Long-term changes in Serengeti-Mara wildebeest and land cover: Pastoralism, population, or policies?

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Declines in habitat and wildlife in semiarid African savannas are widely reported and commonly attributed to agropastoral population growth, livestock impacts, and subsistence cultivation. However, extreme annual and shorter-term variability of rainfall, primary production, vegetation, and populations of grazers make directional trends and causal chains hard to establish in these ecosystems. Here two decades of changes in land cover and wildebeest in the Serengeti-Mara region of East Africa are analyzed in terms of potential drivers (rainfall, human and livestock population growth, socio-economic trends, land tenure, agricultural policies, and markets). The natural experiment research design controls for confounding variables, and our conceptual model and statistical approach integrate natural and social sciences data. The Kenyan part of the ecosystem shows rapid land-cover change and drastic decline for a wide range of wildlife species, but these changes are absent on the Tanzanian side. Temporal climate trends, human population density and growth rates, uptake of small-holder agriculture, and livestock population trends do not differ between the Kenyan and Tanzanian parts of the ecosystem and cannot account for observed changes. Differences in private versus state/communal land tenure, agricultural policy, and market conditions suggest, and spatial correlations confirm, that the major changes in land cover and dominant grazer species numbers are driven primarily by private landowners responding to market opportunities for mechanized agriculture, less by agropastoral population growth, cattle numbers, or small-holder land use.

The extent to which conservation areas can successfully coexist with local users in developing countries is hotly debated, as are the conditions for environmental, social, and economic sustainability of any such coexistence (refs. 1–5 and 44). In East African savannas, habitat loss and wildlife decline are widely perceived and generally attributed to rapid population growth and the spread of subsistence cultivation. Directional trends and causal chains are hard to establish in semiarid lands, however, because rainfall, primary production, grazer populations, and vegetation formations show major unpredictable fluctuations between seasons and years. The 100,000-km^2 Serengeti-Mara Ecosystem (SME) serves as a natural experiment allowing analysis of the long-term outcomes of different policies for conservation on the one hand and community development on the other. The SME comprises contrasting land-use zones with different tenure arrangements, ranging from state-controlled "fortress" conservation areas to private and nonprivate tracts with multiple land uses, some with community-based conservation initiatives, superimposed on a rangeland where ecological, microeconomic, and ethnic continuities make it possible to control for many confounding variables. The SME is bisected by the Kenya/Tanzania border, allowing comparative analysis of the implications of contrasting economic, political, and land tenure contexts of Kenya and Tanzania.

Do land-cover changes and associated wildlife changes in East African rangelands vary with differences in land-use orientations (i.e., use policies, tenure, management strategies)? What specific determinants and causal chains (if any) link policy differences to these outcomes? This article analyzes the long-term outcomes of different land-use practices (and policies) on environment, wildlife (e.g., wildebeest as the dominant grazers), demography, and socio-economic conditions in the SME. It summarizes recent changes in the ecosystem (i.e., land cover and wildebeest), examines those factors potentially driving these changes (i.e., rainfall, human population growth, livestock population, socio-economic trends, land tenure, agricultural policies, and market access) and the fine-scale evidence on the determinants of land-use decisions, and provides simple projections of land conversion trends. A conceptual model is offered for analyzing the dynamics of the changes addressed. These tasks are accomplished by integrating in-depth remote sensing, demographic, and socio-economic studies with meta-analysis of existing extensive long-term data sets on wildlife and livestock and with the existing research knowledge of SME community and ecosystem processes.

Contrary to widely held views, rapid land-cover change and wildlife decline are restricted to the Kenyan part of the system. Correlation and causal analyses demonstrate that major changes in land cover and wildebeest numbers are driven primarily by markets and national land tenure policies, rather than agropastoral population growth. Spread of mechanized agriculture, but not agropastoral land use, is associated with the critical spatial location of changes underlying wildebeest decline.

