - 0.029)
Cattle	27.432	(24.418 - 30.817)	37.093	(33.018 - 41.671)	24.886	(22.152 - 27.957)
Donkey	0.987	(0.769 - 1.265)	0.498	(0.388 - 0.639)	0.652	(0.509 - 0.837)
Eland	---	(--- - ---)	0.167	(0.167 - 0.167)	0.762	(0.762 - 0.762)
Elephant	---	(--- - ---)	---	(--- - ---)	---	(--- - ---)
Giraffe	0.05	(0.04 - 0.063)	1.181	(0.947 - 1.473)	0.979	(0.785 - 1.22)
Gerenuk	---	(--- - ---)	0.078	(0.061 - 0.099)	0.042	(0.033 - 0.053)
G. Gazelle	2.325	(1.987 - 2.72)	1.372	(1.172 - 1.605)	1.169	(0.999 - 1.368)
Impala	0.148	(0.127 - 0.174)	0.404	(0.345 - 0.472)	---	(--- - ---)
Lesser Kudu	---	(--- - ---)	0.016	(0.012 - 0.02)	---	(--- - ---)
Ostrich	0.223	(0.17 - 0.293)	0.153	(0.116 - 0.2)	0.281	(0.214 - 0.369)
Oryx	---	(--- - ---)	0.078	(0.061 - 0.099)	0.053	(0.041 - 0.066)
Shoats	50.488	(50.488 - 50.488)	19.69	(19.69 - 19.69)	8.4	(8.4 - 8.4)
T. Gazelle	---	(--- - ---)	---	(--- - ---)	0.162	(0.138 - 0.19)
Wildebeest	---	(--- - ---)	0.635	(0.462 - 0.874)	2.447	(1.779 - 3.365)
Zebra	0.085	(0.085 - 0.085)	0.373	(0.373 - 0.373)	3.563	(3.563 - 3.563)

Table 3b. Kruskal-Wallis tests for differences in density between areas by species and season. For species with significant differences results from a Kruskal-Wallis multiple comparisons test are also included. For the stated contrasts (H = HIGH, I=INTERMEDIATE, and L=LOW) a 0 indicates no significant difference and a 1 indicates significant differences exist between the two areas ($p<0.05$).

	Dry						Wet					
Species	χ^2	df	pvalue	I v L	I v H	L v H	χ^2	df	pvalue	I v L	I v H	L v H
Camel	---	--	---	---	---	---	0.608	2	0.738	0	0	0
Cattle	161.000	2	<0.001	0	1	1	84.017	2	<0.001	1	1	1
Donkey	7.267	2	0.026	0	0	0	22.235	2	<0.001	0	0	0
Eland	---	--	---	---	---	---	14.282	2	0.001	0	0	0
Elephant	1.468	2	0.480	0	0	0	---	---	---	---	---	---
Giraffe	11.586	2	0.003	0	0	0	27.865	2	<0.001	0	0	0
Gerenuk	3.753	2	0.153	0	0	0	5.954	2	0.051	0	0	0
G. Gazelle	17.622	2	<0.001	0	0	0	10.752	2	0.005	0	0	0
Impala	1.208	2	0.547	0	0	0	10.620	2	0.005	0	0	0
Lesser Kudu	---	--	---	---	---	---	6.994	2	0.030	0	0	0
Ostrich	5.241	2	0.073	0	0	0	2.664	2	0.264	0	0	0
Oryx	2.937	2	0.230	0	0	0	2.176	2	0.337	0	0	0
Shoats	243.358	2	<0.001	0	1	1	312.775	2	<0.001	0	1	1
T. Gazelle	6.669	2	0.036	0	0	0	13.243	2	0.001	0	0	0
Wildebeest	4.229	2	0.121	0	0	0	80.360	2	<0.001	0	0	1
Zebra	33.018	2	<0.001	0	0	0	69.242	2	<0.001	0	0	1

Table 3c. Kruskal-Wallis tests for differences in density between seasons for each species within a LUA.

	OSIL			ESEL		
Species	χ^2	df	pvalue	χ^2	df	pvalue
Camel	---	---	---	1.000	1	0.317
Cattle	0.608	1	0.435	26.440	1	<0.001
Donkey	9.066	1	0.003	1.889	1	0.169
Eland	---	---	---	3.002	1	0.083
Elephant	---	---	---	---	---	---
Giraffe	0.000	1	0.994	7.635	1	0.006
Gerenuk	1.000	1	0.317	0.060	1	0.807
G. Gazelle	27.817	1	0.000	2.107	1	0.147
Impala	4.008	1	0.045	7.406	1	0.007
Lesser Kudu	---	---	---	4.005	1	0.045
Ostrich	0.234	1	0.628	2.219	1	0.136
Oryx	---	---	---	3.002	1	0.083
Shoats	4.923	1	0.026	1.107	1	0.293
T. Gazelle	2.001	1	0.157	---	---	---
Wildebeest	---	---	---	13.461	1	<0.001
Zebra	3.290	1	0.070	2.212	1	0.137

Table 4a. Domestic and Wild biomass densities (kg/km^2) by season and area. Kruskal-Wallis tests for differences between areas by season (*** =p <0.001, ** = p<0.01, * = p<0.05) and multiple comparison tests for differences between areas by season. Different superscript letters indicate significant differences (p <0.05).

	ALL				DRY						WET					
	DRY		WET		HIGH		INTER		LOW		HIGH		INTER		LOW	
	Bio	SE	Bio	SE	Bio	SE	Bio	SE	Bio	SE	Bio	SE	Bio	SE	Bio	SE
Domestic	2912***	232	5873***	381	5737^{a}	511	2994^{b}	459	1231^{c}	262	5975^{a}	548	7096^{ab}	693	4715^{b}	633
Wild	401***	38	1327***	142	147^{a}	38	439^{b}	75	511^{c}	60	179^{a}	32	1199^{ab}	192	2097^{b}	304

Table 4b. Kruskal-Wallis rank sum test results for differences in domestic and wild biomass between seasons for each area.

Domestic				Wild			
Area	χ^2	df	pvalue	Area	χ^2	df	pvalue
HIGH	6.316	1	0.012	HIGH	6.706	1	0.010
INTER	20.248	1	<0.001	INTER	8.766	1	0.003
LOW	14.192	1	<0.001	LOW	11.740	1	0.001

Table 5a. Functional group biomass densities (kg/km^2) by season and LUA. Kruskal-Wallis tests for differences between areas by season (*** =p <0.001, ** = p<0.01, * = p<0.05) and multiple comparison tests for differences between areas by season. Different superscript letters indicate significant differences (p <0.05).

	Functional Group	Dry		Wet		Dry						Wet					
		All		All		HIGH		INTER		LOW		HIGH		INTER		LOW	
		Bio	SE	Bio	SE	Bio	SE	Bio	SE	Bio	SE	Bio	SE	Bio	SE	Bio	SE
Domestic	Grazers	2589***	225	5473***	379	4812^a	483	2778^b	448	1153^b	259	5066^a	529	6742^b	689	4564^c	630
	Mixed	323***	27	400***	29	925^a	95	215^b	35	78^b	19	909^a	78	354^b	52	151^b	30
	Browsers	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Wild	Grazers	175***	18	478***	68	50^a	17	136^a	26	282^a	37	17^a	9	165^a	31	1021^b	163
	Mixed	39**	4	219	52	26^a	6	28^a	5	55^a	8	124	25	145	43	340	122
	Browsers	187***	32	630***	80	71^a	32	275^a	68	173^a	47	38^a	18	889^a	171	735^a	123

Table 5b. Kruskal - Wallis test for seasonal differences in functional group biomass density within LUA.

	Domestic				Wild			
Group	Area	χ^2	df	pvalue	Area	χ^2	df	pvalue
Grazers	HIGH	2.180	1	0.140	HIGH	3.290	1	0.070
	INTER	20.772	1	<0.001	INTER	0.361	1	0.548
	LOW	19.174	1	<0.001	LOW	13.629	1	<0.001
Mixed	HIGH	4.923	1	0.026	HIGH	13.375	1	<0.001
	INTER	1.107	1	0.293	INTER	8.409	1	0.004
	LOW	1.027	1	0.311	LOW	0.754	1	0.385
Browsers	HIGH	---	---	---	HIGH	0.095	1	0.758
	INTER	---	---	---	INTER	7.895	1	0.005
	LOW	---	---	---	LOW	9.853	1	0.002

Table 6a. Mean body weight (kg) for observed domestic and wild species by functional groups, season and area. Kruskal-Wallis test for differences between areas by season(*** =p <0.001, ** = p<0.01, * = p<0.05) and multiple comparison tests for differences between areas by season. Different superscript letters indicate significant differences (p <0.05). Means with no superscript values had no significant differences between areas.

	Functional Groups	All				Dry						Wet					
		Dry		Wet		HIGH		INTER		LOW		HIGH		INTER		LOW	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Domestic	Grazers	175.52***	0.78	175.79	0.62	178.21^{a}	0.68	172.48^{b}	1.72	173.54^{ab}	2.34	174.43	1.13	177.9	0.7	174.61	1.51
	Mixed	18	0	18	0	18	0	18	0	18	0	18	0	18	0	18	0
	Browsers	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wild	Grazers	196.63	1.18	165.27	2.4	200	0	194.62	2.63	197.27	1.37	200	0	165.8	4.93	164.12	2.78
	Mixed	77.76*	10.93	81.42***	4.91	86.76^{a}	7.18	61.83^{a}	5.02	83^{a}	20.12	56.81^{a}	3.87	70.23^{ab}	6.05	106.72^{b}	10.26
	Browsers	613.53	30.92	670.14	18.89	629.17	120.83	601.7	44.6	625.71	46.86	750	0	633.29	31.03	705.38	21.78

Table 6b. Seasonal differences in mean body weight for functional groups within a counting area

		Domestic			Wild		
	Area	χ^2	df	pvalue	χ^2	df	pvalue
Grazers	HIGH	4.218	1	0.040	NA	1	NA
	INTER	15.853	1	<0.001	19.191	1	<0.001
	LOW	0.009	1	0.924	75.630	1	<0.001
Mixed	HIGH	NA	1	NA	8.998	1	0.003
	INTER	NA	1	NA	0.318	1	0.573
	LOW	NA	1	NA	5.838	1	0.016
Browsers	HIGH	—	—	—	0.833	1	0.361
	INTER	—	—	—	0.326	1	0.568
	LOW	—	—	—	1.516	1	0.218

Table 7. Species richness and species density (number of unique species/km^2) for each LUA and season. Pearson's Chi-square tests of species densities reveals no significant ($p < 0.05$) differences between LUAs within a season, or within seasons for each area.

	Number of Species			Number of Species per km^2		
	All	Dry	Wet	All	Dry	Wet
HIGH	7	6	5	0.027	0.023	0.019
INTER	10	7	10	0.025	0.017	0.025
LOW	11	9	9	0.024	0.020	0.020

Table 8. Proportion of Sub Block Zones (1/3 km^2) that contain herds of the following species – i.e. the proportion of sub-blocks in which each species is present. All herd sizes are included

	Dry	Wet	Dry			Wet		
Species	All	All	HIGH	INTER	LOW	HIGH	INTER	LOW
Cattle	0.078	0.123	0.219	0.071	0.030	0.229	0.131	0.073
Shoats	0.069	0.087	0.242	0.046	0.024	0.299	0.058	0.032
G. Gazelle	0.030	0.043	0.011	0.026	0.041	0.083	0.035	0.035
Giraffe	0.022	0.039	0.008	0.029	0.021	0.002	0.050	0.042
Donkey	0.013	0.016	0.017	0.017	0.007	0.042	0.011	0.012
Zebra	0.048	0.045	0.023	0.038	0.067	0.008	0.027	0.077
Ostrich	0.018	0.025	0.028	0.012	0.021	0.030	0.019	0.029
Wildebeest	0.002	0.038	0.000	0.004	0.002	0.000	0.021	0.070
Gerenuk	0.005	0.004	0.000	0.007	0.005	0.000	0.007	0.003
Eland	0.000	0.006	0.000	0.000	0.000	0.000	0.002	0.011
Impala	0.001	0.005	0.000	0.001	0.002	0.006	0.008	0.000
Oryx	0.001	0.002	0.000	0.000	0.002	0.000	0.002	0.003
T.Gazelle	0.000	0.003	0.002	0.000	0.000	0.000	0.000	0.007

Appendix 1

Appendix 1 Table 1. Numbers of observations and mean and expected cluster sizes from DISTANCE analysis. Upper and lower confidence limits ($p < 0.05$) from DISATANCE 4.1. Only those observations with perpendicular distance data and those with more than 20 observations were included.

	Number of Observations			Mean Cluster Size					Expected Cluster Size				
Species	global	Osil	Esel	observed	cv	lcl	ucl	df	expected	cv	lcl	ucl	df
Cattle	423	217	206	44.00	0.05	40.07	48.31	422	36.99	0.07	32.52	42.06	421
Shoats	366	254	112	55.20	0.04	51.05	59.69	365	55.20	0.04	51.05	59.69	365
Donkey	41	28	13	5.17	0.14	3.94	6.78	40	5.17	0.14	3.94	6.78	40
Grants	96	48	48	7.56	0.13	5.83	9.81	95	7.56	0.13	5.83	9.81	95
Giraffe	70	7	63	4.89	0.15	3.66	6.52	69	4.89	0.15	3.66	6.52	69
Ostrich	40	17	23	1.98	0.12	1.55	2.51	39	1.72	0.11	1.39	2.14	38
Wildebeest	26	0	26	6.31	0.22	4.07	9.79	25	4.45	0.25	2.66	7.42	24
Zebra	36	4	32	4.69	0.12	3.72	5.92	35	4.69	0.12	3.72	5.92	35

Appendix 1 Table 2. Numbers of Groups, mean group size (observed) and mean group size (adjusted) from DISTANCE 4.1.

Table 2.

	Numbers of Groups						Mean Group Size						Adjusted Mean Group Size					
	Dry			Wet			Dry			Wet			Dry			Wet		
Species	HIGH	INTER	LOW	HIGH	INTER	LOW	HIGH	INTER	LOW	HIGH	INTER	LOW	HIGH	INTER	LOW	HIGH	INTER	LOW
Camel	---	---	---	---	1	1	---	---	---	---	1	10	---	---	---	---	1.17	11.7
Cattle	179	98	51	221	211	107	32.42	53.48	46.25	27.36	61.13	90.02	37.95	62.59	54.14	32.02	71.55	105.4
Donkey	9	21	9	28	13	14	7.44	4.52	10	4.21	7.23	9.79	16.06	9.76	21.57	9.09	15.6	21.11
Eland	---	---	---	---	4	18	---	---	---	---	17	19.17	---	---	---	---	17	19.17
Elephant	---	---	1	---	---	---	---	---	1	---	---	---	---	---	1	---	---	---
Giraffe	5	37	29	7	64	67	3.4	2.78	2.48	1.29	5.22	4.6	4.89	4.01	3.57	1.85	7.51	6.62
Gerenuk	1	9	6	---	9	4	1	1.78	2.33	---	2.22	3	1.59	2.82	3.7	---	3.52	4.76
G. Gazelle	8	33	63	48	48	45	4.62	3.58	3.54	7.83	7.29	7.38	7.38	5.7	5.65	12.49	11.63	11.77
Impala	---	1	2	4	10	---	---	2	5.5	6	10.3	---	---	3.19	8.77	9.57	16.43	---
Lesser Kudu	---	---	---	---	4	---	---	---	---	---	1	---	---	---	---	---	1.59	---
Ostrich	19	14	28	17	23	39	1.21	1.57	1.75	2.24	1.78	2.15	1.84	2.38	2.65	3.39	2.7	3.26
Oryx	---	---	2	---	3	5	---	---	6.5	---	6.67	3	---	---	10.31	---	10.57	4.76
Shoats	207	73	35	261	119	53	64.02	66.68	55.89	49.91	67.34	71.79	64.02	66.68	55.89	49.91	67.34	71.79
T. Gazelle	2	---	---	---	---	9	8	---	---	---	---	5.11	12.76	---	---	---	---	8.15
Wildebeest	---	5	2	---	26	110	---	11.2	11	---	6.31	6.39	---	17.66	17.34	---	9.95	10.08
Zebra	11	47	94	4	33	131	5.82	4.72	6.41	5.5	4.61	12.32	5.82	4.72	6.41	5.5	4.61	12.32

Appendix 1 Table 3. Detection Probability from DISTANCE 4.1. Confidence limits for $p < 0.05$.

Species	Det Prob	cv	lcl	ucl	df
Cattle	0.854	0.059	0.761	0.960	422
Shoats	1.000	0.000	1.000	1.000	366
Donkey	0.464	0.124	0.361	0.595	40
Grants	0.627	0.079	0.536	0.734	95
Giraffe	0.695	0.111	0.557	0.866	69
Ostrich	0.660	0.135	0.503	0.866	39
Wildebeest	0.634	0.156	0.461	0.872	25
Zebra	1.000	0.000	1.000	1.000	36
GT_WT Mean	0.631	0.117	0.498	0.803	---

Appendix 2

Appendix 2 Table 1. Two part conditional model - logistic regression of presence/absence (logistic) and zero truncated negative binomial model for abundance (count) as a function of distance from settlement given presence. Model parameter estimates, SE and p values. For all areas combined.

		Species	Inter	SE	P value	Dboma	SE	P value	Dboma^2	SE	P value
Logistic	Dry	Cattle	-1.257	0.132	< 0.001	-1.002	0.120	< 0.001	0.117	0.017	< 0.001
		Shoat	-1.276	0.110	< 0.001	-0.703	0.067	< 0.001	---	---	---
		Zebra	-3.891	0.184	< 0.001	0.258	0.040	< 0.001	---	---	---
		Grant's G.	-3.489	0.110	< 0.001	---	---	---	---	---	---
		Giraffe	-4.333	0.244	< 0.001	0.167	0.056	0.003	---	---	---
	Wet	Cattle	-0.895	0.113	< 0.001	-0.864	0.097	< 0.001	0.102	0.014	< 0.001
		Shoat	-0.341	0.132	0.010	-1.588	0.175	< 0.001	0.120	0.034	< 0.001
		Zebra	-4.836	0.337	< 0.001	1.081	0.196	< 0.001	-0.122	0.026	< 0.001
		Grant's G.	-2.789	0.146	< 0.001	-0.115	0.046	0.012	---	---	---
		Giraffe	-5.104	0.377	< 0.001	1.024	0.208	< 0.001	-0.103	0.026	< 0.001
Count	Dry	Cattle	3.830	0.123	< 0.001	0.088	0.118	0.456	-0.001	0.016	0.932
		Shoat	4.440	0.086	< 0.001	-0.085	0.051	0.099	---	---	---
		Zebra	1.707	0.155	< 0.001	0.000	0.033	0.989	---	---	---
		Grant's G.	1.761	0.099	< 0.001	---	---	---	---	---	---
		Giraffe	0.103	1.240	0.934	0.003	0.102	0.979	---	---	---
	Wet	Cattle	3.825	0.090	< 0.001	0.336	0.083	< 0.001	-0.021	0.012	0.075
		Shoat	4.294	0.092	< 0.001	0.191	0.162	0.239	-0.020	0.044	0.651
		Zebra	0.967	0.494	0.050	0.945	0.293	0.001	-0.132	0.041	0.001
		Grant's G.	2.796	0.129	< 0.001	-0.129	0.039	< 0.001	---	---	---
		Giraffe	1.446	0.444	0.001	0.359	0.253	0.157	-0.059	0.033	0.078

Appendix 2 Table 2a. Two part conditional model - logistic regression of presence and absence. Model parameter estimates, SE and p values.

		Species	Inter	SE	P value	Dboma	SE	P value	Dboma^2	SE	P value
DRY	HIGH	Cattle	-0.803	0.203	< 0.001	-0.743	0.286	0.009	---	---	---
		Shoat	0.054	0.215	0.802	-2.072	0.368	< 0.001	---	---	---
		Zebra	-3.733	0.305	< 0.001	---	---	---	---	---	---
		Grant's G.	-4.535	0.450	< 0.001	---	---	---	---	---	---
		Giraffe	-4.760	0.502	< 0.001	---	---	---	---	---	---
	INTERMEDIATE	Cattle	-2.572	0.112	< 0.001	---	---	---	---	---	---
		Shoat	-2.163	0.320	< 0.001	-0.147	0.288	0.610	-0.048	0.049	0.332
		Zebra	-5.066	0.430	< 0.001	0.420	0.077	< 0.001	---	---	---
		Grant's G.	-3.672	0.500	< 0.001	-0.027	0.315	0.933	0.007	0.040	0.856
		Giraffe	-3.515	0.172	< 0.001	---	---	---	---	---	---
	LOW	Cattle	-3.352	0.330	< 0.001	-0.035	0.089	0.696	---	---	---
		Shoat	-2.842	0.325	< 0.001	-0.301	0.112	0.007	---	---	---
		Zebra	-3.234	0.259	< 0.001	0.170	0.060	0.005	---	---	---
		Grant's G.	-3.419	0.482	< 0.001	0.394	0.329	0.231	-0.074	0.049	0.131
		Giraffe	-3.839	0.202	< 0.001	---	---	---	---	---	---
WET	HIGH	Cattle	-1.212	0.110	< 0.001	---	---	---	---	---	---
		Shoat	-0.850	0.101	< 0.001	---	---	---	---	---	---
		Zebra	-2.489	0.109	< 0.001	---	---	---	---	---	---
		Grant's G.	-3.488	0.703	< 0.001	4.492	2.217	0.043	-3.377	1.561	0.030
		Giraffe	-6.153	1.001	< 0.001	---	---	---	---	---	---
	INTERMEDIATE	Cattle	-1.642	0.150	< 0.001	-0.076	0.039	0.054	---	---	---
		Shoat	-1.012	0.198	< 0.001	-0.860	0.121	< 0.001	---	---	---
		Zebra	-3.576	0.176	< 0.001	---	---	---	---	---	---
		Grant's G.	-3.212	0.280	< 0.001	-0.027	0.071	0.703	---	---	---
		Giraffe	-2.938	0.131	< 0.001	---	---	---	---	---	---
	LOW	Cattle	-2.537	0.111	< 0.001	---	---	---	---	---	---
		Shoat	-1.591	0.270	< 0.001	-0.836	0.150	< 0.001	---	---	---
		Zebra	-5.259	0.626	< 0.001	1.484	0.334	< 0.001	-0.164	0.042	1302.290
		Grant's G.	-3.306	0.313	< 0.001	0.000	0.082	1.000	---	---	---
		Giraffe	-5.813	0.845	< 0.001	1.269	0.430	0.003	-0.123	0.052	0.018

Appendix 2 Table 2b. Two part conditional model - zero truncated negative binomial model for abundance as a function of distance from settlement given presence. Model parameter estimates, SE and p values.

		Species	Inter	SE	P value	Dboma	SE	P value	Dboma^2	SE	P value
DRY	HIGH	Cattle	3.585	0.162	< 0.001	0.235	0.243	0.334	---	---	---
		Shoat	4.464	0.144	< 0.001	-0.157	0.257	0.542	---	---	---
		Zebra	1.745	0.176	< 0.001	---	---	---	---	---	---
		Grant's G.	1.771	0.363	< 0.001	---	---	---	---	---	---
		Giraffe	1.602	0.228	< 0.001	---	---	---	---	---	---
	INTERMEDIATE	Cattle	4.224	0.110	< 0.001	---	---	---	---	---	---
		Shoat	4.274	0.311	< 0.001	0.334	0.326	0.305	-0.107	0.060	0.076
		Zebra	1.042	0.298	< 0.001	0.089	0.050	0.076	---	---	---
		Grant's G.	0.910	0.418	0.030	0.428	0.227	0.059	-0.040	0.026	0.122
		Giraffe	-1.016	6.544	0.877	---	---	---	---	---	---
	LOW	Cattle	3.374	0.216	< 0.001	0.210	0.055	< 0.001	---	---	---
		Shoat	3.883	0.294	< 0.001	0.107	0.105	0.310	---	---	---
		Zebra	1.856	0.245	< 0.001	-0.012	0.057	0.832	---	---	---
		Grant's G.	1.439	0.520	0.006	0.269	0.358	0.452	-0.042	0.053	0.426
		Giraffe	-5.218	88.059	0.953	---	---	---	---	---	---
WET	HIGH	Cattle	3.748	0.096	< 0.001	---	---	---	---	---	---
		Shoat	4.218	0.070	< 0.001	---	---	---	---	---	---
		Zebra	1.701	0.216	< 0.001	---	---	---	---	---	---
		Grant's G.	1.503	0.964	0.119	3.579	3.044	0.240	-2.397	2.099	0.253
		Giraffe	1.037	0.637	0.103	---	---	---	---	---	---
	INTERMEDIATE	Cattle	3.920	0.103	< 0.001	0.168	0.026	< 0.001	---	---	---
		Shoat	4.571	0.131	< 0.001	0.116	0.081	0.152	---	---	---
		Zebra	1.473	0.129	< 0.001	---	---	---	---	---	---
		Grant's G.	2.898	0.250	< 0.001	-0.142	0.059	0.017	---	---	---
		Giraffe	1.579	0.342	< 0.001	---	---	---	---	---	---
	LOW	Cattle	4.847	0.095	< 0.001	---	---	---	---	---	---
		Shoat	4.671	0.155	< 0.001	-0.066	0.081	0.412	---	---	---
		Zebra	1.691	0.773	0.029	0.724	0.435	0.096	-0.110	0.059	1302.290
		Grant's G.	2.942	0.213	< 0.001	-0.159	0.057	0.006	---	---	---
		Giraffe	0.906	0.831	0.276	0.743	0.464	0.109	-0.109	0.060	0.068

FIGURES

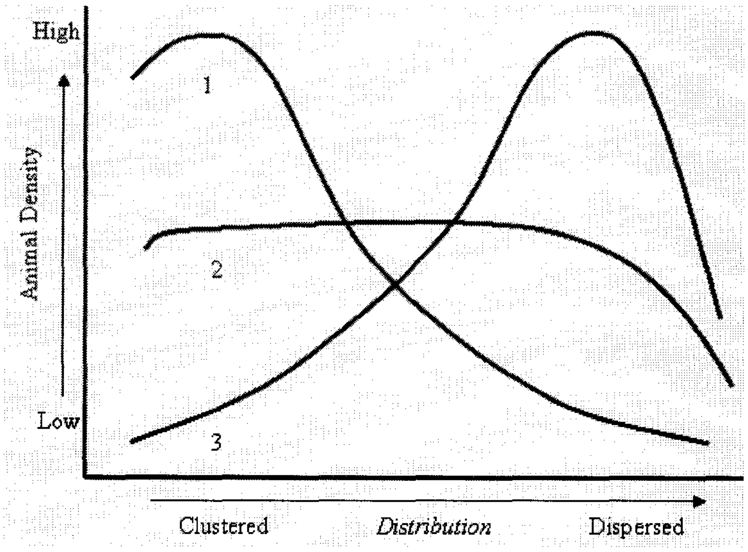


Figure 1.
Hypothetical responses of wildlife density as a function of increasing settlement density and distribution for three different levels of rainfall/ productivity – high > 800mm (1), medium 500 – 800mm (2), and low < 500mm.

