Responses to alternative rainfall regimes and antipoaching in a migratory system

Ricardo M. Holdo,[1,6] Kathleen A. Galvin,[2] Eli Knapp,[3] Stephen Polasky,[4] Ray Hilborn,[5]
and Robert D. Holt[1]

[1]*Department of Biology, University of Florida, Gainesville, Florida 32611 USA*
[2]*Department of Anthropology and Natural Resource Ecology Laboratory, Colorado State University,
Fort Collins, Colorado 80523 USA*
[3]*Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523 USA*
[4]*Department of Applied Economics and Department of Ecology, Evolution, and Behavior, University of Minnesota,
St. Paul, Minnesota 55108 USA*
[5]*School of Aquatics and Fishery Science, University of Washington, Seattle, Washington 98195 USA*

Abstract. Migratory ungulates may be particularly vulnerable to the challenges imposed by growing human populations and climate change. These species depend on vast areas to sustain their migratory behavior, and in many cases come into frequent contact with human populations outside protected areas. They may also act as spatial coupling agents allowing feedbacks between ecological systems and local economies, particularly in the agropastoral subsistence economies found in the African savanna biome. We used HUMENTS, a spatially realistic socioecological model of the Greater Serengeti Ecosystem in East Africa, to explore the potential impacts of changing climate and poaching on the migratory wildebeest (*Connochaetes taurinus*) population, the fire regime, and habitat structure in the ecosystem, as well as changes in the size and economic activities of the human population outside the protected area. Unlike earlier models, the HUMENTS model predicted only moderate declines in the wildebeest population associated with an increasing human population over the next century, with a gradual expansion of agriculture, more poaching, and increases in fire frequency and reduced tree density. Changes in rainfall were predicted to have strong asymmetric effects on the size and economic activity of the human population and on livestock, and more moderate effects on wildlife and other ecological indicators. Conversely, antipoaching had a stronger effect on the ecological portion of the system because of its effect on wildebeest (and therefore on fire and habitat structure), and a weaker effect on the socioeconomic component, except in areas directly adjacent to the protected-area boundary, which were affected by crop-raiding and the availability of wildlife as a source of income. The results highlight the strong direct and indirect effects of rainfall on the various components of socioecological systems in semiarid environments, and the key role of mobile wildlife populations as agents of spatial coupling between the human-dominated and natural portions of ecosystems. They also underscore the fundamental importance of considering the spatial configuration of hunting refuges across the landscape in relation to human populations.

Key words: agropastoral systems; crop-raiding; elephants; hunting; savanna dynamics; socioecological models; spatial coupling; spatial heterogeneity; stochastic rainfall; subsistence agriculture; Tanzania; wildebeest.

Introduction

Ungulates are key ecological and economic players in terrestrial biomes, particularly in many migratory systems (McNaughton et al. 1988, Hobbs 1996, Sinclair et al. 2007). These ecosystems are often characterized by super-abundant species that simultaneously act as ecosystem engineers, tourist attractions, and food resources for human communities (Wilcove 2008). Migratory ungulates may be particularly vulnerable to population collapse, given their requirements for exten-

sive landscapes and the difficulty of containing highly mobile species within protected areas (Berger 2004, Thirgood et al. 2004, Bolger et al. 2008). Movement between protected areas and human-dominated landscapes exacerbates human–animal conflict and exposure to habitat change and hunting pressure (Thirgood et al. 2004, Harris et al. 2009). The development of predictive tools to assess how migratory systems will respond to future challenges, such as global climate change and growing human population density, is essential for conservationists, park managers, and policymakers. Here we present such a tool and conduct an assessment of the prospects for long-term ecological change in an

emblematic migratory system, the Greater Serengeti Ecosystem (GSE hereafter) of East Africa.

Migratory ungulates play dominant ecological roles in ecosystems, as demonstrated by the trophic cascades mediated by elk in Yellowstone and wildebeest in the Serengeti following the reintroduction of wolves and release from rinderpest, respectively (Dobson 1995, Ripple et al. 2001, Fortin et al. 2005, Packer et al. 2005). These trophic cascades have featured widespread impacts on tree populations, key determinants of habitat structure in terrestrial biomes. To these trophic effects we can add impacts on ecosystem function, for example the role of seasonal shifts in habitat use on nutrient cycles (Frank et al. 1994, Holdo et al. 2007), as well as important effects on human livelihoods (Barrett and Arcese 1998, Bekenov et al. 1998, Bennett and McGinnis 2008). Most ecosystems are affected either directly or indirectly by humans living within and around them, and there has, therefore, been a growing realization that they can often be better understood as socioecological rather than purely ecological systems (Matthews 2007, Westley et al. 2002). This is especially true for pastoral and agropastoral systems in developing countries, where small-scale economies are particularly reliant on local ecosystems for raw materials and ecosystem services (Kinyua et al. 2000, Bulte and Horan 2003, Galvin et al. 2006).

Socioecological models have played a crucial role in linking the biophysical realm with models of human economic behavior. These models represent valuable tools for the study of systems that are complex, experimentally intractable, and with dynamics that play out over long time scales. The biophysical component of socioecological models often focuses on the relationship between an economically important animal species (either domestic or wild, harvested destructively or nondestructively) and its abiotic environment and food supply. Pastoral systems have been particularly well studied in this respect (Janssen et al. 2000, Anderies et al. 2002, Walker and Janssen 2002, Thornton et al. 2003, Milner-Gulland et al. 2006, Muller et al. 2007), as have systems that focus on harvesting of wild species (Clark 1990, Schulz and Skonhoft 1996, Skonhoft 1996, 1998, Skonhoft and Solstad 1998, van den Bergh et al. 2006). Such models often consider just one link between human and natural systems (e.g., harvesting or grazing stocking rates and locations). There are a few case studies in which models consider two links, such as hunting and agriculture (Bulte and Horan 2003), or hunting and grazing (Kinyua et al. 2000), but in many systems, multiple economic activities (Hilborn 1995, Costello et al. 2008, Galvin et al. 2008a) can affect and be affected by a wide range of ecological processes. In subsistence agropastoral systems, for example, potential interactions across the human–ecosystem boundary can include livestock competition with wild ungulates for grazing, crop-raiding as a result of land use change, habitat loss from agricultural expansion, forest degradation due to firewood collection and logging, and revenue from ecotourism or hunting of wildlife populations (Homewood et al. 2001, Sitati et al. 2003, Thirgood et al. 2004, Boone et al. 2006a). Where large-scale wildlife migrations are involved, the critical importance of the spatial configuration of wet/dry season or winter/summer ranges of animals in relation to the spatial distribution of human populations often means that a spatially realistic socioecological framework is required for understanding the dynamics of the full system.

In this paper we used as a case study the canonical wildebeest (Connochaetes taurinus) migration of the GSE. The wildebeest are key agents of landscape change via their effects on grass biomass, fire frequency, and tree dynamics (Sinclair et al. 2007, Holdo et al. 2009a). The migration periodically brings large numbers of wildebeest and other ungulates into close proximity with areas of high human population density, generating human–animal conflict through competition for grazing with livestock and crop-raiding. Conversely, humans capitalize on the migration by hunting for bushmeat (Campbell and Hofer 1995, Barrett and Arcese 1998). There has been considerable concern in this system about the future viability of the wildebeest population. These concerns have mainly focused around the possibility of population collapse in the wildebeest as a result of declining rainfall, disease outbreaks, or increased poaching associated with human population growth (Dobson 1995, Pascual and Hilborn 1995, Pascual et al. 1997, Mduma et al. 1999). To date, model-based projections of future wildebeest population decline have ignored the spatial structure of the system and have only explicitly dealt with the dynamics of a single human activity, namely hunting (Pascual et al. 1997, Barrett and Arcese 1998, Mduma et al. 1999). Furthermore, feedbacks to the human system have not been explored. Although valuable first steps, we argue here that a landscape-level approach that incorporates a more complete range of wildlife–human interactions is warranted for understanding the response of the system to future impacts.

The over-arching question we asked is: What is the likelihood of population collapse in the Serengeti wildebeest over the next few decades? We use a spatially explicit simulation model (HUMENTS, short-hand for HUMan-ENvironmenT interactionS) of coupled human and ecological dynamics to investigate the dynamics of wildebeest and human populations in the GSE. We focused on two drivers that could potentially play critical roles in determining the future trajectory of the wildebeest population: rainfall and antipoaching. We conducted a simulation experiment in which we combined alternative rainfall and antipoaching levels to generate six different scenarios, and examined changes in key response variables. Rainfall has been projected to show a generalized decline in the GSE as a result of global climate change (Ogutu et al. 2008, Ritchie 2008); here we examined the effects of both drier and wetter

rainfall regimes than the long-term mean conditions (based on the historical record). Antipoaching is fundamentally linked to macroeconomic conditions at the national and regional level, and it has had a dominant effect on poaching behavior (Sinclair 1995, Hilborn et al. 2006). Our specific objectives were to: (1) predict the trajectory of the wildebeest population in the GSE over the next century under contrasting rainfall and antipoaching conditions, (2) predict the downstream changes in fire extent and tree density, and (3) investigate associated changes in human population density and economic activity.

Materials and Methods

Study system and model overview

The GSE comprises a system of protected areas in Tanzania and Kenya and their surrounding areas. It is approximately defined by the great wildebeest migration (Maddock 1979, Sinclair et al. 2007), plus surrounding areas. Although important human populations, primarily Maasai pastoralists, also occupy much of the eastern boundary of the system in the Loliondo area (the Loliondo Game Controlled Area and the Ngorongoro Conservation Area), we concentrated on the western human population because it has experienced a rapid expansion over the past few decades and it represents the greatest threat to the animal populations of Serengeti (Campbell and Hofer 1995).

