



Research Article

## Central-place analysis and modeling of landscape-scale resource use in an East African agropastoral system

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### Abstract

Most spatial models of grazing assume a global search; that is, the entire paddock or landscape is available to grazers. These ‘unconstrained’ models characterize landscape patches based on absolute properties (i.e., without regard for how individual grazers are situated within them). In most of East Africa cattle are herded and must start and end each day’s grazing at their enclosure. Thus, global search is not a realistic assumption. This implies that the relative location of a patch may be more important than its absolute properties because its quality depends not only on the properties of the patch itself, but also on its location relative to home and to water. Using data from 73 full-day herd follows among a group of agropastoralists in western Tanzania, I build and test an unconstrained model and compare its analytical utility and predictive power to a ‘central-place’ model that defines the landscape relative to herders’ homes (the central place) and dry season water. The central-place model provides analytical insights into the grazing system that are not apparent when using an unconstrained model, and it explains more of the variance in grazing intensity. Because many types of resources are collected around a focal point, central-place models should have wide applicability for analyzing and modeling many kinds of resource use, particularly in the developing world.

### Introduction

Identifying the spatial distribution of impacts is a critical first step in understanding how human resource use affects landscape structure (Forman 1995, Shugart 1998). Spatial models provide a means toward this end (Covich 1976, DeAngelis et al. 1985, Baker 1995, Fox et al. 1996), but many models developed in non-human systems neglect key features of human resource use. In this paper, I use spatial data from agropastoralists’ herding in western Tanzania to compare two types of models<sup>1</sup> for analyzing and predicting

landscape-scale distributions of resource use. While the models themselves deal with grazing intensity, the methods can be applied to a variety of resource types, including fuel and hardwood collection, subsistence hunting, and intertidal gathering. The first type, which I call an ‘unconstrained’ model, has been widely used for modeling grazing systems in North America, Europe and Australia. The second type, a ‘central-place’ model, has a long history in geography, economics and ecology (Haggett et al. 1977, Preston 1992) but to my knowledge has never been used to analyze landscape-level distributions of grazing. In the first two sections I discuss the reasons for ana-

<sup>1</sup>I acknowledge that the term *model* can mean both a conceptual approach and a mathematical representation and have attempted to keep these roles distinct. But because both aspects are explored here I should explicitly state that in analyzing land use I use *model* to

mean a conceptual approach, and in predicting spatial distributions of cattle I use *model* to mean a mathematical representation.

lyzing and modeling pastoral herding, give thumbnail sketches of some existing unconstrained models of grazing systems, and present herding systems from the pastoral literature using a central-place perspective. I then use both approaches to analyze half of a data set on herding practices collected among the Sukuma, a group of agropastoralists in western Tanzania. Based on these analyses I build simple, landscape-scale unconstrained and central-place models and test them using the second half of the same data set. I evaluate the models based on their data requirements, their analytical utility and their ability to predict the spatial distribution of grazing. I conclude by discussing the utility of central-place models for understanding pastoral and other resource use systems, particularly in the developing world.

#### *Why model pastoral herding?*

Pastoral systems provide an excellent example of how spatial modeling can help understand the impacts of human resource use. Virtually all pastoral animals are enclosed at night so daily grazing must start and end at their enclosure (Galaty and Johnson 1990). This 'central-place' constraint has two important effects on herding. First, animals cannot simply stay close to good grazing areas as many wild ungulates do (Estes 1991); they must be driven to and from grazing areas each day. This makes monitoring pastoral animals' densities particularly difficult because aerial censuses, which are generally flown in the morning, do not give an accurate picture of cattle distributions at a landscape scale (Peden 1987). Second, for any particular herder, the utility of a patch depends not just on its quantity and quality of forage, but also on its distance from that herder's settlement and location relative to other resources like water. These two factors can strongly influence the distribution of cattle within pastoral landscapes and may be important considerations in analyzing and modeling pastoral grazing systems. Given the difficulties of monitoring the spatial distribution of pastoral grazing, spatial modeling may offer a more useful method for predicting the distribution of grazing and identifying ecological impacts.

The significance of pastoral land use for biological conservation is widely recognized (Brown 1971, Homewood and Rodgers 1984, Arhem 1985, Sinclair and Fryxell 1985, Lindsay 1989, Enghoff 1990, McCabe 1990, Homewood and Rodgers 1991, McCabe et al. 1992, Prins 1992, Western 1994, Little 1996, Ward et al. 1998, du Toit and Cumming 1999). Indeed,

substantial numbers of wildlife use pastoral areas adjacent to Amboseli National Park, Kenya (henceforth 'N.P.', Western 1975, Lindsay 1989, Western 1994), Maasai Mara Reserve, Kenya (Brotten and Said 1995), Serengeti N.P., Tanzania and Ngorongoro Conservation Area, Tanzania (Homewood and Rodgers 1991, Runyoro et al. 1995), Taringire N.P., Tanzania (Lamprey 1964, Borner 1984, Kahurananga and Silkiluwasha 1997), Lake Manyara N.P., Tanzania (Mwalyosi 1992, Newmark 1996), Mkomazi Game Reserve, Tanzania (Eltringham et al. 1998), and Katavi N.P., Tanzania (TWCM 1992, Caro 1999b). Pastoral land use will likely affect these populations and may strongly influence whether protected areas become insularized. Numerous studies have explored the negative effects of insularization on East Africa's protected areas (Miller and Harris 1977, Soule et al. 1979, East 1981, Western and Ssemakula 1981, Burkey 1995, Newmark 1996), but far fewer have examined the land use systems potentially leading to it. Therefore, an understanding of pastoral land use may assist in promoting successful conservation efforts. The salience of these questions extends beyond East Africa as the links between pastoral land use and conservation are important in Asia (Nyerges 1980, Saberwal 1996, Mishra 1997, Casimir and Rao 1998, Fernandez-Gimenez 1999), the Middle East (Meir and Tsoar 1996) and elsewhere in Africa (Obot et al. 1989, Dodd 1994, Ward et al. 1998, du Toit and Cumming 1999, Kepe and Scoones 1999).

#### *Overview of spatial grazing models*

Two types of grazing models are considered here: 'unconstrained' and 'central-place' models. Unconstrained models examine herbivore distributions based on 'absolute' characteristics of the landscape. These may be abiotic factors like slope, aspect, and distance from water, or biotic attributes like vegetation type, palatability, or the density of other species (Coughenour 1991, Bailey et al. 1996). Unconstrained models implicitly assume global search. In other words, foragers are not tied to a specific place, so the entire landscape or paddock is available to them and absolute characteristics are most appropriate. In contrast, a central-place approach defines landscape characteristics relative to key points (central places) which may change for each user. For example, a particular point may be characterized differently by different herders according to its distance from each one's settlement or direction relative to their particu-

lar water source. Thus the critical idea and crux of a central-place approach is that herders from different households may be using the landscape in qualitatively different ways, even though their animals are occupying the same area.

Unconstrained models have been widely used to examine landscape-scale distributions of grazing. Senft et al. (1983, 1985a, 1985b) use regression models to predict cattle distributions, grazing behavior and choice of resting sites. Pickup and Bastin (1997) apply models developed in Australian rangelands (Pickup 1994) to investigate the effects of paddock shape and the locations of water points in influencing cattle distributions. Other studies use unconstrained landscape-scale models to examine foraging behavior (Turner et al. 1993, Percival et al. 1996), patterns of searching behavior (Anderson 1996), and energetics (Moen et al. 1997).