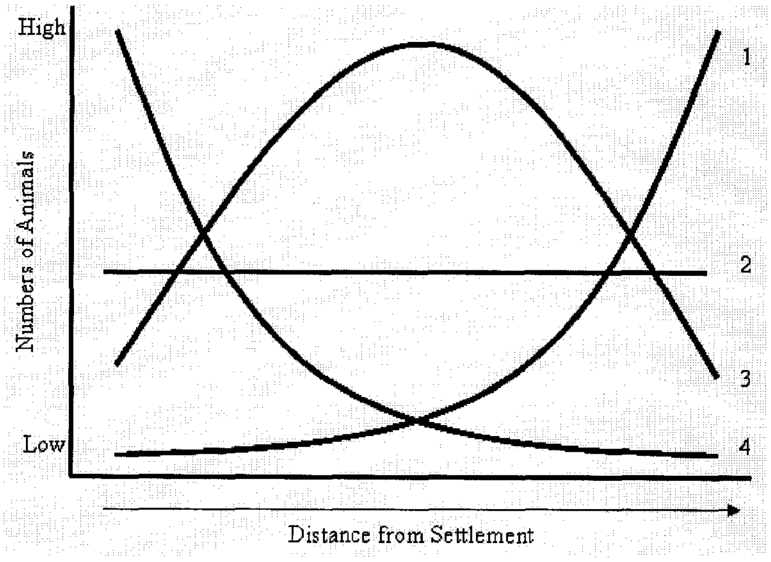


Figure 2. Hypothesized responses of animal density as a function of increasing distance from settlement.

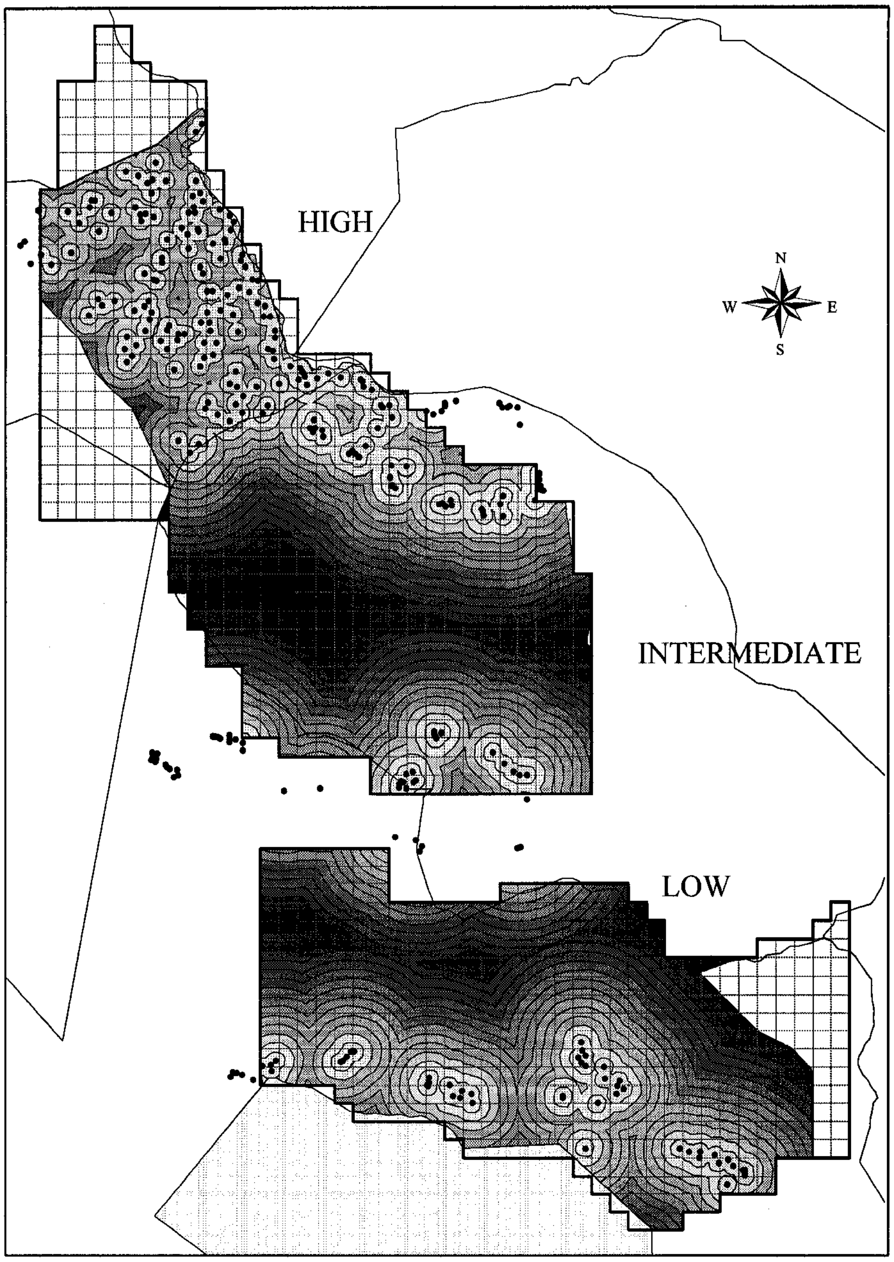


Figure 3. Study Area map indicating each of the three counting areas, permanent settlements for distance to settlement analysis, 1 km distance bands, and group ranch boundaries. Areas covered by the grid but without distance to settlement bands were counted and included in landscape level analyses but were omitted from the settlement level analyses.

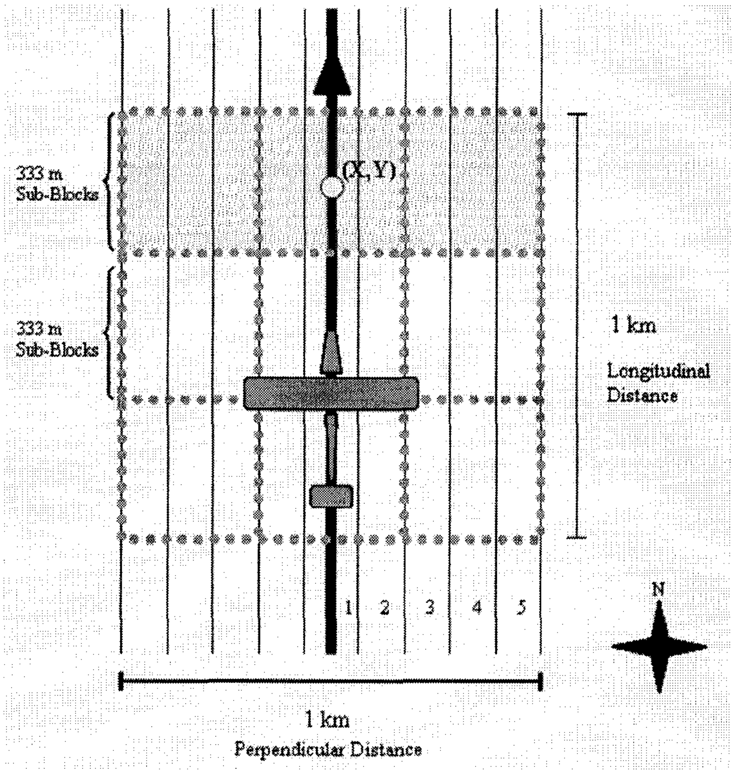


Figure 4. High resolution aerial distance sampling. Transects were placed at one kilometer intervals. Animals were recorded out to 500m on either side of the aircraft and observations were allocated to one of five perpendicular distance bands (1-5). All observations were subsequently aggregated into 1/3 kilometer blocks (shaded) and allocated to a 333m transect segment with a center point at (X,Y).

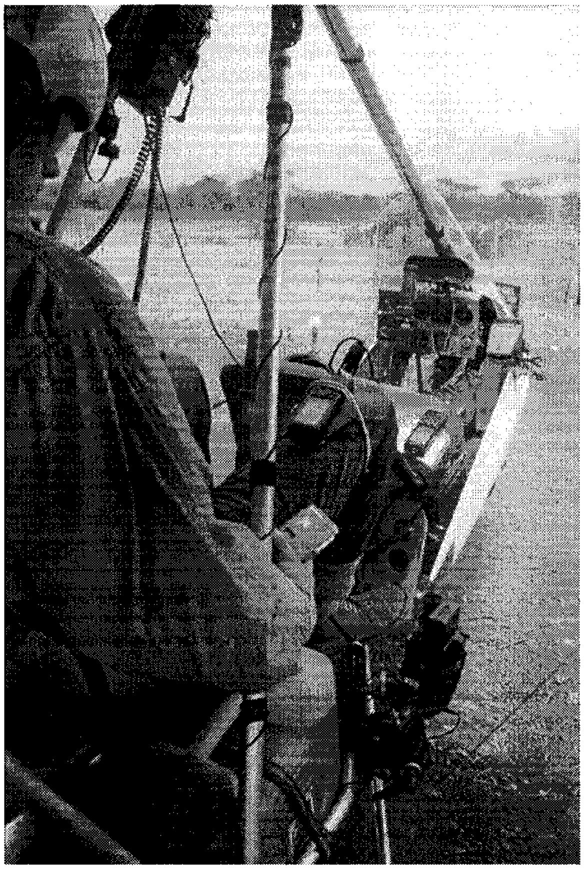


Figure 5. Photographs of the aircraft and equipment used for aerial counts. The seating configuration, with the pilot in the front and the observer behind, and the open structure of the ultra-light allowed for enhanced visibility. GPS units were used for navigation and data collection. Observations were recorded on a micro-cassette. Calibrated perpendicular distance bands were marked on the wing struts.

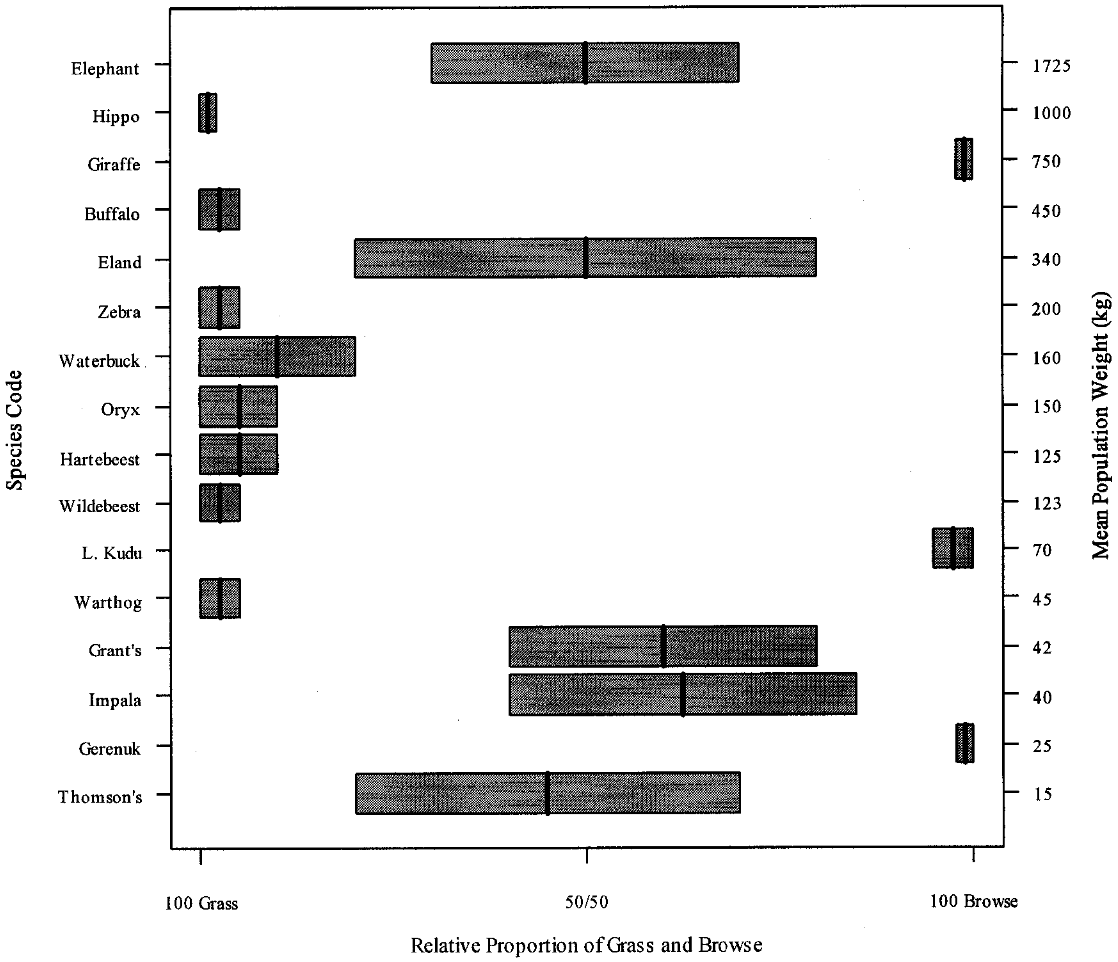


Figure 6. Large herbivore functional groups and foraging guilds. Mean population weights are from Western (1975) and Coe, Cumming, Philipson (1976). See table 1 for species codes. Vertical black lines indicate an estimated mean for the relative proportion of grass vs browse in the annual diet of each species. Horizontal bars suggest the degree of variability in grass:browse ratios. Three functional groups based on diet (Grazers, Mixed Feeders, Browsers) and three groups based on mean body size (Large, Medium, Small) are clearly visible.

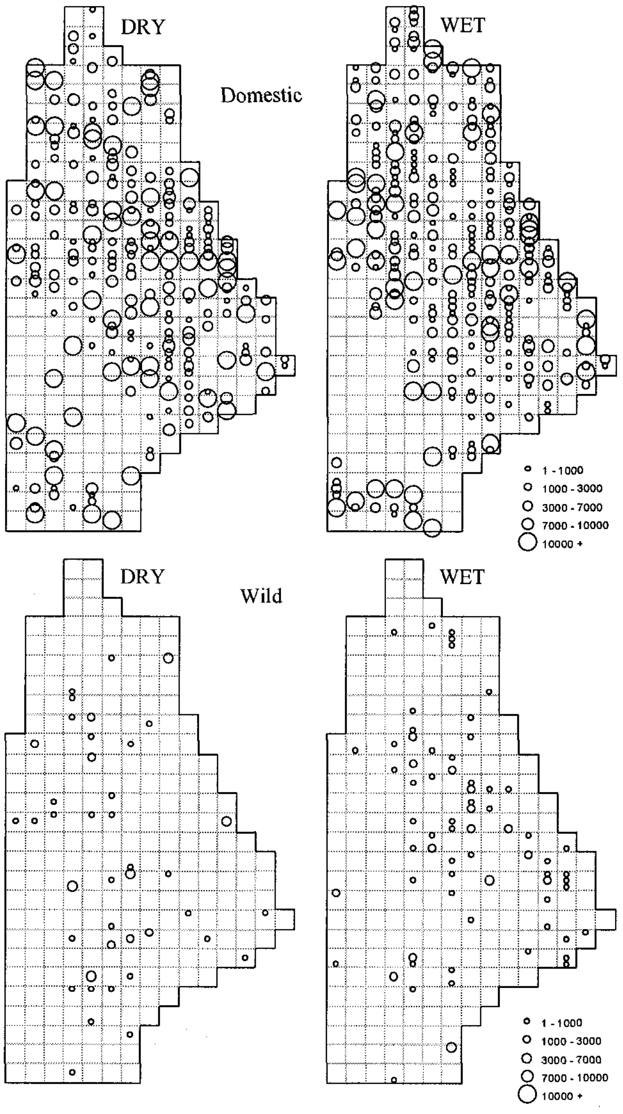


Figure 7. Domestic (top panel) and wild (bottom panel) biomass density (kg/km^2) in the HIGH intensity area for the dry (left) and wet (right) seasons. Points represent biomass density at 1/3 km resolution. The background grid represents 1 km cells. Note that there is very little change in the spatial distribution of domestic animals between seasons. Also, it appears that wild herbivores are avoiding settlements and livestock in the dry season.

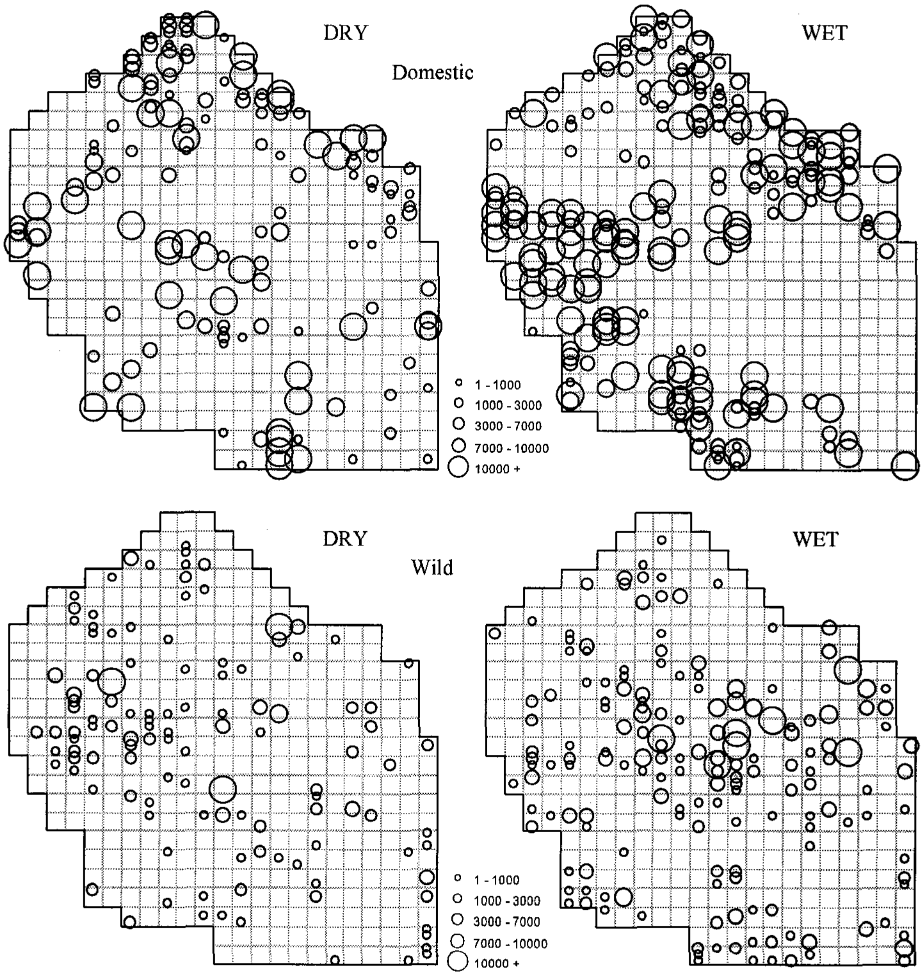


Figure 8. Domestic (top panel) and wild (bottom panel) biomass density (kg/km^2) in the INTERMEDIATE intensity area for the dry (left) and wet (right) seasons. Points represent biomass density at 1/3 km resolution. The background grid represents 1 km cells. Note that livestock are concentrated in the central grazing reserve in the dry season. In the wet season there is a general increase in the distribution and number of domestic animals. In contrast, wildlife appear to generally avoid high concentrations of livestock in both seasons and cluster in the reserve grazing area during the wet season.

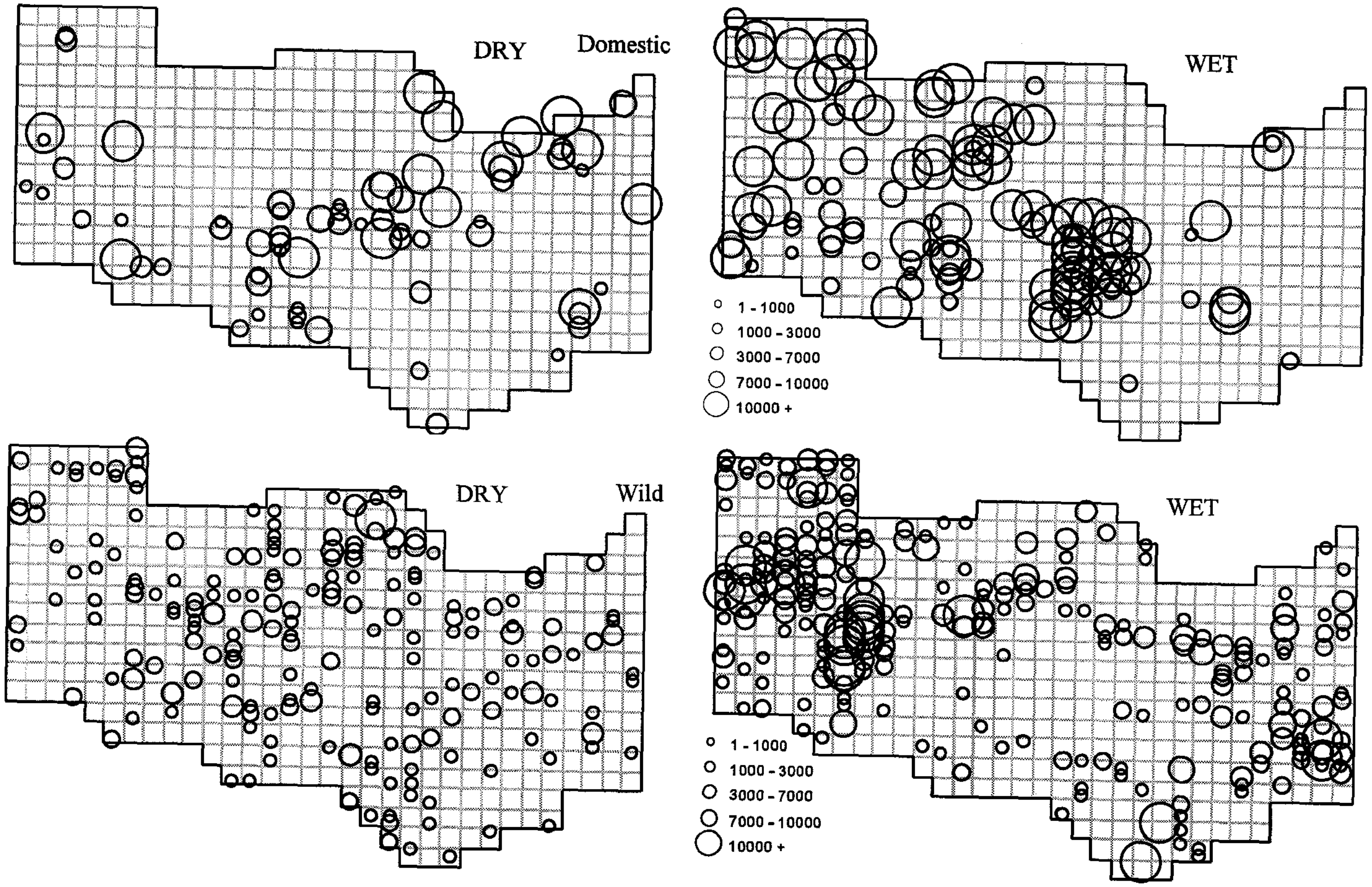


Figure 9. Domestic (top panel) and wild (bottom panel) biomass density (kg/km^2) in the LOW intensity area for the dry (left) and wet (right) seasons. Points represent biomass density at 1/3 km resolution. The background grid represents 1 km cells. Note the line of livestock during the dry season due to the enforcement of grazing stages. Wild herbivores are widely dispersed during the dry season and concentrated during the wet.