HUMENTS is a spatially explicit socioecological model that simulates the dynamics of key ecological processes, human economic activities, and livestock and human population growth. The model couples a pre-existing ecological submodel named SD (Savanna Dynamics), described in detail in Holdo et al. (2009a) with a modified implementation of a socioeconomic household submodel developed by Costello et al. (2008). These modifications and the model equations are described in detail in Appendix A. HUMENTS simulates a subsistence economy in which households allocate labor to three mutually exclusive activities: agriculture, livestock husbandry, and hunting. Other activities such as tree harvesting for timber and firewood can also play an important role in this economy (Holmern et al. 2004, Knapp 2009), and the relative importance of these and other sources of income may shift considerably over the coming decades as pressure on limited resources increases. For simplicity, however, we at present ignored temporal and spatial variation in these activities and treat them as implicit sources of additional fixed income.

For models to be of practical utility for management both inside and outside protected areas, the projected impacts of socioecological interactions must be understood in a spatial context, tailored to the landscape in question. For this reason, the model dynamics are simulated on a spatially realistic lattice, comprised of 10 × 10 km cells covering an area of 40 800 km^2 (Fig. 1a). The GSE lattice in HUMENTS is an extension of the SD model lattice (Holdo et al. 2009a), which defines the boundaries of the wildebeest migration (Fig. 1b). Most of the GSE is either protected within Serengeti National Park (Fig. 1) or game reserves and game management areas in Tanzania and Kenya. Humans and wildlife coexist in portions of the wildebeest range that fall outside protected areas constitute areas, and these are zones where the potential for human–wildlife conflict is high (Fig. 1a). Beyond the wildebeest range, the HUMENTS simulation area extends westward up to 40 km from the protected area boundary to include areas that are almost exclusively human dominated, or at least outside the bounds of formal protection (Fig. 1a). We estimated that this distance encompasses the area over which hunters could make forays into protected areas and thus directly influence the ecology of the GSE.

A strong southeast to northwest rainfall gradient drives the seasonal migration of the wildebeest and other ungulates (Sinclair 1979, Boone et al. 2006b, Holdo et al. 2009b), with important consequences for a range of ecological processes as well as human livelihoods on the periphery of the protected area. When grass production in the Serengeti plains is high during the wet season, the wildebeest migrate south, returning to the northern woodlands as green grass becomes increasingly restricted to areas with dry-season rainfall (McNaughton 1979). The vegetation throughout much of the ecosystem ranges from wooded grassland to woodland. Large areas of pure grassland occur in the southeastern plains due to the presence of a hardpan layer beneath the soil surface that precludes tree growth (Belsky 1990).

Because populated areas to the west of Serengeti National Park have a far greater impact on the park environment than do those to the east, we limited our analysis to this area. We assumed that grazing by livestock occurs only in human-occupied cells, outside the protected areas (Fig. 1a), whereas wildebeest grazing can occur anywhere within the boundaries of the wildebeest range (Fig. 1b). Where these two areas intersect, wildebeest and livestock potentially compete for resources (Fig. 1a). In practice, illegal grazing inside protected areas does occur (E. Knapp, *personal observation*), but we have decided to ignore this particular effect for the time being, given the weak effect of grazing competition between wildebeest and livestock in our model results.

The key players and processes comprising the HUMENTS model are depicted in Fig. 2. In addition to wildebeest, elephants are an important secondary agent of landscape change in the Serengeti (Ruess and Halter 1990, Holdo et al. 2009a). Though far less abundant in the Serengeti than in other African savannas, elephants can nonetheless exert profound effects on the ecology of the system through their effects on tree cover (Croze 1974a, b, Norton-Griffiths 1979, Ruess and Halter 1990), and on human livelihoods via crop-raiding (Sitati et al. 2003, Knapp 2009). As true ecosystem engineers
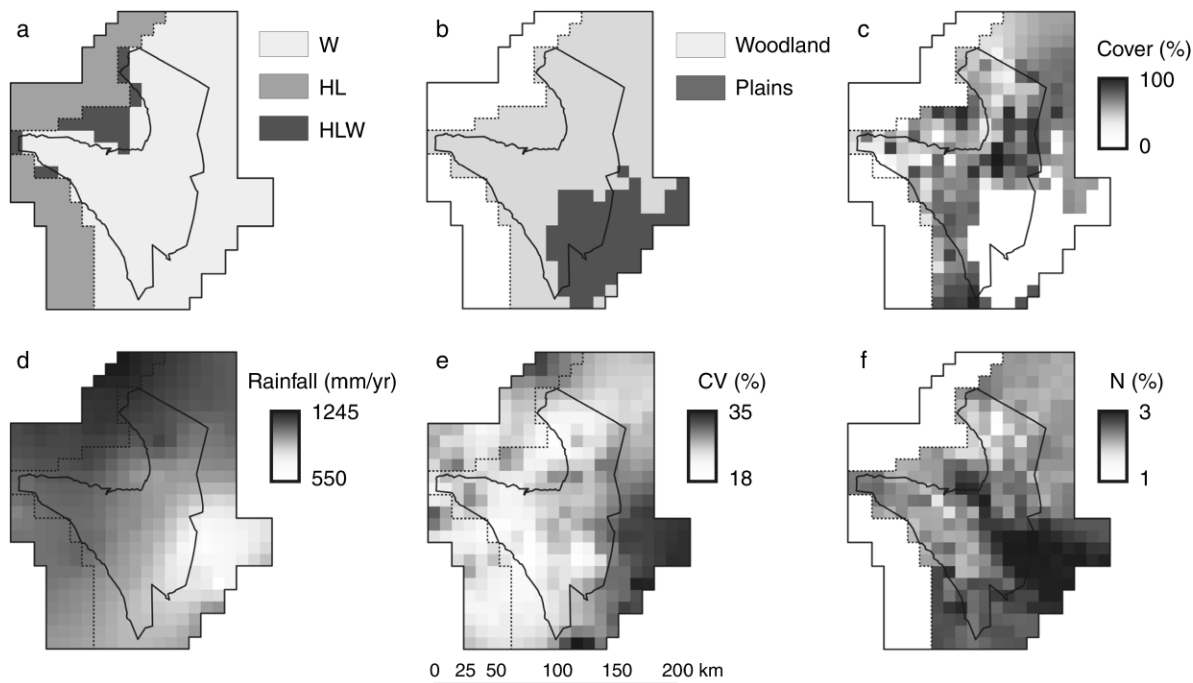
Fig. 1. GIS layers used to drive the spatially realistic, socioecological HUMENTS (HUMan-ENvironmenT interactionS) simulation model for the Greater Serengeti Ecosystem, East Africa. (a) The Greater Serengeti Ecosystem (GSE, outer solid line), showing areas occupied by wildebeest, *Connochaetes taurinus* (W), humans and livestock (HL), and their area of overlap (HLW). The boundary of Serengeti National Park (inner solid line) and the subset of the GSE that bounds the wildebeest migration (dotted line, referred to here as the Serengeti Ecosystem [SE]), are shown. (b) Habitat types modeled in the lattice; (c) canopy cover in the SE in 1972; (d) mean annual rainfall and (e) CV of mean annual rainfall in the SE over the period 1960–2001; and (f) plant nitrogen content in the SE.

(McNaughton et al. 1988, Sinclair 2003), wildebeest and elephants are the dominant grazing and browsing herbivores in this ecosystem, respectively. Although the GSE harbors a large diversity of ungulate and other herbivores (as well as predators), wildebeest are dominant in terms of biomass and their influence on both ecological processes and human livelihoods (Sinclair 1979, Sinclair et al. 2007). Ecologically, wildebeest can regulate the amount of grass biomass in the system, and thus exert a great influence on the frequency and extent of fires, and hence, on tree cover. Wildebeest also represent 55–65% of the total bushmeat harvest in the western Serengeti (Campbell and Hofer 1995, Holmern et al. 2004). Elephants, while less numerous, have a disproportionate influence on tree cover within the protected area (which can indirectly affect the grass layer via tree–grass competition), and are the main source of direct human–wildlife conflict in agricultural areas outside the park (Fig. 2). Following prior models (Barrett and Arcese 1998, Boone et al. 2002, Bulte and Horan 2003), and based on empirical data (Holmern et al. 2004, Knapp 2009), we assumed that humans allocate labor resources to three key economic activities that are both affected by and influence the vegetation structure and wildlife populations within the protected area: agriculture, livestock herding, and hunting (Fig. 2).

The HUMENTS model keeps track of a number of interacting, spatially explicit state variables. These variables describe the size and number of households, livestock herds, wildebeest and elephant population densities, grass biomass, and tree density, all within each lattice cell treated by the model (Fig. 1c). Most of the key model processes (grass production, fire, and agriculture) are either directly or indirectly affected by rainfall, which exhibits a large-scale spatial gradient across the entire system (Fig. 1d), as well as showing smaller scale spatial variation and temporal variability (Fig. 1e). Wildebeest can move between lattice cells, and migrate seasonally in response to the availability of food and nitrogen concentration (Fig. 1f), and therefore serve as agents of spatial coupling in the model. State variables are aggregated within each cell of the lattice, which implies that there is no fine-scale variation among animal and human populations within cells. For the human-occupied portion of the lattice, the socioeconomic submodel of HUMENTS simulates a single representative household per cell, and all households within that cell were assumed to behave identically. To obtain aggregate variables in each cell that can then be coupled with the SD ecological submodel, state variables (e.g., household livestock herd V) are multiplied by the number of households in each cell (hh), which can also vary through time and across space. Throughout the
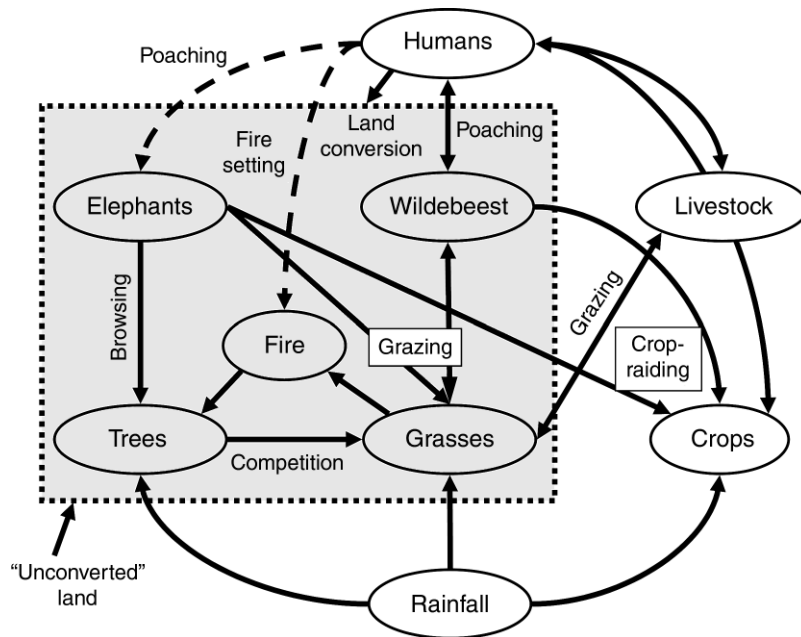
Fig. 2. Key components of the HUMENTS model. The ecological submodel (which simulates vegetation, wildlife, and fire dynamics) is integrated with the socioeconomic submodel (which simulates humans, livestock, agriculture, and hunting) to form a coupled socioecological model. The model operates on multiple time steps: daily for grass dynamics, weekly for animal movement, and annually for tree dynamics and human activity. Humans allocate labor to livestock husbandry, growing crops, hunting, and a general category of economic activity (not shown) that can generate income (e.g., sale of firewood). In addition to direct effects such as hunting, humans can impact ecological processes indirectly through land use change. In areas of wildlife–human coexistence, the amount of land not converted to crops (equivalent to the area available for grazing, A_g in the model equations) varies as a function of human population density. Dashed arrows indicate processes that are not included in the current model version.