A number of authors (citations below) have dealt qualitatively with the central-place constraint in pastoral herding. Their characterizations of pastoral grazing take four basic forms (Figure 1). All these models were presented as conceptual representations of pastoral grazing, but to date, none has been tested quantitatively. Homewood and Rogers (1991) assume that grazing is distributed evenly within an eight kilometer radius around pastoral settlements (Figure 1a). Note that to achieve an even distribution of grazing across the whole circle, herds must spend a disproportionate amount of time at its edges because the area of a circle increases by the radius squared (Figure 1a, center panel). Note also that use is uniform with respect to direction from home (Figure 1a, right panel). Spencer (1973) describes a situation where each settlement's grazing intensity decreases with distance from home and is skewed toward that settlement's water source (Figure 1c). It is easy to imagine an intermediate situation, shown in Figure 1b, where use declines with distance from home but is not skewed toward or away from water. Flat, linear-decreasing, and curvilinear-decreasing relationships between use and distance from home will all produce this type of pattern (Figure 1b and c, center panels); the three curves shown differ only in the degree to which grazing is concentrated around home. Finally, Western (1975) reports that Maasai herders in the Amboseli basin in Kenya water cattle every second day and use areas in the opposite direction on non-watering days (Figure 1d). Intuitively, these models seem better suited to pastoral grazing, but their assumptions and utility relative to conventional models remain untested.

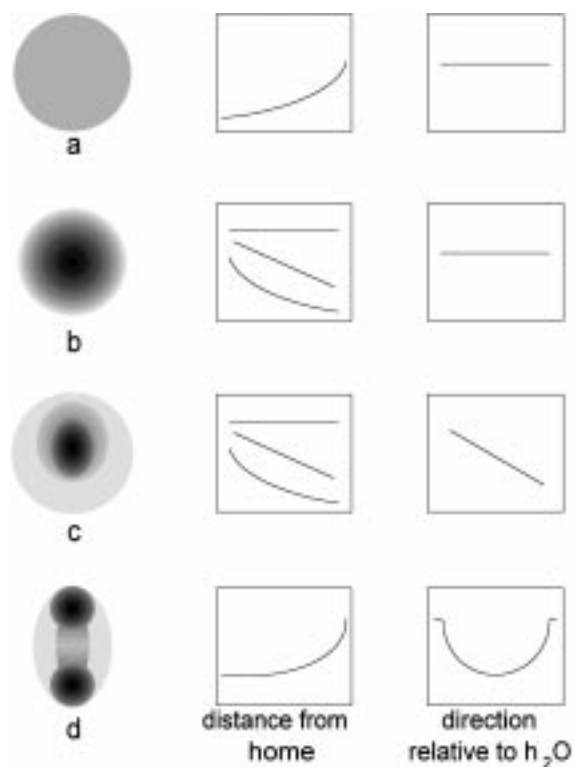


Figure 1. Four Central-place Models of Pastoral Herding. Dark and light areas show high and low grazing intensity respectively. Each settlement is at the center of the circles with its water source directly above. Each distribution is an approximation of a pattern of grazing intensity described in the pastoral literature. The assumptions necessary for each hypothesized distribution in the left column are shown in the panels to the right. The vertical axes in all panels represent use or time spent grazing. The horizontal axes in the center column represent distance from the pastoral settlement and in the right column direction relative to water (ranging from  $0^\circ$  or directly toward water, to  $180^\circ$  or directly away from water). See text for citations and details.

## Study area and data collection

### The Rukwa Valley

Data for this study were collected in the Rukwa Valley, Tanzania (Figure 2). The topography of the Rukwa Valley is mostly flat with some rolling hills reaching elevations around 960 m. Annual precipitation ranges between 600–900 mm and is generally concentrated in a single wet season lasting from early December until early April. Vegetation is a mixture of seasonally flooded grasslands dominated by *Echinochloa pyramidalis*, *Themeda triandra*, and *Sporobolus pyramidalis*, and deciduous Miombo woodlands, dominated by *Brachystegia*, *Julbernardia* and *Acacia* spp. The Rukwa Valley is also an area of high conservation

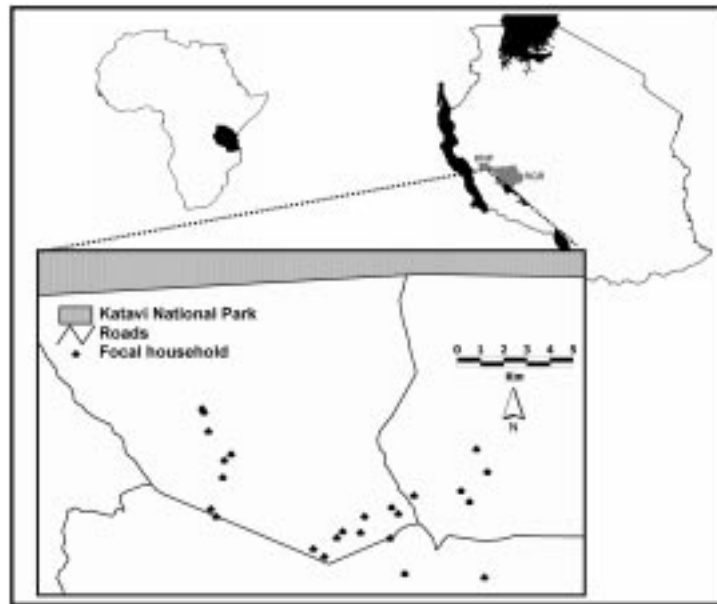


Figure 2. The location of the study area, Katavi National Park (KNP), Rukwa Game Reserve (RGR), and the 24 households included in the study.

value. Home to Katavi National Park, Rukwa Game Reserve, and four contiguous Game Controlled Areas, the Valley supports dense aggregations of large herbivores including buffalo, hippopotamus, elephant, giraffe and a full suite of plains game and carnivores (TWCM 1992, Caro 1999a).

This research was conducted among Sukuma agropastoralists (Abrahams 1967), a Bantu speaking ethnic group who have settled in the Rukwa Valley during the last 25 years. Originally from Shinyanga, Mwanza and Tabora Regions (to the north of Rukwa Region), the Sukuma have spread to every other region in Tanzania (Galaty 1988).

#### *Methods: Data sources*

I constructed a sample of 24 Sukuma households (Figure 2). 'Household' is defined here as an individual herding unit (similar to Dahl and Hjort 1976). Cases where families cultivate separately but herd their animals together are treated as a single household.

To quantify spatial patterns of pastoral land use I recorded the movements of cattle herds from the 24 focal households on 73 full-day herd follows. The primary (adult) cattle herd was followed from the time it was let out in the morning until it was brought home in the evening. I followed each household's herd once during the dry season (September–December 1995), the early part of the wet season (January–early March

1996) and the late part of the wet season (late March–May 1996). 'Herd locations' were recorded (in UTM coordinates) five times per hour using a hand-held global positioning system (GPS) or by interpolating between GPS points. Interpolation assumes that herds move between GPS points in straight lines and at a constant pace, both reasonable assumptions given the frequency of records and the fact that when a herd's pattern of movement changed additional GPS points were recorded. The number of herd locations per unit area reflects the amount of time a herd spent in that area. Throughout the paper I refer to this measure as simply 'grazing intensity.'

All herd locations were entered into a geographic information system (ArcInfo, ESRI, 1997, henceforth: GIS) as text files and referenced according to their distance and compass bearing from home. I also recorded each herd location's direction relative to that household's dry season water source as a value between 0 and 180 degrees (directly toward and away from water, respectively). This allowed every herd location to be plotted on a standardized grid expressing its position relative to that household's home and dry season water source. This standardized coordinate system allows all herd locations to be compared and analyzed collectively.