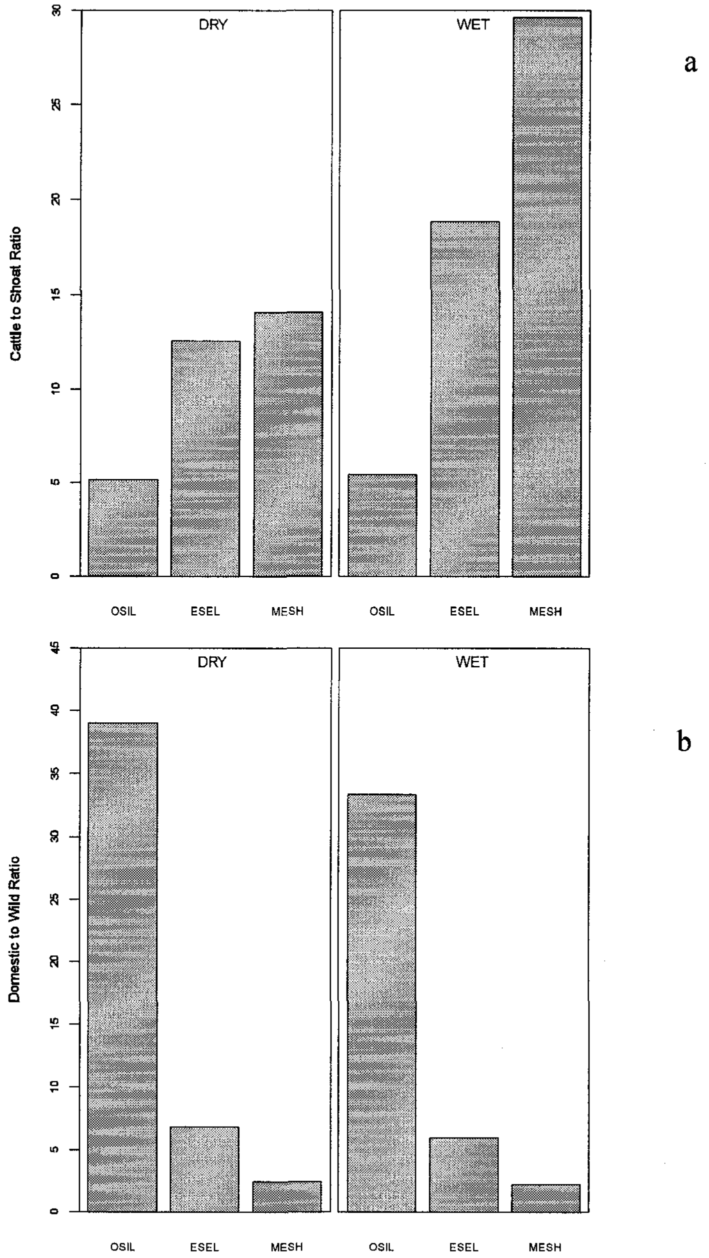


Figure 10. Ratio of cattle to shoat biomass (a) and ratio of domestic to wild herbivore biomass (b) by season and area. Lower ratios suggest more sheep and goats relative to cattle. Note the overall differences between areas within a season as well as the differences within areas between seasons, and especially the lack of change in HIGH. The high ratios of domestic to wild biomass in HIGH indicate a human dominated system, but the seasonal fluctuations in dom:wild ratios across all sites suggest the importance of these areas to seasonally dispersing wildlife from Amboseli National Park.

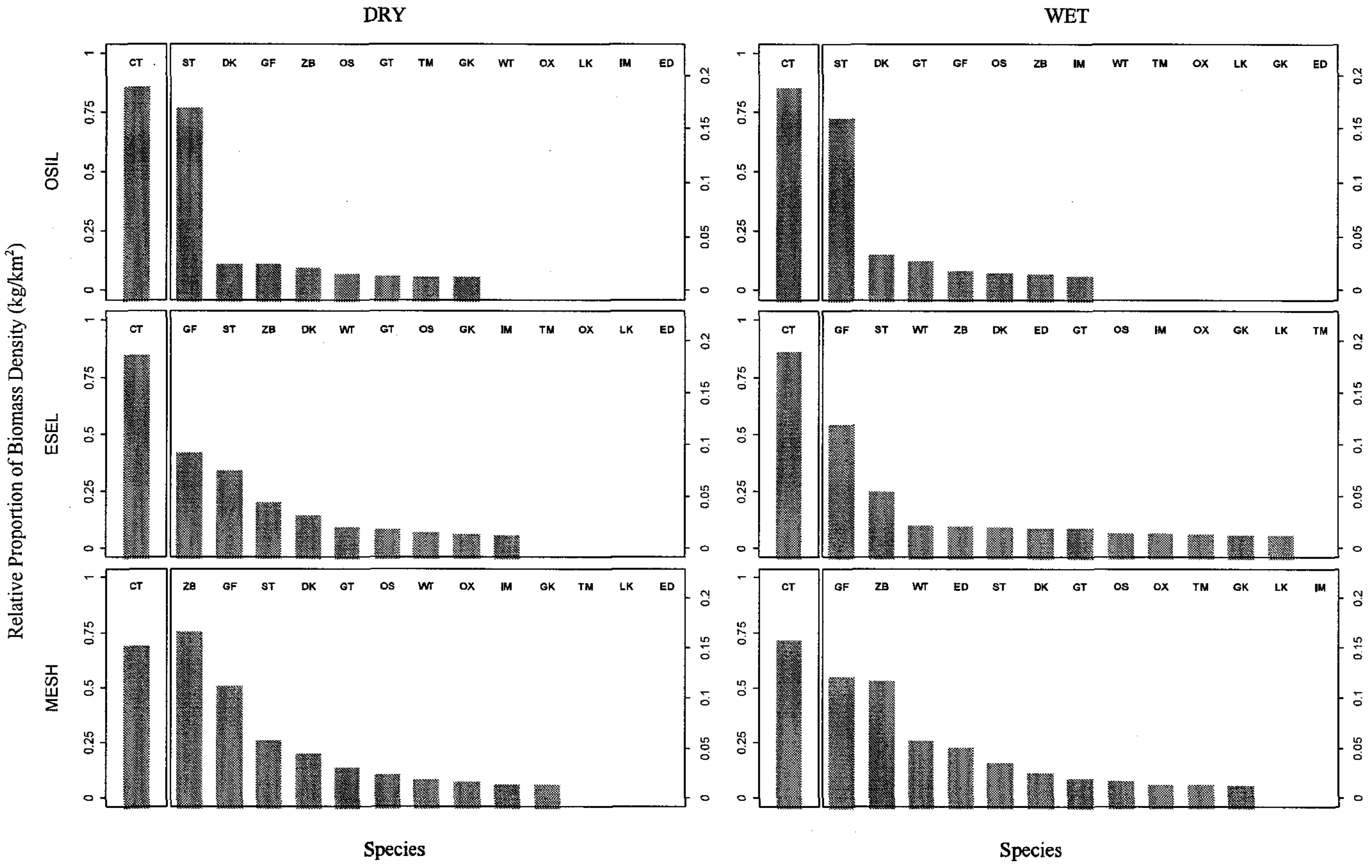


Figure 11. Relative proportion of biomass density (kg/km^2) of different species for dry (panel 1) and wet (panel 2) seasons for each counting area. Note the dominance of cattle in all study areas and seasons (primary Y axis) relative to all other species (secondary Y axis). Also note the relative dominance of domestic animals in HIGH in both seasons. See Table 1 for names of species used and their abbreviations.

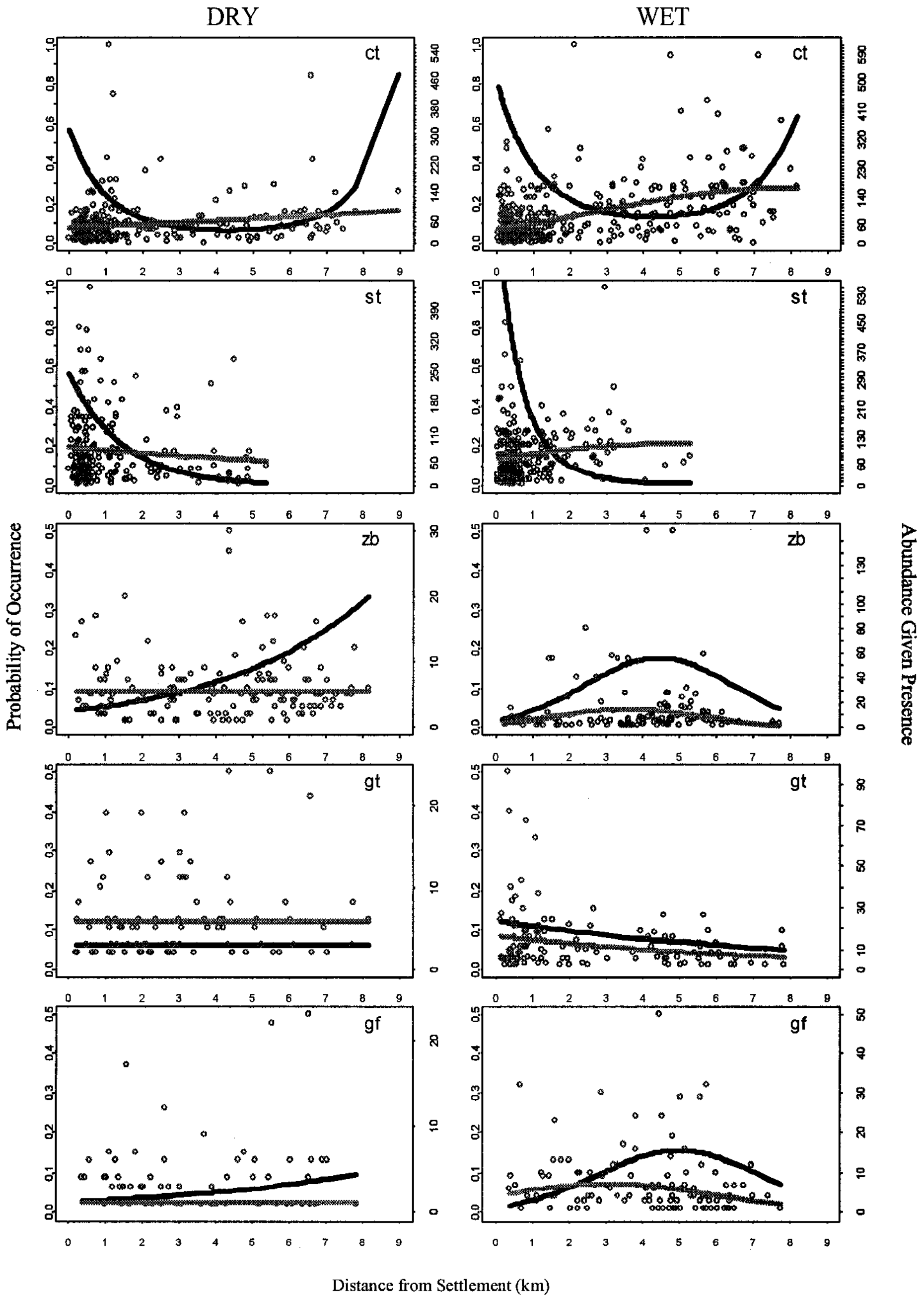


Figure 12. Species distributions as a function of distance from boma across all areas in both seasons. Predicted distributions (lines) are from a two part conditional model. Black lines represent the probability of encountering a herd with increasing distance from settlement (logistic). Grey lines indicate predicted abundance given presence. Open circles represent abundance. Species codes from Table 1.

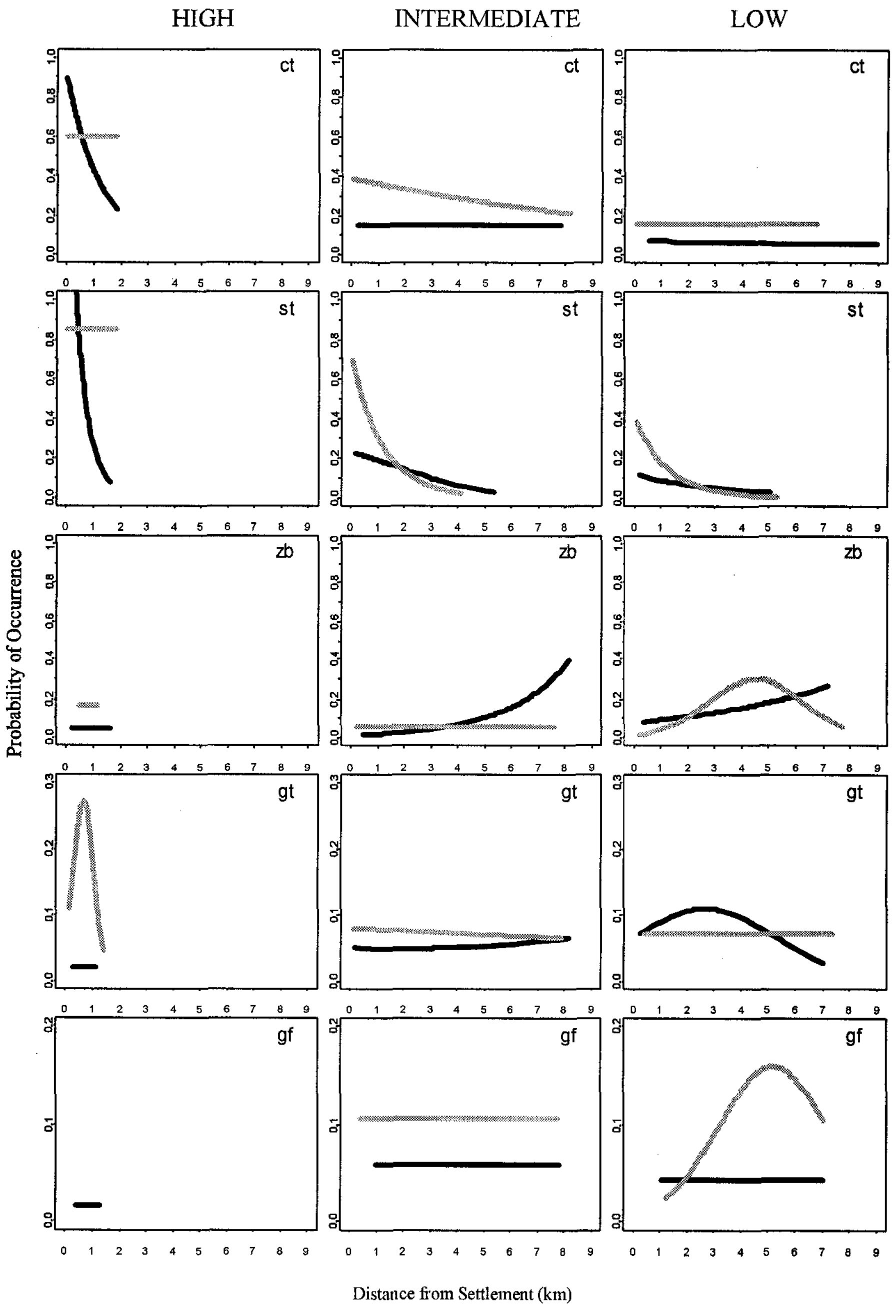


Figure 13. Species distributions as a function of distance from boma by study area and season. Two part conditional model, part 1, the logistic regression model for presence absence as a function of distance from permanent settlement. Solid grey lines indicate wet season and black lines indicate dry season. See Table 1 for species codes.

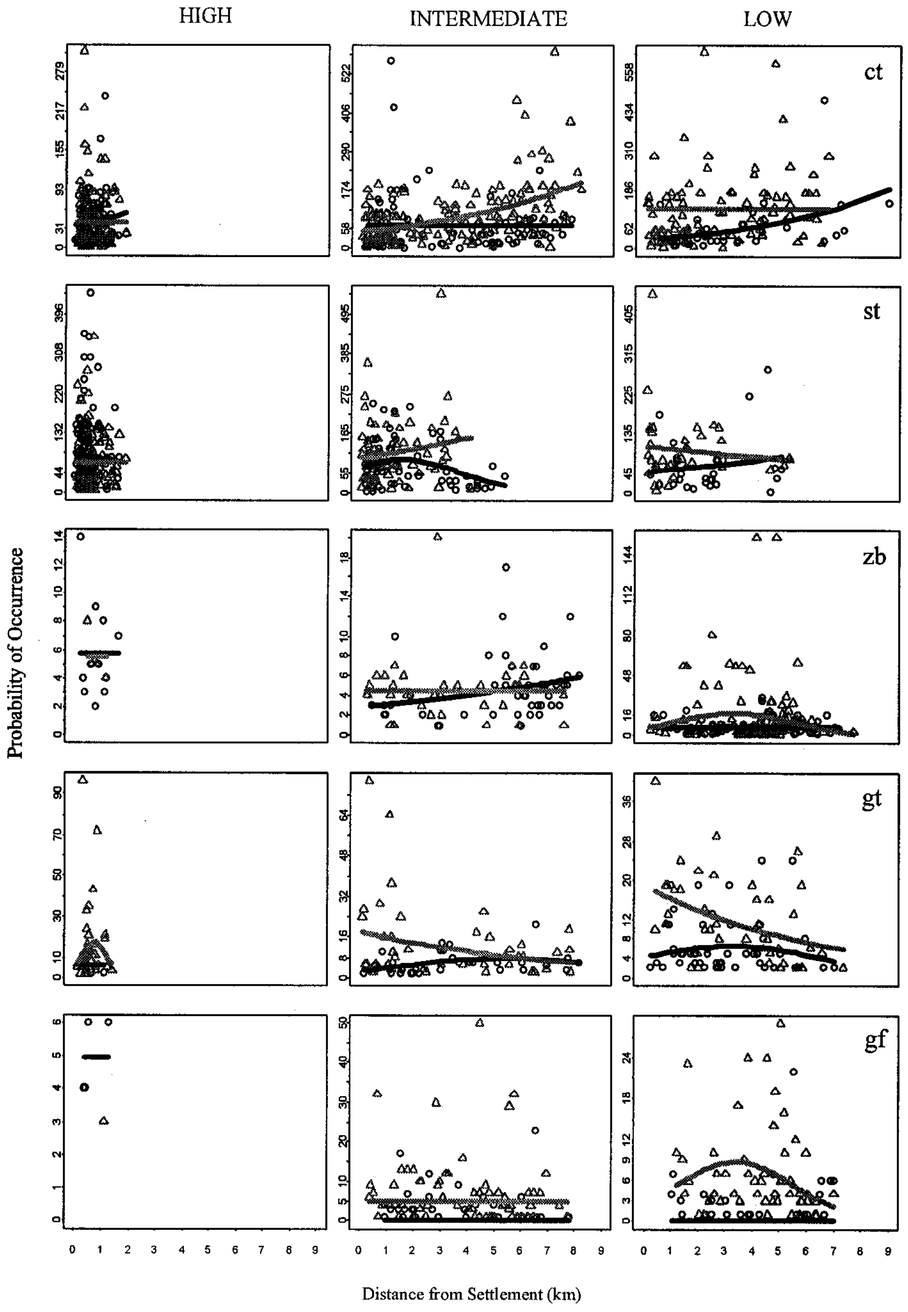
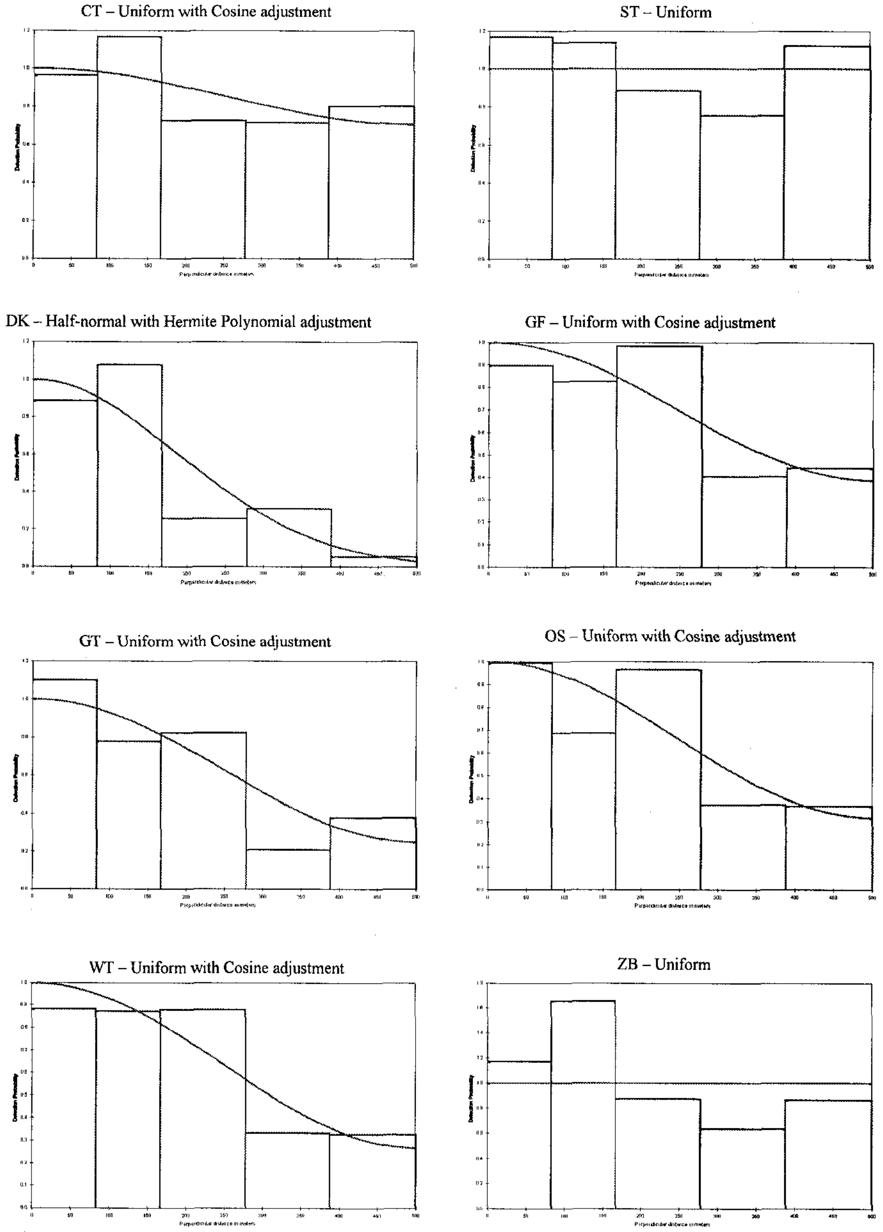


Figure 14. Species distributions as a function of distance from boma by study area and season. Two part conditional model part 2 - zero truncated negative binomial count model. Solid grey lines and open circles indicate wet season and black lines and open triangles indicate dry season. Species codes from Table 1.

Appendix 3



CT – Uniform with Cosine adjustment

ST – Uniform

DK – Half-normal with Hermite Polynomial adjustment

GF – Uniform with Cosine adjustment

GT – Uniform with Cosine adjustment

OS – Uniform with Cosine adjustment

WT – Uniform with Cosine adjustment

ZB – Uniform

Appendix 3 Figure 1. Detection functions from DISTANCE 4.1 software.

CHAPTER 5

LAND-USE CHANGE AND LARGE HERBIVORES IN THE SWAMPS OF THE GREATER AMBOSELI ECOSYSTEM, KENYA

INTRODUCTION

Land-use change and human environmental impacts are widely recognized as fundamentally important forces shaping the structure and function of ecosystems worldwide (Vitousek et al. 1997, Western 2001). Increasing human populations and accelerated land-use change are threatening arid systems across Africa (Ellis and Galvin 1994), as rapid transformation of arable land has resulted in increased pressure on less productive areas. Although this pressure comes from a variety of different sources and manifests itself in myriad ways, the most intense change has focused on key resource areas. Key resource areas for large herbivores are areas of semiarid and arid landscapes that provide forage and water during dry seasons and droughts, thus constituting the resource that ultimately limits herbivore populations (Illius and O'Connor 2000). Consequently, key resource areas are fundamental components of spatially and temporally variable arid and semi-arid ecosystems and important determinants of ecological patterns and processes. They have disproportionate impacts on herbivore and ecosystem vulnerabilities relative to their areas. Land-use change, and especially changes in key resource areas, can have important implications for the structure and function of ecosystems at multiple spatial scales. In the savannas of East Africa, where humans have lived for millennia as important components of the ecosystem (Western 1982b), changes in human land-use in key resource areas could have far reaching implications for entire ecosystems.

