



*LUCID's Land Use Change Analysis as an Approach  
for Investigating Biodiversity Loss and Land Degradation Project*

**Land-Use Impacts on Large Wildlife and Livestock  
in the Swamps of the Greater Amboseli Ecosystem,  
Kajiado District, Kenya  
Part 1, Text and Tables**

**LUCID Working Paper Series Number: 27**

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July 2003

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## A. INTRODUCTION<sup>1</sup>

Land-use change and human environmental impacts are widely recognized as essential components of ecosystems (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. While this pressure comes from a variety of different sources and has manifested itself in myriad ways, the most intense change has focused on key resource areas. By definition, key resource areas are fundamental components of spatially and temporally variable arid and semi-arid ecosystems and important determinants of ecological patterns and processes (Illius and O'Connor, 2000), and therefore represent areas of disproportionate vulnerability. Land-use change, and especially change in key resource areas, can have important implications for the structure and function of ecosystems at a variety of scales. Biodiversity is one component of the system that appears to be particularly susceptible to human induced change. Even in the savannas of East Africa, where humans have lived for millennia as important elements of the ecosystem (Western, 1982), relatively focused changes in human land-use in key resource areas have far reaching implications for the ecosystem as a whole.

Land-use change is a dynamic process – increasing and decreasing through time in response to social, political, economic and ecological factors. The land-use patterns we see in the Amboseli Basin 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, both rainfed and irrigated, 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). While the proximate and ultimate causes of change are a consequence of both internal and external drivers at a variety of scales (Campbell et al., 2003) the primary outcome of these interactions has been the loss of rangeland to crop production and conservation. Focusing on the high potential areas on the foot slopes of Kilimanjaro, and more recently on the swamp systems at the base of the catena, the expansion of agriculture and conservation has resulted in the loss of key resources for both pastoralists and wildlife. As calls for the expansion and intensification of agriculture and conservation increase, it is essential that we develop a quantitative understanding of the implications of these changes for both domestic and wild herbivores alike.

The patterns and processes of land use change have received mounting attention in recent years, and while there is no doubt that current rates of change have increased, it is important to recognize that land-use change is part of an historical continuum. Similarly, we maintain that while most land-use change studies focus on uses that result in direct land conversion, land-use change is not a uni-directional process but rather results in a gradient of interactive changes ranging from blanket protection to human dominance. This is particularly true in African landscapes where humans have played a structural and functional role for millennia. For example, the effects of protection, while different in nature, can be just as severe as the effects of human settlement and agriculture (Western and Gichohi, 1993). For this reason we propose to look at land-use not as a one way process of intensification, but rather as bi-directional – with potential for important environmental impacts at both extremes, and at all points along the continuum (Figure 1).

But what does land-use change mean for biodiversity? This is still the overarching question that lies at the center of our understanding of human impacts on ecosystem integrity, and a necessary component of any successful conservation effort. Despite the pressing need for an enhanced understanding of the direct linkages between land-use change, the spatial and temporal scope of these processes and the systems in which they interact and evolve often prevents comprehensive study. This research is an attempt to collect highly resolved spatial data at a landscape scale in the Amboseli system of southern Kenya – an area that represents an unusual opportunity to examine the effects of a local land-use gradient on wildlife and livestock.

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<sup>1</sup> The contents of this paper will form part of the lead author's PhD thesis from Colorado State University.

The Greater Amboseli system is highly dependent on the swamps as a key resource with wild and domestic herbivore species alike relying on the water and forage in the dry season. Indeed, the spatial and temporal heterogeneity in the Amboseli system created by the presence of these key resource areas supports far more biomass than predicted based on rainfall alone (Western, 1973; Coe et al., 1976). While the swamps have played (and continue to play) a crucial role in maintaining the diverse community of wild and domestic herbivores in the system, they are also the focus of intensifying agricultural pressure (Campbell et al., 2003). The combination of high biodiversity and rapid and intense land-use change within a single system represents an ideal opportunity for examining the effects of land-use change on biodiversity and ecosystem function. The Amboseli swamps represent a microcosm of the myriad forces at work in dryland systems across the globe.

Amboseli National Park and its dispersal areas have been the focus of a number of long term ecological (Western, 1973), behavioral (Altmann et al., 1996; Moss, 2000), and social science studies (Campbell, 1984; Campbell, 1999; Campbell et al., 2003). While each of these studies has recognized the human species as an essential component of the ecosystem, there have been few attempts to directly link the extensive land-use change within the swamps to the distribution and abundance of large mammals. This study establishes a baseline for further longitudinal studies of land-use change and its impacts on the Amboseli ecosystem, but is primarily concerned with quantifying and characterizing the nature of land-use and its spatial interaction with both livestock and wildlife on the landscape at high resolution.

In an effort to increase our understanding of the effects of land-use change on biodiversity in dryland systems our research was guided by three central questions:

- 1) What are the underlying land-use differences between the three swamp systems?
- 2) What are the implications of these differences in land-use for the distribution and abundance of species and functional groups across the three sites?
- 3) What are the general distribution patterns of different species in response to water and domestic livestock, and how are these patterns altered by different land-use regimes?

## **B. STUDY AREA AND METHODS**

The Greater Amboseli Ecosystem of southern Kenya is located along the northern base of Mount Kilimanjaro. The ecosystem is centered on a series of swamps running generally east-west at the base of the catena, 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 – Nov-Jan and Mar – May with a total annual mean of about 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). Once a watershed for the Panagani River system of Tanzania, the swamps now represent an essentially closed system with water inputs from ground water and local run-on. The entire water system originally consisted of 6 independent swamps – Enkongu Narok, Longinyie, Namelok, Kimana, Lenkati, and Esoitpus (from West to East). This study focuses on the primary swamps within this larger system – Amboseli (including Enkongu Narok and Longinyie), Namelok and Kimana.