Data from the relevant sub-section of a 1995 wet season LANDSAT thematic mapper (TM) satellite im-

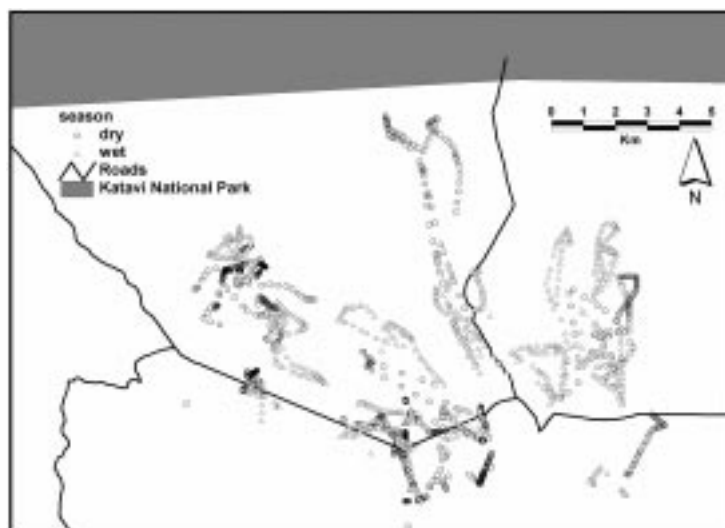


Figure 3. Herd locations observed during dry and wet seasons, plotted in real-world coordinates. Legend as in Figure 2.

age were spatially referenced in ENVI (Environment for Visualizing Images, version 2.5 1996) and imported into the GIS. Vegetation classes were identified based on spectral characteristics and whether or not they occurred within a ‘cultivation mosaic,’ an area where cultivated and regenerating fallow fields dominate the landscape. This mosaic is easily identifiable on the LANDSAT image.

The distribution of all water in the study area was digitized from a 1:50,000 topographic map. Water points actually used by each household were recorded during herd follows. The locations of all cattle-keeping households in the study area were recorded using the GPS.

### Analysis and model building

I split the data set into two halves allocating 12 households to each half. Herding records from the first 12 households were used to derive the parameters for both the unconstrained and central-place models, and data from the other 12 households were used to test the models. To construct the unconstrained model I used absolute landscape attributes (Table 1). For the central-place model I used only relative attributes (Table 2).

#### *Building the unconstrained model*

The unconstrained model is a regression model (Stafford Smith 1988) similar to Senft et al. (1983,

1985a, 1985b). For each 250 m-grid cell in the study area, grazing intensity was calculated as the number of herd locations per unit area. I tested for relationships between grazing intensity and vegetation and landscape characteristics using multiple regression (SPSS, version 7.0, 1995). Individual vegetation classes were tested as categorical variables. I also tested percent woody cover (derived from Pratt et al. 1966), proximity to the nearest settlement ( $1/\text{distance to settlement}$ ) and distance to the nearest water as predictors of grazing intensity (Table 1).

Distance to water was not significantly associated with grazing intensity (Table 1). Of all vegetation classes and percent woody cover, only the cultivated-wooded-grassland class was significantly related to grazing intensity (Table 1). Proximity to the nearest settlement was strongly associated with grazing intensity.

The unconstrained model examines grazing intensity in real-world coordinates only, so herd locations are spread over the entire study area (Figure 3). This meant that relatively few herd locations fell in any given cell, reducing the variation in grazing intensity. Splitting the data set by season would have reduced this variation even further, so a single model was developed for the whole year.

#### *Building the central-place models*

The standardized coordinate system plots all herd locations around a single hypothetical settlement, effectively ‘stacking’ data from different households and

Table 1. Landscape characteristics in the unconstrained model.

Characteristic or vegetation class	Source	<i>P</i> value in unconstrained model
Settlement density	GPS	n.s.
Proximity to nearest settlement	GPS, GIS	$P < 0.0005$
Distance to water	topo map, GIS	n.s.
Dense woodland	LANDSAT TM	n.s.
Dense woodland*	LANDSAT TM	n.s.
Open woodland	LANDSAT TM	n.s.
Open woodland*	LANDSAT TM	n.s.
Wooded grassland	LANDSAT TM	n.s.
Wooded grassland*	LANDSAT TM	$P < 0.001$
Percent woody cover	LANDSAT TM	n.s.

\*Vegetation classes marked with an asterisk were inside the cultivation mosaic (see text for details).

allowing them to be analyzed collectively. This is because each herd location is expressed relative to that herd's home, and all settlement locations lie at the origin in the standardized coordinate system. Recall that these are the same data used to build the unconstrained model, so sample sizes are identical. But because they are stacked, larger numbers of herd locations fall within each cell making it possible to split the data set and still show a general pattern within each season. For this reason I was able to create central-place models for the wet and dry seasons and for both seasons combined.

For each cell in the standardized grid, I recorded distance and direction from the origin (home) and calculated grazing intensity as the number of herd locations in that cell. Assigning each cell the mean of its own and the 8 adjacent cells' values smoothed the grazing intensity data in order to minimize the effects of idiosyncrasies in landscape characteristics. For all central-place models I report both smoothed and unsmoothed results and test all models with like data (i.e., models created with smoothed data are tested on smoothed data).

Next, I used multiple regression to examine the relationships between proximity to home (1/distance to home), direction from home (0 to 180°) and grazing intensity. I also tested for an interaction between distance and direction, which in biological terms, implies that the change in grazing intensity associated with distance from home depends on the direction traveled. Note that proximity to home is not the same as proximity to the nearest settlement used in the unconstrained model. The distinction lies in the fact that proximity to home is calculated using the distance from a herd's location to its own home. Proximity to the nearest

settlement simply uses the distance to whatever settlement is closest to the herd at that moment. The results produced smoothed and unsmoothed models for each season and for both seasons combined (Table 2).

Proximity to home was the strongest predictor variable in the regressions. The direction of water also influenced the distribution of grazing, as direction and the interaction term were often both significant and in no case were they both non-significant (Table 2).

I statistically analyzed the spatial pattern of grazing relative to water by comparing the numerical distribution of directions for standardized herd locations (expressed in degrees from 0–180) with a uniform distribution using a Kolmogorov Smirnov Z statistic. Note that a uniform distribution corresponds to the null hypothesis that the spatial distribution of herd locations (i.e., grazing) is random with respect to water, whereas a departure from uniformity (i.e., a significant K-S Z statistic) indicates that the spatial distribution of grazing is skewed toward or away from water.

## Evaluating the models

### Central-place models

The central-place approach reduces the real-world distribution of herd locations (Figure 3) to the standardized distribution (Figure 4). Visual comparison (Figure 4) and statistical analysis of seasonal patterns of grazing show that the spatial distribution of dry season grazing intensity is skewed toward the dry season water source (K-S  $Z = 8.673$ ,  $P < 0.0005$ ), and wet season grazing is skewed away from it (K-S  $Z = 6.219$ ,  $P < 0.0005$ ).

Table 2. Variables included in the central-place models separated by season and technique.

Season	Smoothing?	Variables	Significance	$r^2$ (adj. $r^2$ )
	smooth	1/distance	$P < 0.0005$	0.842 (0.840)
		direction	n.s.	
		interaction	$P < 0.0005$	
both seasons combined	unsmoothed	1/distance	$P < 0.0005$	0.841 (0.839)
direction		$P < 0.0005$		
interaction		$P < 0.0005$		
dry	smooth	1/distance	$P < 0.0005$	0.826 (0.823)
		direction	$P < 0.0005$	
		interaction	$P < 0.0005$	
dry	unsmoothed	1/distance	$P < 0.0005$	0.708 (0.703)
		direction	$P < 0.0005$	
		interaction	$P < 0.0005$	
wet	smooth	1/distance	$P < 0.0005$	0.784 (0.781)
		direction	n.s.	
		interaction	$P = 0.001$	
wet	unsmoothed	1/distance	$P < 0.0005$	0.798 (0.795)
		direction	n.s.	
		interaction	$P < 0.0005$	

The central-place models were tested in both standardized and real world coordinates. In standardized coordinates, the central-place models derived from the first 12 households were good predictors of grazing intensity around the second 12 households, with  $R$ -squared values ranging from 0.270 to 0.796 (Figure 5). In all cases, smoothing the data increased the amount of variance explained by the model.

So that comparison with the unconstrained model would be valid, the central-place model tested in real-world coordinates was not smoothed and was derived from the whole year. Applying the central-place model to actual settlement patterns and testing it in real-world coordinates, the model explained about 18 percent of the variation in grazing intensity (Figure 6a).

