SCALE Annual Report – 2004-2005

Research and Education Activities

Research Objective 1: Case Study Synthesis and Comparisons
Objective: *Develop a state-of-knowledge publication on complexity, scale, and fragmentation.*

In this research objective the goal is to: 1) synthesize what we know about the drivers of fragmentation, the nature of fragmented landscapes and how ecosystems and people respond to those changes within sites and across sites; 2) present what is known at a workshop, and; 3) to publish the findings in an edited volume. To this end we organized a SCALE workshop in Ithala Game Reserve, South Africa, July 22-24, 2003. The work on the book is on-going, and will be completed in the fall of 2005, for a 2006 printing by Kluwer Academic Publishers. The title of the book is: Fragmentation in Semi-arid and Arid Landscapes: Consequences for Human and Natural Systems.

Research Objective 2: Complexity Framework and Analysis
Objective: *Develop a framework for complexity analysis, apply to all sites, determine herbivore access to complexity for fragmented and un-fragmented grazing orbits (in conjunction with RO 4).*

Activities under Research Objective 2 have been varied. We have applied our herbivore-centric metric of landscape complexity developed in 2003 to all SCALE areas, and have worked with collaborators on socioeconomic measures of complexity and fragmentation. Research on the relationships between heterogeneity and livestock stocking in the US is continuing. Heterogeneity analyses of landscapes in Kenya, Australia, and more generally around the globe are continuing. Boone has refined methods of modeling animal movements using evolutionary programming, and has prepared a manuscript.

Research Objective 3: Herbivore Selection at the Paddock Scale
Objective: *Determine the effects of pasture size on animal diet quality and performance.*

The main aim of the activities covered under this objective is to test whether seasonal variation in the diet quality of cattle is influenced by the sizes of paddocks and the complexity of vegetation enclosed within them. We hypothesize that large paddocks and complex mixes of vegetation provide greater opportunities for selectivity in animal diets, allowing herbivores to better regulate their nutrition, particularly during the dry season when dietary protein levels typically fall below maintenance levels.

There have been three components to our work over the past year:
a) Experimental
We have continued with the collection and analysis of faecal material from selected paddocks in the Dalrymple Shire to compare cattle diet quality to paddock characteristics (e.g., paddock size and landscape complexity).
b) Review

We have reviewed the present and historical drivers and consequences of rangeland fragmentation at both regional and property scales in Australia, with specific emphasis on our study site in the Dalrymple Shire, north east Queensland (book chapter and paper).

c) Metric of Landscape Complexity

We have developed an analysis for quantifying an aspect of landscape complexity, spatially asynchronous variation, that should be of practical significance for how humans and herbivores access heterogeneous resources.

(This work also ties in with two related research projects, one looking at how rangeland systems are affected by the configuration of fencing and water infrastructure, and the other looking at the role of social networks in rangeland systems.)

Research Objective 4: Herbivore Movements in Fragmented vs. Intact Ecosystems
Objective: *Determine effects of fragmentation on herbivore access to ecosystem complexity.*

The following four research activities were undertaken by ILRI from 2004 to 2005:

1. Second year of the assessment of the effects of landscape fragmentation on the movement of pastoral livestock herds in the Kitengela and Mara ecosystems (fully funded by the NSF SCALE grant),
2. Initiation of an MSc on the current and historical livestock movements at local and regional scales in response to fragmentation in the Athi-Kaputiei ecosystem, Kenya (fully funded by the NSF SCALE grant), and
3. Completion of a book chapter on fragmentation processes and effects on wildlife and pastoral livelihoods in the Athi-Kaputiei ecosystem (partially funded by the NSF SCALE grant).

Research Objective 5: Typology of Actual Land Use Patterns
Objective: *Develop a standard format to differentiate and compare land use patterns and management scales within and across study sites.*
Research Objective 7: Factors Driving Contemporary Trends in Land Use Change
Objective: *Investigate how ecological, political, and socio-economic factors interact to influence individual land use decisions.*

"Livestock productivity and mobility in southeast Kazakstan"
SCALE study site 4 and 5

Kazak nomadic pastoralists formerly moved their livestock seasonally between major ecological zones, in response to spatial and temporal variability in the climate and productivity of pastures. Seasonal mobility was interrupted or compressed during the Soviet period, virtually ceased in the immediate post-Soviet 1990s, but is re-emerging as flock numbers rebound from a mid 1990s livestock population crash associated with the collapse of the USSR. However, currently the majority of livestock are managed in fragmented and sedentary systems rather than moving across ecological boundaries.

Previous research in southeast Kazakstan has shown that livestock productivity is directly affected by whether animals are moved to seasonal pastures or are grazed all year around settlements. However, since the economic costs of movement must now be borne by individual pastoral families, this research aims to determine the longer-term costs and benefits to livestock owners of moving their livestock to seasonal pastures. This strategy will be compared to having animals forage in one location throughout the year, with supplementary feeding in winter as necessary. The study covers 2 years, starting in spring 2004 and ending in spring 2006.