Soils in the swamp basins are predominantly saline orthic Solonetz and Solonchaks in the seasonally flooded lakebeds, with patches of mollic Andosols and haplic Chernozems around the edges and chromic Luvisols on the uplands and foot slopes (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) and Odede (2003).

In order to achieve the primary objective of this research - to explore the impacts of human land-use change on the fine-scale interactions of wildlife, livestock and water in the Amboseli swamp systems - we focused our 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 we divided the study site into three zones representing different degrees of human land-use impacts (Figure 2a). In a space for time substitution, 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. While the protected area of Amboseli National Park does represent 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 zone was defined by a 4 kilometer buffer around the boundary of known swamps identified from topographic maps and satellite imagery (Landsat 7 2000). The AMBOSELI National Park zone is centered on the two primary swamps inside Amboseli National Park (Longenyie and Enkongu Narok), which due to its protected status represents the lowest level of human disturbance. NAMELOK represents the highest level of human impact and is 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 KIMANA which is centered on a multipurpose swamp used for livestock, irrigated agriculture, and wildlife conservation (Kimana Sanctuary). For logistical reasons the actual count area also includes some buffer areas outside of the initial 4km (Table 1). While animals in this system may well 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 that are the focus of this study are played out at much finer spatial scales. 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., in prep).

**Table 1.** The number of sub-blocks (333 x 333 m) at distances from original swamp edge

Distance (km)	ZONE					Total
	Amboseli 1	Namelok 2	Kimana 3	Protected	Not Protected	
-	347	54	99	392	108	500
0	203	39	49	215	76	291
1	182	40	48	189	81	270
1	198	48	56	194	108	302
1	204	52	60	197	119	316
2	259	68	81	243	165	408
2	195	62	71	175	153	328
2	168	61	75	139	165	304
3	211	73	100	169	215	384
3	204	74	101	146	233	379
3	233	82	109	166	258	424
4	184	70	86	122	218	340
4	182	72	86	120	220	340
4	215	90	111	152	264	416
5	144	72	86	108	194	302
5	130	70	85	96	189	285
5	32	20	21	28	45	73
6	-	-	-	-	-	-
Totals	3,291	1,047	1,324	2,851	2,811	5,662

Under ideal conditions each of the study zones (treatments) would be separated in space, independent, and replicated. While 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. In an effort to limit some of the potentially confounding effects related to distance analyses in overlapping spheres (eg Namelok and Kimana zones), while at the same time preserving the spatially extensive character of the data, zonal boundaries were determined 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 is analyzed in relation to the nearest primary factor – in this case the swamps - where zones overlap, the overlapping area was divided after the count with each sub-block being assigned to the closest swamp.

### **B.1. Counting technique**

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

The study area was divided into 1 kilometer transects 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 animals larger than Thomson's gazelle (18 kilograms) were included in the count (Table 2). 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 (Figure 3). These data together with the species, total number, group size, and woody canopy cover within a 50m radius of the center of the herd was then recorded on a hand held tape recorder by the primary observer. In order to limit observer bias, all counts were made by the primary observer with the secondary observer assisting in the locating and photographing of herds larger than 20 individuals. Estimates for groups over 20 were replaced with actual counts from the photographs when applicable. Air speeds, 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 ideal altitude of 100m. In order to fulfill the assumptions of the DISTANCE sampling protocol that require the detection of all individuals on the transect line (Buckland et al., 1993) a GPS Video Camera was fixed to the ultra-light to record a swath directly under the aircraft. We intended to use this video data to confirm that all individuals were observed, as well as to develop a detailed habitat map of the area using digital samples from the tape. Unfortunately, these data were stolen before analysis could begin.

### **B.2. Analyses**

Data were transcribed from the micro-cassettes and then entered in Microsoft Excel and Access. Statistical analyses were conducted with SPSS and graphic output was produced in SPSS and Excel. Distance analyses were conducted in ArcView 3.2a (ESRI). After initially entering the data in Excel it was imported into ArcView for projection and confirmation. The actual study area (while very similar to the initial planned area) was defined by the area within 5 km of the swamp edge that was sampled during the flights (areas which were counted but which have no observations were included). The raw data were aggregated into 1/9 km<sup>2</sup> sub-blocks for analysis.

**Table 2.** Species names, biomass and feeding strategies of animals counted in Amboseli swamp in August 2002

Common Name	Scientific Name	Pop. Weight* (Biomass kg)	Feeding Strategy**	Gen. Feeding Strategy***	Water Depend.****
Buffalo	<i>Cyncerus caffer</i> (L.)	450	G	G	Dep
Cattle	<i>Bos indicus</i> (L.)	180	G	G	Dep
Donkey	<i>Equus asinus</i> (L.)	130	G	G	Dep
Eland	<i>Taurotragus oryx</i> (Pallas)	340	B	M	Ind
Elephant	<i>Loxodonta africana</i> (Blumenbach)	1725	M	M	Dep
Giraffe	<i>Giraffa camelopardis</i> (L.)	750	B	M	Ind
Gerenuk	<i>Litocranius walleri</i>	25	B	M	Ind
Grant's Gazelle	<i>Gazella granti</i> (Brooke)	40	M/B	M	Ind
Hippo	<i>Hippopotamus amphibius</i>	1000	G	G	Dep
Impala	<i>Aepyceros melampus</i> (Lichtenstein)	40	B	M	Dep - Ind
Hartebeeste	<i>Alcelaphus buselaphus</i> (Pallas)	125	G	G	Dep - Ind
Ostrich	<i>Struthio camelus</i>	114	B	M	Ind
Oryx	<i>Oryx beisa</i> (Pallas)	150	G	G	Ind
Shoats	<i>Ovis aries</i> (L.) and <i>Capra hircus</i> (L.)	18	G/M	M	Dep
Thomson's Gazelle	<i>Gazella thomsonii</i> (Gunter)	15	M/G	M	Dep
Waterbuck	<i>Kobus ellipsiprymnus</i>	160	G	G	Dep
Warthog	<i>Phacochoerus aethiopicus</i>	45	G	G	Dep
Wildebeest	<i>Connochaetes taurinus</i> (Burchell)	123	G	G	Dep
Zebra	<i>Equus burchelli</i> (Gray)	200	G	G	Dep