Large herbivores have long been key components of East African savanna ecosystems. Herbivores impact the structure and function of ecosystems through direct modification of habitat structure and composition (Laws 1970, Western 2006), nutrient redistribution and cycling (McNaughton et al. 1988, Muchiru et al. in press), and interactions with fire frequency and intensity (Hobbs et al. 1991, Hobbs 1996, van Langevelde et al. 2003). Similarly, herbivore impacts have cascading effects on biodiversity (Cumming et al. 1997, Pringle et al. 2007). The susceptibility of herbivore populations to changes in human land-use has lead to the widespread decline of these important components of savanna ecosystems across East Africa (Norton - Griffiths 1996, Ottichilo et al. 2000, Serneels and Lambin 2001). In this paper I examine the effects of changes in human land-use in the wetlands of the Greater Amboseli Ecosystem on the composition and distribution of large herbivores.

Land-use change is a dynamic process – rates of change accelerate and slow over time in response to social, political, economic and ecological forces. The land-use patterns we see in the Amboseli Basin of southeastern Kenya, are the product of shifting physical and cultural environments over a period of centuries. With this in mind, however, the dominant trends of increased sedentarization and the gradual expansion of agriculture at one extreme and the development of conservation on the other, have a much more recent history. These changes have fundamentally altered the interactions of pastoralists, farmers and wildlife over the past 30 years (Campbell et al. 2000). Although the proximate and ultimate causes of change are a consequence of both internal and external drivers operating at several scales (Campbell et al. 2003) the primary outcome of these interactions has been the loss of rangeland to crop production and conservation areas. Focusing on the high potential areas on the footslopes of Kilimanjaro, and more recently on the wetland systems at the base of the catena, the expansion of agriculture and conservation areas has resulted in the loss of key resources for both pastoralists and wildlife. Because the expansion and intensification of agriculture and conservation is likely to increase, it is essential that we develop a quantitative understanding of the implications of these changes for domestic and wild herbivores.

The Greater Amboseli Ecosystem (GAE) in southern Kenya is centered on a series of swamps that function as key resource areas. Wild and domestic herbivore species rely on the water and forage in these wetlands during the dry season, and the presence of these key resource areas is responsible for a higher biomass of large herbivores in the GAE than would be expected based upon rainfall alone (Western 1973, Coe et al. 1976). Although the swamps play a crucial role in maintaining the diverse community of wild and domestic herbivores in the system, they are also ideal locations for agriculture (Campbell et al. 2003). The Amboseli swamps represent a microcosm of the myriad forces that are changing dryland systems across the globe, presenting an ideal case study of effects of land-use change on biological diversity and ecosystem function.

Amboseli National Park and and the surrounding rangelands have been the focus of a number of long term ecological (Western 1973, Western 2002, Western and Maitumo 2004, Western 2007), behavioral (Altmann et al. 1996, Moss 2000), and social science studies (Campbell 1984, 1999, Campbell et al. 2003). Although each of these has recognized the human species as an essential component of the ecosystem, there have been few attempts to directly link the extensive land-use changes within the swamps to the distribution and abundance of large mammals. Here, I report work that establishes a baseline for further longitudinal studies of land-use change and its impacts on the Amboseli ecosystem, through quantifying and characterizing the nature of land-use and its spatial interaction with both livestock and wildlife on the landscape at high spatial resolution. I address the following questions. How do large herbivore communities respond to land-use change in key resource areas? How are different species and functional groups distributed in relation to water, and how are these patterns altered by different land-use regimes? Finally, I discuss the implications of these distributions and changes in community structure for issues of ecosystem integrity and biodiversity conservation.

Water Dependence and Aridity Tolerance in Large Herbivores – the importance of water in structuring semi-arid savannas

Water is one of the single most important structuring variables in the Amboseli ecosystem (Western 1975). Although the importance of water may be widely appreciated for arid and semi-arid systems, there are surprisingly few studies that document the structural and functional impacts of water on herbivore communities (but see Western 1975a, Owen-Smith 1996, de Leeuw et al. 2001, Redfern et al. 2003, Reid et al. 2003). Western (1975) suggested that large herbivores in the Greater Amboseli system exhibit two general patterns in relation to water - water dependence and water independence. The concept of water dependence/independence was modified by de Leeuw et al. (2001)

to reflect the variability in each species' degree of dependence on surface water (i.e. drinking) to meet its daily moisture needs. I used Aridity Tolerance instead of the more common water dependent/independent classification as it highlights the gradient of daily water requirements within and between species, and avoids confusion between a species' biological requirements and its distribution (i.e. a flat or uniform distribution is "independent" of water). These concepts are useful for predicting the occurrence of different species at broad spatial scales, but it is also important to recognize that herbivore responses to water are more than just responses to water per se. At broad spatial scales, the distribution of herbivores may be constrained by surface water availability. However, within these broad constraints that determine presence/absence, the distribution and abundance of herbivores in relation to water is a function of interactive effects of water, woody vegetation, forage availability and quality, predation risk, and disturbance by humans and their livestock. Hence, the distribution and abundance of large herbivores in response to distance from water, especially at fine spatial scales, is not a just a function of aridity tolerance, but also of body size and feeding strategy.

Body size and feeding strategy have important implications for scale at which herbivores perceive their environment (Fragoso 1999, Mech and Zollner 2002), predation risk (Owen-Smith 1988, Sinclair et al. 2003), vegetation selectivity (Hofmann 1973, 1989), and animal requirements for forage quantity and quality (Prins and Olff 1998, Olff et al. 2002). Recognition of the interactive effects of body size, feeding strategy, and aridity tolerance, or the degree to which a species is able to persist without access to surface water (higher aridity tolerance indicates less dependence on surface water for meeting daily moisture requirements), enables us to make predictions about how different species and functional groups will array themselves along a land-use intensity and distance to water gradient. I expect that large herbivore species and functional groups will exhibit four distinct patterns of abundance distributions relative to distance from water: 1) decreasing, 2) increasing, 3) hump-shaped, or 4) independent (Fig. 1).

Studies of water points in Africa suggest that herbaceous forage quantity and woody vegetation increase with distance from water (Thrash, 1993, Brit et al, 2002). Although this is generally true around man-made water points in the Greater Amboseli Ecosystem (Georgiadis, 1987), there are slight variations in the swamp systems. The presence of abundant surface water results in the production of high quantities of low quality herbaceous forage (Western, 1973) in the swamps themselves. The interaction of herbivore grazing and high herbaceous productivity near the swamps creates a U-shaped (concave) distribution of forage quantity with the highest levels of forage availability occurring both near and far from water. Thus, species that have low aridity tolerance and low forage quality and high forage quantity requirements will decline with increasing distance from water (curve 1, Fig. 1). Herbivores that have high aridity tolerance and lower forage quantity requirements, as well as those that are particularly susceptible to predation pressure and/or human disturbance will increase with increasing distance from water (curve 2, Fig. 1). Species with low to intermediate levels of aridity tolerance, intermediate forage quantity and quality requirements, and high disturbance/predation susceptibility will exhibit a hump-shaped distribution (curve 3, Fig. 1). Finally, herbivores that are truly independent of water and its associated effects on woody and herbaceous vegetation will have flat distributions (curve 4, Fig. 1).

Similarly, large herbivore species and functional groups will exhibit variable responses to a gradient of increasing human land-use intensity. I expect that wildlife biomass will generally decline with increasing land-use intensity (curve 1, Fig.1). Increasing land-use intensity will impact species and functional groups differentially with large bodied disturbance susceptible species such as buffalo and elephant declining the most. Competition for herbaceous forage associated with increasing livestock populations and disturbance around water points will also negatively impact grazers and species with low aridity tolerance (curve 1, Fig. 1). In contrast, I expect mixed- feeders and browsers to be relatively unaffected by intensification (curve 4, Fig. 1) due to their dependence on browse and generally higher aridity tolerance. The expected responses of each species to increasing land-use intensity and distance from water are summarized in Table 1.

METHODS

Study Area

The Greater Amboseli Ecosystem (GAE) of southern Kenya lies in the northern rain shadow of Mount Kilimanjaro. The ecosystem is centered on a series of swamps running generally east-west at the base of the catena formed by the mountain, and is delineated by the dry season dispersal movements of the dominant large herbivores (Western 1975). Mean elevations for each of the swamps are Amboseli 1140 m, Namelok 1156 m, and Kimana 1199 m. Annual rainfall is concentrated in two seasons – November-January and March – May with an annual mean of approximately 350 mm. Temperatures range from highs of 35° C in February/March and lows of 12° C in July with monthly means between 21° and 25° C (Altmann et al. 2002). The swamps represent an essentially closed system with water inputs from ground water and local run-on (Meijerink and Van Wijngaarden 1997). The network of wetlands is made up of six swamps – Enkongu Narok, Longinyie, Namelok, Kimana, Lenkati, and Esoitpus (from West to East) – in various states of protection and utilization for livestock and agriculture. This study focuses on the primary swamps within this larger system – Amboseli (including Enkongu Narok and Longinyie), Namelok and Kimana.

Soils in the Amboseli Basin are extremely diverse, with highly saline clays (Solonetz) in the seasonally flooded lakebeds, with patches of humus-rich (Chernozems) and volcanically derived (Andosols) soils around the edges. The upland and foot-slope areas are predominantly brown Luvisols of aeolian, alluvial or colluvial origin (Touber 1983). Dominant vegetation communities range from *Acacia tortilis* woodland in the south to mixed Acacia/Commiphora woodland north of the swamps. The swamps and seasonally flooded areas are dominated by *Cyperus immensus* and *Acacia xanthophlea*, and *Salvadora persica* respectively. A detailed description of historical vegetation communities and distributions can be found in Western (1973) with updates on more recent vegetation changes in select areas documented in Atieno (2000), Odede (2003), and Western (2006).

Large herbivores in this system appear to respond to the effects of water up to 30 kms away (Western 1975). The dominant set of interactions between human land-use, livestock, wildlife, and water are played out at much finer spatial scales, however. Indeed, evidence from similar counts in the Masai Mara Game Reserve of Kenya suggest that the primary response of most wildlife species to water in the dry season occurs within 4 km (Ogutu et al. submitted). To explore the impacts of human land-use change on the fine-scale interactions of wildlife, livestock and water in the Amboseli swamp systems I focused my counting efforts around the immediate vicinity of the swamps. To examine the primary effects of human land-use change on the spatial distribution of wildlife and livestock I divided the study site into three zones representing different degrees of human land-use intensity – PARK, INTER, CROP (Fig. 2). Each swamp along the northern base of Mt. Kilimanjaro – Amboseli, Namelok, and Kimana - represents a point along the land-use continuum ranging from intensive irrigated agriculture to protected area. Although the protected area of Amboseli National Park (PARK) represents the least human impact, and therefore gives us a sense of what the system might look like in the absence of humans, within this conceptual framework protected areas do not represent "controls" but rather treatments along the gradient.

Each Land Use Area (LUA) was defined using a four kilometer buffer around the boundary of known swamps identified from topographic maps and satellite imagery (Landsat 7 2000). The PARK area was centered on the two primary swamps inside Amboseli National Park (Longenyie and Enkongu Narok), and represented the lowest level of human disturbance. CROP represented the highest level of human impact and was centered on the Namelok swamp which was fenced in 1999 to protect emerging irrigated agriculture from wildlife impacts. Intermediate levels of human impact are represented by INTER which is centered on a multipurpose swamp used for livestock, irrigated agriculture, and wildlife conservation (Kimana Sanctuary).

Ideally, each of the Land Use Areas (LUA) would be separated in space, independent, and replicated. Although the reality of landscape scale research necessitates some degree of pseudoreplication (Hurlbert 1984) it does, however, open a new realm of discovery heretofore unavailable to traditional plot level research. A one kilometer grid was overlaid on the study area and each grid cell was subsequently divided into nine sub-blocks. In an effort to limit some of the potentially confounding effects related to distance analyses in overlapping spheres (e.g. CROP and INTER areas) LUA boundaries were established by assigning each sub-block to the nearest swamp edge. This central point approach, building on the extensive literature on piosphere effects, recognizes that the ecological effect of water decreases with increasing distance away from the source (Andrew 1988, Thrash and Derry 1999). In this way each point in space is associated with the swamp that exerts the greatest effect. To ensure that each sub-block was analyzed in relation to the nearest swamp overlapping areas were divided after the count with each sub-block being assigned to the closest swamp.

Data Collection

The data presented here were collected with an ultra-light aircraft in a dry season aerial count during August 2002. To take advantage of favorable counting conditions (light, weather, animal activity) all counts were conducted during the morning (0730 to 1130) and afternoon (1430 to 1830) hours over a three-day period, from the 21 to 23 August 2002 . Ideally, all counts would have been conducted in the morning hours of each day, but it was essential to complete the count as rapidly as possible to limit the effects of animal movement on counting accuracy – e.g. double counts and missed animals (Thompson et al. 1998). The flight patterns, which include morning and afternoon flights in each zone, were allocated to reduce bias associated with time of day and transect direction.

The study area was divided into one kilometer transects based on the UTM grid with the flight line recorded as a route in the GPS (Garmin 12xl). The counting team consisted of a primary observer/recorder, and a secondary observer/pilot. All individuals and groups of herbivores larger than Thomson's gazelle (18 kilograms) were included in the count (Table 1). Groups were counted and recorded separately for all species except sheep and goats which were combined as "shoats" at the time of counting due to the difficulty in differentiating them from the air. When an individual or group was noted within the 500m strip on either side of the transect line the longitudinal location of the observation along the transect was recorded on the GPS with a waypoint, and the perpendicular distance to the transect line was estimated as one of five distance classes (Fig. 3). These data together with the species and group size were then recorded on a hand held micro-cassette tape by the primary observer. To limit observer bias, all counts were made by the primary observer with the secondary observer assisting with locating and photographing of herds larger than 20 individuals. Air speed, altitude and counting and flight conditions were recorded at different points along each transect. Transects were oriented north-south in response to the prevailing wind conditions, terrain, shape of the study area, and swamp distribution. Transects were flown at an altitude of 100 m.

I collected data on the distribution and abundance of human settlements (including house numbers and types), domestic animals (cattle, sheep and goats, donkeys, and dogs), agricultural plots, vehicles and infrastructure to quantifying the intensity and distribution of human land-use impacts in the swamp systems of the Greater Amboseli

Area. Data on fencing type and presence were not collected during the aerial count, but were recorded during ground surveys of the study area (J. Worden unpublished data, E. Wangui unpublished data). Fences in this area have been constructed to restrict access by wildlife of all sizes ranging from elephants to Thomson's gazelle, but periodic failures of the fence allow some animals temporary access to the agricultural areas. The electric fences in CROP and INTER were built in 1999 with assistance from the European Union as part of a larger effort to support and stabilize irrigated agriculture in the area. The CROP fence encircles the entire Namelok swamp system except for one in-flowing spring in the southeast. All agriculture in the CROP area takes place within the protective confines of the fence. In the INTER area the fence is centered on the town of Kimana (to the south of the study area) and its associated springs. The Kimana swamp itself, which is the focus of this study, was not fenced. The INTER area does include a small section of the Kimana town fence, however. The PARK area contains no agricultural fencing, but does have some small experimental exclosures and a large exclosure around the lodges in the center of the park which differentially limit access by herbivores. Although important for research on the impacts of herbivory and plant community composition (Western and Maitumo 2004, Sarkar 2006), these exclosures have little impact on herbivore community composition and distribution within the National Park and are therefore excluded from this analysis.

Data Processing and Analysis

All data were transcribed from the micro-cassettes by the primary observer. All individual species groups were preserved for analysis in DISTANCE 4.1 software

(Thomas 2004). Detection functions (Appendix 1 - Fig. 1) were generated for all species with sufficient observations (Appendix 1 - Table1). Abundance estimates at the group level were adjusted using the detection probabilities from DISTANCE (Appendix 1-Table 2). Abundance estimates for species with insufficient observations to calculate reliable detection functions were pooled into classes with species of similar body size and coloration. To avoid bias associated with differential detection as a function of distance from the transect line all adjusted species counts were aggregated at the transect segment level.

Human land-use was quantified using four primary variables: house type (type of roofing material used) and the presence or absence of agriculture, fencing, and domestic animals. The presence and status, either cultivated or fallow, of agricultural plots was recorded. For these analyses I combined both cultivated and fallow plots to identify all areas altered by agricultural practices. Sub-blocks indicated as agriculture contained at least one agricultural field and may or may not have been entirely covered by agriculture. Values for the aerial extent of agriculture were based on the area of all sub-blocks containing agricultural fields rather than the actual area of all fields on the ground. Agricultural data were maintained at the sub-block level.

The distance to water for the center of all transect segments was calculated in ArcView 3.2a (ESRI) from the distribution of water points collected in the aerial count. Water data were collected as the number of points and source type, but were summarized as present/absent at the transect segment level for these analyses. I differentiated water sources that were available to wild and domestic animals. Domestic animals had access to all water points on the landscape (even water within protected areas, although officially off limits, is in practice used by domestic stock). Wildlife had access to open water points only, including open water, springs, open troughs, and leaky pipelines. All "open" water points within agricultural fences were considered to be unavailable to wildlife.

Each species was placed in one of three functional categories based on body mass, feeding ecology, and the degree of dependence on surface water for meeting daily water requirements (Table 1). Population unit weights from Western (1975) and Coe et al (1976) were used to allocate species into the following Body Size classes: SMALL (< 50 kg), MEDIUM (50 to 400 kg), and LARGE (> 400 kg). Species were allocated to three categories of feeding strategy based upon the relative proportion of grass and browse in their diets across all seasons (Estes 1991) - GRAZERS, BROWSERS, and MIXED feeders (Table 1). Aridity tolerance (after de Leeuw et al, 2001) represents a species' degree of dependence on surface water (i.e. drinking) to meet its daily moisture needs. As with feeding guilds, there is large seasonal variability among animal species in water requirements both within and between species depending on temperature, forage moisture content, and dew (Western and Finch 1986). Individual species were classified as HIGH, LOW or INTERMEDIATE (Table 1) based upon Western (1975b) and de Leeuw et al (2001).

Domestic biomass density (kg/km^2) was calculated as the sum of the total biomass for all domestic animals (Cattle, Shoats and Donkeys) for each season divided by the area in square kilometers. Wild biomass density (kg/km^2)was calculated in a similar fashion for all the remaining (non-domestic) species. Species richness was taken as the number of all wild species observed in a Land Use Area. To facilitate comparisons between counting areas of different size the total number of species was divided by the total km^2 for each LUA to get a species density, or number of species per km^2.

Statistical Analyses

Data were checked for normality and transformations were applied where appropriate. Transformations generally failed to achieve normality or substantially reduce skewness so non-parametric Kruskal – Wallis tests were used to determine significant differences between areas for species abundance, domestic and wild biomass density, and functional group biomass density. For describing species and functional group distributions in relation to water I used a two part conditional model and model-selection (Burnham and Anderson 2002). High resolution count data contain an excessive number of zero values because animals are not normally distributed on the landscape and therefore fail to meet the necessary assumptions of standard statistical analyses (Cunningham and Lindenmayer, 2005). Two part conditional regression, or hurdle, models account for these excess zeros and have the added benefit of providing separate parameter estimates for presence/absence and abundance data (Cunningham and Lindenmayer 2005). First, a logistic model was fit to the data to predict the probability of a transect segment containing one or more individuals of a given species. Then, all zeros were removed and a negative binomial count model was fit to the data to determine predicted values for the abundance of each species given presence. I considered the following three models: 1) intercept alone, 2) linear, and 3) quadratic, based on the hypothesized relationships between herbivore presence and abundance as a function of distance from water summarized in Figure 1.

The following logistic regression model was used to determine the probability of a transect segment containing an individual of a particular species:

$$Pr = exp(z)/(1 + exp(z))$$

where z is one of the following:

$$z = a$$

$$z = a + bX$$

$$z = a + bX + cX^2$$

with X being distance from water, and a, b, c being model parameters. Three zero truncated negative binomial models with similar terms were fitted to the abundance data.

The evidence for each model as the best fit for the data given the set of candidate models was determined using the Akaike information criterion (AIC) (Burnham and Anderson, 2001). Similar models were used for the logistic and count steps in the two part conditional model and the best fit models were selected based on the lowest AIC values and their support in the data. R 2.4.0 was used for all statistical analyses (R Core Development Team, 2006).

RESULTS

Spatial Patterns

The spatial distribution of domestic and wild animals varied across the Land Use Areas (Fig. 4). In PARK domestic animals were primarily limited to the periphery of the LUA with a few herds deep inside the National Park. There was also a concentration of domestic animal biomass inside the fenced agricultural area in CROP and along boundaries of the protected sanctuary in INTER. In contrast, wild biomass was concentrated in the swamps in PARK and in the small protected area in INTER. There was a spatial separation of domestic and wild biomass in all areas with the clearest differences occurring in the INTER and CROP areas. Wild species exhibited variable patterns with wildebeest clustered in the protected areas of PARK and INTER (Fig. 4) and zebra more widely distributed across all habitats. Elephants and buffalo were centered on the protected swamps and impala, giraffe, and Grant's gazelle were relatively evenly distributed across the more wooded southern areas.

Functional group biomass density varied across Land Use Areas (Fig. 5). Grazers were spread across the protected areas in PARK and INTER. There were also some scattered groups on the periphery of INTER and CROP in areas with fewer herds of livestock. Mixed feeder biomass was spread fairly evenly across the study areas except for empty patches in CROP and INTER where they were displaced by livestock. The high biomass densities for mixed feeders in the protected areas were dominated by elephant. As predicted, browser biomass density was highest outside of protected areas where woody vegetation was more prevalent. A notable exception was the relatively high biomass of browsers in Kimana Sanctuary which still had relatively diverse habitat structure. Individual species had similarly diverse distributions (Fig. 6). The medium and large bodied grazers and mixed feeders such as buffalo, elephant, eland, and wildebeest were almost exclusively limited to the protected areas in PARK and INTER. This contrasts markedly with zebra which were present in both the protected and unprotected areas of all LUAs. Giraffe, Grant's gazelle and impala were even more widely distributed with most observations outside of protected areas.

Human Land Use/Impact

Human impacts were minimal in the protected areas with lodges and camps within the boundaries and scattered settlement on the edges. Human pressure in the form of settlements and agriculture was notably higher around the periphery of INTER than in PARK. Large concentrations of settlements and agricultural plots were found in both CROP and INTER. No agriculture was observed in the vicinity of Amboseli National Park. House type (materials used for construction) is an indicator of permanence and may serve as a surrogate for mobility and its correlate, intensity of human disturbance. Mud and dung houses were found in settlements throughout the study area, but grass-roofed and tin-roofed houses were primarily concentrated in or near the irrigated zones of CROP and INTER (Table 2).

Summary data for each Land Use Area are presented in Table 2. The PARK area had the lowest human impact with 3.6% of the total number of settlements and 15.63% of the total number of houses. Similarly, the types of houses in the PARK area were primarily mud and dung (95.9%) while most of the houses in CROP and INTER were grass (68.9 % and 65.9%) and tin-roofed (33.1% and 18.2%). No agriculture plots were recorded in the PARK area, but CROP and INTER had 6.69% and 6.42% of their area covered in agriculture, respectively (Table 2). The cattle:shoat ratio was highest in PARK with the lower ratios in INTER and CROP indicative of pastoral intensification and an increasing market orientation.

Large Herbivore Response

All species combined yielded a total mean biomass density of 10,337 kg/km^2. PARK had the highest total mean biomass density (13,662 kg/km^2) followed by INTER (7578 kg/km^2) and CROP (3218 kg/km^2). Domestic animals contributed 14.5%, 49.9%, and 76.0% to the biomass totals of PARK, INTER and CROP respectively. Wild and domestic mean biomass density (kg/km^2) was significantly different ($p < 0.05$) across the land-use intensity gradient (Table 3 and Fig. 7a). Domestic mean biomass density was highest in the INTER area and lowest in the PARK area. As expected, wild biomass density was significantly higher in the PARK area and lowest in CROP. Similarly, domestic functional group biomass density in PARK and CROP were significantly different with the highest densities in INTER and lowest in PARK (Table 4).

Wild functional group biomass density was more variable (Table 5 and Fig. 7b). As expected, grazers declined significantly with increasing land-use intensification. Browsers, however, had their highest biomass density in INTER and CROP, with PARK having just over 25% of that found in INTER. Mixed feeders were not significantly different between Land Use Areas, but their biomass density generally declined with increasing land-use intensity. Elephants make up the vast majority of mixed feeder biomass, however, and their preference for the protected areas in PARK and INTER distort the biomass density distribution between LUAs. When elephants were excluded from the mixed feeder category there were still no significant differences in mean biomass density between areas, but interestingly the highest density was in CROP, followed by PARK and finally INTER.

Species level responses to land-use intensification are highly variable (Table 3a). Ten of the 16 wild and two of the three domestic species biomass densities were significantly different between LUAs (Table 3b). As expected, most of the grazer species including hippopotamus, oryx, warthog, wildebeest, and zebra all declined with increasing land-use intensification. The other two wild grazers, hartebeest and waterbuck, were only found in the INTER area. Interestingly, of the mixed feeders and browsers, only elephant, ostrich, and Thomson's gazelle were highest in PARK. The biomass density of all the other mixed feeders and browsers, including eland, giraffe, gerenuk, Grant's gazelle, and impala was highest in the INTER area. Cattle, donkey and shoat biomass densities were also highest at intermediate levels of land-use intensity.