Study Area and Policy Zones

The SME has a conservation core, consisting of the Serengeti National Park (SNP) in Tanzania, continuous with the Masai Mara National Reserve (MMNR) in Kenya (Table 1, Fig. 1). Wildlife tourism is the only land use allowed in these fortress conservation zones. The core areas are surrounded by a ring of buffer zones: inner and outer group ranches (GR) in Kenya; Ngorongoro Conservation Area (NCA), Loliondo Game Controlled Area (LGCA), and Maswa, Grumeti, and Ikorongo game reserves in Tanzania. The Kenyan SME wildlife dispersal areas are privately owned or GR land scheduled for subdivision into private parcels. Private ownership means individual residents can engage in any or all of herding, small-scale farming, mechanized commercial farming, and wildlife tourism enterprises; only hunting is forbidden. Tanzanian game reserves allow only tourism and licensed hunting enterprises, with no settlement. The LGCA allows settlement, cultivation (including mechanized commercial farming), pastoralism, tourism, and licensed hunt-

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Abbreviations: GR, group ranch; SME, Serengeti-Mara Ecosystem; SNP, Serengeti National Park; NCA, Ngorongoro Conservation Area; LGCA, Loliondo Game Controlled Area; MMNR, Masai Mara National Reserve.

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Table 1. Land-use zones and policies in the study area

Country	Zone	Policy	Tenure
Kenya	MMNR	Wildlife tourism and conservation; excludes local land use	County Council Trust
	Inner GRs (Siana, Koiyaki, Ol Choro Oirua, etc.)	Multiple land uses: herding, farming, wildlife tourism	Private plots, some areas are communal property (in trust)
	Outer GRs (Lemek, Nkorinkori etc)	Multiple land uses: mechanized commercial farming, smallholder farming, herding, some wildlife tourism	Privately owned
Tanzania	SNP	Wildlife tourism and conservation; excludes local land use	State controlled
	NCA	Wildlife tourism and conservation; local land use restricted to herding and small-scale farming	State controlled
	LGCA	Herding, small-scale farming, wildlife tourism, hunting leases, mechanized commercial farming	State; registered villages hold title to their land; state allows some private land purchases
	Maswa Game Reserve	Wildlife tourism, hunting leases	State controlled
	Ikorongo Game Reserve	Wildlife tourism, hunting leases	State controlled
	Grumeti Game Reserve	Wildlife tourism, hunting leases	State controlled

ing. The NCA allows settlement, tourism, livestock herding, and small-scale, but not mechanized, cultivation. Tourism, hunting, and mechanized cultivation in Tanzania are state controlled, but despite economic liberalization in 1985, these enterprises remain beyond the reach of most local residents. Most Tanzanian land is state controlled, although some LGCA villages have registered communal title to their land.

Many different community-based conservation initiatives exist throughout the buffer zones; these vary in approach, levels of community participation, and in type and scale of potential returns to communities (ref. 6 and M.T. and K.H., unpublished work). The international border bisecting the SME creates parallel zones of different land-use and conservation orientations linked to different policies and conditions existing in the two countries: Kenya has private land ownership, relatively developed transport and market infrastructure, and strong private enterprise ethos, whereas Tanzania (7) has state ownership and/or common property management of land, poorly developed transport, poor market access, and a centrally controlled economy (8) (Fig. 1, Table 1).