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

\*\* original feeding strategies from Western (1975)

\*\*\* generalized feeding strategies were developed in response to seasonal variability in feeding habits based on descriptions from Estes (1991)

\*\*\*\* water dependency based on Western (1975)

Distance to water was calculated in ArcView from the distribution of water points collected in the aerial count. Water data was collected as the number of points and source type, but was summarized as present/absent for these analyses. We produced 2 water layers in order to differentiate sources that were available to wild and domestic animals. Domestic animals have 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 only have access to open water points, including open water, springs, open troughs, and leaky pipelines.

For the wildlife analyses presented here all “open” water points within wildlife proof fences were excluded. Distances to water at the sub-block level were aggregated into 333 m. classes in keeping with the grain of the study. The distribution of water and shape of the study area resulted in fewer sub-blocks in the more distant classes (Table 3). To limit the effects of small sample area we eliminated all classes with less than 1km sq from the analysis. When results were disaggregated into study zones, the shortest maximum distance to water was used as a limit for all three zones.

The distance of each observation to domestic animals (cattle, donkey, shoats) was calculated with the GIS as well. As with the water analyses, distances were reclassified into 333 m. distance bands for analysis. Distance classes with less than 1 km sq were eliminated from the analysis and the shortest maximum distance was used as a limit for comparisons between zones.

**Table 3.** The number of sub-blocks (333 x 333m) at different distances away from water (layers one and two\*) and livestock in Amboseli, August 2002

Distance to water 2				Distance to water 1				Distance to Domestic			
Distance (km)	Frequency	%	Cumulative %	Distance (km)	Frequency	%	Cumulative %	Distance (km)	Frequency	%	Cumulative %
-	410	7	7	-	413	7	7	-	274	5	5
0	369	7	14	0	381	7	14	0	619	11	16
1	384	7	21	1	408	7	21	1	684	12	28
1	349	6	27	1	382	7	28	1	826	15	42
1	512	9	36	1	569	10	38	1	639	11	54
2	432	8	43	2	506	9	47	2	643	11	65
2	317	6	49	2	389	7	54	2	422	8	73
2	291	5	54	2	372	7	60	2	323	6	78
3	330	6	60	3	423	8	68	3	308	5	84
3	297	5	65	3	376	7	75	3	264	5	88
3	291	5	70	3	344	6	81	3	244	4	93
4	226	4	74	4	239	4	85	4	163	3	96
4	208	4	78	4	209	4	89	4	113	2	98
4	255	5	83	4	236	4	93	4	90	2	99
5	189	3	86	5	162	3	96	5	30	1	100
5	183	3	89	5	132	2	98	5	9	0	100
5	116	2	91	5	69	1	99	5	6	0	100
6	78	1	93	6	38	1	100	6	5	0	100
6	50	1	93	6	12	0	100	6	5	0	100
6	42	1	94	6	2	-	100	Total	5,662	100	
7	40	1	95	Total	5,662	100					
7	38	1	96								
7	39	1	96								
8	37	1	97								
8	34	1	97								
8	35	1	98								
9	30	1	99								
9	26	1	99								
9	24	0	100								
10	13	0	100								
10	11	0	100								
10	6	0	100								
Total	5,662	100									

\* Number of sub-blocks and percent of the study area at distances from water and domestic animals. Distance to water 2 includes only "open" water sources which are accessible to both wildlife and livestock. Distance to water 1 includes all water sources (both "open" and "closed") and represents water available to livestock only. Distances to domestics were calculated using the distribution of cattle, donkeys, and shoats.

## C. RESULTS

### C.1. Spatial Patterns

The spatial distribution of groups across the study area varied significantly by species (Figures 4a-l). The protected areas (Amboseli National Park and Kimana Sanctuary) contained the highest mean biomass density (13,725.81 kg/km<sup>2</sup> for protected areas vs. 4045.18 kg/km<sup>2</sup> for the non-protected areas) and the highest mean species richness (0.34 vs. 0.12 species per sub-block). Domestic livestock (cattle and shoats) were distributed across the area with some groups entering the swamps near human settlements on the periphery of Amboseli, but the highest concentrations occurred in the densely settled areas near Namelok and Isinet. Wild species exhibited variable patterns with wildebeest clustered in the protected areas of Amboseli and Kimana (Figures 4a-l) and zebra more widely distributed across all habitats. Elephants and buffalo, were centered on the protected swamps while impala, giraffe, and Grant's gazelle were relatively evenly distributed across the more wooded southern areas.

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 Kimana than in Amboseli. Large concentrations of settlements (bomas) and agricultural plots (sub-blocks with at least some agriculture) were found in both Namelok and Kimana (Figures 4a and 4b). 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. Dung houses are found in settlements throughout the study area, but grass roofed and tin roofed houses are primarily concentrated in or near the irrigated zones of Namelok and Kimana (Figures 4c and 4d).