paper, we refrain from using subscripts to refer to spatial position, unless required for clarity.

The model combines multiple time steps to accommodate fast (e.g., grass growth) and slow (e.g., tree dynamics) processes. The sequence of events simulated in a single annual cycle is shown in Fig. 3. At the beginning of the wet season, a rainfall surface realization for the next 12 months is generated by randomly sampling from the historical rainfall record. Using rain gauge data collected at monthly intervals across the entire ecosystem over several decades, we generated monthly rainfall surfaces for the period 1960–2006 using inverse distance weighting. Sampling entire years of rainfall data from the historical record preserves the spatial structure and seasonal patterns of rainfall that occur in wet and dry years, for example. Our simulation approach draws years independently and therefore does not capture multiyear rainfall cycles driven by the El Niño phenomenon (Ogutu et al. 2008), but it does preserve spatial and spatiotemporal rainfall patterns within dry and wet years in the GSE.

Once the annual and monthly rainfall totals for each cell have been determined, households allocate their labor supply to alternative economic activities according to prior information on ecological conditions, such as rainfall, grass biomass, and wildebeest abundance. These variables, in conjunction with labor inputs, determine economic output, by influencing crop yields, crop losses to wildlife, livestock survivorship, and hunting offtake. As in many previous socioeconomic subsistence models, we assumed that households produce crops, livestock, and game meat using land and labor as inputs (de Janvry et al. 1991, Barrett and Arcese 1998, Costello et al. 2008). Production functions then convert these inputs into products, conditional on environmental conditions. We assumed that labor is allocated to alternative production activities in such a way as to maximize income. We also assumed that, within certain constraints, crops, livestock, and game meat can be traded. This departs from Barrett and Arcese's (1998) model for the Serengeti, in which game meat is considered a non-tradable product used only for within-household consumption. Published evidence (Loibooki et al. 2002) and our own observations (E. Knapp, *unpublished data*) suggest that hunting can be regarded primarily as a cash-generating activity that is influenced by household economic status. The subsistence economy of the GSE can be characterized as one of incomplete markets with limited inter-village trade, so a perfect market framework does not adequately describe this system (de Janvry et al. 1991, Barrett and Arcese 1998, Polasky et al. 2008). As a result, instead of modeling the supply and demand functions for agricultural and livestock products, we made the simplifying
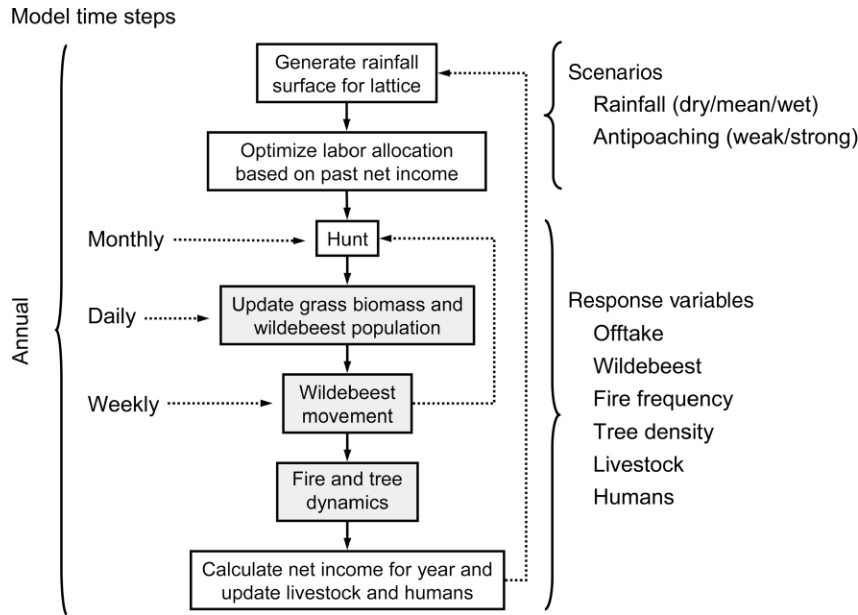
Fig. 3. Schematic representation of the key variables and processes that form part of the HUMENTS model. The model integrates a household submodel representing an agropastoral economy (open boxes) with a nested ecological submodel (shaded boxes). Two drivers (rainfall and antipoaching) are manipulated to explore the effects of six simulation scenarios (mean, dry, and wet rainfall regimes combined with weak and strong antipoaching) on key response variables.

assumption, based on empirical data, that both crop and livestock prices are determined by climate, which in a subsistence economy is the single most important determinant of crop yield and livestock production (de Janvry et al. 1991, Dercon 1996, Barrett et al. 2003). At the end of each year, surplus income is used to purchase livestock, which can be regarded as a savings mechanism that provides a buffer against future economic downturns (Dercon 1996).

HUMENTS also departs from previous socioecological models of the GSE (Barrett and Arcese 1998, Costello et al. 2008) in assuming that that decisions related to labor allocations are based on expectations of environmental variables, given historical precedent. As a result, actual economic returns will often fall short of expectations, because the decision-making will be suboptimal when compared to "perfect knowledge." To implement this, we assumed that allocations to alternative productive activities are based on running averages of three key variables: relative crop yield (Y_{ra}), which depends on rainfall; grass standing biomass (G_{ra}), which affects livestock production; and mean wildebeest abundance ($\bar{W}_{ra}$), which determines hunting income and thus affects both crop yield (through crop-raiding) and livestock production (via competition). The number of years used to compute the running average (t_{ra}) determining "expectation" can vary: A small value of t_{ra} indicates a short-term response, while a large value of t_{ra} heavily weights the past.

Following the labor allocation process, the SD submodel is used to simulate grass biomass dynamics, fire (which occurs on a fixed day during the dry season,

depending on the probability of an ignition event) and wildebeest dynamics (using a daily time step over the course of a year). The SD submodel is described in detail elsewhere (Holdo et al. 2009a), but for convenience its equations are provided in Appendix B. We inserted within the SD submodel a hunting component that iterates monthly (as described in the *Herbivore dynamics* section of Appendix B), to allow for poaching effects on wildebeest population dynamics. This differs from the other components of the socioeconomic submodel, which update annually to accommodate seasonal changes in wildebeest distribution. Labor allocation to hunting is made at the beginning of the year based on the expected average occupancy patterns of wildebeest over the course of the year ($\bar{W}_{ra}$), but actual wildebeest offtake depends on realized occupancy patterns during each month (W). This allows offtake for each human-occupied cell to reflect seasonal changes in wildebeest abundance.

The net revenue for each household is then calculated based on the realized value of crop and livestock productions, as well as wildlife offtake in each cell. Changes in livestock herd numbers are determined by ecological conditions and labor inputs, and by decisions to buy or sell animals at the end of the annual cycle. Finally, the human population increases or declines depending on whether net revenue exceeds or falls short of household requirements, respectively.

Model simulations

Effects of rainfall and antipoaching.—We conducted simulations with three rainfall (dry, mean, and wet) and

two antipoaching (strong and weak enforcement) scenarios and examined the behavior of six key response variables: wildebeest, livestock, and human population sizes, wildebeest offtake, fire, and tree density. The mean (baseline) rainfall scenario was generated by randomly drawing annual rainfall surfaces from the 1960–2006 historical record. Rainfall in the GSE has shifted between relatively wet and dry phases over this period (Appendix C). For the dry and wet scenarios, we drew rainfall surfaces from the 1980–1999 and 1960–1979 periods, which exhibited below- and above-average rainfall compared to the long-term mean, respectively. Hilborn et al. (2006) identified distinct phases of poaching intensity (associated with antipoaching) in the recent history of the Serengeti. Widespread poaching occurred between 1978–1990, but poaching has abated substantially since then (Hilborn et al. 2006). In our model, a single parameter, φ, controls the probability of getting caught hunting per unit labor (Table A1 in Appendix A), and serves as a proxy for antipoaching. We assign φ values of 0.15 and 0.05 (Appendix A) to correspond to periods of strong (the baseline) and weak antipoaching, respectively. We initialized the model variables (wildebeest and livestock populations, tree density, etc.) with our most recent estimates. The exceptions were the initial spatial patterns of human and livestock population densities, for which we lack historical data, so we assumed uniform distributions for these variables. We also assumed that human labor allocation decisions take into account ecological conditions over the previous five years (i.e., $t_{ra} = 5$ years). This time period reflects an intermediate response to temporal stochasticity, resulting in neither highly volatile nor rigidly fixed labor allocation dynamics. Finally, we used a constant elephant population of 3000 animals (the approximate present-day population) in all simulations. Although the elephant population of Serengeti is currently expanding, in the past it has fluctuated widely, alternating between periods of rapid growth and decline (Sinclair et al. 2007), so future dynamics are difficult to predict.