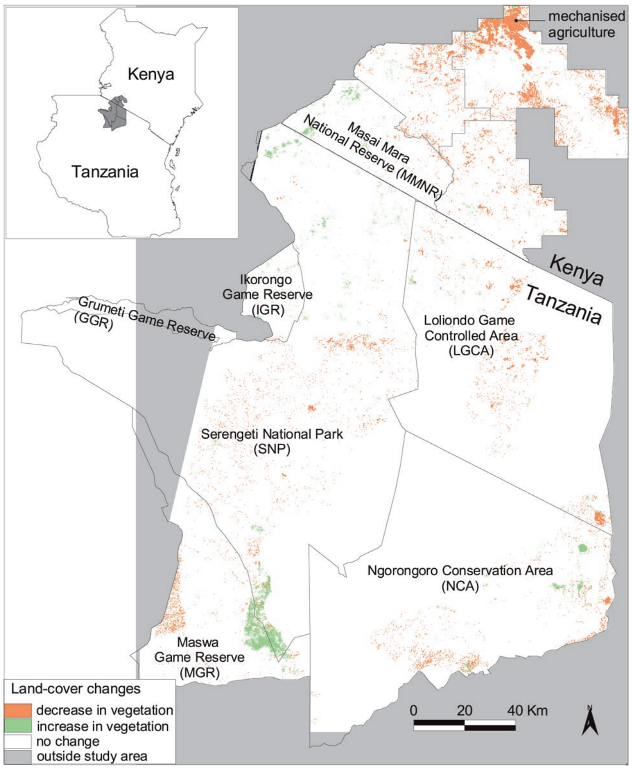

Fig. 1. Land-cover changes in the SME 1975–1995.

Despite an overall rainfall gradient from the dry southeastern plains (500 mm per year) to the wet northwest in Kenya (1,200 mm per year; ref. 9), topography and the influence of Lake Victoria generate such a diversity of local climates that comparable growing conditions and vegetation types are repeated across different zones and on both sides of the border. These range from the seasonally very productive short-grass associations that characterize the Serengeti Plains (and formerly, the Loita Plains in Kenya), to taller stands of grass in wetter areas, grading into bush, thicket, and *Acacia* woodland (9, 10). In addition to these vegetation formations, cultivation ranges from hand- or ox-based small holder to broad stretches of mechanical-based, commercial systems.

The SME is generally taken as the area defined by the movements of the migratory wildebeest (9), covering some 25,000 km^2 centered on the SNP. The present study emphasizes the interdependence of SME ecological processes and outcomes with those in the surrounding buffer zones (Fig. 1). It excludes, however, the western part of the SME, together with the westernmost buffer zones, for two reasons. These areas differ markedly from the rest of the study area in terms in climate, vegetation, buffer zone population composition and density, and importance of poaching (11, 12), and their coverage would require separate satellite imagery. In this article, the terms Kenya SME and Tanzania SME refer to the Kenyan and Tanzanian parts of the study area respectively, and thus include buffer zone areas not necessarily covered in other studies (9) (Fig. 1).

Methods

This study integrates a range of data, methods, and approaches: broad single-round regional to fine-scale intensive multiround survey; land-use policy and economic assessment linked with long-term vegetation and habitat change; human, livestock, and wildlife population data; and information on agropastoralist land-use strategies. Remote sensing, rainfall, and aerial census data quantified ecological dynamics from 1975 to 2000 (13). Landsat time-series data measured the expansion of large-scale wheat and small-holder agriculture, based on a differencing of successive image data and controlling for interannual variability in climate conditions. Wildebeest and livestock trends were calculated from 1960–1990 aerial censuses (datasets made available by Department of Resource Surveys and Remote Sensing, Serengeti Ecological Monitoring Programme, Institute of Resource Assessment/Tanzanian Natural Resources Information Centre, Arusha Conservation Information Centre, and Natural Resources International). Wet-season (November-May) and dry-season (June-October) wildebeest dispersal area rainfall was calculated from monthly rainfall records of 1975–1997. A multivariate regression model of the time series of wildebeest population estimates (12 surveys flown between January and May 1978–1997) against rainfall and livestock was computed for 1978–1997. Before the statistical analysis, all data were detrended and log-transformed to remove nonstationary variance in the series. Further, mean wildebeest density per km^2 was calculated for each sampling unit (5×5 km grid cell) over each period with stable overall population estimates (1978–1979, 1980–1985, and 1986–1997). Mann–Whitney U and Wilcoxon signed-rank tests demonstrated significant differences in wildebeest density among spatial units characterized by different land uses (farming vs. rangeland zones in Loita) in a given period, or in different periods for a given land use or eco-unit (14).