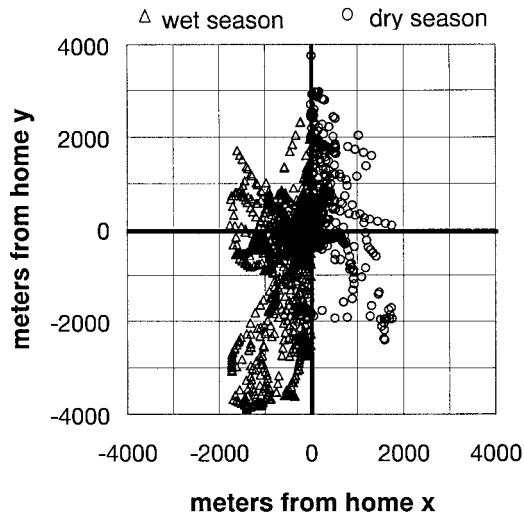


Figure 4. Dry (right) and wet (left) season herd locations plotted using the standardized coordinate system. The pastoral settlement is at the origin and dry season water lies directly above on the vertical axis. Wet and dry season data are plotted on opposite sides of the vertical axis for visual comparison.

#### Unconstrained model

Under the unconstrained model, distance to the nearest settlement and one categorical vegetation variable (wooded grassland in the cultivation mosaic) were significantly associated with grazing intensity (Table 1). This suggests that settlements can be relevant landscape features in predicting grazing intensity. The significance of the categorical vegetation variable suggests that more grazing happens within the wooded grassland portion of the cultivation mosaic. The unconstrained model explained about 15 percent of the variance in grazing intensity (Figure 6b).

## Discussion

#### Biological relevance

What is the biological relevance of these models? The central-place approach shows that of the models presented (Figure 1), Spencer's (Figure 1c 1973) most nearly approximates Sukuma dry-season herding. The wet season situation is a mirror image of Figure 1c, with grazing intensity skewed away from dry season water. Interestingly, this reveals similarities between the Sukuma herding system and other savanna grazing systems. Western (1975) found that wild herbivores in the Amboseli ecosystem in Kenya stayed close to dry season water, but with the first rains (when water

was widely available) they moved away from perennial water to areas with more palatable forage. The seasonal shift in Sukuma herding practices follows this pattern, but because herds are tied to their home settlements, the shift is less extreme. This similarity is especially interesting considering that the Rukwa Valley is much wetter than Amboseli (*ca.* 800 *vs.* *ca.* 200 mm rainfall).

A central-place model of grazing intensity over the whole year, highlights the spatial heterogeneity of grazing intensity in pastoral systems (Figure 7). Analyses of pastoral grazing and its ecological effects may miss important spatial variation if this landscape-scale heterogeneity is ignored (e.g., when stocking rates are calculated for administrative units, Peden 1987). Heterogeneity is also important for ecosystem-level analyses of pastoral systems (Coughenour et al. 1985, Ellis and Swift 1988). Ellis and Swift (1988) argue that temporal variability in cattle numbers can lead to low proportions of net primary productivity being consumed by livestock. The data presented here suggest that landscape-scale heterogeneity in grazing intensity may create spatial variability as well. McCabe (1990) and Conant (1982) describe how social and ecological factors can restrict the distribution of grazing at regional scales. Heterogeneity at both landscape and regional scales may affect savanna biodiversity by providing spatial refugia for species sensitive to pastoral grazing, or by influencing the extent to which pastoral landscapes insularize or connect protected areas.

In the Sukuma system the distribution of grazing is primarily driven by the locations of central places (cattle-keeping settlements). This raises the question of what dictates the location of settlements. Addressing similar questions, Western and Dunne (1979) examined the settlement site decisions of Maasai pastoralists and Schoener (1983) and Covich (1976) provide theoretical predictions for the spacing of central places. The Sukuma, however, cultivate in addition to raising cattle (Abrahams 1967, Brandström 1985) and report that sufficient area and suitable soil for cultivation are the most important characteristics for choosing a site (Borgerhoff Mulder 1995 unpublished data). Thus, by dictating the spacing of central places, arable land and fallowing practices may be the ultimate drivers of grazing intensity.

Central-place models may be useful in other contexts as well. The models built and tested here analyze the Sukuma grazing system and predict the relative distribution of grazing based on the amount of time



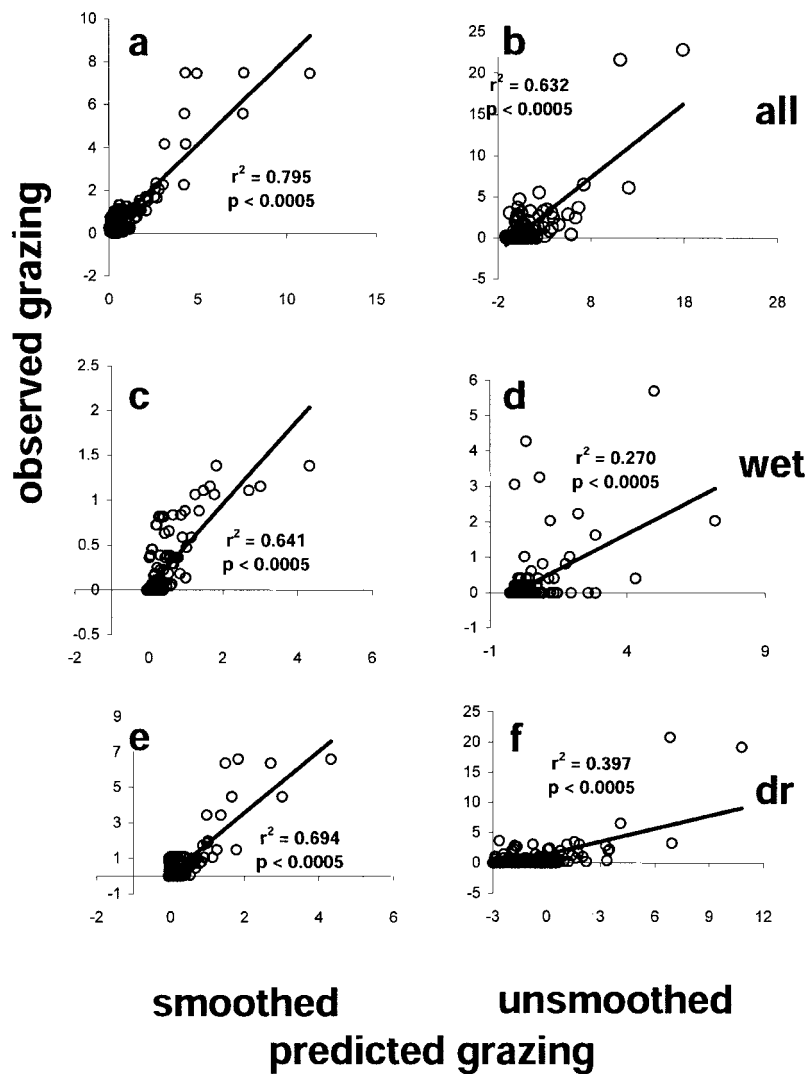


Figure 5. Scatter plots showing the relationships between observed grazing intensity (vertical axes) and grazing intensity predicted by the central-place models (horizontal axes) in standardized coordinates. Panels show smoothed (a, c and e) and unsmoothed (b, d and f) central-place models for both seasons combined (a and b), the dry season (c and d), and the wet season (e and f).

animals spend in different parts of the landscape. They provide only a snapshot of grazing intensity since they have no time dimension. The metric used is simply the number of times herds are recorded per unit area. Presumably, this measure provides an aggregate measure of impacts, including herbivory, trampling or nutrient redistribution (e.g., Turner 1998b, 1998a). More specific measures of impact (e.g., stocking density, grazing pressure or stocking rate *sensu* Coughenour 1991) would only require scaling these values so that the overall mean for one settlement equals the number of animals kept (or tropical livestock units or kilograms of biomass) divided by the area used. There is

also no reason why a central-place model cannot incorporate a time dimension or disaggregate behaviors to explore a particular process in greater depth.