## **C.2. Zonal Comparisons**

### *C.2.a. Human Land Use/Impact*

Quantifying the intensity and distribution of human land-use impacts in the swamp systems of the Greater Amboseli Area was one of the primary objectives of this research. To this end we 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. We quantify human land-use impact as a function of four primary variables: house type (type of roofing material used), presence/absence of agriculture, fencing, and domestic animals.

Summary data for the entire study area and each separate zone are presented in Table 4. The Amboseli NP area has the lowest quantifiable direct human impact with 3.6% of the total number of bomas and 15.63% of the total number of houses. Similarly, the types of houses in the Amboseli area are primarily mud and dung (95.9%) while most of the houses in Namelok and Kimana are grass (68.9 % and 65.9%) and tin roofed (33.1% and 18.2%). House type is used as an indicator for sedentarization and the ratio of mud to grass and tin houses (Figure 5) suggests the permanency of human settlement and therefore the intensity of human impact.

The presence or absence of agricultural plots is also an indicator of human impact as well as a quantifiable variable of land-use change. We recorded the presence of agricultural plots and whether they were currently cultivated or fallow. For these analyses all agricultural plots were pooled in order to indicate all areas altered by agricultural practices. Sub-blocks indicated as agriculture contain at least one agricultural field but are not necessarily covered entirely by agriculture. The following area values are based on the area of all sub-blocks containing agricultural plots rather than the actual area of all plots on the ground. While there were no agriculture plots recorded in the Amboseli area, Namelok and Kimana each had 6.69% and 6.42% of their area covered in agriculture (Table 4).

Another indicator of human impact in the Amboseli system is fencing. Fencing data was not collected during the aerial count, but fence distribution is well known and has been recorded elsewhere (Worden unpublished data, Wangui unpublished data). Fences in this area have been designed and constructed to restrict access by wildlife of all sizes ranging from elephants to Thomson's gazelle (periodic failures of the fence allow some animals temporary access to the agricultural areas). The electric fences in Namelok and Kimana 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 Namelok swamp encircles the entire Namelok swamp system except for one in-flowing spring in the southeast. All agriculture in the Namelok area takes place within the protective confines of the fence. In Kimana the fence is centered on the town of Kimana (to the south of our study area) and its associated springs. The Kimana swamp itself, which is the focus of our study, is not currently fenced. The Kimana study area does include a small section of the Kimana town fence, however. The Amboseli study zone contains no agricultural fencing, but does have some small experimental enclosures limiting access to different species. There is also a larger enclosure around the lodges in the center of the park. While significant for research, these fences have little impact on the species composition and distribution within the park and are therefore excluded from this analysis. Fencing summary data is presented in Table 4.

**Table 4.** General Characteristics and Human Impacts in the swamps of Amboseli, August 2002

	Amboseli	Namelok	Kimana	Protected*	Not Protected	Total
Area (sq. km)	365.7	116.3	147.1	316.8	312.3	629.1
Land Use	Protected	Agro-Pastoral	Mixed - Agr-Pastoral/ Protected	Protected	Agro-Pastoral	N/A
Human Impact	Low	High	Intermediate	Low	High	N/A
Fence	No Fences***	Swamp Fenced for agriculture	Swamp not fenced (some non-swamp)	No Fences***	Some agricultural fencing	Mixed
Fenced area (sq km)	-	17.89	5.56	-	23.44	23.44
% of area Fenced	-	15.38	3.78	-	7.51	3.73
Area protected (sq km)	287.00	5.22	24.56	316.80	-	316.80
Percent of area protected	78.49	4.49	16.69	100.00	-	53.30
Area original swamp** (sq km)	39.00	6.00	11.00	43.56	12.00	56.00
Percent of zone covered by original swamp	10.42	5.16	7.48	13.75	3.84	8.90
Area within 3km of original swamp	254.33	68.22	88.56	238.33	172.78	411.11
Percent of area within 3 km of original	65.97	54.54	55.89	72.22	50.62	65.35
Agriculture (% of area covered)	-	6.69	6.42	.70****	4.80	2.74
agriculture	-	59.26	37.37	4.80****	46.30	44.52
Settlement (Boma) Density - no./sq km	0.04	1.87	1.07	0.00	1.24	0.62
Boma Den within 3 km of original swamp	0.05	1.75	0.88	0.02	1.10	0.56
Mud Roof Density (no./sq km)	0.70	0.56	0.77	-	1.39	0.69
Grass Roof Density (no./sq km)	-	4.28	3.19	-	3.10	1.54
Tin Roof Density (no./sq km)	0.03	1.38	0.88	0.01	0.96	0.48
Percent of all house = Mud	95.86	8.99	15.85	-	25.47	25.44
Percent of all houses = Grass	-	68.88	65.92	-	56.94	56.87
Percent of all houses = Tin	4.14	22.13	18.23	100.00	17.59	17.69
Ratio of Mud to Grass and Tin houses	23.18	0.10	0.19	-	0.34	0.34
Domestic animal density (no/km <sup>2</sup> )	19.61	38.16	45.25	18.52	39.70	29.04
Domestic Biomass density (kg/km <sup>2</sup> )	1,965.20	2,489.36	3,640.39	2,050.83	2,862.44	2,453.80
% cattle (by number)	50.24	29.16	38.31	56.63	33.27	40.77
% shoats (by number)	49.05	70.84	61.35	42.50	66.55	58.82
% of total cattle (by number)	48.39	17.37	34.24	44.62	55.38	N/A
% of total shoats (by number)	32.74	29.26	38.00	23.21	76.79	N/A

Protected".

indicator of the extent of swamps in the area prior to changes in land-use

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

\*\*\*\*Agr. in the protected area may be encroachment or inaccurate recording of boundaries on the ground or in the GIS

The final variable in our conceptual model of human impact is domestic livestock. In this study domestic animals are both an independent as well as a response variable. In the context of human impacts, the number, distribution and herd composition of domestic animals has important implications for competition with wildlife. On the other hand, as will be demonstrated in the section on Herbivore Response below, domestic animals also respond to both direct and indirect human induced land-use changes. As a component of the human land-use system, we found that Kimana had the highest overall density (42.3 individuals per km<sup>2</sup>) and biomass density (3640.12 kg/km<sup>2</sup>). Of that total biomass, 85.7% consisted of cattle and 13.7% of shoats. Similarly, Kimana contained 34% of the total number of cattle and 38% of the shoats over the whole study area (summary data see Table 4).