National censuses on human population (Tanzania: 1967, 1978, 1988; Kenya: 1962, 1969, 1979, 1989), demographic and health surveys [1991–1992, 1996 (Tanzania); 1989, 1993, 1998 (Kenya)], national archives, and project literature on conservation and land-use policies defined spatially explicit demographic, policy, and socio-economic information. Multiround surveys of 174 Tanzanian and 288 Kenyan Maasai households, complemented by broader single-round surveys, quantified land-use choices, economic returns, and land conversion to cultivation (M.T. and K.H., unpublished work). Demographic survey established agropastoralist reproductive histories, mortality, fertility, economic factors, settlement size trends, migration, and education [$n = 14,928$ Maasai and 1,545 Maasai households (15) in Narok, Kajiado, and Ngorongoro; socio-economic work gathered comparative data for Loliondo].

Using geographic information system (GIS) techniques, interrelations between biophysical, cultural, socio-economic and political variables, proximate and underlying causes were analyzed for land units and pooled into policy categories (Table 1). Remote sensing and household survey data were linked at the household level. Spatial logistic multiple regression models were built, using as the dependent variable land conversion to mechanized agriculture between 1975–1985 and 1985–1995 and, as independent variables, distance to roads, to the nearest village, to the district capital, and to permanent water, group ranch type, population density in 1979 and 1989, change in population density 1979–1989, agro-climatic zone, elevation, and soil suitability for agriculture (16). A conceptual model of the competition between different land uses was then developed and key relationships were evaluated based on the evidence.

Land Cover and Wildlife Population Changes 1975–2000

Remote sensing analysis shows that land-use changes from 1975 to 1995 were significantly widespread and rapid in Kenya (13). Mechanized farming around MMNR spread from 4,875 ha to a total of 47,600 ha in this time frame (13), concentrated in the Loita Plains. Other land changes in the Kenyan SME include the expansion of settlements of small holders, mostly around the MMNR's gates at Talek, Sekanani, and Aitong, including an increase in the number of Maasai bomas (17) and their associated modifications in vegetation cover, and small-scale maize farming. The last account for at most 13,400 ha, dispersed in small patches around scattered settlements. Rangeland modifications were also detected in the northeastern area of the Kenyan SME. The Tanzanian part of SME showed climate-driven fluctuations and some forest succession, but negligible habitat conversion (Fig. 1). Here the SNP protects the main wildlife migration routes from ecologically significant and ecosystem-scale change. In contrast, most of the dispersal area in Kenya is unprotected.

Most species for which comparable long-term aerial census data are available show rapid decline in Kenya, but not in Tanzania. The total nonmigratory wildlife population in the Kenyan SME declined by 58% in the 1970s–1990s (18). Giraffe, topi, buffalo, and warthog decreased by 73–88%, and waterbuck, Thompson's gazelle, kongoni, Grant's gazelle, and eland by about 60%. Impala, elephant, and ostrich showed no trend in population during the 1970s–1990s (18). By contrast, Serengeti wildlife species witnessed few significant changes. Buffalo and rhino had localized declines (and roan became locally extinct). Topi increased from 1977 to 1991, then declined in 1996. Elephants decreased by 81% between 1970 and 1986 (11), then partially recovered to 53% of their 1970s numbers by the early 1990s (19).

Wildebeest dominate SME wildlife numbers and biomass, and their migrations define the ecosystem. After an initial increase (20), the Tanzanian SME (Serengeti) wildebeest population has fluctuated around 1,227,000 animals since 1977, whereas the Kenyan SME population decreased by 75% over the past 20 years. Serengeti wildebeest are regulated by density-dependent mortality through dry-season food shortage (21, 22). Kenyan SME wildebeest population fluctuations are strongly correlated with both wet- and dry-season Kenya SME rainfall, and therefore with wet- and dry-season food supply (adjusted $R^2 = 0.51$; $P < 0.01$). Can the difference between Serengeti and Kenyan SME wildebeest population trends be attributed to habitat conversion in the Kenyan part of SME? Expansion of mechanized agriculture took place on the wet-season rangelands that were fenced to exclude wildlife. Wildebeest are excluded from their former wet-season range as the area is converted to wheat farming, with the period 1985–1997 showing the most marked decrease in wildebeest density ($Z = -3.34$; $P < 0.001$). Neither temporal nor spatial correlations support the idea that increased competition with cattle directly drives the decline in wildebeest numbers. Other studies suggest disease, predation, and poaching are not major factors either, although poaching may cause local declines (12). The data do not allow comparable levels of analysis for other wildlife species, but the same logic applies. Most Kenyan wildlife populations show a major decline whereas Tanzanian populations do not. Yet, no significant differences in the two areas exist in terms of long-term climate trends, human or livestock population densities or growth rates, or rates of uptake of small-holder agriculture.