Community composition varied across Land Use Areas. Cattle, shoats, and donkeys were present in all LUAs except CROP where donkeys were absent, but the relative proportion of cattle and shoats differed across areas (Table 2). Wild species composition differed between sites as well with no oryx observed in INTER and hartebeest and waterbuck absent from PARK. No buffalo, hippo, hartebeest, oryx, waterbuck, or warthog were observed in CROP. Overall species richness differed significantly between LUAs (Table 6 and Fig 8) but there were no significant differences for species density (number of species per km^2). However, the general pattern of higher species numbers and density at intermediate levels of human land-use intensity was consistent in both measures.

Large Herbivore Distributions in relation to Water

Overall, livestock and wildlife had similar distributions in relation to water (Fig. 9). The probability of encountering domestic and wild herbivores decreased gradually with increasing distance from water. However, although wildlife occupied nearly 50% of all transect segments adjacent to water (Fig. 9b), domestic animals appeared to occupy just less than 20% (Fig. 9a). When wildlife were present they also concentrated in much larger aggregations close to water than farther away. In contrast, livestock biomass given presence was relatively constant at all distances (Fig 9a, grey line).

As predicted, wildlife functional groups differed in their responses to water (Fig. 10). The probability of encountering grazers declined with increasing distance from water as expected. Also as predicted, the probability of encountering browsers and mixed feeders varied little out to eight kilometers from water. Biomass distributions given presence differed very little between functional groups, however, with the biomass of all groups declining gradually with increasing distance from water.

Land-use intensity has important implications for functional group distributions in relation to water (Fig. 11). In PARK, the probability of encountering grazers and grazer biomass given presence declined sharply with increasing distance from water before increasing again slightly at around four to five kilometers. In contrast, grazer encounter probability in INTER increased with distance from water while biomass given presence declined. In CROP, both grazer encounter probability and biomass appeared to be independent of water. As predicted, land-use intensity had very little impact on browser distributions with the encounter probability and biomass given presence being essentially independent of water in all Land Use Areas. In keeping with their diverse feeding strategies and variable body sizes, mixed feeder distributions across LUAs were complex. In PARK mixed feeder encounter probability and biomass both declined gradually with distance from water. As with PARK, mixed feeder distributions in INTER were similar to those observed in grazers, but biomass given presence declined more rapidly, and the encounter probability was hump-shaped with the highest probabilities at intermediate distances from water. In CROP, mixed feeder encounter probability and biomass given presence trended in opposite directions with the former increasing and the latter decreasing with increasing distance from water. The mean number of species per km^2 also declined with increasing distance from water (Fig. 12).

Overall species distributions in relation to water were highly variable (Fig. 13). As with livestock generally (Fig. 9), the probability of encountering both cattle and shoats declined with increasing distance from water while the number of individuals in a transect segment, given presence, increased slightly. For moderately and highly abundant wildlife species encounter probability and abundance distributions closely resembled predicted responses based on aridity tolerance, feeding strategy, and body size (Fig. 13). For grazers such as zebra and wildebeest both encounter probability and abundance declined gradually with increasing distance from water. The distribution of the larger-bodied and more water-dependent buffalo was far more limited. Buffalo were only observed within 1.5 kilometers from water and the probability of encountering them within this range declined rapidly with distance. The encounter probability of giraffe, the only abundant browser, was nearly independent of distance from water, but increased slightly with increasing distance. Giraffe abundance given presence, declined with increasing distance from water. As expected, mixed feeder distributions were highly variable with large and small-bodied species with low aridity tolerance, such as elephant and Thomson's gazelle, having their highest probabilities and abundances close to water. The mixed feeders of intermediate body size and intermediate to high aridity tolerance such as impala, ostrich and Grant's gazelle were more independent of water. Encounter probability and abundance was independent of water for impala and slightly decreasing for ostrich. Grant's gazelle encounter probabilities were highest at intermediate distances from water while abundance declined gradually to approximately four kilometers where it leveled off.

Livestock distributions in relation to water varied with land-use intensity (Fig 14a). Both cattle and shoat distributions were independent of water in PARK. Under increasing levels of land-use intensification encounter probabilities declined with distance from water in INTER and CROP for both species. Abundance given presence also declined in both cattle and shoats in INTER, but it appeared that the extreme levels of intensification in CROP were pushing larger herds farther from water in search of forage. Wild grazer distributions were increasingly decoupled from water across the land-use intensification gradient. Although buffalo patterns in PARK were similar to the overall distribution, the few observations in INTER appeared to be independent of water, and buffalo were absent entirely from CROP. Wildebeest and zebra showed similar trends with the encounter probabilities of both species displaced from water in INTER with probability and abundance highest at intermediate distances for wildebeest, and encounter probability gradual increasing and abundance decreasing with increasing distance from water for zebra (Fig 14b). Both species had water independent distributions in CROP where wildebeest were all but absent. As expected, giraffe distributions were independent of water in all Land Use Areas (Fig 14a).

It is also important to note that all wildlife species were displaced from water at least one kilometer in CROP, while some species such as elephant were not observed within two kilometers of water. Elephant encounter probabilities declined as a function of distance from water in PARK and INTER and were independent of water in CROP. In contrast, elephant abundance declined with distance from water in CROP and INTER and was independent of water in PARK. The smaller bodied mixed feeders such as Grant's gazelle, impala, and Thomson's gazelle were distributed independently of water in CROP and INTER (Fig. 14b). The one exception was for Grant's which had generally similar patterns of highest encounter probabilities at intermediate distances in both INTER and PARK. Distributions of all three of these species in PARK were similar to their overall patterns presented in Figure 13.

DISCUSSION

Land-use change in the swamp systems of Greater Amboseli has had a profound impact on the distribution and abundance of both wild and domestic herbivores. Previous studies have noted changes in key species such as elephants (Western and Lindsay 1984, Moss 2001), woodlands (Western and Gichohi 1993, Western and Maitumo 2004), and browsers (Western 2006) within Amboseli National Park. Although these studies have enhanced our understanding of population dynamics in the context of ecosystem change, they have only considered one end of the land-use gradient. By examining the responses of herbivores across a land-use gradient that includes high intensity irrigated agriculture, a mixed agro-pastoral-protected system, and a national park, the effects of land-use change on large herbivore communities and the role of humans in modifying ecosystem structure and function emerge. My observations suggest that large herbivore responses to land-use intensification in key resource areas are broadly predictable based on the interaction of aridity tolerance, feeding strategy, and body size. The impact of land-use intensification on different species and functional groups was apparent in the spatial distribution and community patterns at the Land Use Area level, as well as in the distributional patterns of large herbivores in relation to water. These results indicate that human land-use intensification in key resource areas of savanna ecosystems has potentially profound effects on large herbivore distributions, abundance, and community structure.

Land Use Area Comparisons

The process of land-use intensification in the key resource swamp areas of the Greater Amboseli Ecosystem has been characterized by agricultural expansion, increases in settlement density and permanence, fence construction, and changing patterns of livestock herd structure and density. As expected, domestic animals were primarily found in the vicinity of settlements in both CROP and INTER, but long distance incursions of domestic stock into Amboseli National Park occurred daily (personal observation). Wildlife biomass was more broadly distributed reflecting fundamental differences in aridity tolerance, feeding strategy, and body size. For example, wildebeest, one of the dominant grazers in the system, were concentrated in Amboseli National Park (PARK) and the Kimana Sanctuary (INTER) and essentially absent from the non-protected areas. The absence of wildebeest from the non-swamp and converted areas suggests that their low aridity tolerance and preference for intermediate densities of high quality forage (Andere 1981) was responsible for their elimination under intensifying land-use. As land-use intensifies human and livestock disturbance displace wildlife from water points (Williams 1998). Similarly, intensive livestock grazing reduces grass biomass to below the intermediate density preferred by many species, and removes high quality forage. In contrast, the ability of zebra to utilize relatively high quantity poor quality forage may partially explain their presence on the drier periphery of the study zones at some distance from both water and settlement where forage density remains high because of low offtake from domestic and wild herbivores. Zebra are just as water dependent as wildebeest are. However, they require higher forage biomass than wildebeest do. Thus, it appears that for zebra, forage limitations associated with increasing land-use intensification (livestock grazing, conversion to cropland) may override the preferences for areas closer to water.

Further indications of the vulnerability of particular species to land-use intensification were apparent in the distributions of Grant's gazelle, giraffe, and impala. The relative aridity tolerance and browser and mixed feeder strategies of Grant's gazelle, giraffe, and impala were evident in their preference for relatively woody habitats in the south of PARK and away from the primary settlement areas in CROP and INTER. As predicted, these species appeared to be relatively resilient to moderate levels of land-use intensification, and in a very real sense may be more threatened by the polarization of habitats that occurs with the segregation of the human and wild systems (Western and Gichohi 1993) at opposite ends of the land-use gradient. Indeed, the densities of all of these species, as well as eland, gerenuk, and waterbuck, were highest in the intermediate land-use area (INTER). For these species which appear to be more tolerant of land-use intensification the issue may ultimately be one of maintaining a sufficiently dynamic system in both time and space, with a heterogeneous mosaic of habitats, rather than the spatial extent and intensity of human induced land-use change per se. Although it appears that Grant's gazelle, giraffe, and impala may be less vulnerable to habitat loss associated with the conversion of key resources to agriculture, changes in human attitudes towards wildlife as a result of agricultural expansion may lead to the direct consumption and elimination of certain species (especially giraffe) through time.

The combined effects of habitat loss and increasing human-wildlife conflict associated with the transition from pastoral to agricultural production were apparent in the distributions of the relatively large-bodied and aridity intolerant buffalo and elephant. These two species were primarily found in the protected areas and appeared to be particularly vulnerable to land-use intensification. The large body sizes and forage requirements of these species may partially explain their preference for protected areas, but another possible explanation, is that these species, more than any other except the predators, have significant direct negative impacts on people, livestock, and agriculture. Buffalo are a known reservoir of disease for livestock (Grootenhuis 1999) and like elephants can cause injuries and fatalities to people when both depend upon the same resources. Similarly, elephants have been known to kill livestock over competition for water sources (especially in the dry season) and their destruction of crops and other agricultural infrastructure is well known.

Buffalo and elephant are the most visible representatives of a suite of species that will require protected areas to survive in the face of land-use intensification in the Greater Amboseli Ecosystem. Even with protection, however, the porous boundaries and inherent mobility of both wildlife and livestock combined with the direct negative impacts of buffalo and elephant on livestock and agriculture contributes significantly to the polarization of both habitats – protected and heavily modified by elephants on one hand, and unprotected and modified by humans on the other - and attitudes as human-wildlife conflicts increase.

Species and Functional Group Patterns

These data corroborate other studies that suggest that habitat changes within Amboseli National Park are impacting biodiversity (Struhsaker 1976, Western and Maitumo 2004, Western 2006). There appears to have been a shift in community structure with grazers and elephants concentrating in the protected areas near water with browsers and mixed feeders pushed to the periphery. This is also apparent in the relative abundance patterns of grazers, browsers, and mixed feeders along a land-use intensity gradient. Habitat polarization at both extremes of the land-use intensity gradient simplify the large herbivore community. For example, the densities of browsing species (e.g. giraffe and gerenuk) are considerably lower in Amboseli National Park. This is almost certainly the result of the massive decline in woodlands within the park boundaries (Western and Maitumo 2004, Western 2006) resulting from the interaction of various factors ranging from increasing soil salinity and shifting water tables (Western and van Praet 1973) to compression of an increasing elephant population (Western and Lindsay 1984). Furthermore, if we consider the Amboseli National Park alone (excluding the immediate surrounding area included in the PARK area), four species from the observed regional pool were not represented – gerenuk, impala, hartebeest, and waterbuck. These absences may be an artifact of the counting technique in which extremely rare species may not be detected, but their presence in other zones does suggest that the National Park alone is insufficient for preserving biodiversity in this region.

It must be noted, however, that while some of the rare species may not be abundant in the National Park, it does seem to provide essential protection for some important species such as buffalo, hippo, ostrich, oryx, and Thomson's gazelle. Similarly, the park represents the primary aggregations of the ecosystem's most abundant wild grazers, wildebeest and zebra, and an essential refuge for elephants. In this regard, the National Park continues to operate as the core dry season habitat for the majority of the ecosystem's wildlife. When this central protected area and its low human land-use intensity buffer zone are combined with other smaller protected areas in the context of a mixed land-use system (Kimana Sanctuary) all of the observed wildlife species are represented. It is also important to note the large number of livestock that are using the resources within the park. Due to the collapse of man-made water sources on the periphery of the park (Western 1982a) pastoralists and their livestock continue to depend on the swamps for water and, to a lesser degree, forage in the dry season.

And what of the other swamps in the system – Namelok (the "sweet place" in Maasai) (CROP) and Kimana (INTER), that were historically important stepping stones for wildlife between Amboseli and Tsavo and Chyulu National Parks (David Western, personal communication)? CROP currently represents the land-use extreme of intensive human impacts and over 50% of the original swamp being converted to agriculture. The beginnings of irrigated agriculture were evident in Namelok (CROP) by 1973, with a major expansion of area under crop production coinciding with a period of intense drought in the early 1980s (Campbell et al. 2003, Campbell et al. 2005). As Namelok swamp became an increasingly important focal point (relief valve) for pastoralists faced with increased competition for dwindling resources, conflict with wildlife inevitably intensified. In an effort to limit the negative interactions of wildlife and agriculture, an electric fence, essentially impervious to wildlife, was constructed around the swamp, effectively excising this historically important resource from wildlife.

The conversion and subsequent fencing of the swamp has resulted in the local extinction of buffalo and hippo, and the virtual collapse of elephant, zebra, and wildebeest populations. All of these species show extreme preference for areas close to water and their declines suggest a significant response to conversion and excision of the swamp habitat. In contrast to PARK, the browsers and mixed feeders have relatively high densities. These more aridity tolerant species are less affected by the loss of the swamp and may in fact benefit from an increase in woody plant species that has been observed with sedentarization and intensification (e.g.. Western 1989, Tobler et al. 2003) and the loss of ecosystem engineers (Jones et al. 1994) such as elephants and rhino (van Wjingaarden 1985, Owen-Smith 1988, 1989, Western and Gichohi 1993). It is also interesting to note that while CROP in many ways represents the most human dominated system it does not have the highest livestock biomass density. Although this may be an expected pattern in peri-urban and urban environments, the low livestock density relative to that found in INTER corroborates the hypothesis that the intensification of human land-use in the swamps has negative implications for both livestock and wildlife.

INTER is a mixed production system that encompasses elements of pastoral, agricultural, and protected systems. Although the spread of cultivation occurred somewhat later in Kimana (INTER) (Campbell et al. 2003), its proximity to a major rural road has meant a rapid intensification and expansion of agriculture in recent years. Concomitant with agricultural expansion has been an increasing interest in conservation that culminated in the establishment of the Kimana Sanctuary in 1998. In many respects the dynamic and diverse collection of land-use patterns and processes of change represented in INTER are indicative of larger landscape level patterns. As a microcosm of patterns at broad spatial and temporal scales INTER may serve as an indicator of possible outcomes given a heterogeneous mosaic of mixed land-use systems.

As hypothesized, INTER had intermediate levels of total herbivore biomass. There were some significant exceptions, however, and species such as eland, giraffe, gerenuk, grants, hartebeest, impala, and waterbuck, had higher densities in INTER. Hartebeest and waterbuck are both rare grazers while the others are relatively aridity tolerant mixed feeders and browsers. Domestic biomass density was considerably higher in INTER than in either PARK or CROP. The data did not appear to corroborate the suggestion by Western (1989) that mixed wildlife/livestock systems support more overall biomass than either livestock or wildlife dominated systems. In a sense, however, PARK itself acts as a mixed system as livestock frequently make use of the resources within the park boundaries despite its protected status. But even if we remove all the livestock from

PARK there is still more biomass in the wildlife only system. Although there may be lingering effects of livestock in the PARK system (i.e. the facilitative effects of livestock on wildlife may be more important than the sum of their biomass would suggest), this is unlikely considering livestock numbers are relatively low. It is also possible that this is a result of the relatively focused nature of the sampling design. However, I think it is more likely that the impacts of high settlement densities combined with agriculture, even at low levels, results in an environment that is sufficiently hostile to wildlife to prevent the realization of the synergistic effects of a strictly livestock/wild system, as referred to by Western (1989). Indeed, the very nature of land-use intensification in the swamps has resulted in a fundamental alteration of human-wildlife interactions, changing a relatively benign/neutral pastoral relationship to an inherently antagonistic agricultural-wildlife relationship.

Herbivore Distributions in relation to Water

Water is an essential resource in the arid savannas of East Africa, and the swamps of Amboseli are well known as a fundamental component of this seasonally dynamic ecosystem (Western 1973). Although the effects of water on community structure at broad spatial scales have been documented (Western 1975, de Leeuw et al. 2001), the responses of herbivores to water at finer spatial scales are less well understood (Redfern et al. 2003, Redfern et al. 2005). A clear understanding of the fine scale responses of herbivores to water, and the influences of land-use on these relationships, is an essential first step in understanding the impact of herbivore distribution patterns on ecosystem structure and function. High-resolution spatial data of herbivore distributions enables us to link land-use change with our understanding of the potential for herbivores to modify their environment (Laws 1970, Hobbs 1996, Augustine and McNaughton 1998, Adler et al. 2001). This linkage is especially important in arid and semi-arid systems where herbivores have potentially severe impacts on vegetation around water points (Georgiadis 1987, Andrew 1988, Georgiadis and McNaughton 1990, Thrash and Derry 1999).

At a general level many of these patterns are consistent with our existing understanding of the influence of water in arid systems, but two points warrant further consideration: the scale at which these interactions occur, and the influence of land-use on the relationship between water and herbivores. Western (1975) noted that the Amboseli herbivore community could be divided into two communities – water dependent (low aridity tolerance) and water independent (high aridity tolerance) – with 99% of the total biomass of the former found within 15km of water. The high degree of clustering around water by "water-independent" species mirrors that found in this study, but at much broader spatial scales. The high spatial resolution counting technique used here demonstrated similar patterns of "attraction" to water for low aridity tolerant species at much finer spatial scales, suggesting that much of the broad scale pattern observed by Western (1975) is actually driven by localized interactions between herbivores and water. This characteristic is particularly important in systems like Amboseli that are dominated by highly vulnerable key resource areas.

Water distribution was an important factor in structuring the Greater Amboseli Ecosystem. Generally, both wild and domestic herbivores declined with increasing distance from water. Livestock abundance was relatively independent of water, however, reflecting the role of herding in altering their spatial distributions. As predicted from patterns of aridity tolerance and body size, wild herbivore functional group distributions differed in relation to water. Relatively low aridity tolerance and dependence on relatively low quality herbaceous forage means that grazers generally cluster near the swamps in the GAE. The generally higher aridity tolerance and dry season dependence of browsers and mixed feeders on relatively nutritious browse results in less water dependent distributions. The distributions of grazers and mixed feeders appeared to be the most susceptible to variations in land-use intensity, while browsers were distributed independently of water across the gradient. These results indicate that land-use intensification in key resource areas may differentially impact wild herbivore functional groups with cascading effects on habitat heterogeneity and biodiversity. Indeed, the general response of species richness as a function of water suggests that the excision or homogenization of the swamps may have profound implications for composition of the large herbivore community in the GAE.

These patterns of differential susceptibility to land-use intensification are clear in species level distributions as a function of water. As with the functional group response, the distributions of grazing species such as buffalo, wildebeest and zebra are altered and constrained under land-use intensification. Key species such as buffalo, elephant, and wildebeest are confined to narrow strips adjacent to water under intermediate land-use intensity (INTER) and all but eliminated under intensive use (CROP). Giraffe are distributed independently of water in all areas, and mixed feeders appear to be increasingly decoupled from water under intermediate and intense land-use change. It is possible that the adaptable diets of mixed feeders enables them to shift from herbaceous to woody forage with increasing land-use intensification, thus potentially avoiding competition with livestock for scarce dry season resources.

CONCLUSIONS

Land-use change in the swamps of the Greater Amboseli Ecosystem has had a significant impact on the composition and spatial structure of the large herbivore community. Spatially confined changes in land-use ranging from subsistence pastoralism to fine scale cultivation with parallel changes in settlement pattern and intensity can drive fundamental impacts on the community and spatial structure of both wildlife and livestock. Not only does the removal of key resources from the "grazing" system have cascading effects on biodiversity and ecosystem resilience/resistance, but it also alters fundamentally the interaction of local peoples with their environment (e.g. Newmark et al. 1994). Observations at the extreme end of land-use intensification (CROP) demonstrated that the extensive loss of habitat observed in the swamps has an effect that is far larger than their total area would suggest. Thus, although the outlook for wildlife in CROP looks bleak, it does suggest that more porous boundaries may offer some hope to both wildlife and livestock. The absence of particular species from the core protected area, in turn, suggests that a balanced approach between protection and human use is essential. The swamps represent the heart of Amboseli's diversity and dynamism, and the loss of these critical habitats to agriculture at one extreme and the extensive habitat modification due to compression at the other, has potentially far reaching implications for the ecosystem as a whole. Central to the survival of Amboseli's diversity and abundance is a conservation and development strategy that maintains a flexible system of management that recognizes the role of aridity tolerance, feeding strategy, and body size in mitigating species responses to intensification, and the importance of heterogeneity and key resource areas to the resilience and stability of dynamic ecosystems.

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TABLES

Table 1. Species names, biomass, functional groups, and hypothesized functional relationships to surface water and land-use intensification. Numbers in the last two columns correspond to the hypothetical response curves in Figure 1.

Common Name	Scientific Name	Species Code	Population Unit Weight (kg)*	Body Size Class**	Feeding Strategy***	Aridity Tolerance****	Landscape Response	Water Response
Cattle	*Bos indicus* (L.)	CT	180	Medium	Grazer	Intermediate	3	1
Donkey	*Equus asinus* (L.)	DK	130	Medium	Grazer	Low	1	1
Shoats	*Ovis aries* (L.) and *Capra hircus* (L.)	ST	18	Small	Mixed	Intermediate	2	1
Buffalo	*Cyncerus caffer* (L.)	BF	450	Large	Grazer	Low	1	1
Eland	*Taurotragus oryx* (Pallas)	ED	340	Medium	Mixed	High	4	3
Elephant	*Loxodonta africana* (Blumenbach)	EL	1725	Large	Mixed	Low	4	3
Gerenuk	*Litocranius walleri*	GK	25	Small	Browser	High	3	4
Giraffe	*Giraffa cameleopardis* (L.)	GF	750	Large	Browser	High	3	4
Grant's Gazelle	*Gazella granti* (Brooke)	GT	40	Small	Mixed	High	4	3
Hartebeeste	*Alcelaphus buselaphus* (Pallas)	HT	125	Medium	Grazer	Intermediate	1	1
Hippo	*Hippopotamus amphibius*	HP	1000	Large	Grazer	Low	1	1
Impala	*Aepyceros melampus* (Lichtenstein)	IM	40	Small	Mixed	Intermediate	4	3
Lesser Kudu	*Tragelaphus imberbis*	LK	70	Medium	Browser	High	3	4
Ostrich	*Struthio camelus*	OS	114	Medium	Mixed	High	4	4
Oryx	*Oryx beisa* (Pallas)	OX	150	Medium	Grazer	High	1	2
Thomson's Gazelle	*Gazella thomsonii* (Guntter)	TM	15	Small	Mixed	Low	4	1
Waterbuck	*Kobus ellipsiprymnus*	WB	160	Medium	Grazer	Low	1	1
Warthog	*Phacochoerus aethiopicus*	WH	45	Small	Grazer	Low	1	1
Wildebeest	*Connochaetes taurinus* (Burchell)	WT	123	Medium	Grazer	Low	1	1
Zebra	*Equus burchelli* (Gray)	ZB	200	Medium	Grazer	Low	1	1

* all body weights from Western (1975) except for gerenuk, lesser kudu, waterbuck, warthog, and wildebeest which are from Coe etal (1976)

** body size classes as follows: Small (< 50 kg), Medium (50 to 400 kg), and Large (> 400 kg)

*** Grazer (G), Browser (B) or Mixed (M) feeder based on descriptions from Estes (1991)

**** the degree to which a species depends on surface water to meet its water requirements (after de Leeuw et al, 2001) - animals that need to drink daily have a low tolerance while those that can meet most of their requirements from moisture in vegetation have a high aridity tolerance - Western (1975) and de Leeuw et al (2001) differ on STs

Table 2. Land-use characteristics for each of the Land Use Areas in the study area.

Table 2.