### C.2.b. Herbivore Response

We counted a total of 35,412 individuals of 19 species (3 domestic, 16 wild). Biomass values for each species were calculated based on a population weight (Table 2). All species combined yielded a total biomass of 5,611,376.89 kg, or a total mean biomass density of 8919.69 kg/km<sup>2</sup>. Amboseli had the highest total mean biomass density (11,584.5 kg/km<sup>2</sup>) followed by Kimana (6830.1 kg/km<sup>2</sup>) and Namelok (3185.8 kg/km<sup>2</sup>). Domestic animals contributed 17.0%, 53.3%, and 78.1% to the biomass totals of Amboseli, Kimana and Namelok respectively. Species level totals for the entire counting area, each study zone, and protected and non-protected areas are summarized in Table 5.



Species richness (number of species) was calculated for wild species only. The overall mean species richness (mean number of species per sub-block) was 0.29. A comparison between the zones reveals that Amboseli had the highest mean richness 0.291 followed by Kimana 0.173 and Namelok 0.102 (Figure 6).

All species were allocated to a functional group based on their feeding habits. Typical functional classifications for large herbivores are based on Hofman (1989) with three general categories of grazers, browsers and mixed feeders. Most species, while showing general patterns of forage preference, have the potential for remarkable flexibility under certain circumstances (Estes, 1991). This is especially true of the browsers and mixed feeders who shift feeding preferences in response to the seasonal availability of high quality forage. This variability is particularly important in a highly seasonal system like Amboseli where forage quality is extremely heterogeneous in both space and time. In recognition of this variability and the low number of browsers and mixed feeding species relative to grazers (browsers=5, mixed=4, and grazers=10), the first two categories were lumped into a single mixed feeder class. Species classification was based on Western (1975) with modifications from Estes (1991) ( see Table 2).

Total grazer biomass density (15038.48 kg/km<sup>2</sup>) was higher than that of mixed feeders (6560.95 kg/km<sup>2</sup> and 2358.01 kg/km<sup>2</sup> excluding elephants), and this pattern held through out all zones. Similarly, the biomass density of both grazers and mixed feeders was higher in Amboseli than in either Kimana or Namelok (Fig. 7). While the nature of this decline was consistent between grazers and mixed feeders, mixed feeder biomass density declined more severely between Amboseli and Kimana (43.14% vs 40.11%) with the decline in grazer biomass density marginally more between Kimana and Namelok (53.75% vs 52.44%). Overall, grazer and mixed feeder biomass density declined 72.3% and 73.0% between Amboseli and Namelok respectively.

### **C.3. Distance to Water**

Water is one of the single most important structuring variables in the Amboseli ecosystem (Western, 1975). While 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, 1975; Owen-Smith, 1996; Redfern et al., 2003; Reid et al., 2003). In this study one of our explicit goals was to document the impact of water on the distribution and abundance of different species and functional groups and the role that human land-use plays in mitigating and altering these relationships/interactions.

The distribution and abundance of herbivores over the whole study area in relation to water differed markedly by species (Figures 8a-l). Total mean biomass, total wild and total domestic biomass are all highest near water (Figure 9). At the species level, however, there are important differences in the peak positions of the curves and the magnitude of biomass between species, with two general patterns of water dependence and water independence emerging (classification after Western, 1975).

Water dependence is clearly evident in the distribution of buffalo, elephant, Thomson's gazelle, waterbuck, wildebeest and zebra as well as cattle and donkeys. Other water dependent species such as shoats and warthog show a less defined pattern, but still exhibit a general tendency to occur near water (shoats appear to exhibit an independent pattern which may be a result of the long distances traveled to water in the park – see zonal comparisons below, or possibly may reflect the local Maasai perspective that shoats are essentially water independent). Water independent species, including gerenuk, giraffe, and Grant's gazelle, show no clear association with water (and a possibly negative response from gerenuk). Other independent species such as eland, impala, and ostrich appear to have a slight attraction to water with peaks in the intermediate distances between 1 and 3 kilometers.

Species richness at the level of the entire study area is positively correlated with water (Figure 10). Similarly, mean grazer biomass is considerably higher near water, and decreases sharply to about



2 kilometers from water where it begins to decline less severely (Figure 11a). The mean biomass of mixed feeders shows a similar pattern, with a somewhat sharper decline, if elephants are included (Figure 11b). If we exclude elephants, however, there appears to be no clear association with water (Figure 11c). This lack of water dependence is consistent with the primarily “concentrate selector” (Hofmann, 1989) feeding strategy of these species.