For nonmigratory wildlife species, however, the causes of population decline in the Kenyan SME are likely to be more complex and less related to expansion of mechanized farming. Candidate driving forces are droughts, poaching (12), and loss of woody vegetation. For a few species, increase in Maasai settlements (17) may have more than a local effect (R. Reid, personal communication).

Determinants of Land Cover and Wildebeest Changes

Cross-border and policy zone differences in SME land cover and wildebeest population fluctuations were tested against potential driving forces of change, including rainfall, human population growth (natural increase and in-migration), livestock population trends, level of agropastoral well-being (testing the claim that poverty drives degradation), land tenure, and agricultural and market policies. Of these potential explanatory variables, rainfall, Maasai natural population increase, agropastoralist population density, and livestock population trends do not differ significantly between the two countries. Both wet- and dry-season rainfall show high interannual variation but no temporal trend between 1975 and 1997 in either part of the SME. The Maasai are the largest ethnic group living around the SME. Our large demographic survey showed a high Maasai natural increase of 3.9% per annum in both the Kenyan and Tanzanian buffer zones [compare widely cited estimate of 2.2% per annum (23); national rates in each zone, respectively, 2.9%, 3.2%]. Total population growth rate in the Ngorongoro District (Tanzania) (24) was 3.6% per annum in 1978–1988. The Narok District as a whole has twice this rate (6.4% per annum, 1979–1989) (25) due to rapid in-migration of non-Maasai, but not into the MMNR-adjacent areas. The MMNR buffer zone populations are overwhelmingly Maasai (15), with population densities, growth rates, and land use comparable to those round the Serengeti (26).

MMNR buffer zone aerial census data for the wet season indicate no significant change in cattle population from 1977 to 1997. Cattle graze postharvest stubble on large-scale farms. Frequent NCA ground counts show no long-term trend in either cattle numbers or livestock equivalents from the 1970s to 1990s (27, 28). Kenyan buffer zone Maasai are wealthier than those around the Serengeti, with nearly double the livestock equivalents per reference adult (LE.RA^{-1}) (8.21 LE.RA^{-1}, SD = ±4.97, $n = 237$ compare 4.43 LE.RA^{-1}, SD = ±3.09, $n = 137$), more improved (tin-roofed) housing (47.8% of Kenyan compared to 3.6% of NCA Maasai) and more Maasai children 7–12 yr attending primary education (32%; compared to 9% in NCA: national averages, 65.0% and 47.4%, respectively). These differences result partly from NCA conservation policies, but both Kenya and Tanzania Maasai are poorly integrated into national health and education services.

The Kenyan SME buffer zone values for changes in land cover were compared with respect to landscape and socioeconomic variables (29). Multiple logistic regression models show the location of conversion to large-scale wheat farming in the Loita Plains is largely explained by agro-climatic potential (for 1975–1985, $\rho^2 = 0.63$, $n = 20{,}000$: mechanized agriculture is progressively less likely in more arid agro-climatic zones) and proximity to Narok town (16). For 1985–1996 distance to Narok remains important (odds ratio = 0.885, $P = 0.0001$, $n = 20{,}000$), agro-climatic potential becomes less so. Conversely, communication difficulties between Serengeti buffer zones and Mwanza or Arusha constrain marketing in Tanzanian parts of SME (30), despite the presence of potential farmland. In Kenya, cereal prices and imports are high (31); there is significant demand for large-scale mechanized cultivation, and 1973–1974, 1984, and 1993–1994 droughts were followed by rapid reinvestment into mechanized cultivation. In Tanzania, experimental parastatal-sponsored mechanized wheat cultivation trials begun in Loliondo in 1987 were abandoned by 1992. Agricultural conversion was rapid in Kenya during 1980–1985, and even faster during 1985–1995.