In all simulations, we computed mean values for the response variables across 100 model runs. This number of runs was large enough to enable us to capture the dominant temporal trends of the model output. We present both means and 95% percentiles for the trajectories of the response variables. For the purposes of the present paper, the probability of worst-case outcomes for the wildebeest population is as (or more) important than the mean trend. To evaluate these probabilities, we computed the proportion of runs for each model scenario for which the wildebeest population was predicted to fall below three arbitrary population size thresholds (1.00, 0.75, and 0.50 million animals).

Sensitivity analysis.—To examine the robustness of our predictions as a function of the model parameters, and to identify the model components that are most likely to affect its dynamics, we conducted a global sensitivity analysis on 23 parameters corresponding to the socioeconomic submodel. We did not include parameters from the ecological submodel (SD) in the analysis because these results are reported elsewhere (Holdo et al. 2009a). We assumed normal distributions for the parameters, with means centered on the default parameter estimates (Table A1) and standard deviations drawn from the literature, our own data, or our best judgment (see Appendix D). We ran 1500 iterations of the model using random normal deviates from these distributions for each of the 23 parameter values. We assumed baseline conditions for rainfall, elephant population size, and antipoaching. In each case, we ran the model for 50 years and used the means of the wildebeest and human populations over the final 25 years as our response variables. We conducted simple regressions of the response variables against each parameter using R version 2.7.1 and used adjusted-R^2 values and the regression slopes to assess the influence of each parameter (R Development Core Team 2008). We used the slopes to derive a standard measure, SA, of parameter influence:

$$\text{SA}_i = \frac{|Y(\bar{p}_i + p_i^{\text{SD}}) - Y(\bar{p}_i - p_i^{\text{SD}})|}{\bar{Y}} \times 100 \qquad (1)$$

where SA_i is the value of SA for parameter i, $\bar{p}_i$, and p_i^{SD} are the mean and standard deviation of parameter i, $\bar{Y}$ is the mean value of the response variable, and $Y(p_i)$ is the value of Y at parameter value p_i (based on the regression equation).

RESULTS

Trajectories under baseline conditions

On average, the model predicted a gradual decline in the wildebeest population over the next century (Fig. 4a), driven both by increases in the size of the human population (Fig. 4b) and hunting offtake (Fig. 4d). Livestock numbers were projected to remain relatively stable for the foreseeable future under baseline conditions (Fig. 4c). The rate of decline of the wildebeest population slowed down after 100 years, as did the rate of increase of the human population (Fig. 4a, b). Most of the change in the wildebeest population occurred over the first 25 years of the simulations, whereas the increase in the human population continued beyond this point. The wildebeest population decline resulted in more widespread fire (Fig. 4e) as a result of greater standing grass biomass, and the increase in fire was in turn predicted to reduce the amount of woody cover (Fig. 4f).

Effects of rainfall and antipoaching

Most of the response variables were influenced by rainfall and/or antipoaching (Fig. 4). The wildebeest population was sensitive to both (Fig. 4a), whereas the human population was primarily affected by rainfall (Fig. 4b). Human population growth decelerated after
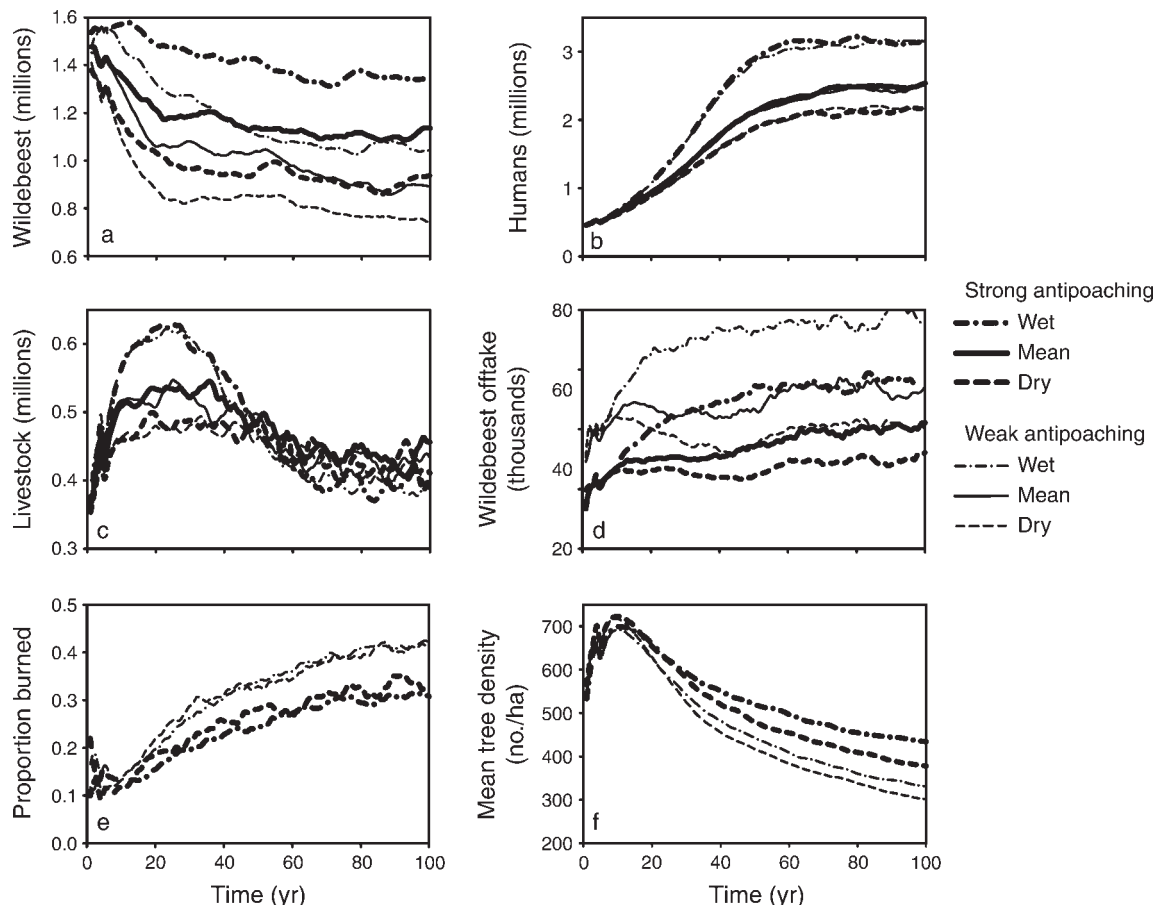
Fig. 4. Spatially aggregated results for the factorial combinations of three rainfall scenarios (dry, mean, and wet conditions, based on historical records) and two antipoaching scenarios (weak 1970s enforcement vs. stronger present-day enforcement): (a) wildebeest population; (b) human population; (c) livestock numbers; (d) wildebeest harvest; (e) annual area burned as a proportion of the total; and (f) mean tree density across the entire GSE. Shown are weighted moving averages (with a five-year window) based on mean values for 100 runs of each scenario over 100 years. The results for mean rainfall conditions are omitted from panels (e) and (f) to increase legibility.

about 50 years, and the carrying capacity of the system for humans was strongly but asymmetrically dependent on rainfall, i.e., the positive effect of wet conditions was more evident than the negative effect of persistently dry conditions (Fig. 4b).

Wet conditions increased the carrying capacity of the system for wildebeest, but the effect of rainfall on the wildebeest population appeared to be somewhat stronger when there was less poaching (the difference in wildebeest numbers between strong vs. weak antipoaching is more evident in the wet scenario; Fig. 4a). This occurred because when enforcement was lax, hunting effort increased (Appendix D, panel c), resulting in greater wildebeest offtake (Fig. 4d). This enhanced hunting pressure constrained the degree to which wildebeest could respond to environmental conditions and forage availability.

Under altered (wet or dry) rainfall conditions, the short- and long-term prospects for livestock also shifted. In the wet scenario, livestock numbers initially increased

with rainfall (Fig. 4c), but declined over time (Fig. 4c) because rapid human population growth, coupled with high crop production, limited the amount of land available for livestock grazing, as well as its relative profitability. In the dry scenario, in contrast, the viability of agriculture was reduced, owning livestock became an increasingly important activity, and the long-term size of the livestock herd ultimately converged with the predictions for the wet scenario. Although the effects of antipoaching were evident in the trajectories of the wildebeest population and offtake (Fig. 4a, d), antipoaching was predicted to have little or no effect on either the overall size of the human population or the livestock herd in the GSE (Fig. 4b, c).

Rainfall and antipoaching had downstream effects on fire and canopy cover in the ecosystem (Fig. 4e, f). The amount of fire in the system (fire frequency) was higher (and tree density lower) under weak antipoaching, because this resulted in more offtake, a smaller wildebeest population, and less grass consumption than

the strong antipoaching scenario. The rainfall scenarios had stronger effects on tree density than on fire (Fig. 4e, f) because fire is tightly coupled with wildebeest grazing, whereas tree dynamics are influenced by both fire and precipitation (Fig. 4e, f).

The high variability of rainfall led to substantial variation around the mean trends. We present 95% percentiles for the 100 runs conducted for each scenario around the response variable means shown in Fig. 4 (Appendix E: Table E1). The response variables exhibited approximately normal distributions around these means. Both dry conditions and weak antipoaching increased the probability of the wildebeest population falling below certain population thresholds (Table 1), with increased poaching being more likely to push the population below half a million animals than dry conditions alone. In general, <1% of the runs in any given scenario led to the wildebeest population dropping below this level (Table 1).