In order to determine the effect of land-use on the herbivore-water relationship we plotted mean biomass density as a function of distance from water for each species, including biomass and functional groups, in each zone (Figs. 12 and 13). While most water independent species such as eland, giraffe and gerenuk show little directional change in their distributions, some species such as Grant’s, impala, and ostrich show a stronger association with water in the Amboseli park area than in Namelok or Kimana. This pattern is even more apparent in the water dependent species such as elephants, Thomson’s, wildebeest and zebra. Plots of the functional aggregations (grazers and mixed feeders) reveal similar trends with markedly higher biomass near water in Amboseli, a slight tendency to occur near water in Kimana, and little or no association with water in Namelok (grazers may even be avoiding water in Namelok).

Similar patterns emerge for species richness and functional group distributions between zones. While species richness in Amboseli reflects the trend of decreasing richness with increasing distance from water observed for the whole study area, in both Namelok and Kimana species richness appears to have no association with distance from water (Figure 13). Grazer biomass also decreases with distance from water in Amboseli and less severely in Kimana, but Namelok reveals a slightly more complicated pattern with slightly higher biomass both close to and farther from water with lower mean biomass at intermediate distances. This may be due in part to competition with cattle that appear to occur primarily at intermediate distances from water in Namelok (Figure 14a). The biomass distribution of mixed feeders, is similar to grazers in Amboseli and Kimana, but appears to be independent of water in Namelok (Fig 14b).

We suggest that the key variable in this differential distribution between the zones is human settlement. Settlement (boma) distributions, while concentrated within the first three kilometers across the entire study area (Figure 15a), reveal a strong tendency to cluster near water in Namelok and slightly less so in Kimana (Fig 15b). Clustering of settlements around water points alters the spatial and temporal structure of the herbivore community, which has important implications for ecosystem function as a result of the differential susceptibility between species to human disturbance.

#### **C.4. Distance to Domestic Animals**

In contrast to settlements (boma), which represent a form of indirect competition through displacement of wildlife, domestic animals have the potential to compete directly with wildlife for resources. One measure of the nature and intensity of the interaction between wildlife and domestic stock is their relative spatial distribution.

We plotted the distribution of all wild species (except for hartebeest and oryx due to small sample sizes), total wildlife biomass density, species richness, and functional groups in relation to domestic animals (cattle, donkeys, and shoats). Total wildlife biomass (Figure 17a) and mean wild species richness (Figure 17b) increase with increasing distance from domestic livestock. Grazers show a similar trend with the highest biomass densities occurring furthest from livestock, but mixed feeders appear to congregate at intermediate distances from domestics (Figure 17c). At the study area level three patterns of individual species distributions emerge (Figure 16). The distribution of gerenuk, Grant’s and impala show little relationship to domestic animals. Wildebeest and especially buffalo and zebra, on the other hand, appear to be actively avoiding livestock. Elephant, giraffe and warthog (and possibly eland, ostrich, and waterbuck) occur at intermediate distances from domestics. The effects of land-use on the spatial interactions of wildlife and domestic animals are apparent when we disaggregate the data into each study zone (Figs 18 and 19). For example, wildebeest appear to only avoid livestock in Kimana where the

permanent presence of settlements and domestic animals may result in direct competition for forage. Zebra on the other hand appear to be avoiding livestock in Amboseli and to a lesser degree Namelok, but occupy intermediate distances in Kimana. While there are some notable exceptions, including the increase in mean species richness at intermediate distances in Kimana (Figure 18a), the general patterns for functional groups (Figures 18b and c) and species level responses (Figure 19) at the study area level appear to hold between zones.

#### **D. 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 Moss personal communications), woodlands (Western and van Praet, 1973), and browsers (Western, personal communication) within Amboseli National Park. While these studies have added to our understanding of population dynamics in the context of ecosystem change, they have only considered one end of the land-use gradient (Fig 1). 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 an impression of the effects of land-use change on biodiversity and the role of humans in modifying ecosystem structure and function emerges.

These data corroborate other studies that suggest that habitat change within Amboseli National Park is impacting biodiversity (Western, personal communication). In particular, biomass densities of mixed feeding species (and especially those that are almost exclusively browsers, eg giraffe and gerenuk) are considerably lower in Amboseli National Park (Table 5). This is almost certainly the result of the massive decline in woodlands within the park boundaries resulting from as yet unequivocally identified 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 National Park alone (excluding the immediate surrounding area included in the Amboseli zone 1), four species from the regional pool sampled in this count are 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 system.

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 elephant. 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 infrastructure on the periphery of the park (Western, 1982) 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) and Kimana, which used to look like a “miniature Amboseli”- that were historically important stepping stones for wildlife between Amboseli and Tsavo and Chyulu National Parks (Western, personal communication)? Namelok currently represents the opposite land-use extreme of intensive human impacts and over 50% of the original swamp converted to agriculture (Table 4). The beginnings of irrigated agriculture were evident in Namelok by 1973, with a major expansion of area under crop production coinciding with a period of intense drought in the early 1980's (Campbell et al., 2003). 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 Amboseli, the browsing end of the mixed feeders (gerenuk and giraffe) have relatively high densities. These water independent 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 (eg. Western, 1989; Tobler et al., 2003) and the loss of ecosystem engineers such as elephants and rhino (van Wjingaarden, 1985; Owen-Smith, 1988; Owen-Smith, 1989; Western and Gichohi, 1993). It is also interesting to note that while Namelok in many ways represents the most human dominated system it does not have the highest livestock biomass density. While this may be an expected pattern in peri-urban and urban environments, the low livestock density relative to that found in Kimana corroborates the hypothesis that the intensification of human land-use in the swamps has negative implications for both livestock and wildlife in 1999.

Kimana is a mixed production system that encompasses elements of pastoral, agricultural, and protected systems. While the spread of cultivation occurred somewhat later in Kimana (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 which 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 Kimana are indicative of larger landscape level patterns. As a microcosm of larger scale patterns Kimana may serve as an indicator of possible outcomes given a heterogeneous mosaic of mixed land-use systems.