Although land and biota changes are more pronounced in the Kenyan than the Tanzanian side of the ecosystem, rainfall, land of agro-ecological potential, human population growth, and livestock population trends display no major difference between countries. Cross-border land tenure and market conditions differ fundamentally and are more likely to explain the observed differences in land cover and wildlife.

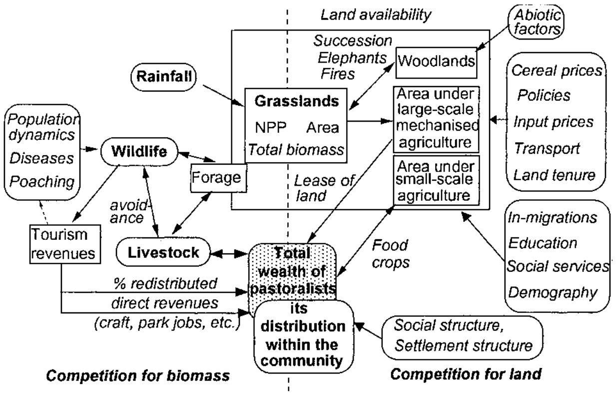

Fig. 2. Conceptual model of land-use dynamics in the SME.

Conceptual Model

The conceptual model set out is developed from a range of theories and prior models, referenced in the outline below, that address different facets of land-cover change in the SME and elsewhere. Empirical and statistical observations of component relationships indicate the validity of the model that analyzes the dynamics of ecosystem change in terms of competition for land and competition for biomass (Fig. 2). The total land area of the ecosystem is in demand for both subsistence and mechanized cultivation (M.T. and K.H., unpublished work), for fuel wood extraction from forests and woodlands, and for grazing for livestock and wildlife (9, 27, 32). These land demands are controlled by biophysical and socio-economic factors, but also compete for limited space. The transition between forest/woodlands and grasslands is driven largely by edaphic factors and disturbances such as fires, heavy browsing by elephants, and natural succession (33–37), although many of these processes have underlying human drivers (38, 39). Foremost among these is land conversion to agriculture (ref. 40 and M.T. and K.H., unpublished work), especially the expansion of broad-scale mechanized farming, which is controlled by agro-climatic potential and economic factors, such as cereal and input prices, access to the market, and transportation costs (16). Kenyan Maasai landowners can lease their land to farmers or cultivate small plots themselves. These decisions are associated with changes in lifestyles, demography, and education.

Wildlife and livestock compete for biomass and access to water and display disease interactions (27, 41). Along with poaching (12), these factors contribute to regulating wildlife population (21, 22). The size of the livestock population is linked to pastoralists' decisions and their wealth. Around conservation areas, however, a significant portion of pastoralist wealth potentially derives from wildlife-related tourism activities (ref. 5 and M.T. and K.H., unpublished work), with redistribution of tourism incomes to adjacent communities (as cash or through the provision of social services) or through park-related incomes (rangers, handicraft industry, vegetable production for or employment in park lodges). A possible tradeoff exists for pastoralists between increasing livestock holdings and maintaining tourist-related incomes through wildlife conservation. Similar tradeoffs have to be made by pastoralists concerning the leasing of their land for mechanized agriculture and the expansion of small-scale cultivation. These complex decisions are influenced by the proportion of total pastoralist income that is (or could potentially be) derived from the different land-use options. Three major factors determine this income composition: (*i*) who decides and benefits from different land-use activities; (*ii*) the natural and cultural landscape attributes of different locations that influence land use (14) (agro-climatic potential, access to markets, roads and water, proximity to high wildlife density areas); and (*iii*) policies that encourage, exclude, restrict, or give a comparative advantage to some land uses (e.g., agricultural subsidies, cultivation bans, redistribution of tourism revenues, improvement of transportation infrastructure, provision of social services, land tenure). Policy instruments in particular affect