#### *Analytical and predictive utility*

A central-place analysis makes it possible to examine herding days from different settlements collectively. This is important because during a single day, herders use only a portion of the area used over a longer period and patterns are difficult to recognize. However, over many days a general pattern becomes clear. Figure 4 and the statistical analyses demonstrate that

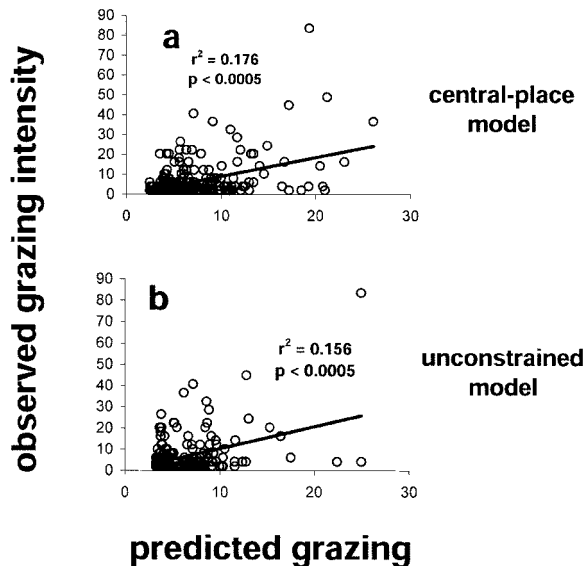


Figure 6. Relationships between observed grazing intensities (vertical axes) and the predicted grazing intensities (horizontal axes) from central-place (a) and unconstrained (b) models in real-world coordinates.

the central-place approach can reveal relatively subtle differences in seasonal patterns of herding even after splitting the data set; this is achieved by ‘stacking’ data from multiple households (and hence, multiple days of herding).

Another advantage of the central-place approach is that it is highly generalizable. Virtually all pastoralists corral their animals at night and have to water them at least infrequently (Hill 1995), so data requirements will not vary between different pastoral groups. This means that central-place models can provide a framework for comparative studies of herding, even in drastically different environments. This is in contrast to regression models (Stafford Smith 1988) which are not comparable across sites (Bailey et al. 1996) or even across seasons (Senft et al. 1985a).

The central-place approach is also flexible. The standardized data presented here are not scaled; the distances from the origin for standardized points are the same as the distance from home for the real-world herd locations. It is possible however, to scale the distances so that the dry season water source lies at (1,0). This would standardize the data to an even greater degree by eliminating the variance introduced by differences in households’ distance to water. Also, impacts and use need not be distributed evenly around the central place. By incorporating directionality and interaction between distance and direction from the central

place, it is possible to analyze or model anisotropic distributions of resource use (similar to ‘expanded distance decay’ parameters for gravity models, Eldridge and Jones 1991).

For this paper I have focused on characterizing the Sukuma herding system as a whole rather than examining variability within the system, but this is not a prerequisite for a central-place analysis. Elsewhere (Coppolillo 2000), I have used a central-place approach to analyze the factors affecting individual households’ herding practices and livestock productivity.

In terms of predictive power, the central-place model was comparable to the unconstrained model in predicting the spatial distribution of grazing intensity in real-world coordinates (Figure 6). Using standardized coordinates however, the central-place model performed far better than the unconstrained model which can only be expressed in real-world coordinates (Figure 5 a–f vs. Figure 6b).

There are however, some disadvantages to a central-place approach. First, data collection may be more difficult, since it is necessary to know where each herd comes from. Thus it may be necessary to follow individual herds for entire herding days or foraging trips, which could slow data collection. With handheld GPS units available for below US\$ 100, it may be possible to use multiple units and teach a number of herders to record their own positions throughout the day. This could facilitate data collection and allow pastoralists themselves to be involved in monitoring and assessment of environmental impacts (e.g., see Lewis 1995). A second disadvantage is that central-place modeling in real-world coordinates requires that each settlement is selected and modeled independently and values from all settlements are summed to produce the aggregate, landscape-scale distribution of grazing. This process is considerably more cumbersome than building an unconstrained model, which can be created in a single step. Finally, while vegetation preferences can be analyzed using a central-place approach (see above) or modeled in real-world coordinates, vegetation types cannot be incorporated into a standardized coordinate system.

The unconstrained model demonstrated that distance to the nearest settlement was significantly associated with grazing intensity, suggesting that settlements are relevant landscape features when predicting grazing intensity even if herds’ home settlements are not identified. The unconstrained approach did not resolve the effects of water availability on grazing;

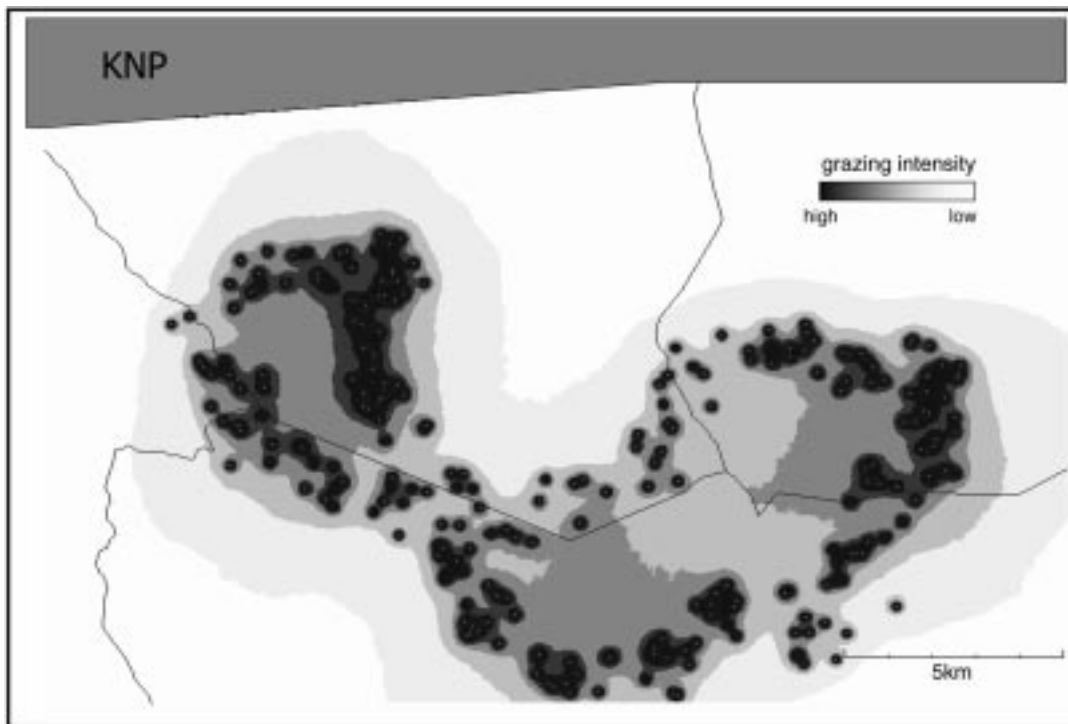


Figure 7. The spatial distribution of grazing intensity over the entire year when a central-place model is applied to every cattle-keeping settlement in the study area. Settlements are shown as tiny white dots. Roads are shown in black. KNP is shaded for consistency with Figures 2 and 3, but is not grazed by livestock.

distance to water was not significantly associated with grazing intensity in the unconstrained analysis. The importance of water is widely recognized in other grazing systems (Coppock et al. 1986, McCabe 1990, Coughenour 1991, Homewood and Rodgers 1991, Bailey et al. 1996), and the seasonal shifts revealed by the central-place approach make it clear that water is important in the Sukuma herding system as well (see also Coppolillo 2000). It appears that the central-place constraint confounded the unconstrained model's ability to resolve this effect.