	PARK	INTER	CROP
Wetland Name	Amboseli NP	Kimana	Namelok
Area (km^2)	364.7	142.7	115
Land Use	Protected Area	Agro-Pastoral and Protected	Agro-Pastoral
Human Impact	Low	Intermediate	High
Degree of Fencing around Wetlands	Not Fenced*	Not Fenced **	Swamp Fenced***
Fenced area (km^2)	0.00	5.56	17.89
Percent of total area fenced	0.00	3.89	15.56
Area protected (km^2)	287.00	24.56	5.22
Percent of area protected	78.69	17.21	4.54
Number of Settlements	14	158	217
Settlement Density - no./km^2	0.04	1.11	1.89
Percent of all house = Traditional	95.86	15.85	8.99
Percent of all houses = Grass	0.00	65.92	68.88
Percent of all houses = Tin	4.14	18.23	22.13
Cattle:Shoat ratio	1.30	0.58	0.45

* No agricultural fences, but there are some small exclosures around experimental plots and tourist facilities

** the swamp is not fenced, but there is a fence in the southern part of the area that encloses non-swamp agriculture

*** the entire swamp area is fenced off for agricultural production

Table 3a. Density (kg/km^2) estimates and lower and upper confidence limits for all domestic and wild species by Land Use Area.

Table 3a.

	Park			Mixed			Crop		
Species	Density	LCL	UCL	Density	LCL	UCL	Density	LCL	UCL
Buffalo	1.793	*1.793*	*1.793*	0.694	*0.694*	*0.694*	—	—	—
Cattle	10.123	*10.123*	*10.123*	17.589	*17.589*	*17.589*	11.104	*11.104*	*11.104*
Donkey	0.112	*0.112*	*0.112*	0.161	*0.161*	*0.161*	—	—	—
Eland	0.022	*0.022*	*0.022*	0.294	*0.294*	*0.294*	0.078	*0.078*	*0.078*
Elephant	2.896	*2.311*	*3.627*	0.827	*0.660*	*1.036*	0.157	*0.125*	*0.196*
Giraffe	0.126	*0.126*	*0.126*	0.505	*0.505*	*0.505*	0.270	*0.270*	*0.270*
Gerenuk	0.003	*0.002*	*0.003*	0.217	*0.174*	*0.271*	0.139	*0.112*	*0.174*
Grant's Gazelle	2.643	*2.118*	*3.298*	3.532	*2.831*	*4.407*	2.017	*1.617*	*2.517*
Hippo	0.378	*0.302*	*0.474*	0.098	*0.078*	*0.123*	—	—	—
Hartebeeste	—	—	—	0.021	*0.021*	*0.021*	—	—	—
Impala	0.472	*0.378*	*0.588*	1.072	*0.859*	*1.338*	0.322	*0.258*	*0.401*
Ostrich	1.124	*0.907*	*1.393*	0.126	*0.102*	*0.156*	0.200	*0.161*	*0.248*
Oryx	0.022	*0.022*	*0.022*	—	—	—	—	—	—
Shoats	7.765	*7.765*	*7.765*	30.168	*30.168*	*30.168*	24.896	*24.896*	*24.896*
Thomson's Gazelle	0.622	*0.499*	*0.777*	0.308	*0.247*	*0.385*	0.548	*0.439*	*0.684*
Waterbuck	—	—	—	0.126	*0.126*	*0.126*	—	—	—
Warthog	0.132	*0.105*	*0.164*	0.063	*0.051*	*0.079*	—	—	—
Wildebeest	20.293	*20.293*	*20.293*	2.684	*2.684*	*2.684*	0.017	*0.017*	*0.017*
Zebra	13.175	*13.175*	*13.175*	4.835	*4.835*	*4.835*	0.713	*0.713*	*0.713*

Table 3b. Kruskal Wallis test for differences between areas by species. Significant comparisons are indicated with a 1. Species which were found in only one of the three LUAs are indicated with a ---.

Table 3b.

	χ^2	df	pvalue	P vs C	P vs M	C vs M
Buffalo	15.372	2	<0.001	0	0	0
Cattle	75.863	2	<0.001	1	1	0
Donkey	3.104	2	0.212	0	0	0
Eland	7.841	2	0.020	0	0	0
Elephant	12.248	2	0.002	0	0	0
Giraffe	13.156	2	0.001	0	0	0
Gerenuk	12.597	2	0.002	0	0	0
Grant's Gazelle	12.683	2	0.002	0	0	0
Hippo	3.638	2	0.162	0	0	0
Hartebeeste	3.362	2	0.186	---	---	---
Impala	1.974	2	0.373	0	0	0
Ostrich	16.271	2	<0.001	0	0	0
Oryx	1.414	2	0.493	---	---	---
Shoats	102.116	2	<0.001	1	1	0
Thomson's Gazelle	0.358	2	0.836	0	0	0
Waterbuck	13.470	2	0.001	---	---	---
Warthog	3.580	2	0.167	0	0	0
Wildebeest	154.796	2	<0.001	1	1	0
Zebra	60.209	2	<0.001	1	0	0

Table 4. Wild and Domestic mean biomass density (kg/km^2) for the entire area and each LUA. *** indicates significant differences between areas ($p<0.001$). Different subscript letters indicate significant differences based on Kruskal-Wallis multiple comparisons test ($p<0.05$).

Table 4.

	All		Park		Crop		Mixed	
	Biomass	SE	Biomass	SE	Biomass	SE	Biomass	SE
Domestic	2465.8***	321	1976.8^a	462.5	2446.9^b	380.3	3730.9^b	682.8
Wild	7872.1***	778.9	11685.8^a	1240.7	771.6^b	200.5	3847.5^c	1115.8

Table 5. Mean biomass density (kg/km^2) and SE for domestic and wild functional groups for the entire area and individual Land Use Areas.

Table 5.

		All		Park		Mixed		Crop	
		Biomass	SE	Biomass	SE	Biomass	SE	Biomass	SE
Domestic	Grazers	2176.6***	311.5	1837^a	452.3	3187.8^b	651.8	1998.8^b	358.0
	Mixed	289.2***	35.1	139.8^a	38.4	543.2^b	92.5	448.1^b	87.1
	Browsers	---	---	---	---	---	---	---	---
Wild	Grazers	4131.1***	360.2	6326.3^a	591.2	1733.5^b	336.6	144.7^c	44.6
	Mixed	3559.4	646.3	5264.8	1045.9	1730.1	861.2	421.2	178.9
	Mixed - No EL	255.4	25.5	269.6	35.1	151.2	33.5	303.3	60.1
	Browsers	181.5***	35.9	94.7	29.5	383.9	127.2	205.7	62.1

Table 6. The total number of species and the number of species per km^2 (species density) for each Land Use Area. Pearson's Chi-square test suggests significant differences in species richness ($\chi^2 = 8.6172$, df = 2, p-value = 0.01345) but no significant differences for species density.

Table 6.

	Richness	Species Density
Park	14	0.038
Mixed	15	0.105
Crop	10	0.087

FIGURES

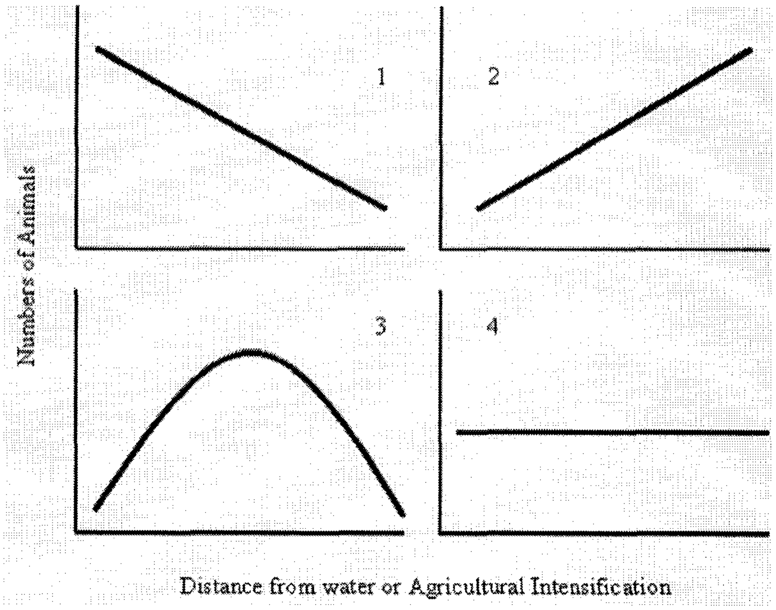


Figure 1. Hypothetical responses of large herbivore biomass or density to a distance to water or increasing agricultural intensity gradient. Predicted responses emerge from differences in feeding strategy (functional group) and body size.

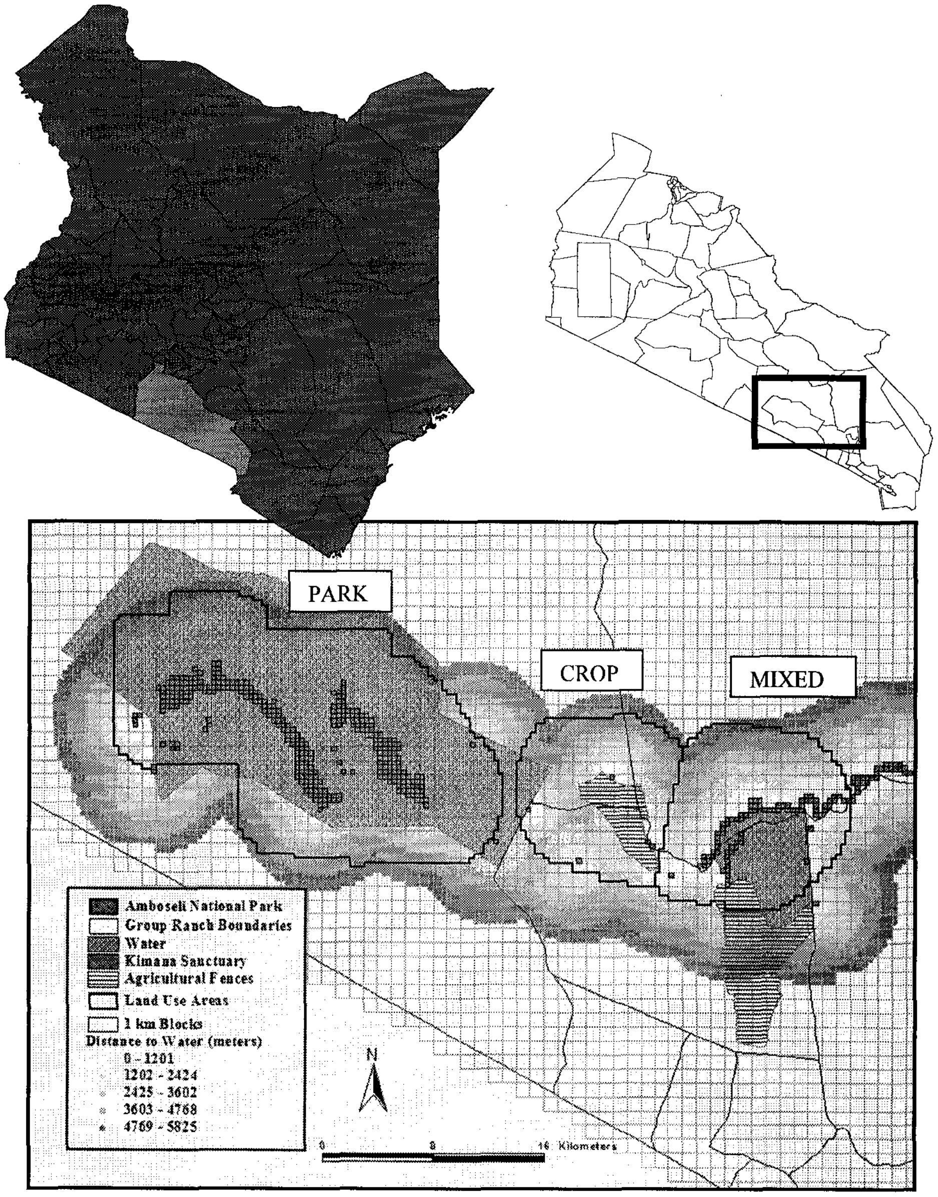


Figure 2. Study area map. This study was conducted in the core wetlands of the Greater Amboseli Ecosystem, Kajiado District, Kenya. Three wetland Land Use Areas were selected along a land-use intensity gradient ranging from protected (PARK) to mixed agro-pastoral and protected (INTERMEDIATE) and intensive agro-pastoral (CROP). Black polygons dilineate the Land Use Areas.

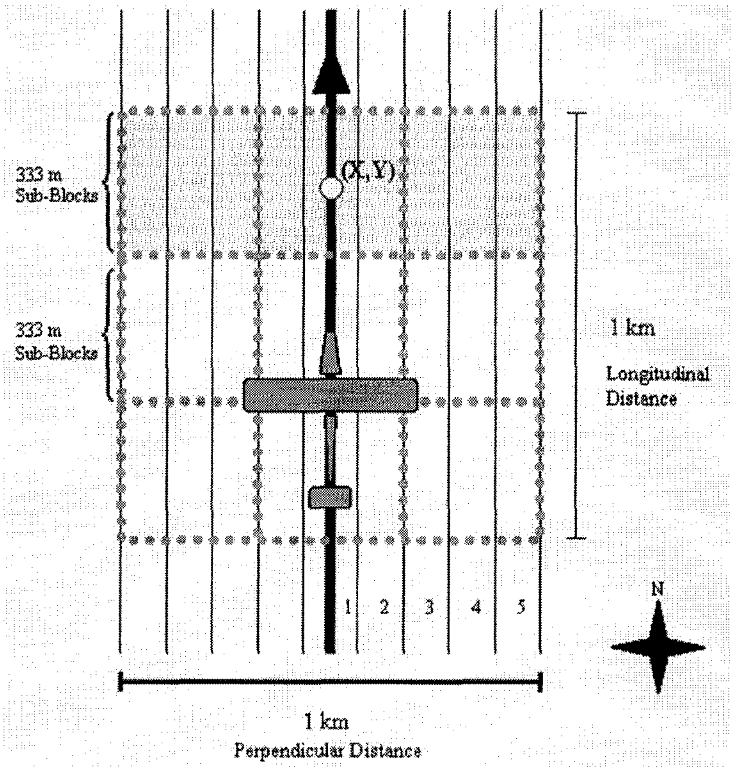


Figure 3. High resolution aerial distance sampling. Transects were placed at1 kilometer intervals. Animals were recorded out to 500m on either side of the aircraft and observations were allocated to one of five perpendicular distance bands (1-5). All observations were subsequently aggregated into 1/3 kilometer blocks (shaded) and allocated to a 333m transect segment with a center point at (X,Y).

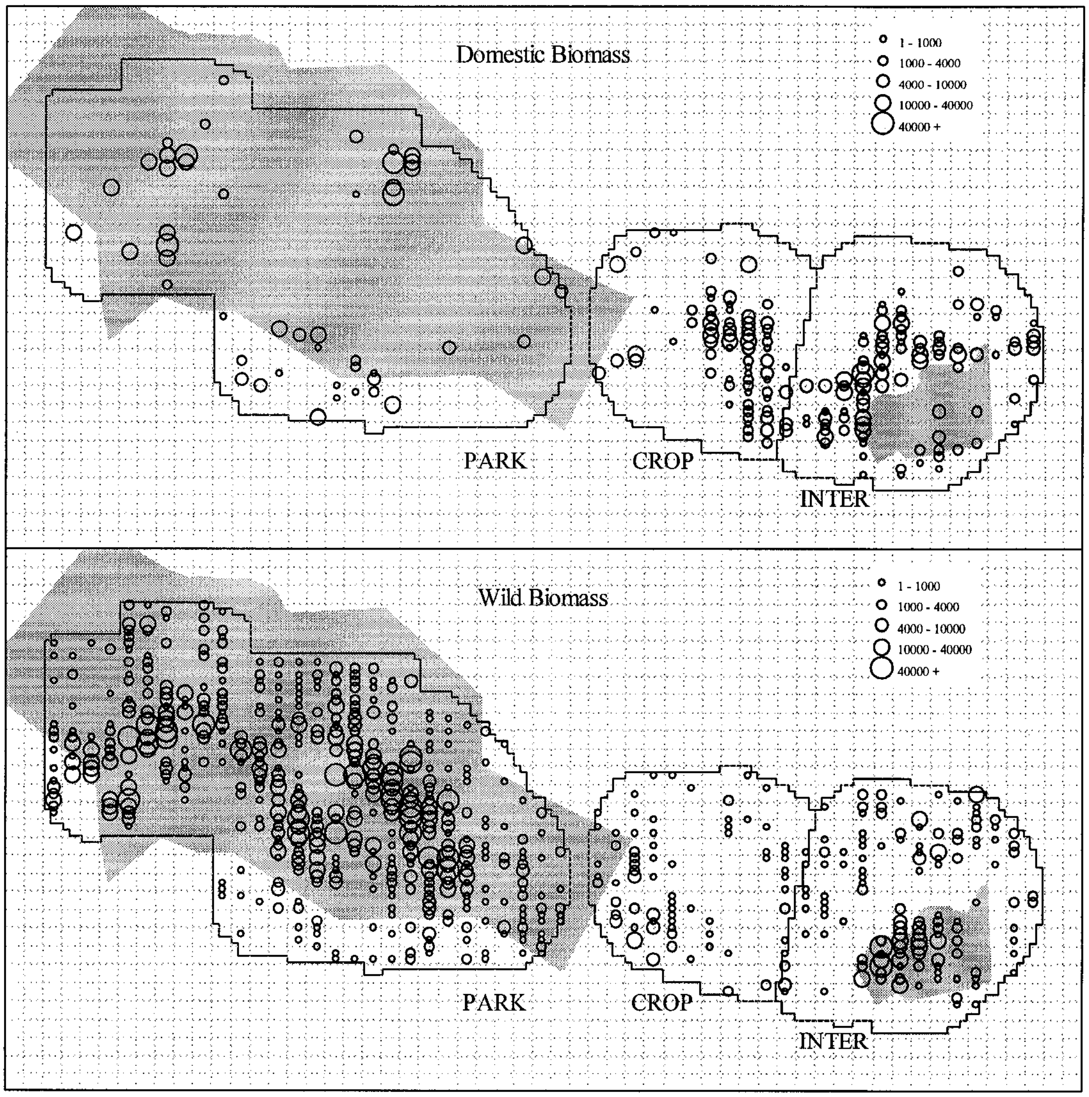


Figure 4. Spatial distribution of domestic and wild large herbivore biomass. All points indicate kilograms per transect segment (.33km^2). Note the spatial separation of domestic and wild herbivores in all Land Use Areas. Also note the concentration of wildlife around water in Amboseli National Park, the total exclusion of wildlife in the agricultural zone in CROP, and the aggregation of wildlife in the Kimana Wildlife Sanctuary (INTERMEDIATE). Shaded grey polygons represent protected areas – Amboseli National Park in the left and Kimana Sanctuary on the right.

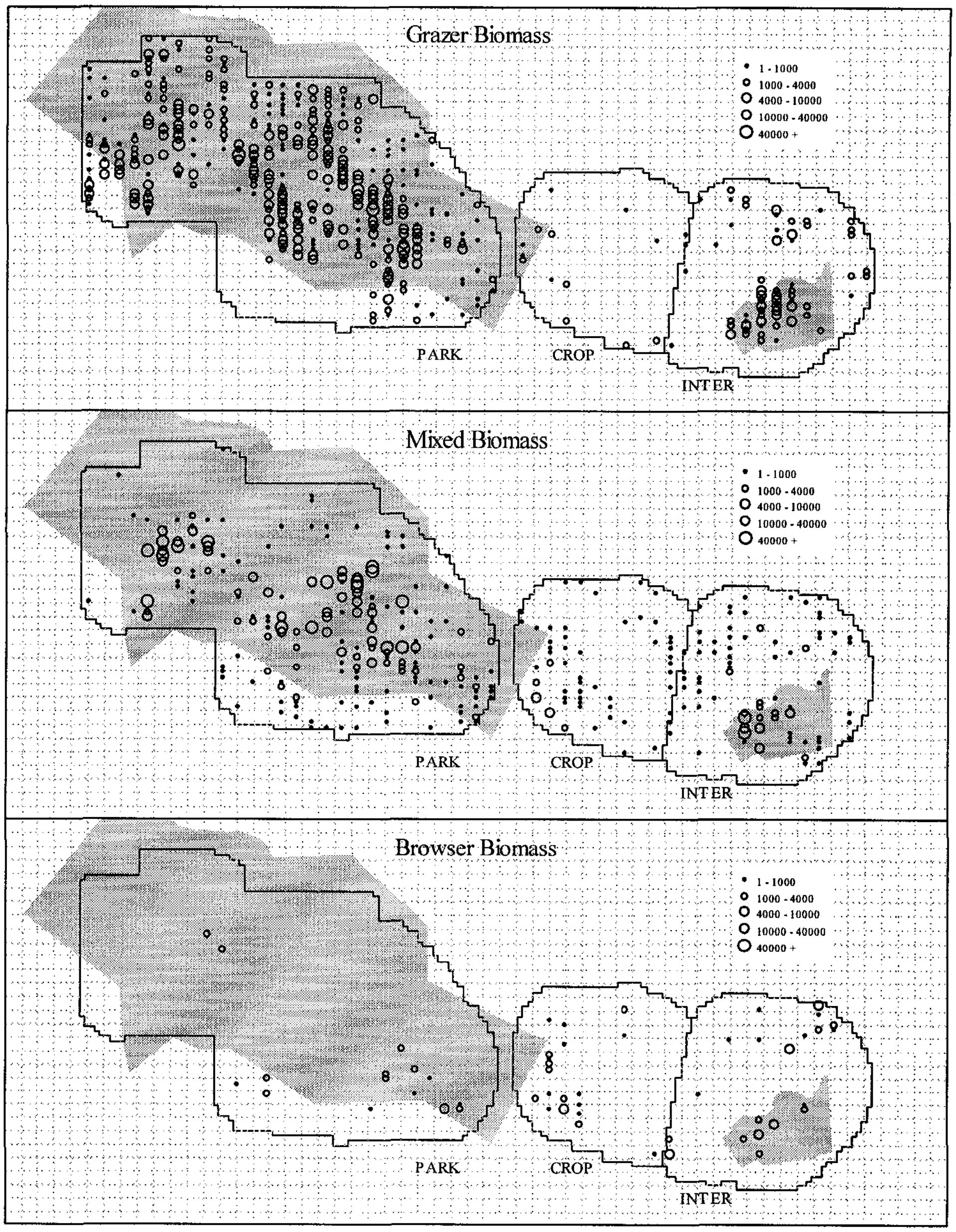
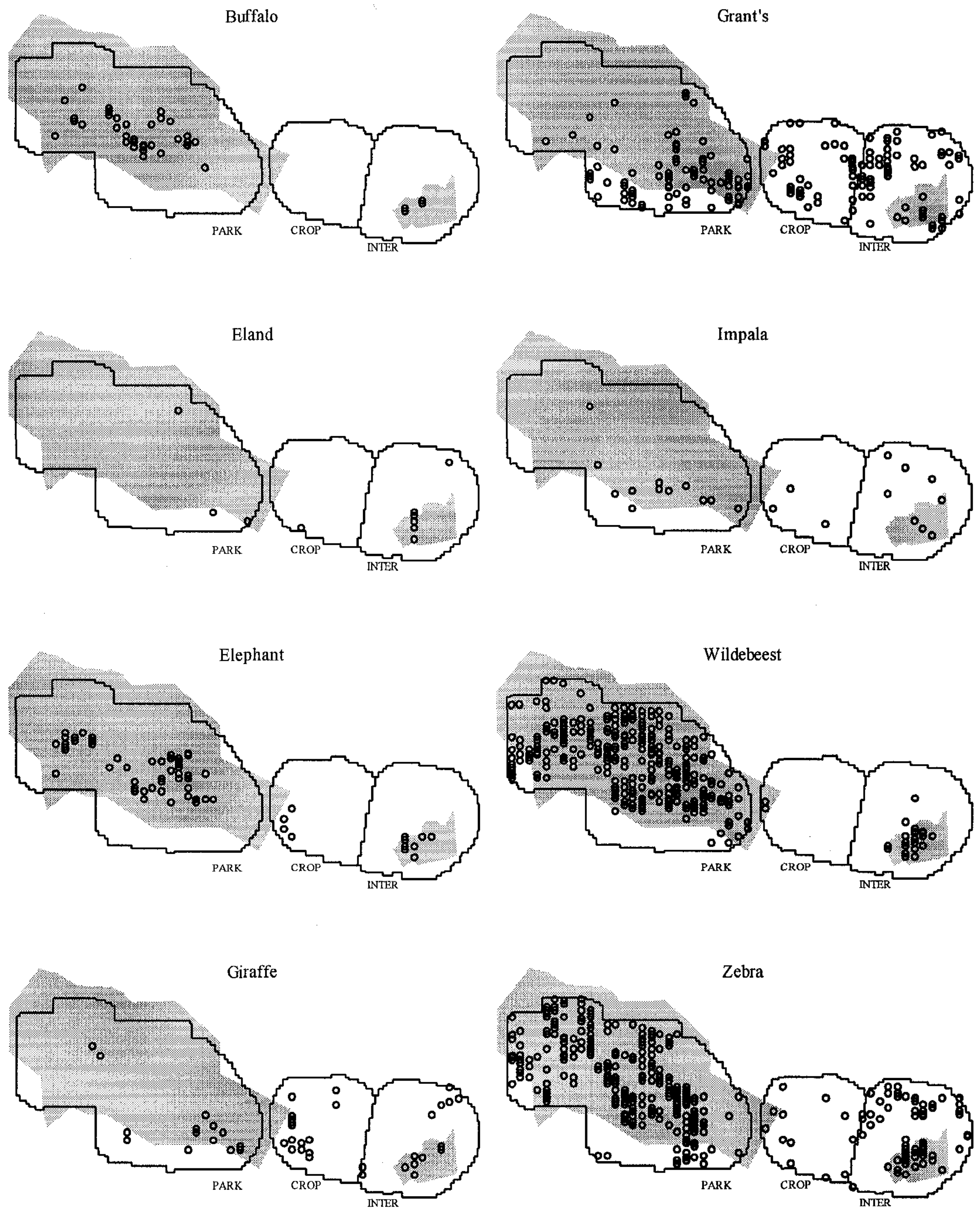


Figure 5. Spatial distribution of large herbivore wild biomass density by functional group. All points indicate kilograms per transect segment (.33km^2). Shaded grey polygons represent protected areas – Amboseli National Park in the left and Kimana Sanctuary on the right.