Spatial patterns

At the end of the 100-year simulation, the human population showed a spatially bimodal distribution (Fig. 5a), being highest just north and south of the western corridor of the Serengeti, and increasing as a function of distance to the protected area boundary. The decline in population density as a function of distance to the protected area resulted from losses to agriculture sustained as a result of crop-raiding, as suggested by the lower labor investment into crops in areas close to the protected area boundary (Fig. 5b). Spatial patterns of human population density and labor allocation to crops were also determined by relative crop yields (Fig. 5e), as influenced by rainfall patterns (Fig. 1d, e). Crop yields generally increased with rainfall along a south-to-north gradient, but they were also influenced by the spatial pattern of unpredictability in precipitation as quantified by the coefficient of variation in rainfall (Fig. 1e). In the pocket of lower crop yields in the central west of the ecosystem (Fig. 5e), the model predicted that crops should tend to give way to higher investments in livestock (Fig. 5c) and hunting (Fig. 5d) as alternative sources of income, and lead to a higher livestock to human ($V{:}H$) ratio (Fig. 5h). There was also a predicted east-to-west gradient in livestock ownership: $V{:}H$ and labor allocation to livestock increased towards the park boundary (where crops were less viable) in the southern portion of the ecosystem (Fig. 5c, h). This gradient was less evident in the northern part of the ecosystem, where agriculture and livestock were replaced by hunting as the dominant economic activity (Fig. 5d). Generally, hunting was most prominent within or near the areas of human–wildlife coexistence north of the western corridor (Figs. 5d and 1a) that also overlap with the dry season range of the wildebeest (Fig. 5g). Patterns of fire (Fig. 5i) were at least in part associated with wildebeest distribution patterns (Fig. 5f, g), with highly grazed portions of the ecosystem (which have lower standing

TABLE 1. Percentage of simulation years (100 years × 100 runs) during which the wildebeest (*Connochaetes taurinus*) population fell below a specified population threshold for each factorial combination of rainfall and antipoaching.

Rainfall	Population threshold (millions of wildebeest)	Antipoaching	
		Strong (%)	Weak (%)
Mean	1.00	25	48
	0.75	4	13
	0.50	0	<1
Dry	1.00	55	78
	0.75	12	32
	0.50	<1	1
Wet	1.00	4	26
	0.75	<1	3
	0.50	0	0

grass biomass) having lower fire frequency. The distribution of fire across the landscape was in turn predicted to affect the spatial pattern of woody cover in the long term (Fig. 5j). The model predictions for the response variables largely matched landscape-level historical patterns observed in the Serengeti, including: seasonal wildebeest distribution patterns (Pennycuick 1975, Maddock 1979, Holdo et al. 2009b); the occurrence of two main areas of high fire frequency (Fig. 5i), in the northern Serengeti and west of the plains (Dempewolf et al. 2007), and patterns of increasing tree density in Maswa Game Reserve (southwest of Serengeti National Park) and central Serengeti National Park, with declines elsewhere (Fig. 5j), especially in the northern Serengeti (Norton-Griffiths 1979).

Effects of rainfall and antipoaching across space

The effects of rainfall and antipoaching were highly variable across space, and several response variables showed complex spatial patterns (Figs. 6 and 7). Human population density and labor allocations showed both positive and negative changes across the landscape in response to drier conditions (Fig. 6a–d) and reduced antipoaching (Fig. 7a–d). These results are particularly striking considering the relatively weak mean effects of rainfall and antipoaching on labor allocation (Appendix F). On average, a reduction in rainfall (dry vs. mean rainfall scenario) had a relatively small effect on the total size of the human population (Fig. 5b), but when this change was mapped out across space, the model suggested a strong east–west gradient in population density decline, with areas immediately north and south of the western corridor showing the greatest decline (Fig. 6a). The greatest changes were observed in the central portion of the ecosystem, where a relative shift in labor occurred from crops to livestock (Fig. 6b, c).

The decline in the wildebeest herd predicted in the dry scenario (Fig. 4a) also had spatially heterogeneous effects: People who live near the protected area boundary in both the western corridor and northern GSE are strongly dependent on hunting for their income (Fig. 5d), but a rainfall-driven decline in the size of the wildebeest herd would lead to less hunting in the west
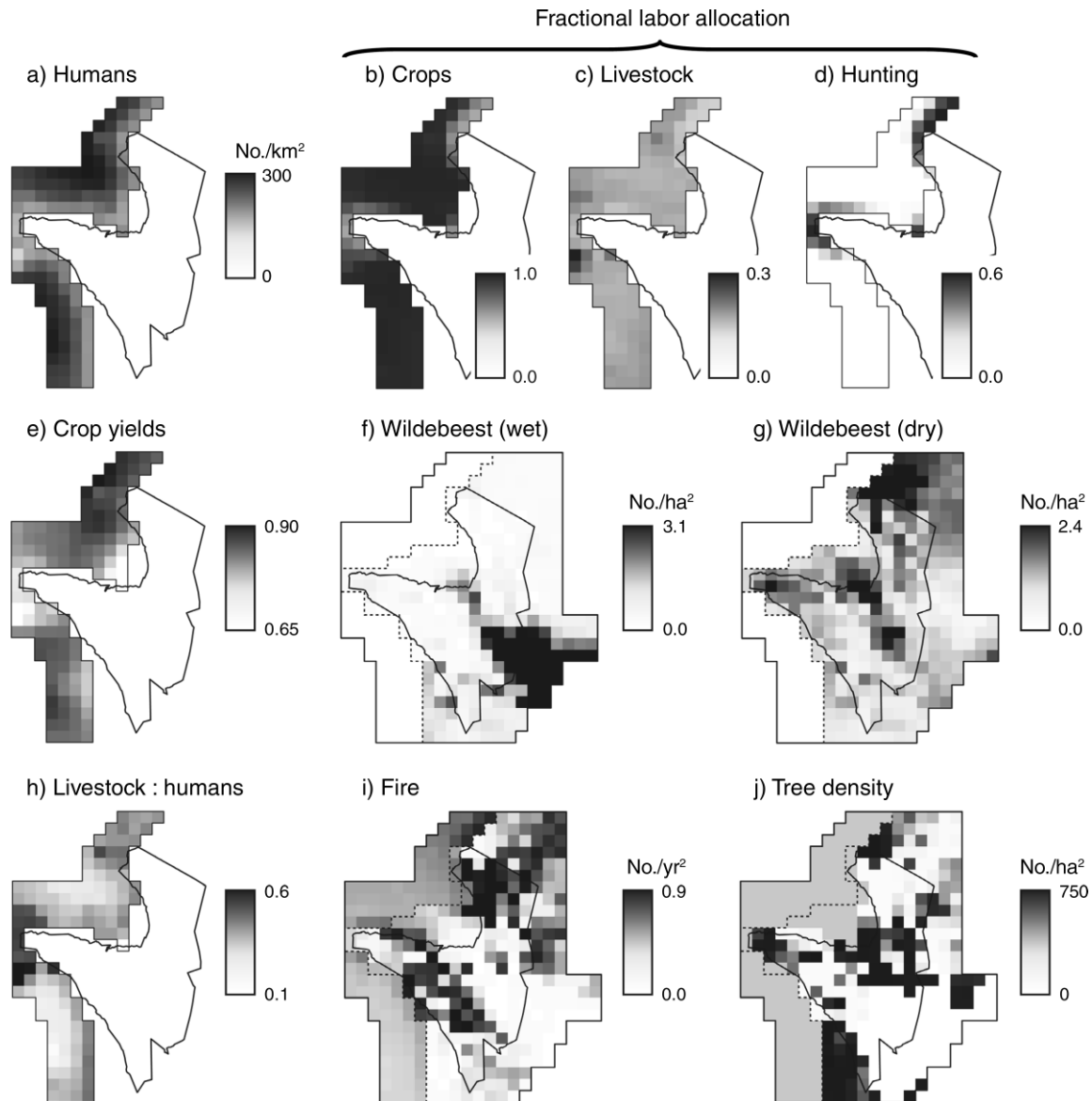
FIG. 5. Predicted spatial distribution of (a) human population density; labor allocation to (b) crops, (c) livestock, and (d) hunting (inside and outside the protected area combined); (e) relative crop yield (proportion); (f) wet- and (g) dry-season wildebeest population density; (h) livestock to human ratio per household; (i) fire frequency; and (j) tree density across the entire GSE after 100 years (based on means computed for 100 runs), assuming baseline conditions (mean rainfall and strong antipoaching).

and more in the north. Similarly, the simulated relaxation of antipoaching was predicted to have only a marginal effect on human population density overall, but not in areas that rely strongly on hunting for income (Fig. 7a). In these areas, there was little change in labor allocation to livestock as a result of reduced enforcement, but there was a strong shift from crops to hunting in areas with high wildlife density adjacent to the protected area (Fig. 7b–d).

The socioeconomic indicators in the model (human population density and labor allocation) generally showed strong spatial variation in relation to distance from the protected area boundary of the GSE (Figs. 6a–