The unconstrained model was not informative in clarifying the role of vegetation in influencing the distribution of grazing. Of six vegetation classes and the composite measure (percent woody cover), only wooded grassland within the cultivation mosaic was significantly associated with higher grazing intensities in the unconstrained model. This is an unsurprising result given that all the households in the study area fall within this vegetation type. The lack of association with other vegetation characteristics is probably not because herders do not discriminate between vegetation types, but more likely because the central-place constraint restricts their ability to do so. Calculating

preference values for each household by comparing observed use to the availability of vegetation classes around that household, rather than the whole study area, would help clarify this question.

Overall, the central-place model provided analytical insights not apparent using the unconstrained model and more effectively predicted the distribution of grazing intensity. Further, the more modest data requirements make seasonal comparisons and the use of smaller data sets possible and provide a framework for comparative studies of pastoral systems.

#### *When are central-place models appropriate?*

The importance of human dominated ecosystems and the human dimensions of conservation problems are increasingly recognized in landscape ecology and conservation biology (see Forman 1995, Clayton et al. 1997, Forman and Collinge 1997, Terman 1997, Zavala and Burkey 1997, Bignal 1998, Kremen et al. 1998, Lawrence et al. 1998, McIntyre and Hobbs 1999). Spatial modeling can provide the essential link between the anthropogenic processes driving resource use and resultant landscape-level changes. Spatial

models have been used to point to specific areas where anthropogenic impacts are most acute (e.g., Fox et al. 1996), to provide a foundation for decision making (Campbell and Hofer 1995), to evaluate alternative management options (Ellis and Coughenour 1996) and to explore the long-term effects of heterogeneity in resource use (Weber et al. 1998).

The models presented here capture a critical element of pastoral land use: the need to start and end resource collection at a central place. This constraint affects other kinds of resource use, particularly in rural parts of the developing world where most resources are collected locally and on foot. Therefore, central-place models may apply to many types of resources and extraction systems. In cases where search radii are smaller than or equal to the spacing of central places, this approach will offer insights that might otherwise be missed. When resources are clumped or if resource users travel very far from home, a central-place model might not provide any additional information because the assumption of global search is less severely violated.

The models presented here are superficially similar to central-place (Shaffer 1989), gravity (Haynes and Fotheringham 1984, Eldridge and Jones 1991) and diffusion models (Haggett et al. 1977) used in geography and economics. However, they differ in one important respect: the economic and geographic models are primarily concerned with interactions between points. The models presented here deal with the effects of points (pastoralists' settlements and water sources) on surrounding landscape elements. These models also differ from central-place foraging studies which tend to focus on foragers' intake rates (Orians and Pearson 1979, Kacelnik 1984), load sizes (Wetterer 1989, Cuthill and Kacelnik 1990) and processing decisions (Metcalf and Barlow 1992, Bettinger et al. 1997, Bird and Bliege Bird 1997). However, the data collected for all central-place models are relatively similar. Intake rates will likely reflect foragers' location (but see Coppolillo 2000), so the different models should inform each other by focusing on parts of the same process. Thus, coupling the economic, behavioral and spatially-explicit models presented here is possible, and may lead to a more unified central-place framework.

By linking the spatial distributions of use and impacts to individuals' behavior, a 'combined' central-place model would be a powerful tool for understanding spatial patterns of resource use. Equally importantly, because these models capture critical elements

of resource use, they help identify why extraction systems take the forms that they do. This makes it easier to recognize conditions under which resource use may be destructive and helps identify what to do about it. With the growing prevalence of conservation strategies engaging local people (Western et al. 1994, Stevens 1997, Hackel 1999) it is increasingly imperative to monitor and understand human resource use (Kremen et al. 1994, Brandon 1998). Clearly, central-place models can make a contribution to landscape ecology and conservation biology in applied as well as theoretical contexts.

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### References

- Abrahams, R. G. 1967. The Peoples of Greater Unyamwezi, Tanzania. International African Institute, London, UK.
- Anderson, D. C. 1996. A Spatially-Explicit Model of Search Path and Soil Disturbance by a Fossorial Herbivore. *Ecological Modelling* 89: 99–108.
- Århem, K. 1985. Pastoral Man in the Garden of Eden: The Maasai of the Ngorongoro Conservation Area, Tanzania. University of Uppsala, Uppsala, Sweden.
- Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift and P. L. Sims. 1996. Mechanisms that Result in Larger Herbivore Grazing Distribution Patterns. *Journal of Range Management* 49: 386–400.