Table 2. Economic returns from main land uses and for different socio-economic groups

Activity	GR member ($/household/year per 100 acres)	Elite (GR leaders; local, district or national officials; politicians and outside entrepreneurs) ($/household/per year per 100 acres)
Conservation-compatible uses		
Livestock	530	530
Small-scale cultivation + farming association	51 + 103	548 + 103
Tourism: campsite + GR Wildlife Association (WA) + elite WA + lodge shares	276 + 126 + 0 + 0	7,294 + 3,500 + 3,638 + 3,976
Total conservation compatible uses	1,205	19,589
Large-scale cultivation (lease)	2,444	2,444
Large-scale cultivation (own)	—	14,964

Conservation-compatible uses (livestock, small-scale cultivation, game viewing) allow retention of wildlife habitat in the SME wet-season dispersal area. By contrast large-scale cultivation entails permanent conversion to land cover incompatible with wildlife persistence.

the decision-making process of agropastoralists and, therefore, modify land-use changes and their impacts on the ecosystem. The three factors above lead to considerable spatial variability in preferred land-use options, as manifested both on the remote sensing images and by fine-scale socio-economic surveys.

Socio-Economic and Spatial Factors in Local Decisions over Land Use

The great majority of Maasai around the SME have taken up cultivation over the last 10 years. Despite great intersite variability, 88% of Tanzanian Maasai households and 46% of the Kenyan currently cultivate [$n = 1{,}545$ households (15); 10 years ago 2% and 19%, respectively]. Land tenure and policy restrictions, however, result in few mechanized cultivation opportunities for the Maasai in the Tanzanian buffer zone. Maasai NCA farm sizes are similar to Kenya hand-hoe areas (0.86 ha, SD = ±0.71, $n = 67$), but hectarage is significantly larger in LGCA and Kenya GRs (2.92 ha, SD = ±2.01, $n = 64$; $P < 0.001$) where other techniques (animal draught and tractor) are allowed. Maasai wheat areas in Loita Plains commercial farms average 4.44 ha (SD = ±3.49, $n = 27$). Households close to protected areas may receive tourism incomes (Talek 86.4%, NCA 12%, LGCA 3%). These earnings can be significant in the case of some Kenyan SME Maasai households (M.T. and K.H., unpublished work), but are rarely the principle income (NCA 0.2%, Narok 1.3%). There is no evidence that greater income from tourism and larger livestock holdings (relative to Tanzania) translate into increasing total livestock populations around the MMNR.

Both potential revenues and actual land-use strategies differ between Maasai households according to socio-economic factors. A statistical clustering of 278 Kenyan households in the broad-scale survey gave four land-use strategy groups, combining livestock production with, respectively, subsistence cultivation (54 households), tourism (136 households), mechanized wheat farming/leasing (29 households), or a diversified strategy with both tourism and maize cultivation (59 households). Wage earning *per se* had little explanatory power in the clustering process. Households in the baseline group (livestock production with subsistence cultivation) were less likely to have a leadership position than households in any of the other clusters (29). For a subsample of 162 household heads, leadership (elite) status (GR chairman, treasurer, or secretary) was strongly associated with involvement in mechanized farming (odds ratio 467.2, $P = 0.0007$) or in diversified livelihoods (combining livestock, tourism and maize cultivation: odds ratio 41.3, $P = 0.0052$) as were education (odds ratios 5.64, $P = 0.002$; 3.67, $P = 0.0264$) and wealth (expressed as livestock holdings: odds ratios 3.72, $P = 0.0113$; 3.01, $P = 0.0029$). Leadership status and networks are used to secure lands favorable for development or cultivation and to tap revenues from distant sources (M.T. and K.H., unpublished work). Leadership positions are negatively associated with formal education. Accessibility factors were important determinants of land-use strategy (43). Tourism is associated with proximity to MMNR and mechanized cultivation with distance from the reserve/proximity to wheat belt and markets, (odds ratio 1.4, $P = 0.0001$). Socio-economic factors and natural landscape factors (slope, elevation, and agro-ecological zone) were lesser determinants.