d and 7a–d). The spatial response of the ecological variables, in contrast, was independent of the boundary (Figs. 6e–g and 7e–g). Under dry conditions, wildebeest population declines (Fig. 6e) were predicted to be more prominent in the Serengeti plains (Fig. 1b), where forage is more sensitive to changes in rainfall than in the wetter northern woodlands. The wildebeest decline in the plains was in turn predicted to lead to more fire (because of lower grass consumption), even as fire declined in the north of the ecosystem as a result of lower fuel production (Fig. 6f). This decrease in fire frequency led to a recovery in tree density in the northern portion of the ecosystem (Fig. 6g). The spatial patterns of
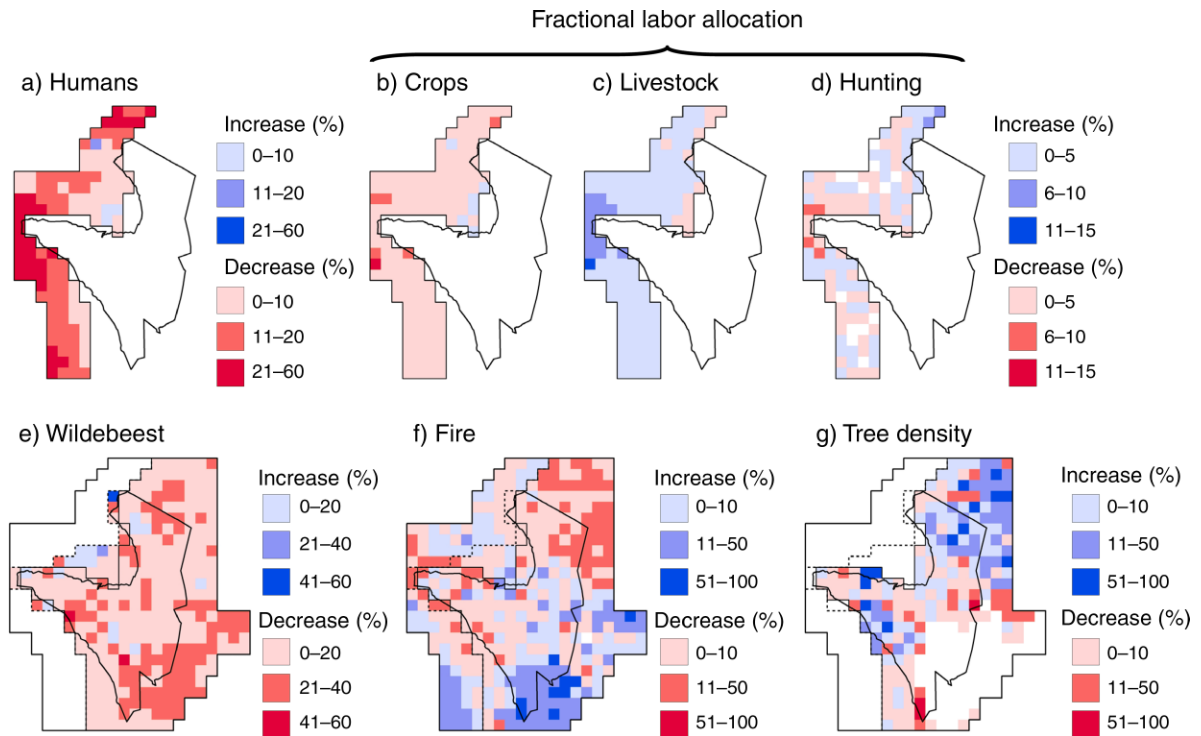
Fractional labor allocation

FIG. 6. Predicted changes in (a) human population density; labor allocation to (b) crops, (c) livestock, and (d) hunting; (e) the mean wildebeest distribution calculated across an annual cycle; (f) fire frequency; and (g) tree density across the entire GSE after 100 years (based on means computed for 100 runs) under a dry (vs. mean) rainfall regime.
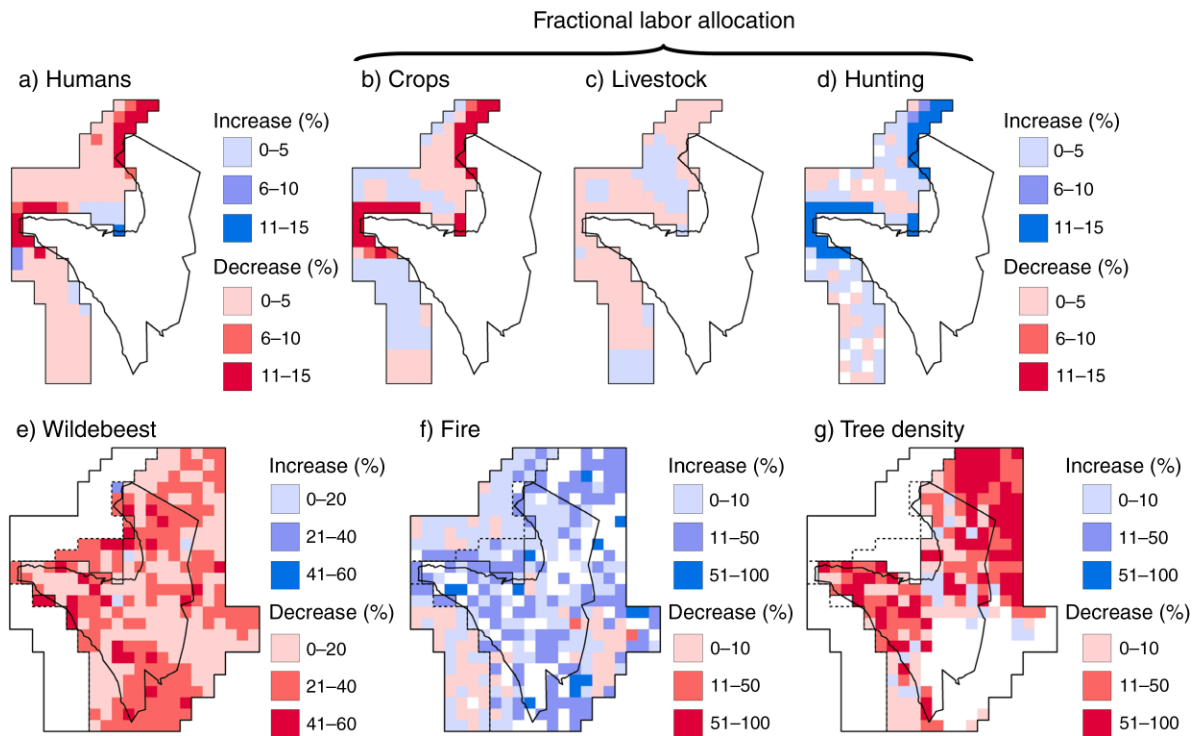
Fractional labor allocation

FIG. 7. Predicted changes in (a) human population density; labor allocation to (b) crops, (c) livestock, and (d) hunting; (e) the mean wildebeest distribution calculated across an annual cycle; (f) fire frequency; and (g) tree density across the entire GSE after 100 years (based on means computed for 100 runs) under weak (vs. strong) antipoaching.

changes in fire and tree density under dry conditions were the product of an interaction between the direct effects (production) and indirect effects (the modulating influence of wildebeest consumption) of rainfall on fuel standing biomass. The patterns predicted under conditions of reduced antipoaching were the product of increased hunting near the protected area boundary (Fig. 7d). This increase in hunting resulted in a generalized reduction in the wildebeest population (Fig. 7e), associated increases in fire, and declines in tree density throughout the ecosystem (Fig. 7f, g). Thus, even though both dry conditions and weak antipoaching caused declines in the wildebeest population, the spatial pattern of these declines and their downstream consequences for ecological processes differed in the two scenarios.

Sensitivity analysis

Model output was most strongly influenced by uncertainty in parameters associated with agriculture (crop price p_A, crop yield γ, and the Cobb-Douglas production coefficient β), human demography (the human caloric requirement during stress years c' and the maximum rate of human population growth r_H), and the price of bushmeat p_H (Appendix D). This is an indicator of the strong dependence of model outcome on human population growth and the viability of agriculture as a driver of economic wellbeing and an alternative to hunting. Even though we used relatively narrow estimates for p_A and γ (based on extensive household survey data), small levels of error in these parameters were shown to be influential. In contrast, a number of parameters for which we had insufficient data (and thus wide error estimates), such as the crop-raiding parameters λ_E and λ_W and the price-adjustment coefficients s_A and s_L, had negligible effects on model behavior (Appendix D).

DISCUSSION

Effects of climate

Our model results underscore the fundamental role of climate in regulating feedbacks between social and ecological components in savanna agropastoral systems. Rainfall plays a multifaceted role in these ecosystems because it directly affects not only grass and tree growth but also crop yields. Indirectly, rainfall determines livestock production, wildebeest population growth, and ultimately human population growth and income (Fig. 2). These multiple effects help to explain some of the nonlinear dynamics of the system. For example, in the short term, the wet scenario increases the carrying capacity of the system compared to the mean rainfall scenario for both wild and domestic ungulates (Fig. 4), but over the longer term wetter conditions lead to fast human population growth, agricultural expansion, and a lower carrying capacity for livestock than would be the case under mean conditions.

The model presently focuses strictly on the consequences of alternative precipitation regimes, and not on some of the other environmental changes that are to be expected under global climate change scenarios. Such changes may include, in addition to a decline in mean rainfall, greater variability in precipitation (more frequent and extreme drought events; Hansen et al. 2006), temperature and atmospheric CO_2 increases (Hulme et al. 2001, Ogutu et al. 2008), and altered patterns of N deposition. Temperature increases in particular will likely influence soil moisture dynamics and fire regimes, and temperature and CO_2 both have direct implications for grass and tree growth rates (Tietjen and Jeltsch 2007, Bond 2008, Ritchie 2008).

Effects of poaching

Previous models of wildebeest poaching (Pascual et al. 1997, Barrett and Arcese 1998, Mduma et al. 1999) predicted far steeper future declines in the wildebeest population than observed in our model. Those studies include both relatively simple models with fixed hunting pressure (Pascual et al. 1997, Mduma et al. 1999) and a more complex socioecological model that allows for human population increases and dynamic hunting behavior (Barrett and Arcese 1998), but in all cases space is treated implicitly. In the HUMENTS model, marked increases in human population size failed to drive the wildebeest population below about half a million animals, even in the "worst-case" scenario (dry conditions and weak antipoaching; Table 1). This is largely due to the potentially high opportunity cost of hunting: To hunt deep in the protected area, hunters must travel long distances, which is both time consuming and increases the probability of arrest. Wildebeest can find refuge from hunting in a system as large as the Serengeti. Given an avoidance response to areas of intense hunting (which we do not simulate but have seen clear evidence of; G. Hopcraft, *unpublished data*), the risk to wildebeest due to over-harvesting may actually be lower than suggested by our present model. Our overall conclusion that the wildebeest population could remain quite sizeable over the next few decades may seem counterintuitive, given the prevailing notion that migratory ungulate populations are particularly vulnerable to human pressure (Berger 2004, Wilcove 2008, Harris et al. 2009). Much of this has to do with the design of Serengeti National Park and adjoining conservation areas; this system of protected areas is remarkable for the degree to which it preserves the landscape covered by the migration (Thirgood et al. 2004). This is a case where the initial spatial design for a set of reserves makes biological sense from the perspective of sustaining a key ecological process.