- Baker, W. L. 1995. Longterm Response of Disturbance Landscapes to Human Intervention and Global Change. *Landscape Ecology* 10: 143–159.
- Bettinger, R. L., R. Malhi and H. McCarthy. 1997. Central place models of acorn and mussel processing. *Journal of Archaeological Science* 24: 887–899.
- Signal, E. M. 1998. Using an ecological understanding of farmland to reconcile nature conservation requirements, EU agriculture policy and world trade agreements. *Journal of Applied Ecology* 35: 949–954.
- Bird, D. W. and R. L. Bliege Bird. 1997. Contemporary Shellfish Gathering Strategies among the Meriam of the Torres Strait Islands, Australia: Testing the Predictions of a Central Place Foraging Model. *Journal of Archaeological Science* 24: 39–63.
- Borner, M. 1984. The Increasing Isolation of Tarangire National Park. *Oryx* 19: 91–96.
- Brandon, K. 1998. Perils to Parks: The Social Context of Threats. *in Parks in peril : people, politics, and protected areas*. Pp. 415–439. Edited by K. Brandon, K. H. Redford and S. E. Sanderson. Island Press, Nature Conservancy, Washington, D.C., USA.
- Brandström, P. 1985. The Agro-Pastoral Dilemma: Underutilization or Overexploitation of Land Among Sukuma of Tanzania. African Studies Programme, University of Uppsala, Uppsala, Sweden.
- Brotten, M. D. and M. Said. 1995. Population trends of ungulates in and around Kenya's Masai Mara Reserve. *in Serengeti II: Dynamics, Management and Conservation of an Ecosystem*. Pp. 169–193. Edited by A. R. E. Sinclair and P. Arcese. University of Chicago Press, Chicago.
- Brown, L. H. 1971. The Biology of Pastoral Man as a Factor in Conservation. *Biological Conservation* 3: 93–100.
- Burkey, T. V. 1995. Faunal Collapse in East African Game Reserves Revisited. *Biological Conservation* 71: 107–110.
- Campbell, K. and H. Hofer. 1995. People and Wildlife: Spatial Dynamics and Zones of Interaction. *in Serengeti II Dynamics, Management and Conservation of an Ecosystem*. Pp. 534–570. Edited by A. R. E. Sinclair and P. Arcese. University of Chicago Press, Chicago.
- Caro, T. M. 1999a. Abundance and distribution of mammals in Katavi National Park, Tanzania. *African Journal of Ecology* 37: 305–313.
- Caro, T. M. 1999b. Densities of mammals in partially protected areas: The Katavi ecosystem of western Tanzania. *Journal of Applied Ecology* 36: 205–217.
- Casimir, M. J. and A. Rao. 1998. Sustainable herd management and the tragedy of no man's land: An analysis of west Himalayan pastures using remote sensing techniques. *Human Ecology* 26: 113–134.
- Clayton, L., M. Keeling and E. J. Milner Gulland. 1997. Bringing home the bacon: A spatial model of wild pig hunting in Sulawesi, Indonesia. *Ecological Applications* 7: 642–652.
- Conant, F. P. 1982. Thorns Paired, Sharply Recurved: Cultural Controls and Rangeland Quality in East Africa. *in Desertification and Development. Dryland Ecology in Social Perspective*. Edited by S. B. and H. S. Mann. Academic Press, London, UK.
- Coppock, D. L., J. E. Ellis and D. M. Swift. 1986. Livestock Feeding Ecology and Resource Utilization in a Nomadic Pastoral Ecosystem. *Journal of Applied Ecology* 23: 573–583.
- Coppolillo, P. B. 2000. The landscape ecology of pastoral herding: Spatial analysis of land use and livestock production in East Africa. *Human Ecology* 28: 527–560.
- Coughenour, M. B. 1991. Spatial Components of Plant-Herbivore Interactions in Pastoral, Ranching, and Native Ungulate Ecosystems. *Journal of Range Management* 44: 530–542.
- Coughenour, M. B., J. E. Ellis, D. M. Swift, D. L. Coppock, K. Galvin, J. T. McCabe and T. C. Hart. 1985. Energy Extraction and Use in a Nomadic Pastoral Ecosystem. *Science* 230: 619–625.
- Covich, A. P. 1976. Analyzing Shapes of Foraging Areas: Some Ecological and Economic Theories. *Annual Review of Ecology and Systematics* 7: 235–257.
- Cuthill, I. C. and A. Kacelnik. 1990. Central Place foraging: A Reappraisal of the 'Loading Effect'. *Animal Behavior* 40: 1087–1101.
- Dahl, G. and A. Hjort. 1976. Having Herds. Pastoral Herd Growth and Household Economy. University of Stockholm, Stockholm, Sweden.
- DeAngelis, D. L., J. C. Waterhouse, W. M. Post and R. V. O'Neill. 1985. Ecological Modelling and Disturbance Evaluation. *Ecological Modelling* 29: 399–419.
- Dodd, J. L. 1994. Desertification and Degradation in Sub-Saharan Africa Livestock. *Bioscience* 44: 28–34.
- du Toit, J. T. and D. H. M. Cumming. 1999. Functional Significance of Ungulate Diversity in African Savannas and the Ecological Implications of the Spread of Pastoralism. *Biodiversity and Conservation* 8: 1643–1661.
- East, R. 1981. Species-Area Curves and Populations of Large Mammals in African Savanna Reserves. *Biological Conservation* 21: 111–126.
- Eldridge, J. D. and J. P. Jones. 1991. Warped Space – a Geography of Distance Decay. *Professional Geographer* 43: 500–511.
- Ellis, J. E. and M. B. Coughenour. 1996. The Savanna Integrated Modeling System. International Workshop on Sustainable Use of Rangelands and Desertification Control, Jeddah, Saudi Arabia.
- Ellis, J. E. and D. M. Swift. 1988. Stability of African Pastoral Ecosystems: Alternate Paradigms and Implications for Development. *Journal of Range Management* 41: 450–459.
- Eltringham, S. K., I. A. Cooksey, W. J. B. Dixon, N. E. Raine, C. J. Sheldrick, N. C. McWilliam and M. J. Packer. 1998. Large Mammals of Mkomazi. *in Mkomazi: The Ecology, Biodiversity and Conservation of a Tanzanian Savanna*. Pp. 485–504. Edited by M. Coe, N. C. McWilliam, G. Stone and M. J. Packer. Royal Geographic Society (with The Institute of British Geographers), London, UK.
- Enghoff, M. 1990. Wildlife Conservation, Ecological Strategies and Pastoral Communities. *Nomadic Peoples* 25–27: 93–107.
- Estes, R. D. 1991. *The Behavior Guide To African Mammals*. University of California Press, Berkeley, USA.
- Fernandez-Gimenez, M. E. 1999. Reconsidering the role of absentee herd owners: A view from Mongolia. *Human Ecology* 27: 1–27.
- Forman, R. T. T. 1995. *Land mosaics : the ecology of landscapes and regions*. Cambridge University Press, Cambridge/New York.
- Forman, R. T. T. and S. K. Collinge. 1997. Nature conserved in changing landscapes with and without spatial planning. *Landscape and Urban Planning* 37: 129–135.
- Fox, J., P. Yonzon and N. Podger. 1996. Mapping Conflicts Between Biodiversity and Human Needs in Lantang National Park, Nepal. *Conservation Biology* 10: 562–569.
- Galaty, J. G. 1988. Pastoral and Agropastoral Migration in Tanzania: Factors of Economy, Ecology and Demography in Cultural Perspective. *in Production and Autonomy*. Pp. 163–183. Edited by Bennett, J. W. and Bower, J. R. Lanham: University Press of America: Society for Economic Anthropology, 1988.
- Galaty, J. G. and D. L. Johnson. 1990. Introduction: Pastoral Systems in Global Perspective. *in The World of Pastoralism: Herding Systems in a Global Perspective*. Edited by J. G. Galaty and D. L. Johnson. Belhaven Press, New York, NY, USA.