Buffalo

Grant's

Eland

Impala

Elephant

Wildebeest

Giraffe

Zebra

Figure 6. Spatial distribution of large herbivore species. All points indicate presence within a transect segment (.33km^2). Shaded grey polygons represent protected areas – Amboseli National Park in the left and Kimana Sanctuary on the right.

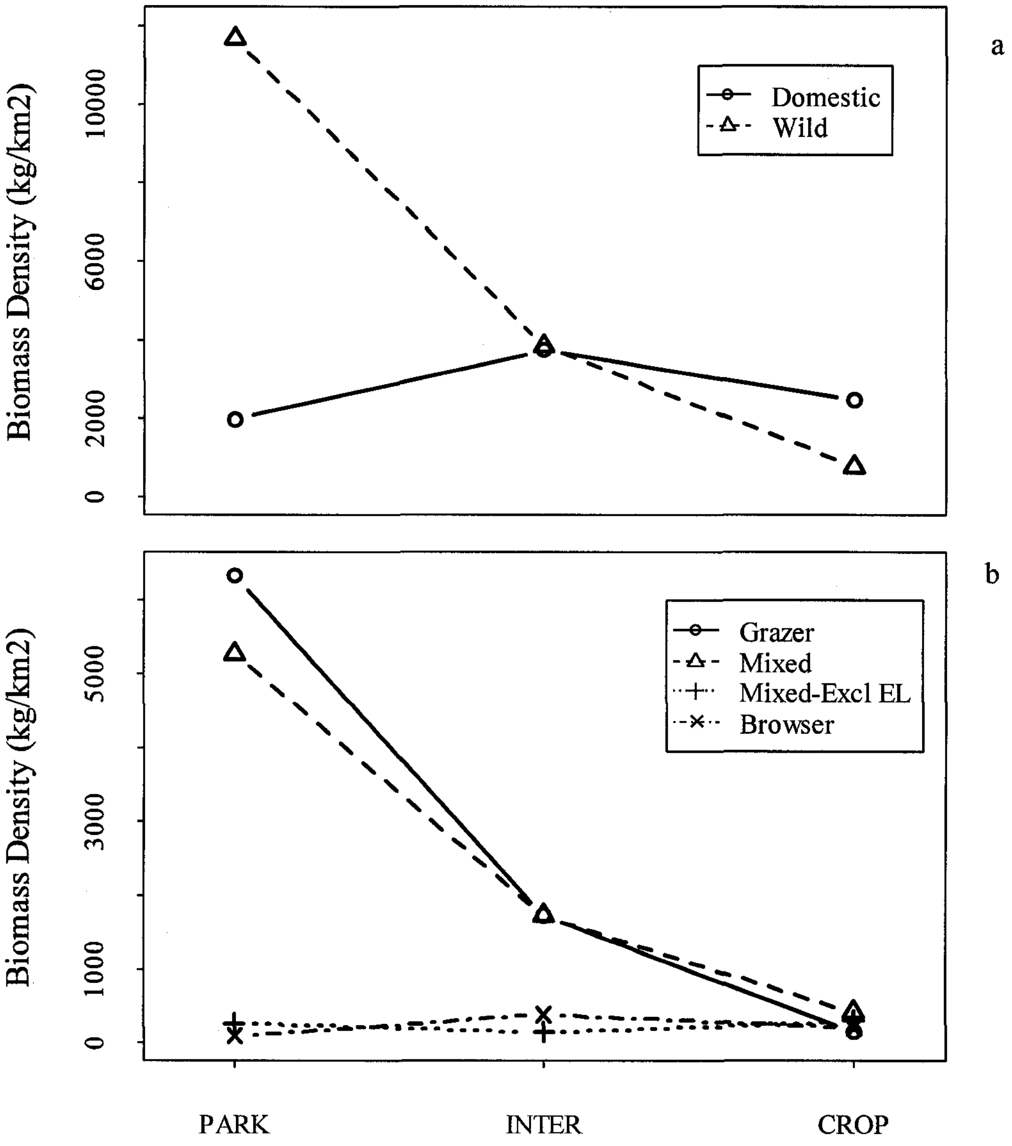


Figure 7. Biomass density (kg/km^2) for wild and domestic herbivores (a), and wild herbivores by functional group (b) by Land Use Area. Note that domestic biomass peaks at intermediate land-use intensity (INTER).

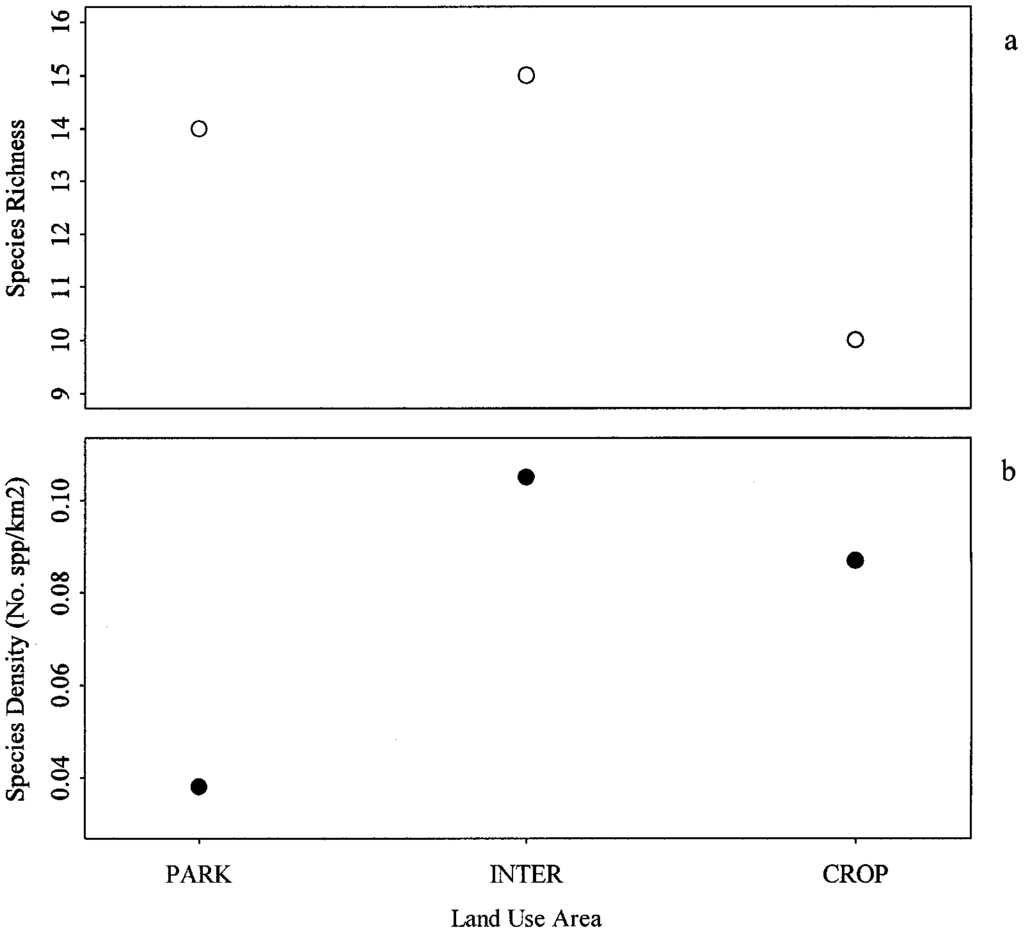


Figure 8. Wild species richness (total number of unique species per Land Use Area) (a) and species density (number of unique species per km^2) (b) by Land Use Area.

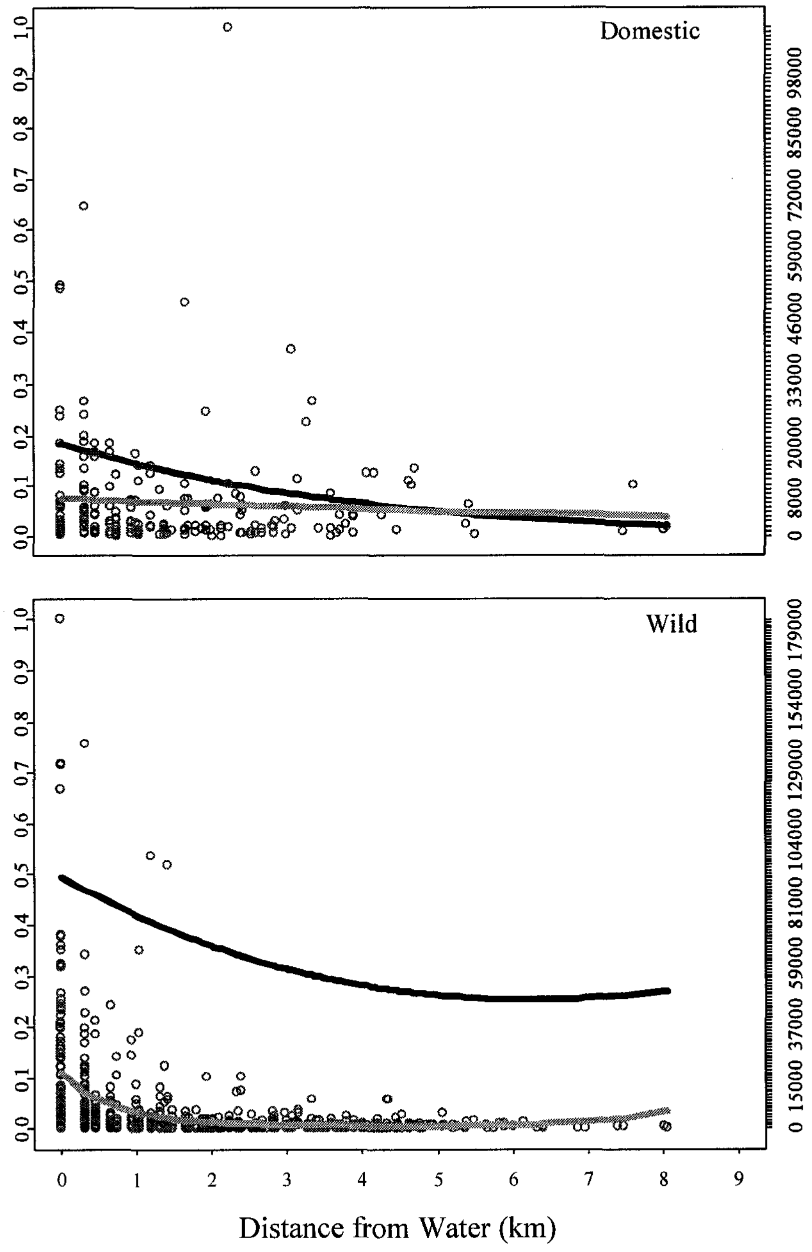


Figure 9. Domestic and wild biomass (kg) distributions as a function of distance from water. A two part conditional model was used to generate a predicted response for the probability of encountering one or more animals in a transect segment (black line) and the abundance of animals given presence (grey line). Actual count data is presented as open circles.

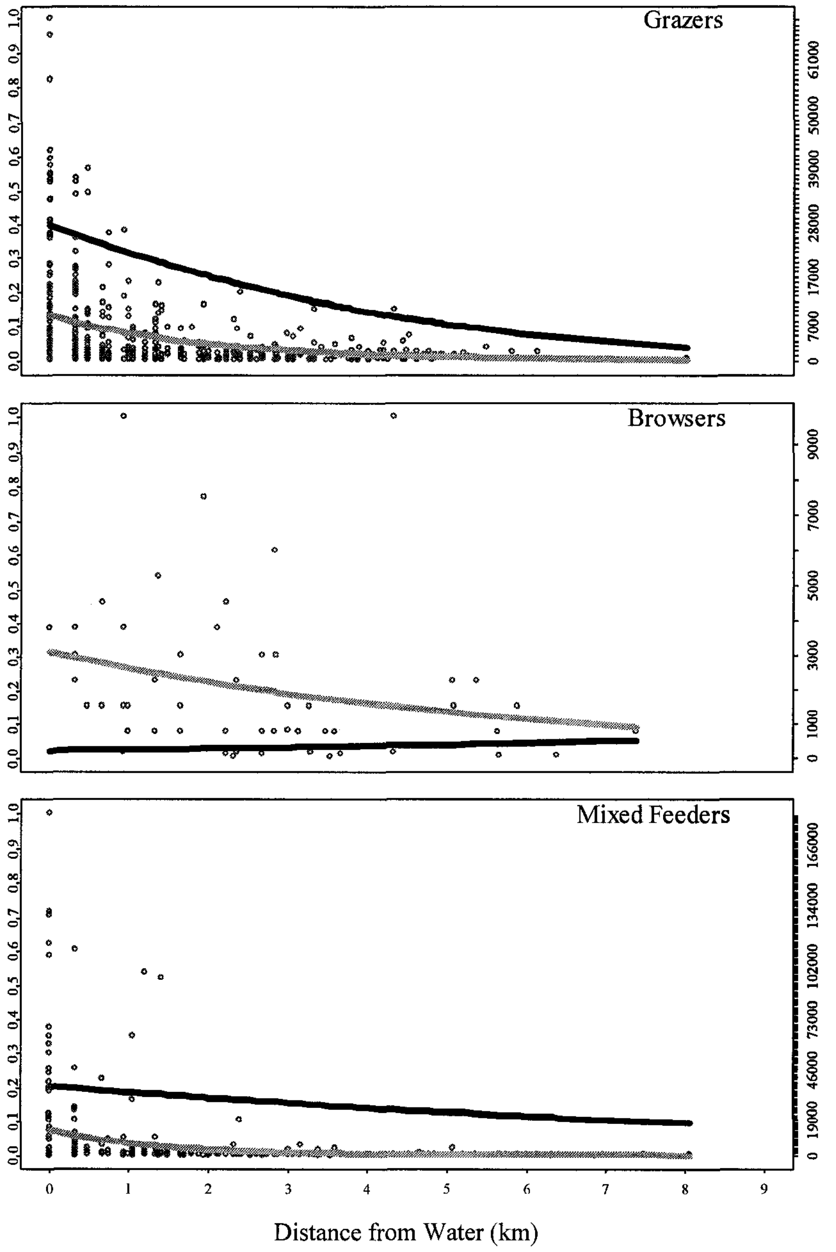


Figure 10. Functional group wild biomass (kg) distributions as a function of distance from water. A two part conditional model was used to generate a predicted response for the probability of encountering one or more animals in a transect segment (black line) and the abundance of animals given presence (grey line). Actual count data is presented as open circles.

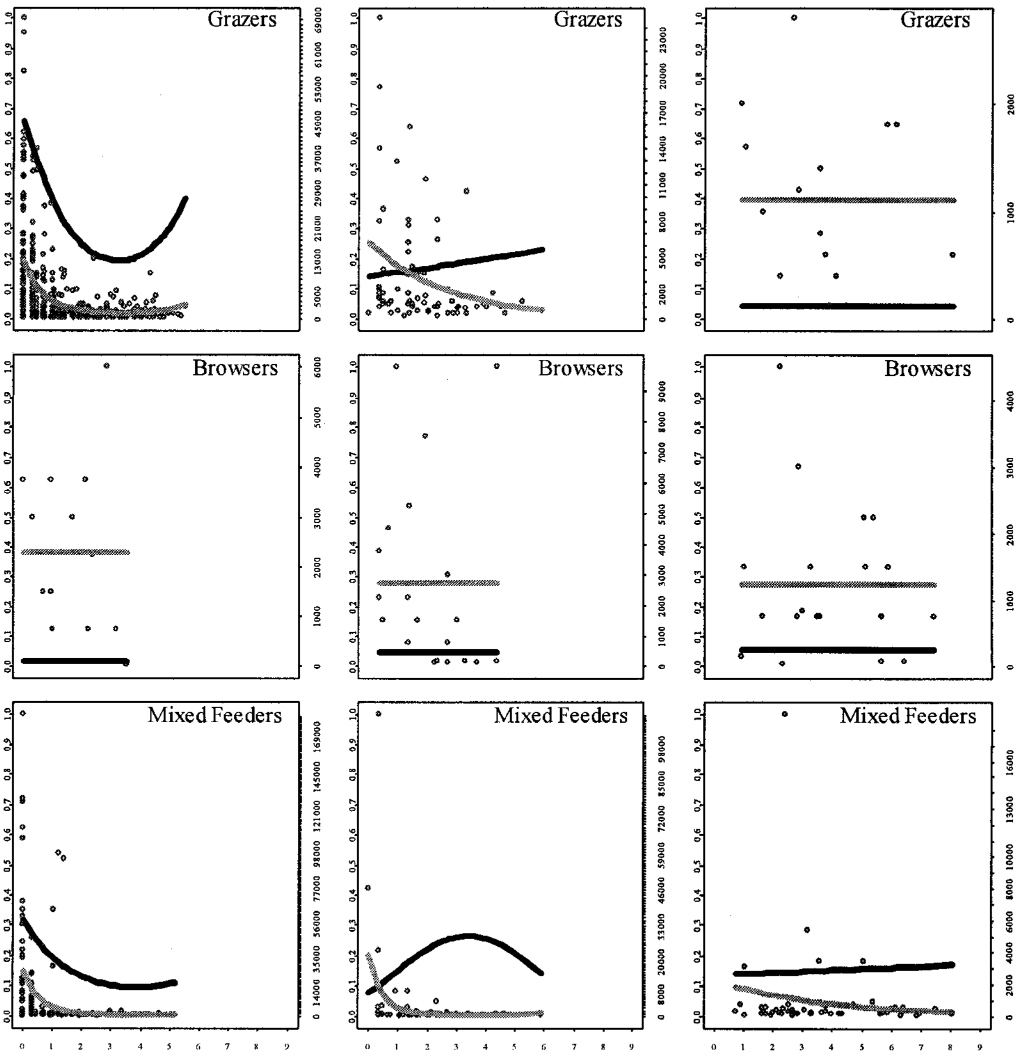


Figure 11. Functional group wild biomass (kg) distributions as a function of distance from water by Land Use Areas. A two part conditional model was used to generate a predicted response for the probability of encountering one or more animals in a transect segment (black line) and the abundance of animals given presence (grey line). Actual count data is presented as open circles.

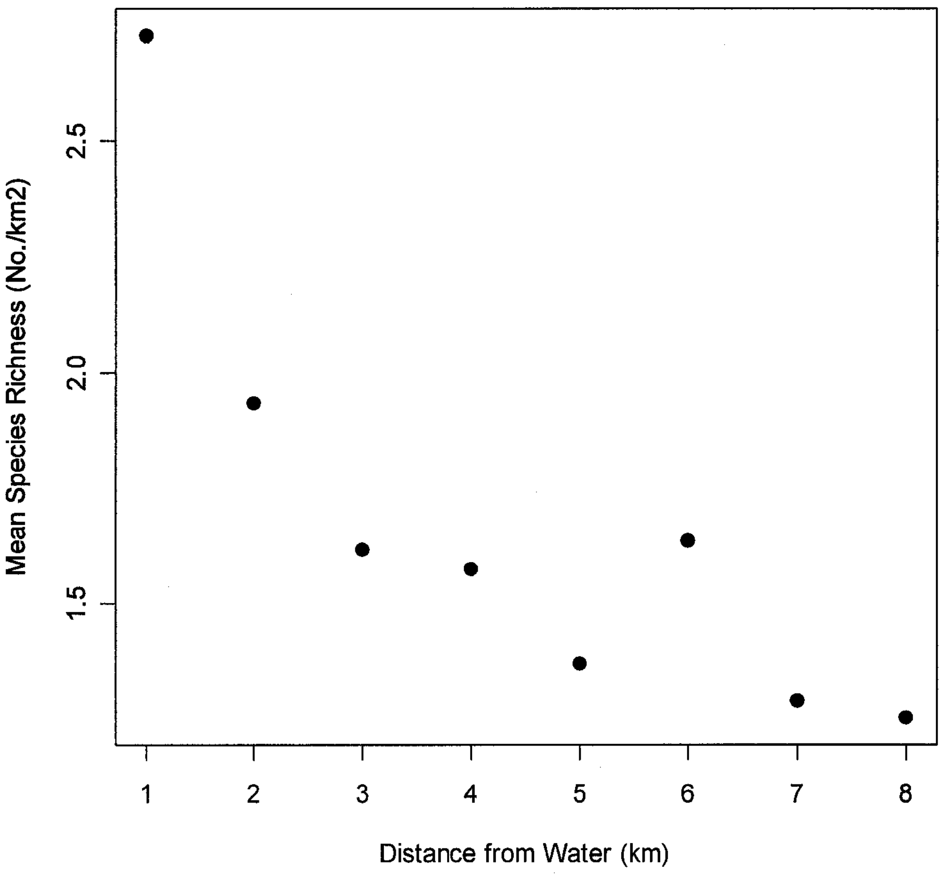


Figure 12. Mean wild species richness (number per km^2) as a function of distance from water. Only grid cells with observations were used.

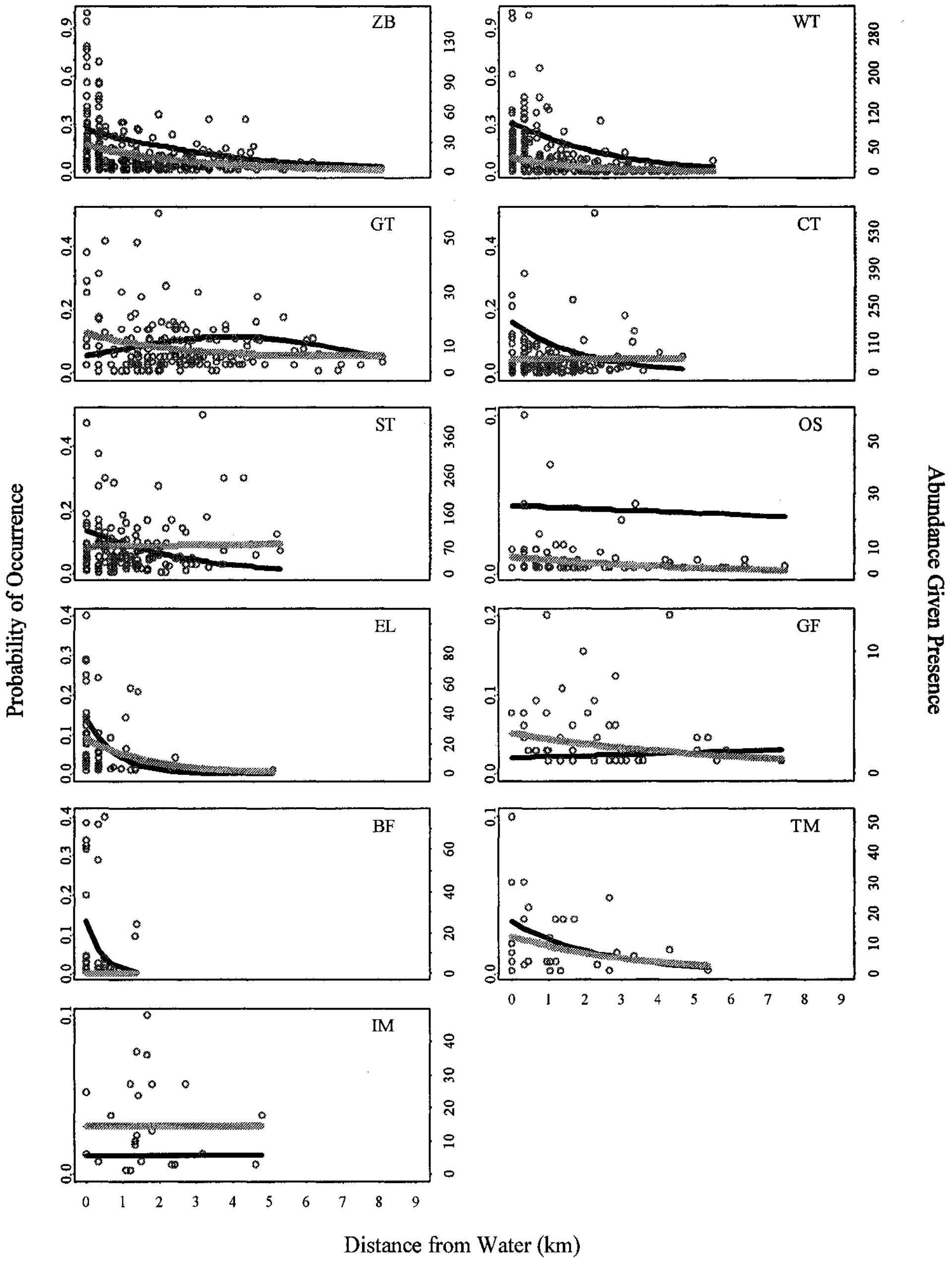


Figure 13. Two part conditional model of herbivore abundance as a function of distance from water for all swamps in the Greater Amboseli study area. Black lines indicate the probability of encountering a group of greater than or equal to one individual at different distances to water. Grey lines are predicted values of the zero truncated negative binomial model of group sizes as a function of distance from water. Open circles are actual abundance data. Species codes from Table 1.