The importance of space in migratory systems

Beyond the simulated effects on the size of the wildebeest population, our model results highlight the importance of spatial variation for large socioecological

systems. We have already emphasized the key role that the shape of the protected portion of the GSE plays for the wildebeest migration. Beyond the importance of shape, human–wildlife interactions (e.g., crop-raiding and poaching) vary in intensity as a function of distance to the boundary between the protected and settled portions of the ecosystem. As a result, global values of the response variables do not necessarily reflect local responses. This "distance effect" has important consequences for the overall dynamics of the system and the spatial pattern of impacts. For example, Fig. 5 shows that changes in the allocation of labor as a result of shifting rainfall or antipoaching are greater in areas that are strongly influenced by proximity to wildlife (either because of changes in the availability of bushmeat or of crop yields, as a result of crop-raiding). These boundary effects are more important for the human population outside the protected areas than for some of the ecological processes inside them. This is demonstrated by the fact that the distributions of fire frequency and woody vegetation generated by the model across the landscape appear unrelated to proximity to the park boundary (Fig. 6). This occurs because the effects of human activities (primarily hunting, secondarily habitat loss) on the ecological processes are mediated by the highly mobile wildebeest, which act as vectors for transmitting ecological perturbations across space. Any spatial signature in wildebeest population density arising from the localized nature of hunting near the park boundary is rapidly diffused well away from the edge, and changes in the wildebeest population caused by hunting are propagated spatially throughout the landscape, leading to cascading changes in fire and tree density at large spatial scales. If the keystone herbivores in the system were resident grazers (such as buffalo), we might expect much stronger gradients in fire frequency and tree density change towards the park boundary associated with hunting spatial patterns (Campbell and Hofer 1995). The mobile nature of animals in migratory socioecological systems therefore not only affects their sensitivity or resistance to hunting pressure, but also their impact on the broader ecology and landscape structure of ecosystems.

The role of temporal variability

In addition to the importance of space, the highly stochastic nature of rainfall in this system leads to patterns that differ from those expected in a purely deterministic model. This is particularly striking with respect to crop yields, which are highly dependent on the temporal pattern of soil moisture availability during the growing season. In the rain-fed agricultural systems of the western Serengeti, crop yields are completely dependent on current-year rainfall. The reliability and distribution of growing-season rainfall are more important than the total amount, and even though the average change in the total amount of growing-season rainfall (compared to mean conditions) is similar in the wet and

dry scenarios, rainfall is more reliable in the wet scenario. Under these conditions, with drought less likely and crop production more dependable, people will tend to make allocation decisions with predictable outcomes, i.e., those most likely to maximize income and lead to population increase. This asymmetry is shown by the strong effect that wet (but not dry) conditions have on household crop production compared to mean conditions (Appendix F). Even though modeled crop production generally declined over time (due to a reduction in land availability caused by overcrowding), the positive effect on household agricultural output under wetter-than-normal conditions was quite striking (Appendix F). This asymmetry has direct consequences for the size of the human population, which is strongly dependent on crops for its economic wellbeing, and for livestock. Livestock are impacted by variable rainfall both directly and indirectly: On the one hand, livestock carrying capacity is mainly governed by rainfall; on the other, market conditions for livestock sales are largely determined by crop yields.

Caveats

The model produced good fits to data when used for parameter estimation, and generated reasonable predictions when validated against data quantifying hunting levels as a function of distance from the park boundary (Appendix G). A future challenge will be to improve and refine the model by comparing simulated changes in human population densities and land cover with observed spatial patterns for these variables. Introduction of new elements to the model may enhance biological and socioeconomic realism (albeit at the cost of increased complexity). Some potential additions to the model are: a better understanding of human impacts on tree density (both inside and outside protected areas); resident as well as migratory wildlife species; explicit modeling of movement and population dynamics of elephants; and disease dynamics, given the key historical role of disease outbreaks in regulating both wildebeest and livestock populations (Dobson 1995, Sinclair 1995). In particular, we highlight that in the present model, the maintenance of dry and wet ranges for the wildebeest are assumed to be far more critical than the details of the migration routes that link these ranges. Our movement model is a "redistribution" model rather than a true movement model (Holdo et al. 2009b). Future model innovations might explore the importance of preserving migration routes as well as ranges, particularly given the potential threat to current migration routes posed by human population increase around the so-called "western corridor" of Serengeti NP (Thirgood et al. 2004). On the human side, potential areas for model improvement could include the introduction of economic activities such as firewood gathering, wage labor, and ecotourism as explicit components of the model, and a more sophisticated model of human demography.

Conclusions

The linkages between local economies and biological processes in socioecological models have been relatively understudied compared to the potential importance of each individual component in determining the dynamics of these systems. Our model highlights the importance of some of these linkages for understanding the spatiotemporal dynamics of wildlife populations, and shows the long-term dynamics that emerge from analyses of socioecological systems that incorporate two-way feedbacks between human behavior and ecological processes. Our results also bring to the forefront the importance of an explicit consideration of space and of environmental stochasticity, particularly in semiarid ecosystems with small-scale economies (Galvin et al. 2004, 2008b).

A fundamental future challenge is to understand how the resilience and adaptation of societies and ecological systems are linked, and how they respond in the face of both short-term shocks and long-term drivers of change (Anderies et al. 2002, Ludwig et al. 2002, Walker and Janssen 2002). Understanding changes in land use and ecosystems and the implications for global environmental change for people and for sustainability is a major research challenge (Turner et al. 2007). The problem includes understanding what determines land use change, and assessments of system outcomes such as behavioral adaptation and transformation. Policymakers seek environmental solutions that often take into account a single problem, rather than adopting a systems-level perspective, and therefore dramatic and radically simplified assumptions are made regarding the governing and use of land (Reid et al. 2008). Only rarely, however, is the socioecological system addressed as a truly integrated system. Our present model achieves this to an extent, and it has added value in terms of understanding the trade-offs of particular land uses for people and the ecosystem, while highlighting spatial and temporal trends that have direct implications for policy and management of protected areas.

Literature Cited

Anderies, J. M., M. A. Janssen, and B. H. Walker. 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. Ecosystems 5:23–44.
Barrett, C. B., and P. Arcese. 1998. Wildlife harvest in integrated conservation and development projects: linking harvest to household demand, agricultural production, and environmental shocks in the Serengeti. Land Economics 74:449–465.
Barrett, C. B., F. Chabari, D. Bailey, P. D. Little, and D. L. Coppock. 2003. Livestock pricing in the Northern Kenyan rangelands. Journal of African Economies 12:127–155.
Bekenov, A. B., I. A. Grachev, and E. J. Milner-Gulland. 1998. The ecology and management of the Saiga antelope in Kazakhstan. Mammal Review 28:1–52.
Belsky, A. J. 1990. Tree-grass ratios in East African savannas: a comparison of existing models. Journal of Biogeography 17:483–489.
Bennett, D., and D. McGinnis. 2008. Coupled and complex: human-environment interaction in the Greater Yellowstone Ecosystem, USA. Geoforum 39:833–845.
Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18:320–331.
Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.
Bond, W. J. 2008. What limits trees in C4 grasslands and savannas? Annual Review of Ecology, Evolution, and Systematics 39:641–659.
Boone, R. B., M. B. Coughenour, K. A. Galvin, and J. E. Ellis. 2002. Addressing management questions for Ngorongoro Conservation Area, Tanzania, using the SAVANNA modelling system. African Journal of Ecology 40:138–150.
Boone, R. B., K. A. Galvin, P. K. Thornton, D. M. Swift, and M. B. Coughenour. 2006a. Cultivation and conservation in Ngorongoro Conservation Area, Tanzania. Human Ecology 34:809–828.
Boone, R. B., S. J. Thirgood, and J. G. C. Hopcraft. 2006b. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology 87:1987–1994.
Bulte, E. H., and R. D. Horan. 2003. Habitat conservation, wildlife extraction and agricultural expansion. Journal of Environmental Economics and Management 45:109–127.
Campbell, B. M., and H. Hofer. 1995. People and wildlife: spatial dynamics and zones of interaction. Pages 534–570 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.
Clark, C. W. 1990. Mathematical bioeconomics: the optimal management of renewable resources. Second edition. John Wiley and Sons, New York, New York, USA.
Costello, C., N. Burger, K. A. Galvin, R. Hilborn, and S. Polasky. 2008. Dynamic consequences of human behavior in the Serengeti ecosystem. Pages 301–324 in A. R. E. Sinclair and C. Packer, editors. Serengeti III: human-environment interactions. University of Chicago Press, Chicago, Illinois, USA.
Croze, H. 1974a. The Seronera bull problem: the elephants. East African Wildlife Journal 12:1–27.
Croze, H. 1974b. The Seronera bull problem: the trees. East African Wildlife Journal 12:29–47.
de Janvry, A., M. Fafchamps, and E. Sadoulet. 1991. Peasant household behavior with missing markets—some paradoxes explained. Economic Journal 101:1400–1417.
Dempewolf, J., S. Trigg, R. S. DeFries, and S. Eby. 2007. Burned-area mapping of the Serengeti-Mara region using MODIS reflectance data. IEEE Geoscience and Remote Sensing Letters 4:312–316.
Dercon, S. 1996. Risk, crop choice, and savings: evidence from Tanzania. Economic Development and Cultural Change 44:485–513.
Dobson, A. 1995. The ecology and epidemiology of rinderpest virus in Serengeti and Ngorongoro Conservation Area. Pages 485–505 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.
Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk

movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26:163–188.

Galvin, K. A., S. Polasky, C. Costello, and M. Loibooki. 2008a. Human responses to change: modeling household decision making in Western Serengeti. Pages 325–346 in A. R. E. Sinclair and C. Packer, editors. Serengeti III: human-environment interactions. University of Chicago Press, Chicago, Illinois, USA.

Galvin, K. A., R. S. Reid, R. H. Behnke, and N. T. Hobbs. 2008b. Fragmentation of semi-arid and arid landscapes: consequences for human and natural systems. Springer, Dordrecht, The Netherlands.