- Hackel, J. D. 1999. Community conservation and the future of Africa's wildlife. *Conservation Biology* 13: 726–734.
- Haggett, P., A. E. Frey and A. D. Cliff. 1977. Locational analysis in human geography. Arnold, London, UK.
- Haynes, K. E. and A. S. Fotheringham. 1984. Gravity and Spatial Interaction Models. Sage Publications, Beverly Hills, CA, USA.
- Hill, D. H. 1995. The Cattle and Buffalo of Africa: Management. *Outlook on Agriculture* 24: 155–161.
- Homewood, K. M. and W. A. Rodgers. 1984. Pastoralism and Conservation. *Human Ecology* 12: 431–441.
- Homewood, K. M. and W. A. Rodgers. 1991. Maasailand Ecology: Pastoralist Development and Wildlife Conservation in Ngorongoro, Tanzania. Cambridge University Press, Cambridge, UK.
- Kacelnik, A. 1984. Central Place Foraging in Starlings (*Sturnus vulgaris*): Patch Residence Time. *Journal of Animal Ecology* 53: 283–299.
- Kahurananga, J. and F. Silkiluwasha. 1997. The migration of zebra and wildebeest between Tarangire National Park and Simanjiro Plains, northern Tanzania, in 1972 and recent trends. *African Journal of Ecology* 35: 179–185.
- Kepe, T. and I. Scoones. 1999. Creating grasslands: Social institutions and environmental change in Mkambati area, South Africa. *Human Ecology* 27: 29–53.
- Kremen, C., A. M. Merenlender and D. D. Murphy. 1994. Ecological Monitoring – a Vital Need For Integrated Conservation and Development Programs in the Tropics. *Conservation Biology* 8: 388–397.
- Kremen, C., I. Raymond and K. Lance. 1998. An Interdisciplinary Tool for Monitoring Conservation Impacts in Madagascar. *Conservation Biology* 12: 549–563.
- Lamprey, H. F. 1964. Estimation of the Large Mammal Densities, Biomass and Energy Exchange in the Taringire Game Reserve and Masai Steppe in Tanzania. *East African Wildlife Journal* 1: 1–46.
- Lawrence, D., D. R. Peart and M. Leighton. 1998. The Impact of Shifting Cultivation on a Rainforest Landscape in West Kalimantan: Spatial and Temporal Dynamics. *Landscape Ecology* 13: 135–148.
- Lewis, D. M. 1995. Importance of GIS to Community-Based Management of Wildlife: Lessons From Zambia. *Ecological Applications* 5: 861–871.
- Lindsay, W. K. 1989. Integrating Parks and Pastoralists: Some Lessons from Amboseli. *in Conservation in Africa*. Pp. 149–167. Edited by Anderson, D. and Grove, R. Cambridge University Press, New York, USA.
- Little, P. D. 1996. Pastoralism, Biodiversity, and the Shaping of Savanna Landscapes in East Africa. *Africa* 66: 37–51.
- McCabe, J. T. 1990. Turkana Pastoralism: A Case Against the Tragedy of the Commons. *Human Ecology* 18: 81–103.
- McCabe, J. T., S. Perkin and C. Schofield. 1992. Can Conservation and Development Be Coupled Among Pastoral People: An Examination of the Maasai of Ngorongoro Crater, Tanzania. *Human Organization* 51: 353–366.
- McIntyre, S. and R. Hobbs. 1999. A Framework for Conceptualizing Human Effects on Landscapes and Its Relevance to Management and Research Models. *Conservation Biology* 13: 1282–1292.
- Meir, A. and H. Tsoar. 1996. International Borders and Range Ecology – the Case of Grazing. *Human Ecology* 24: 39–64.
- Metcalfe, D. and K. R. Barlow. 1992. A Model For Exploring the Optimal Trade-Off Between Field Processing and Transport. *American Anthropologist* 94: 340–356.
- Miller, R. I. and L. D. Harris. 1977. Isolation and Extirpations in Wildlife Reserves. *Biological Conservation* 12: 311–315.
- Mishra, C. 1997. Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation* 24: 338–343.
- Moen, R., J. Pastor and Y. Cohen. 1997. A Spatially Explicit Model of Moose Foraging and Energetics. *Ecology* 78: 505–521.
- Mwalyosi, R. B. B. 1992. Influence of Livestock Grazing On Range Condition in South-West Masailand, Northern Tanzania. *Journal of Applied Ecology* 29: 581–588.
- Newmark, W. D. 1996. Insularization of Tanzanian parks and the local extinction of large mammals. *Conservation Biology* 10: 1549–1556.
- Nyerges, A. E. 1980. Traditional Pastoralism and Patterns of Rangeland Degradation. *in Browse in Africa. The Current State of Knowledge*. Pp. 465–471. Edited by H. N. Le Houérou. International Livestock Center for Africa, Addis Ababa, Ethiopia.
- Obot, E. A., M. Oyatogun and M. Wari. 1989. Response of Woody Vegetation of Nwari Grazing Reserve to Utilization by Nomadic Livestock. *Environmental Conservation* 16: 165–169.
- Orians, G. H. and N. E. Pearson. 1979. On the Theory of Central Place Foraging. *in Analysis of Ecological Systems*. Edited by D. J. Horn, R. D. Mitchell and C. R. Stairs. Ohio State University Press, Columbus, OH, USA.
- Peden, D. G. 1987. Livestock and Wildlife Population Distributions in Relation to Aridity and Human Populations in Kenya. *Journal of Range Management* 40: 67–71.
- Percival, S. M., W. J. Sutherland and P. R. Evans. 1996. A spatial depletion model of the responses of grazing wildfowl to the availability of intertidal vegetation. *Journal of Applied Ecology* 33: 979–992.
- Pickup, G. 1994. Modelling Patterns of Defoliation by Grazing Animals in Rangelands. *Journal of Applied Ecology* 31: 231–246.
- Pickup, G. and G. N. Bastin. 1997. Spatial distribution of cattle in arid rangelands as detected by patterns of change in vegetation cover. *Journal of Applied Ecology* 34: 657–667.
- Pratt, D. J., P. J. Greenway and M. D. Gwynne. 1966. A Classification of East African Rangeland. *Journal of Applied Ecology* 3: 369–382.
- Preston, R. E. 1992. Christallers Research On the Geography of Administrative Areas. *Progress in Human Geography* 16: 523–539.
- Prins, H. H. T. 1992. The Pastoral Road to Extinction: Competition Between Wildlife and Traditional Pastoralism in East Africa. *Environmental Conservation* 19: 117–123.
- Runyoro, V. A., H. Hofer, E. B. Chausi and P. D. Moehlman. 1995. Long Term Trends in the Herbivore Populations of the Ngorongoro Crater, Tanzania. *in Serengeti II: Dynamics, Management and Conservation of an Ecosystem*. Pp. 146–168. Edited by A. R. E. Sinclair and P. Arcese. University of Chicago Press, Chicago, IL, USA.
- Saberwal, V. K. 1996. Pastoral Politics: Gaddi Grazing, Degradation and Biodiversity Conservation in Himachal Pradesh, India. *Conservation Biology* 10: 741–749.
- Schoener, T. W. 1983. Simple Models of Optimal Feeding-Territory Size: A Reconciliation. *The American Naturalist* 121: 608–629.
- Senft, R. L., L. R. Rittenhouse and R. G. Woodmansee. 1983. The Use of Regression Models to Predict Spatial Patterns of Cattle Behavior. *Journal of Range Management* 36: 553–557.
- Senft, R. L., L. R. Rittenhouse and R. G. Woodmansee. 1985a. Factors Influencing Patterns of Cattle Grazing Behavior on Shortgrass Steppe. *Journal of Range Management* 38: 82–87.
- Senft, R. L., L. R. Rittenhouse and R. G. Woodmansee. 1985b. Factors Influencing Selection of Resting Sites by Cattle on Shortgrass Steppe. *Journal of Range Management* 38: 295–299.

- Shaffer, R. 1989. *Community Economics: Economic Structure and Change in Smaller Communities*. Iowa State University Press, Ames, Iowa, USA.
- Shugart, H. H. 1998. *Terrestrial ecosystems in changing environments*. Cambridge University Press, Cambridge, UK.
- Sinclair, A. R. E. and J. M. Fryxell. 1985. The Sahel of Africa: Ecology of a Disaster. *Canadian Journal of Zoology* 63: 987–994.
- Soule, M. E., B. A. Wilcox and C. Holtby. 1979. Benign Neglect: A Model of Faunal Collapse in the Game Reserves of East Africa. *Biological Conservation* 15: 259–272.
- Spencer, P. 1973. Nomads in Alliance. *Symbiosis and Growth Among the Rendille and Samburu of Kenya*. Oxford University Press, London, UK.
- Stafford Smith, M. 1988. Modeling: Three Approaches to Predicting How Herbivore Impact is Distributed in Rangelands. New Mexico Agricultural Experiment Station, Las Cruces.
- Stevens, S., Ed. 1997. *Conservation Through Cultural Survival: Indigenous Peoples and Protected Areas*. Island Press, Washington D.C., USA.
- Terman, M. R. 1997. Natural links: naturalistic golf courses as wildlife habitat. *Landscape and Urban Planning* 38: 183–197.
- Turner, M. D. 1998a. Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: 2. Effects of a phosphorus gradient on spatial patterns of annual grassland production. *Journal of Biogeography* 25: 683–694.
- Turner, M. D. 1998b. Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: I. Gradients in the chemical composition of rangeland soils and vegetation. *Journal of Biogeography* 25: 669–682.
- Turner, M. G., Y. Wu, W. H. Romme and L. L. Wallace. 1993. A Landscape Simulation Model of Winter Foraging by Large Ungulates. *Ecological Modelling* 69: 163–184.
- TWCM. 1992. Katavi-Rukwa census, November 1991, Tanzania Wildlife Conservation Monitoring, Arusha, Tanzania.
- Ward, D., B. T. Ngairorue, J. Kathena, R. Samuels and Y. Ofran. 1998. Land degradation is not a necessary outcome of communal pastoralism in arid Namibia. *Journal of Arid Environments* 40: 357–371.
- Weber, G. E., F. Jeltsch, N. Van Rooyen and S. J. Milton. 1998. Simulated Long-Term Vegetation Response to Grazing Heterogeneity in Semi-Arid Rangelands. *Journal of Applied Ecology* 35: 687–699.
- Western, D. 1975. Water Availability and Its Influence on the Structure and Dynamics of a Savannah Mammal Community. *East African Wildlife Journal* 13: 265–286.
- Western, D. 1994. Ecosystem Conservation and Rural Development: The Case of Amboseli. *in* *Natural connections: perspectives in community-based conservation*. Pp. 15–52. Edited by D. Western, R. M. Wright and S. C. Strum. Island Press, Washington D.C., USA.
- Western, D. and T. Dunne. 1979. Environmental Aspects of Settlement Site Decisions among Pastoral Maasai. *Human Ecology* 7: 75–98.
- Western, D. and J. Ssemakula. 1981. The Future of the Savanna Ecosystems: Ecological Islands or Faunal Enclaves? *African Journal of Ecology* 19: 7–19.
- Western, D., R. M. Wright and S. C. Strum. 1994. *Natural connections: perspectives in community-based conservation*. Island Press, Washington D.C., USA.
- Wetterer, J. K. 1989. Central Place Foraging Theory: When Load Size Affects Travel Time. *Theoretical Population Biology* 36: 267–280.
- Zavala, M. A. and T. V. Burkey. 1997. Application of ecological models to landscape planning: the case of the Mediterranean basin. *Landscape and Urban Planning* 38: 213–227.