As hypothesized, Kimana had intermediate levels of overall biomass. There were some significant exceptions, however, with a number species having higher densities in Kimana – eland, giraffe, gerenuk, grants, hartebeest, impala, and waterbuck. Hartebeest and waterbuck are both rare grazers while the others are relatively water independent mixed feeders. Domestic biomass density was considerably higher in Kimana than in either Amboseli or Namelok. The data we present here does not appear to corroborate the suggestion by Western (1989) that mixed systems support more overall biomass than either livestock or wildlife dominated systems. In a sense, however, Amboseli 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 Amboseli there is still more biomass in the wildlife only system. While there may be lingering effects of livestock in the system (ie their impacts are more than just the sum of their biomass), we feel that this is unlikely considering there low numbers overall. It is also possible that this is a result of the relatively focused nature of our sampling design. We think it more likely that the impacts of high settlement densities combined with agriculture, even at low levels, results in an environment which is sufficiently hostile to wildlife to prevent the realization of the synergistic effects of a strictly livestock/wild system. Indeed, the very nature of land-use intensification in the swamps results in the fundamental alteration of human-wildlife interactions, changing a relatively benign/neutral pastoral relationship to an inherently antagonistic agricultural-wildlife relationship

The interactions of individuals and their environments in space are a central component of landscape ecology. The high resolution aerial counting methodology that we use here stems from over a decade of work in the development of ground based high-resolution techniques (Rainy et al, unpublished data, Reid et al., 2003; Ogotu et al., in prep) in a variety of savanna ecosystems in East Africa. While we are still in the process of refining the aerial methodology it has been

successfully applied to other areas in the Greater Amboseli ecosystem. One of the primary achievements of these high-resolution techniques is the effective elimination of overlap in the detection of domestic and wild species which, because of its ubiquity in coarser resolution studies, prevents a detailed understanding of the interactions between pastoralists, livestock and wildlife (Reid et al., 2001). Similarly, the continuous nature of the data enables us to consider it geographically as map layers in a GIS (Fig 4 a-l) as well as graphically (see distance to water and livestock plots above).

If we consider the map output in Figure 4, the nature and extent of different land-use patterns within the three study zones is clear. Of particular importance to our discussion here is the high density and clustering of agriculture and settlements both within and on the periphery of the swamps in Namelok and Kimana. The intensity of human impact is further indicated by the relative abundance and density of “permanent” structures in the form of grass (and also tin) roofs. As might be expected, domestic animals are primarily found in the vicinity of settlements in both Namelok and Kimana, but it is interesting to note the long distance incursions into Amboseli National Park that occur on a daily basis (personal observation). Fundamental differences in biology are also reflected in the observed distribution of wild species on the landscape. For example, wildebeest and zebra, the dominant grazers in the system, show similar distributions in Amboseli and the Kimana Sanctuary but fundamentally different patterns in the non-protected areas. The absence of wildebeest from the non-swamp and converted areas suggests that their extreme water dependency and preference for intermediate levels of high quality forage (Andere, 1981; Estes, 1991) results in their virtual elimination in the face of intensifying land-use. In contrast, the ability of zebra to utilize relatively high quantity poor quality forage results in their presence on the drier periphery of the study zones at some distance from both water and settlement. It appears that forage requirements as mitigated through competition with livestock over ride the inherent water dependence of zebra at fine spatial scales.

Further indications of the vulnerability of particular species to changes in land-use are apparent in the distributions of Grant’s gazelle, giraffe, impala, buffalo, and elephant. The relative water independence and concentrate selector strategy (preference for high quality forage in relatively low quantities) of grants, giraffe, and impala is evident in their preference for relatively woody habitats in the south of Amboseli and away from the primary settlement areas in Namelok and Kimana. These species appear 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. For these more tolerant species 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. While it appears that grant’s, giraffe, and impala may be less vulnerable to habitat loss associated with the conversion of key resources to agriculture, it is important to note that the resulting change in human attitudes towards wildlife may result in 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 are apparent in the distributions of buffalo and elephant. These two species are primarily found in the protected areas and appear to be particularly vulnerable to land-use intensification. Buffalo are only found in the protected areas. Elephants are more common in protected areas, but are known to be wide ranging and spend significant amounts of time in the non-protected areas. The large body sizes and forage requirements of these species may partially explain their preference for protected areas.

Another possible explanation, however, 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 direct physical damage to people when both depend on 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.

These two species 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 Amboseli. 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 and attitudes as human-wildlife conflicts increase.

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). While the effects of water on community structure at broad spatial scales have been documented (Western, 1975), the responses of herbivores to water at finer spatial scales are less well understood. We suggest that 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 the study area level (all zones combined) the two general patterns of water dependence and independence suggested by Western (1975) are corroborated here with some significant inter species variation. As mentioned above, while most of the water dependent wildlife species are most commonly found near water (eg buffalo, elephant, Thomson's, waterbuck, wildebeest, and zebra) the response of the water independent species is more variable. Collectively, we can summarize these distributions as: 1) attraction, 2) neutrality, 3) intermediate, 4) repulsion and 5) push-pull (Figure 20).

It is important to note that these curves do not necessarily describe an attraction or repulsion for water *per se*, but rather the preference for a suite of characteristics associated with proximity to water in a particular landscape (eg. forage quantity and quality, predation pressure, etc). The water dependent species exhibit some form of curve 1 (except warthog), and the water independent species variations of curves 2 (giraffe and Grant's), 3 (eland and impala), and 4 (gerenuk). Ostriches appear to show some slight attraction to water despite their general water independence. These general responses are similar to those found in the Masai Mara Ecosystem (Ogutu et al., in prep), with some intra species variation and the notable exception of a U-shaped distribution with higher densities both near and far from water (Figure 20).