The broad regional survey (288 households), multiround survey (57 households), and contingent valuation survey (169 households) in the Kenyan part of the study area allow estimates of economic returns from different enterprises to different socio-economic groups (M.T. and K.H., unpublished work). The results are summarized in Table 2. GR members are likely to get more from cultivation. Elite households have privileged access to and control of MMNR dividends, GR wildlife association revenue, select campsites, lodge shares, and wage-earning positions in the tourist industry and derive considerable returns from tourism. Tourism depends on landscapes and wildlife, however, which are vulnerable to land conversion. Where distance from the park reduces tourist attraction, and market access and agro-ecological conditions favor commercial cultivation, elites can command significant returns from agriculture, especially where they secure landholdings that are many times the standard individual plot allocation.

These figures reflect site- and zone-specific tradeoffs between policy constraints, economic returns, and local aspirations. Kenya Maasai pursue the most lucrative land-use options. The percentage of land converted to cultivation correlates with income from leasing for cultivation (linear regression's $R^2 = 0.804$, $P < 0.05$; $n = 5$), and inversely with percentage of households receiving income from tourism. Similarly, cultivation correlates with market access (16). In Tanzania, policy and/or infrastructure govern land-use options. Serengeti buffer zones do not display the spread of agriculture seen around MMNR, at either the ecosystem or intensive study site level (<3% of 5-km radius area around each study site was converted to agriculture during 1985–1995).

Conclusions

These findings do not support the widespread assumption that the main drivers of land-cover change are agropastoralist population growth and land use. Decisions over land use are driven by tradeoffs between different economic opportunities (as described in the conceptual model) and not by population pressure. Private land tenure makes possible and market conditions encourage commercial cultivation, which leads to major land-cover change and wildebeest decline in the Kenyan SME. Conversely, state control of land, policies restricting mechanized cultivation, and market constraints reduce land-use options, land-cover change, and any associated impacts on wildlife in the Tanzanian SME.

Local vegetation change over a radius of a few kilometers around new Maasai settlements close to the MMNR could be contributing to declining numbers for some nonmigratory wildlife species. But changes in vegetation cover associated with the expansion of settlements has affected a much smaller area compared with rangelands conversion for mechanized farming, over the last decades, and a similar overall density and growth rate of the Maasai population in the Tanzanian SME did not lead to declining wildlife numbers.

Simple projections for 2010, assuming high population growth rate (6.4%), maize yields of 2.5 tons/ha, and yearly maize consumption of 0.18 tons/person, suggest the area needed for subsistence agriculture to feed the population of Narok District remains small (102,400 ha, 5.75% of the total available). Large-scale wheat cultivation represents only 2.80% of the total area, but its location in the core area of the wildebeest breeding and calving grounds and wet-season grazing range led to a 75% decrease in the Kenyan SME wildebeest during 1977–1997. The ecosystem could accommodate future population growth at low ecological cost provided land zoning manages settlement, subsistence agriculture, and their access to and impact on key resources (e.g., swamps, water holes, wildlife migration routes).

Zoning of the Serengeti and adjacent buffer zones into national parks, reserves, NCA, and LGCA has played a crucial role in conserving the Tanzanian system. Conversely, partial conversion of wet-season dispersal and/or calving areas to mechanized cultivation has precipitated major wildebeest losses in the Kenya part. Current attempts to establish "bottom-up" zoning in Kenyan SME depend not only on enforcement, but also on provision of incentives to agropastoralists—particularly a distribution of conservation revenue that makes conservation worth their while (43, 44).

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