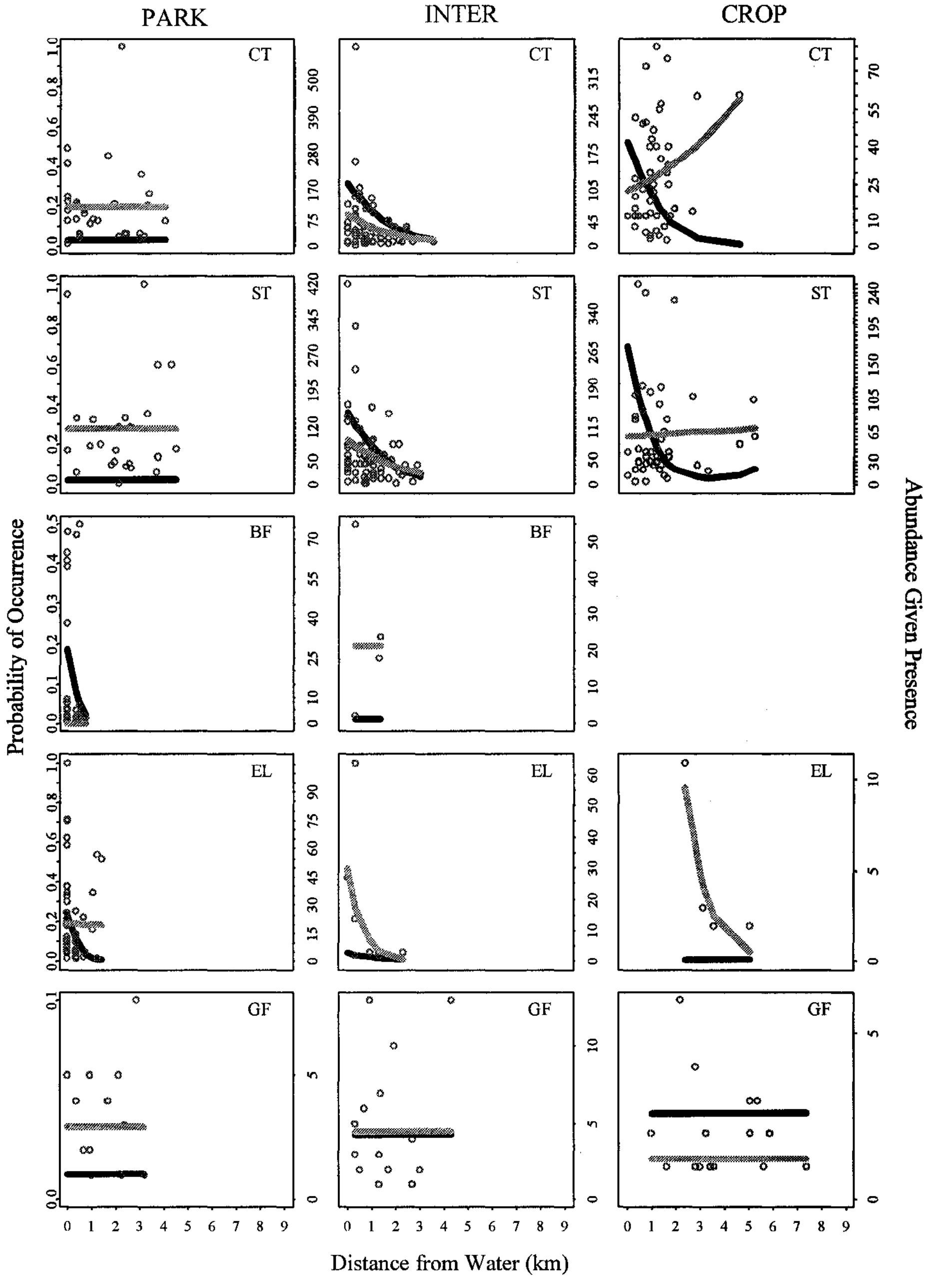


Figure 14a. Two part conditional model of herbivore abundance as a function of distance from water for each of the swamps in the Greater Amboseli study area. Black lines indicate the probability of encountering a group of greater than or equal to one individual at different distances to water. Grey lines are predicted values of the zero truncated negative binomial model of group sizes as a function of distance from water. Open circles are actual abundance data. Species codes from Table 1.

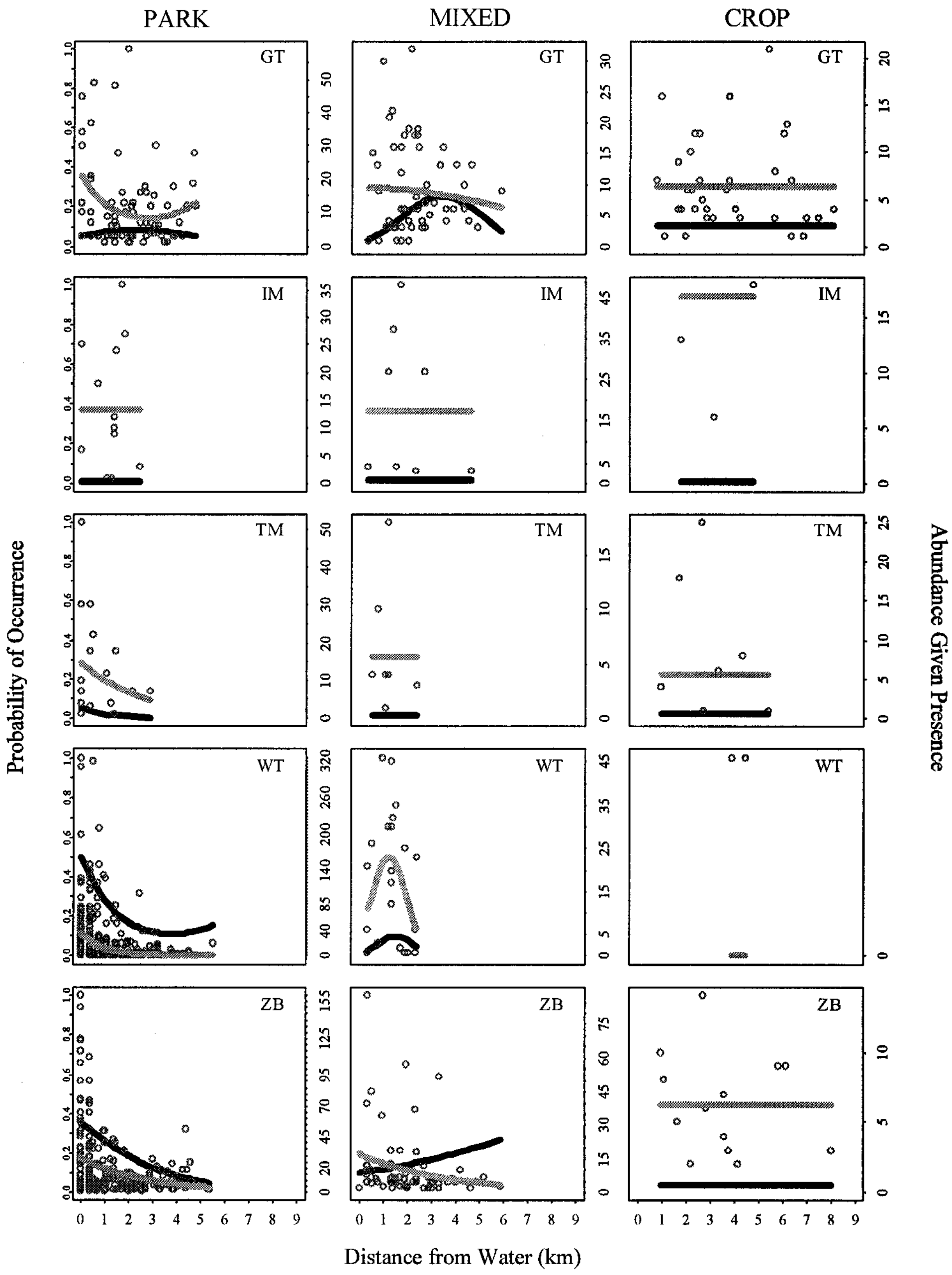


Figure 14b. Two part conditional model of herbivore abundance as a function of distance from water for each of the swamps in the Greater Amboseli study area. Black lines indicate the probability of encountering a group of greater than or equal to one individual at different distances to water. Grey lines are predicted values of the zero truncated negative binomial model of group sizes as a function of distance from water. Open circles are actual abundance data. Species codes from Table 1.

Appendix 1

Appendix 1 Table 1. Total number of groups, number used in DISTANCE calculations, and number per study area by species. Detection functions were calculated for all highlighted species. Species abbreviations are shown in Table 1.

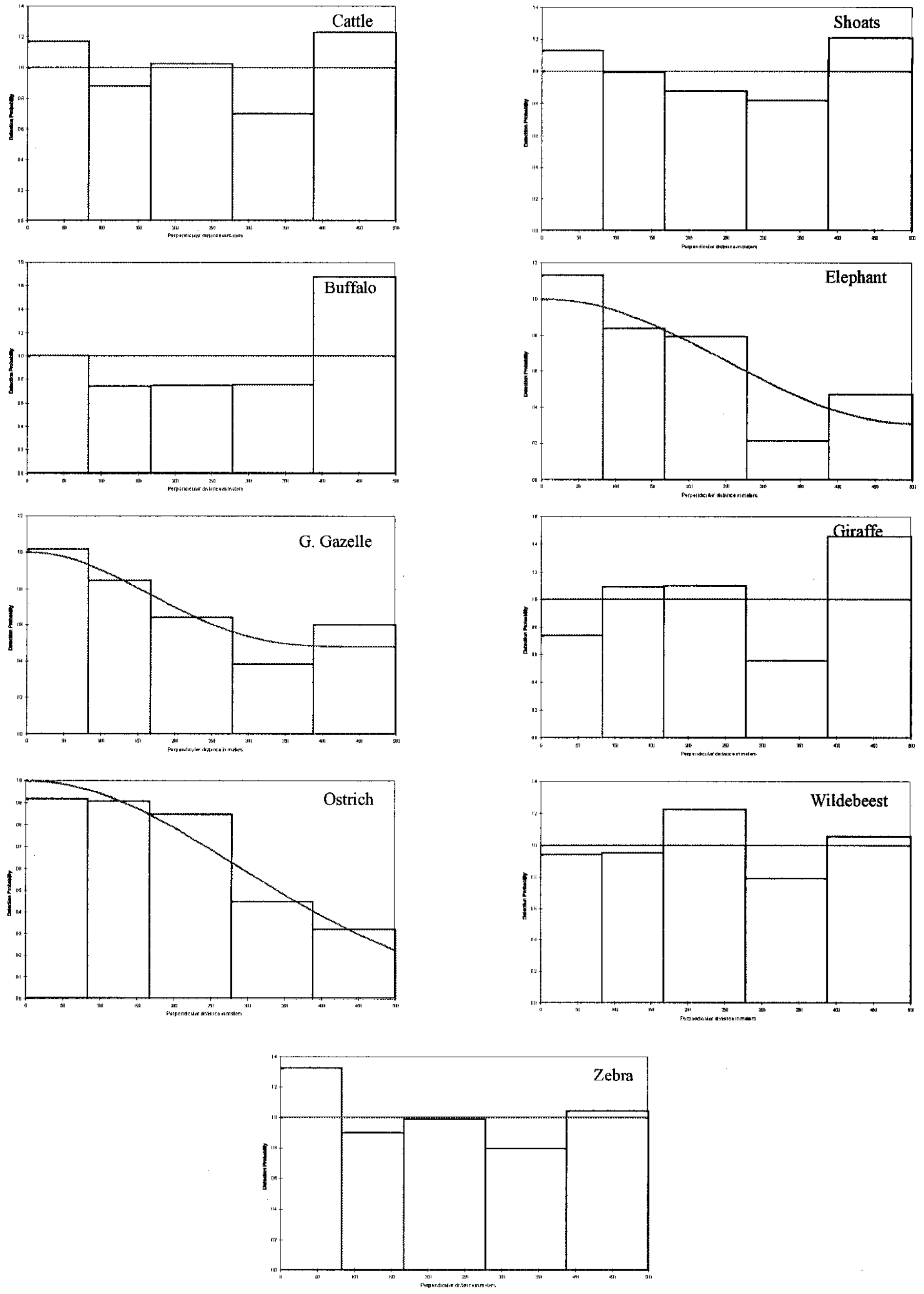
Appendix 1 Table1.

Numbers of Groups - Entire study area				Numbers of Groups - by study area					
All		Used in DISTANCE		Amboseli		Namelok		Kimana	
Species	Number of Groups	Species	Number of Groups	Species	Number of Groups	Species	Number of Groups	Species	Number of Groups
WT	517	ZB	291	WT	489	CT	81	ST	99
ZB	493	WT	287	ZB	392	ST	80	CT	94
CT	225	GT	175	GT	90	GT	48	ZB	82
ST	215	CT	149	EL	76	GF	19	GT	62
GT	200	ST	144	OS	69	ZB	19	WT	26
EL	91	OS	74	CT	50	OS	10	GF	17
OS	85	EL	56	BF	40	TM	8	EL	9
GF	52	GF	49	ST	36	EL	6	IM	8
BF	45	TM	25	TM	18	GK	5	ED	7
TM	33	BF	24	GF	16	IM	3	TM	7
IM	24	IM	23	IM	13	WT	2	GK	6
WH	14	WH	13	WH	11	ED	1	OS	6
GK	12	GK	12	HP	8	HT	1	BF	5
ED	11	ED	9	DK	3			WB	4
HP	9	HP	5	ED	3			DK	3
DK	6	DK	4	OX	2			WH	3
WB	4	WB	3	GK	1			HP	1
OX	2	OX	2						
HT	1	HT	1						

Appendix 1 Table 2. Detection probabilities, CV and lower and upper confidence limits for all species. A value of 1 for detection function indicates that this species had sufficient observations to calculate its own detection function. Species indicated as 0 utilize the most appropriate detection probability based on species similarity in body size and coloration.

Appendix 1 Table 2 .

Species	value	cv	lcl	ucl	Detection Function
Cattle	1.000	---	1.000	1.000	1
Donkey	1.000	---	1.000	1.000	0
Shoats	1.000	---	1.000	1.000	1
Buffalo	1.000	---	1.000	1.000	1
Eland	1.000	---	1.000	1.000	0
Elephant	0.656	0.113	0.523	0.821	1
Gerenuk	0.671	0.113	0.538	0.837	0
Giraffe	1.000	---	1.000	1.000	1
Grant's Gazelle	0.671	0.113	0.538	0.837	1
Hartebeeste	1.000	---	1.000	1.000	0
Hippo	0.656	0.113	0.523	0.821	0
Impala	0.671	0.113	0.538	0.837	0
Lesser Kudu	1.000	---	1.000	1.000	0
Ostrich	0.664	0.108	0.535	0.823	1
Oryx	1.000	---	1.000	1.000	0
Thomson's Gazelle	0.671	0.113	0.538	0.837	0
Waterbuck	1.000	---	1.000	1.000	0
Warthog	0.671	0.113	0.538	0.837	0
Wildebeest	1.000	---	1.000	1.000	1
Zebra	1.000	---	1.000	1.000	1



Appendix 1. Figure 1. Detection functions for individual species. Data was pooled across all Land Use Areas.

CHAPTER 6

CONCLUSIONS AND SYNTHESIS

Rangeland fragmentation in the Greater Amboseli Ecosystem (GAE) has greatly altered pastoral land-use patterns. Subdivision and sedentarization has led to divergent patterns of settlement and an emerging polarization of the landscape into areas of under and over utilization. The concentration of settlement associated with communally managed group ranches, and the dispersion of settlements in private lands have important implications for the creation and maintenance of forage reserves and therefore pastoral mobility at multiple scales. Altered disturbance regimes associated with declines in the dynamism of settlement and movement have important implications for the distribution and abundance of wildlife in rangeland areas. Fragmentation has also altered land-use patterns in the key resource areas of the GAE with important implications for the large herbivore community across the land-use intensity gradient.

In this dissertation I have demonstrated the importance of fragmentation and its effects on pastoral settlement patterns for the structure and function of ecosystems through human induced disturbance regimes and the spatial and temporal patterns of livestock and wildlife utilization. In Chapter 2 I presented evidence that fragmentation has played an important role in shaping the contemporary structure of pastoral interactions with the environment through its impacts on the scale of ecological and social interactions. The interaction of fragmentation and settlement pattern at multiple scales had cascading effects on the spatial and temporal dynamics of Maasai land-use. Through the opportunities and constraints associated with a central place foraging system, these new settlement patterns had important implications for the structure and function of savannas, the creation and maintenance of grazing reserves, and the vulnerability of pastoralists and their livestock to drought.

At the regional scale, national and international constraints on movement and expansion, the excision of key resource areas, land tenure change, and the development of water resources for livestock in previously inaccessible areas initiated a process of rangeland fragmentation and an associated decline in inter and intra-cultural connectivity. Subsequent increases in human and livestock population densities and shifts in broad scale settlement patterns have resulted in the emergence of forage availability, as opposed to forage access as a function of water distribution, as the proximate constraint on livestock production. This, in turn, necessitated a shift from the traditional wet season to a dry season dispersal system, and a corresponding emphasis on preserving dry forage biomass as opposed to maximizing access to ephemeral high quality forage resources.

Within this larger regional context, fragmentation at the landscape level has been exacerbated by further reduction in the scale of land tenure (group ranch adjudication and subdivision) and sedentarization. Changes in the disturbance pattern associated with the creation and abandonment of settlements had important implications for the mosaic of grassland patches in savanna ecosystems. In subdivided areas settlements were widely dispersed across the landscape resulting in a relatively homogeneous distribution of human impacts. In contrast, the communally managed areas took an alternative trajectory in which sedentarization in the context of increasing forage constraints led to a highly clustered pattern of settlement with distinct grazing stages and seasonal movements. Clustered distributions concentrated human disturbance at intermediate distances from water thereby conserving grazing reserves and balancing access to forage and water. Although this may have enhanced control over the spatial and temporal distribution of grazing, it also resulted in a collapse of the dynamic shifting mosaic of abandoned settlements and promoted a polarization of the landscape into over and under utilized areas. The loss of flexibility and dynamism in both scenarios may have important implications for the stability of plant herbivore systems as heterogeneity declines and the shifting mosaic of patches in different states of recovery from settlement and grazing collapses (Coughenour 1991). A longitudinal analysis of settlement patterns in the Eselenkei area indicated that this shift in the spatial patterning of settlements was accompanied by a parallel decline in settlement turnover rates.

At the local level, fragmentation has altered the physical and social structure of settlements. Subdivision and the associated individualization of production has resulted in more numerous smaller settlements with reduced internal social networks. Although settlement ages were found to be generally younger, increasing investments in permanent housing suggests that this was primarily a result of recent subdivision and allocation and that over time settlement ages will increase significantly. Even though settlements were being occupied for increasingly longer periods in the communally managed areas, they continued to act as hubs for linking people and landscapes. These larger multi-family settlements prevent the complete collapse of traditional multi-scale social networks that once linked cultures, sections, landscapes, settlements, and households.

Results from Chapter 3 demonstrated that subdivision and sedentarization reduced mobility at the daily to seasonal time scales, but had unanticipated consequences for inter-annual or drought-induced mobility. Similarly, although there was some evidence that movement increased herder's access to green forage, this was less than expected suggesting that there may be fundamental changes in the nature of mobility in the increasingly constrained rangelands of East Africa. Finally, although there were clear differences in the herd sizes supported under normal conditions in the privately and communally managed systems, the persistence of open access areas and drought mobility in the face of, or possibly because of, subdivision and sedentarization resulted in little difference in the overall number of cattle and proportion of the herd lost to drought, indicating that drought-induced mobility continued to be an important strategy for stabilizing pastoral livestock populations despite increasing fragmentation.

Data presented in Chapter 4 indicated that increasing pastoral land-use intensity, as represented by land privatization and distributed settlement patterns, had important implications for the density, distribution, and structure of the wild large herbivore community. I have shown that species and functional group responses to pastoral land-use intensification at multiple spatial and temporal scales were generally predictable based on body size and feeding ecology. Grazers were most susceptible to competitive exclusion at high levels of pastoral land-use intensity while browsers appeared to exhibit a threshold response to intensification at the landscape scale. Mixed feeders generally appeared to be independent of intensification in keeping with the seasonal adaptability of their diet. Large bodied herbivores all but disappeared under high levels of pastoral land-use. There were important exceptions however, and more in-depth research into the differential responses of large herbivores to direct and indirect pastoral impacts is required. At the settlement level, the spatial distributions of all three of the wild species analyzed here supported the idea that low intensity pastoral land-use may seasonally "facilitate" wildlife utilization of semi-arid savannas. Furthermore, this study demonstrates the importance of high resolution counting and detailed investigations of pastoral wildlife interactions for furthering our understanding of pastoral development and land-use change and its implications for the structure and function of East African savanna ecosystems.

In Chapter 5 I demonstrated that land-use change in the swamps of the Greater Amboseli Ecosystem had a significant impact on the composition and spatial structure of the large herbivore community. These data suggested that spatially limited changes in land-use, ranging from subsistence pastoralism to fine scale cultivation with parallel changes in settlement pattern and intensity, impacted the community and spatial structure of both wildlife and livestock. Not only does the removal of key resources from the "grazing" system have cascading effects on biodiversity and ecosystem resilience, but it also alters fundamentally the interaction of local peoples with their environment (e.g. Newmark et al. 1994). The extreme end of land-use intensification (CROP) demonstrated that the extensive loss of habitat observed in the swamps had an effect that was far larger than their total area would suggest, and while the outlook for wildlife in CROP looked bleak it does suggest that more porous boundaries may offer some hope to both wildlife and livestock. The absence of particular species from the core protected area, in turn, suggested that a balanced approach between protection and human use is essential.

The swamps represent the heart of Amboseli's diversity and dynamism, and the loss of these critical habitats to agriculture at one extreme and the extensive habitat modification due to compression at the other, has potentially far reaching implications for the ecosystem as a whole. This is particularly clear in light of species and functional group responses to distance from water under different land-use intensities. As pastoral land-use intensity increased the combination of increased competition for water and forage resources in its vicinity resulted in the displacement of some species and functional groups thus fundamentally restructuring the spatial patterns of large herbivore utilization. Central to the survival of Amboseli's diversity and abundance is a conservation and development strategy that maintains a flexible system of management that recognizes the role of aridity tolerance, feeding strategy, and body size in mitigating species responses to intensification, and the importance of heterogeneity and key resource areas to the resilience and stability of dynamic ecosystems.

Fragmentation in the Greater Amboseli Ecosystem has impacted Maasai settlement patterns, pastoral mobility, and the abundance, distribution, and diversity of the large herbivore community at multiple scales. Unfortunately, policies that were designed to enhance and stabilize pastoral production in variable environments have created a system that is more constrained and less flexible. This in turn has led to the solidification of a once dynamic disturbance regime associated with the creation, maintenance, and abandonment of pastoral settlements. Ironically, the underlying unpredictability of these systems, the very characteristic that managers seek to control and to limit, may have enhanced their stabilities by increasing spatial heterogeneity, flexible and opportunistic movement, and a diversity of functions on the landscape

(Coughenour 1991). As managers seek to reduce unpredictability and variation through restrictions on mobility, disease prevention, and water provision, pastoralists have had to seek new ways to compensate for the loss of dynamism and movement. In the Greater Amboseli Ecosystem this has been achieved through two divergent strategies, the one involving forage resources conservation and a focus on quantity rather than quality, and the other individualization and privatization. Both strategies have potentially far reaching implications for pastoral vulnerability and ecosystem stability. Ultimately, policy and development interventions in pastoral systems need to embrace heterogeneity and work within the context of fragmentation to enhance the availability of forage in space and time.

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COLORADO STATE UNIVERSITY

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JEFFREY S. WORDEN ENTITLED FRAGMENTATION AND SETTLEMENT PATTERN IN MAASAILAND – IMPLICATIONS FOR PASTORAL MOBILITY, DROUGHT VULNERABILITY, AND WILDLIFE CONSERVATION IN AN EAST AFRICAN SAVANNA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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