Galvin, K. A., P. K. Thornton, R. B. Boone, and J. Sunderland. 2004. Climate variability and impacts on East African livestock herders. African Journal of Range and Forage Science 21:183–189.

Galvin, K. A., P. K. Thornton, J. R. de Pinho, J. Sunderland, and R. B. Boone. 2006. Integrated modeling and its potential for resolving conflicts between conservation and people in the rangelands of East Africa. Human Ecology 34:155–183.

Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and M. Medina-Elizade. 2006. Global temperature change. Proceedings of the National Academy of Sciences USA 103:14288–14293.

Harris, S., S. Thirgood, G. Hopcraft, J. Cromsigt, and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7:55–76.

Hilborn, R. 1995. A model to evaluate alternative management policies for the Serengeti-Mara ecosystem. Pages 617–637 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Hilborn, R., P. Arcese, M. Borner, J. Hando, G. Hopcraft, M. Loibooki, S. Mduma, and A. R. E. Sinclair. 2006. Effective enforcement in a conservation area. Science 314:1266.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Holdo, R. M., R. D. Holt, M. B. Coughenour, and M. E. Ritchie. 2007. Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna. Journal of Ecology 95:115–128.

Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009a. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. Ecological Applications 19:95–109.

Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009b. Opposing rainfall and nutrient gradients best explain the wildebeest migration in the Serengeti. The American Naturalist 173:431–445.

Holmern, T., A. B. Johannesen, J. Mbaruka, S. Mkama, J. Muya, and E. Røskaft. 2004. Human-wildlife conflicts and hunting in the western Serengeti, Tanzania. NINA Project Report 26:1–26.

Homewood, K., E. F. Lambin, E. Coast, A. Kariuki, I. Kikula, J. Kivelia, M. Said, S. Serneels, and M. Thompson. 2001. Long-term changes in Serengeti-Mara wildebeest and land cover: pastoralism, population, or policies? Proceedings of the National Academy of Sciences USA 98:12544–12549.

Hulme, M., R. Doherty, T. Ngara, M. New, and D. Lister. 2001. African climate change: 1900–2100. Climate Research 17:145–168.

Janssen, M. A., B. H. Walker, J. Langridge, and N. Abel. 2000. An adaptive agent model for analysing co-evolution of management and policies in a complex rangeland system. Ecological Modelling 131:249–268.

Kinyua, P. I. D., G. C. van Kooten, and E. H. Bulte. 2000. African wildlife policy: protecting wildlife herbivores on private game ranches. European Review of Agricultural Economics 27:227–244.

Knapp, E. 2009. Western people shall not die: examining the effects of household wealth on the resilience of a coupled human-natural system in Tanzania. Dissertation. Colorado State University, Fort Collins, Colorado, USA.

Loibooki, M., H. Hofer, K. L. I. Campbell, and M. L. East. 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. Environmental Conservation 29:391–398.

Ludwig, D., B. H. Walker, and C. S. Holling. 2002. Models and metaphors of sustainability, stability, and resilience. Pages 21–50 in L. H. Gunderson and L. Pritchard, Jr., editors. Resilience and the behavior of large-scale systems. Island Press, Washington, D.C., USA.

Maddock, L. 1979. The "migration" and grazing succession. Pages 104–129 in A. R. E. Sinclair and M. Norton-Griffiths, editors. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Matthews, R. 2007. Modelling the sustainability of rural systems: concepts, approaches and tools. Journal of Agricultural Science 145:636–641.

McNaughton, S. J. 1979. Grassland-herbivore dynamics. Pages 46–81 in A. R. E. Sinclair and M. Norton-Griffiths, editors. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. Bioscience 38:794–800.

Mduma, S. A. R., A. R. E. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: a 40-year record. Journal of Animal Ecology 68:1101–1122.

Milner-Gulland, E. J., C. Kerven, R. Behnke, I. A. Wright, and A. Smailov. 2006. A multi-agent system model of pastoralist behaviour in Kazakhstan. Ecological Complexity 3:23–36.

Muller, B., A. Linstadter, K. Frank, M. Bollig, and C. Wissel. 2007. Learning from local knowledge: modeling the pastoral-nomadic range management of the Himba, Namibia. Ecological Applications 17:1857–1875.

Norton-Griffiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. Pages 310–352 in A. R. E. Sinclair and M. Norton-Griffiths, editors. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Ogutu, J. O., H. P. Piepho, H. T. Dublin, N. Bhola, and R. S. Reid. 2008. El Nino-Southern Oscillation, rainfall, temperature and Normalized Difference Vegetation Index fluctuations in the Mara-Serengeti ecosystem. African Journal of Ecology 46:132–143.

Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A. R. E. Sinclair. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. Science 307:390–393.

Pascual, M. A., and R. Hilborn. 1995. Conservation of harvested populations in fluctuating environments: the case of the Serengeti wildebeest. Journal of Applied Ecology 32:468–480.

Pascual, M. A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology 11:966–976.

Pennycuick, L. 1975. Movements of the migratory wildebeest population in the Serengeti areas between 1960 and 1973. East African Wildlife Journal 13:65–87.

Polasky, S., J. Schmitt, C. Costello, and L. Tajibaeva. 2008. Larger-scale influences on the Serengeti ecosystem: national and international policy, economics, and human demography. Pages 347–378 in A. R. E. Sinclair and C. Packer,

editors. Serengeti III: human-environment interactions. University of Chicago Press, Chicago, Illinois, USA.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, R. S., K. A. Galvin, and R. S. Kruska. 2008. Global significance of extensive grazing lands and pastoral societies: an introduction. Pages 1–24 in K. A. Galvin, R. S. Reid, R. H. Behnke, and N. T. Hobbs, editors. Fragmentation of semi-arid and arid landscapes: consequences for human and natural systems. Springer, Dordrecht, The Netherlands.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227–234.

Ritchie, M. E. 2008. Global environmental changes and their impact on the Serengeti. Pages 183–208 in A. R. E. Sinclair and C. Packer, editors. Serengeti III: human-environment interactions. University of Chicago Press, Chicago, Illinois, USA.

Ruess, R. W., and F. L. Halter. 1990. The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. African Journal of Ecology 28:259–275.

Schulz, C. E., and A. Skonhoft. 1996. Wildlife management, land-use and conflicts. South African Journal of Wildlife Research 26:151–159.

Sinclair, A. R. E. 1979. Dynamics of the Serengeti ecosystem: process and pattern. Pages 1–30 in A. R. E. Sinclair and M. Norton-Griffiths, editors. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Sinclair, A. R. E. 1995. Serengeti past and present. Pages 3–30 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Sinclair, A. R. E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. Philosophical Transactions of the Royal Society of London B 358:1729–1740.

Sinclair, A. R. E., S. A. R. Mduma, J. G. C. Hopcraft, J. M. Fryxell, R. Hilborn, and S. Thirgood. 2007. Long-term ecosystem dynamics in the Serengeti: lessons for conservation. Conservation Biology 21:580–590.

Sitati, N. W., M. J. Walpole, R. J. Smith, and N. Leader-Williams. 2003. Predicting spatial aspects of human-elephant conflict. Journal of Applied Ecology 40:667–677.

Skonhoft, A. 1996. Wildlife management, illegal hunting and conflicts. Environment and Development Economics 1:165–181.

Skonhoft, A. 1998. Resource utilization, property rights and welfare-wildlife and the local people. Ecological Economics 26:67–80.

Skonhoft, A., and J. T. Solstad. 1998. Investing in wildlife: Can wildlife pay its way? Journal of African Economies 7:237–262.

Thirgood, S., A. Mosser, S. Tham, G. Hopcraft, E. Mwangomo, T. Mlengeya, M. Kilewo, J. Fryxell, A. R. E. Sinclair, and M. Borner. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. Animal Conservation 7:113–120.

Thornton, P. K., K. A. Galvin, and R. B. Boone. 2003. An agro-pastoral household model for the rangelands of East Africa. Agricultural Systems 76:601–622.

Tietjen, B., and F. Jeltsch. 2007. Semi-arid grazing systems and climate change: a survey of present modelling potential and future needs. Journal of Applied Ecology 44:425–434.

Turner, B. L., E. F. Lambin, and A. Reenberg. 2007. The emergence of land change science for global environmental change and sustainability. Proceedings of the National Academy of Sciences USA 104:20666–20671.

van den Bergh, J. C. J. M., J. Hoekstra, R. Imeson, P. A. L. D. Nunes, and A. T. de Blaeij. 2006. Bioeconomic modelling and valuation of exploited marine ecosystems. Springer, Dordrecht, The Netherlands.

Walker, B. H., and M. A. Janssen. 2002. Rangelands, pastoralists and governments: interlinked systems of people and nature. Philosophical Transactions of the Royal Society of London B 357:719–725.

Westley, F., S. R. Carpenter, W. A. Brock, C. S. Holling, and L. H. Gunderson. 2002. Why systems of people and nature are not just social and ecological systems. Pages 103–120 in L. H. Gunderson and C. S. Holling, editors. Panarchy: understanding transformations in human and natural systems. Island Press, Washington, D.C., USA.

Wilcove, D. S. 2008. No way back: the decline of the world's great animal migrations. Island Press, Washington, D.C., USA.

APPENDIX A

Description and equations for the household submodel of HUMENTS (*Ecological Archives* A020-010-A1).

APPENDIX B

Equations and parameters used by the ecological submodel of HUMENTS (*Ecological Archives* A020-010-A2).

APPENDIX C

A figure showing mean annual rainfall trends in the GSE over the past half century (*Ecological Archives* A020-010-A3).

APPENDIX D

Results of global sensitivity analysis (*Ecological Archives* A020-010-A4).

APPENDIX E

Error bounds for response variables (*Ecological Archives* A020-010-A5).

APPENDIX F

A figure showing the effects of rainfall and antipoaching on labor allocation patterns (*Ecological Archives* A020-010-A6).

APPENDIX G

A figure showing HUMENTS model fits to data (*Ecological Archives* A020-010-A7).

SUPPLEMENT

C source code and data files for HUMENTS model (*Ecological Archives* A020-010-S1).