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 similar patterns of association with water across the greater Amboseli ecosystem, but at much larger spatial scales. With our high spatial resolution counting technique we demonstrate similar patterns at much finer spatial scales revealing some degree of fractal similarity while at the same time suggesting that much of the larger scale pattern is actually driven by very localized interactions between herbivores and water. This characteristic is of particular importance in systems like Amboseli that are dominated by highly vulnerable key resource areas.

The potential implications of human land-use change in these key resource areas is apparent when the relationship between herbivores and water is plotted by study zone, or land-use treatment, independently. A close examination of the graphs in Figure 12 reveals a wide range of species-

specific responses to water as a function of land-use. For example, a number of the water dependent species such as elephant, zebra, and wildebeest exhibit a displacement from areas near water in the mixed and high human land-use zones of Kimana and Namelok. This displacement is also apparent in the functional group responses (Figure 14) with both grazers and mixed feeders showing a higher tendency to be found near water in Amboseli. There appears to be little significant change in the water independent species, with the exception of both Grants' and ostriches, which suggest some minor degree of displacement.

Livestock exhibit similar types of responses to land-use. In particular it is important to note how the preference for areas near water exhibited by livestock in the mixed system (Kimana) is altered under intensive human use (Namelok) and protection (Amboseli). In Amboseli the lack of association with water may be a function of the management of herds as they enter the park for water to avoid congestion at water points, or alternatively may suggest that livestock are drawn to the park for forage as much as for water. In Namelok, the displacement of both shoats and cattle from around water is an indication of the impacts that an intensification of crop production might have on the pastoral system.

The direct impact livestock in Amboseli through vegetation modification (eg. Georgiadis and McNaughton, 1990; Augustine and McNaughton, 1998; Adler et al., 2001) and the redistribution of nutrients represents only part of their total effect on the ecosystem. Another significant impact of livestock is the indirect impact they exert through their influence on the distribution of other species (eg. Boydston et al., 2003; Reid et al., 2003; Ogutu et al., in prep). The distribution patterns of wildlife in relation to livestock in the Amboseli swamps during the dry season of 2002 fall within the same general categories as for water (Figure 20). As with water, however, it is difficult to attribute the observed response to a single factor as it represents a suite of effects and factors such as direct competition for forage, facilitation, convergence in habitat preference, and displacement by herders. While an examination of underlying factors may require experimentation, the implications of these factors as revealed in the spatial associations of livestock and wildlife under different land-use regimes is apparent.

In this paper we have focused on water and livestock as two of the primary variables driving the distribution of livestock and wildlife in the Amboseli system. While this is consistent with research in other areas (eg Maasai Mara) there are some other important variables that may warrant further consideration. The most important one, which we have only touched on here, is the type and distribution of pastoral settlements. Initial analyses of this data set suggested strong edge effects due to known settlements outside of the sampling area and we are currently developing a distribution layer for settlements on the edges of the study area for analysis. Other potentially important variables that require further exploration include habitat variables such as available forage, tree cover, and soil type, as well as infrastructure such as roads, towns, and tourist camps and lodges. We are also in the process of examining the spatial associations between wild species (inter and intra-specific distances). Although a consideration of feeding strategy and water dependence are central to any analysis of herbivore distribution patterns, future analyses based on other species attributes including body size, and its associated biological characteristics such as metabolic and reproductive rates and mobility, reproductive strategies, and susceptibility to poaching and predation are also warranted.

## **E. CONCLUSION**

Land-use change in the swamps of Amboseli has had a significant impact on the composition and spatial structure of the large herbivore community. The data we present here demonstrate how spatially limited changes in land-use - from subsistence pastoralism to small scale cultivation with parallel changes in settlement pattern and intensity - impact the community 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 (eg. Newmark et al., 1994). The salient features of land-use change in the Amboseli swamp system have been on the

one hand, extreme habitat modification due to protection and compression, and on the other an increasing intensification of human impacts in the form of sedentarization, crop expansion, and fence construction. In general, we see that intensification results in a decrease in total biomass, wildlife and livestock biomass, grazer and mixed feeder biomass, and species richness. The grim outlook that this portrays for wildlife in the Amboseli swamps is somewhat mitigated by the impressive density of livestock biomass supported in Kimana, and the reasonable levels of species richness and wildlife biomass supported in the Kimana Sanctuary. While the effects of land-use are clear at both ends of the spectrum, it is important to note that the lack of significant differences in house density and sedentarization as indicated by roof structures, as well as percent of the area cultivated, suggest that the important differences between Namelok and Kimana may be primarily the result of resource excision (fencing) and associated habitat homogenization. Namelok demonstrates that the extensive loss of habitat observed in the swamps has an effect that is far larger than their total area would suggest, and while the outlook for wildlife in Namelok 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 and recognizes both the importance of heterogeneity and the central role of key resource areas to the resilience and stability of dynamic ecosystems.

In summary, we suggest that these spatially focused land-use changes have far reaching implications for both conservation and development, with the following points in particular warranting further consideration:

- both livestock and wildlife are impacted by the loss of key resource areas
- fine scale shifts in species composition and spatial structure associated with human land-use will have impacts across spatial scales
- both extremes of human land-use (protected and converted) result in the homogenization of habitats and herbivore communities
- land-use change fundamentally alters the interactions of pastoralists, livestock and wildlife
- protected areas are essential, but not sufficient, for the conservation of large mammals in the Greater Amboseli Ecosystem

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