Twelve pastoral households and their flocks of sheep and goats are being monitored in two ecological regions of southeast Kazakstan (Scale study site 4 Balkhash Basin, and study site 5 Moinkum Desert). In each of two villages, selected owners comprise two households managing their animals all year around the village, two keeping livestock year-round at outlying barns more than 5 km from the village, and two owners who move their livestock each season to different pasture zones, from 20 km up to 300 km distant from the villages. The biological and economic returns to seasonal livestock movement are compared to circum-village and sedentary grazing management.

Data on each of the 12 households have been gathered in three surveys – spring and fall 2004, spring 2005. Two further surveys will be carried out in fall 2005 and spring 2006. Data are collected from the 12 households on:

- Live weight of 20 adult ewes and 20 adult nanny goats (480 smallstock total)
- Viability of their offspring (lambing/kidding rate, mortality, weight gain to 1 year)
- Flock growth through reproduction
- Pasture measurements of yield and livestock feed value at each grazing location
- Costs of seasonal movement to pastures (labor, fuel, transport)
- Costs of winter supplementary feeding
- Asset ownership necessary for seasonal movement (wagons, vehicles, tents, etc).
- Cash income from market sales of live animals, wool and fiber
- Subsistence income from home slaughter and animal by-products

Research Objective 8: Economic Surveys and Analysis
Objectives: *Gather information on household economic performance and the economic dimensions of livestock production systems in relation to scale and resource access.*

Activities for this objective involve gathering data on household economic performance and the economic dimensions of livestock production in relation to scale and resource access. Survey data and secondary sources are being used to assess household economic viability, spatial resource access patterns and level of material subsidy. The major objective of this RO is to provide adequate information to enable relatively simple socio-economic modelling to be carried out in tandem with the Savanna ecosystem model. Scenario analyses can then be undertaken to look at the interactions between ecological complexity and household well-being in case-study environments.

Kajiado

A journal article on scenario analyses for the Kajiado case study was submitted, revised and accepted for publication in the journal Agricultural Systems. The paper describes a simple rule-based model that tracks cash flow and calories in agro-pastoral households and its linkages to the Savanna model.

Kazakstan

During the year, data were collected to generate the information needed to specify a PHEWS module for Kazakstan. Survey data were collected from a total of 58 households in two villages, Ay Daly in the Almaty Oblast and Sary Ozek in the Zhambyl Oblast, and these data have been summarized using descriptive statistics.

Research Objective 9: PHEWS (Pastoralist Household Economic Welfare Simulator) Model Assessments

Objective: Determine economic-ecological interactions resulting from alternative land use practices.

Kajiado & Kazakstan

During the year, PHEWS was reprogrammed to allow it to be specified essentially as an agent-based model. Instead of using representative households of different types, a whole distribution of individual households can be simulated on the landscape, whose collective characteristics match observed data. PHEWS now operates by reading a data input file with the “global” (unchanging) data needed for the run. At each iteration of the model, it reads a household file, with one record per household, the model is run through, and the household file is written out again with the changes that have occurred during that time period (such as changes in livestock numbers due to births, deaths, purchases and sales, etc). This file then becomes the input household file for the next iteration. At the same time, a set of “history” files is written out with key model variables at each iteration (one record per iteration per file), for as many households as are being simulated. These history files include herd numbers over time, cash flow over time, food consumption in the household by source of calories over time, and key output indicator variables by household over time.

Related Savanna-PHEWS modelling work is planned to look at further sets of scenarios. These include the following:

- Quantify the benefits and costs of maintaining pure and mixed-breed herds, and identify a mix of breeds that maximizes animal productivity and expected returns.
- Quantify the usefulness of maintaining some portion of group ranch lands as communal grazing.
- Identify potential pathways for diversification within livelihood groups defined through cluster analyses, and identify how the options for diversification vary across the landscape, and how they may vary for wealth levels.

Development of PHEWS for Kazakstan using the results of the new household survey data will be undertaken in the coming months.

Research Objective 11: Spatial Complexity, Temporal Variability and Population Patterns

Objective: *Develop competing models linking animal populations to spatial complexity.*

Last year’s research activity on spatial and temporal heterogeneity and ungulate population dynamics included three major parts.

1. Implementation of an empirical Bayesian method for the state-space model (SSM) to estimate the strength of density dependence of ungulate populations and the additive effects of climate on the dynamics of ungulate populations. This new implementation allows for estimating the uncertainty of the estimates of the strength of density dependence and climate effects by constructing 95% confidence intervals or bootstrapping the variances of the estimates. It also takes into account autocorrelation and measurement errors in time series data.
2. Implementations of the Unscented Kalman filter, the Gibbs sampler and the adaptive Metropolis algorithm to estimate the parameters of the theta-logistic models and the Ricker model. The Bayesian nonlinear SSM model accounts for autocorrelation and measurement errors in time series data.
3. Applications of the linear and nonlinear Bayesian SSM model and the Markov chain Monte Carlo simulations (MCMC) to test hypotheses regarding the effects of spatial and temporal heterogeneity on the dynamics of ungulate populations (**H1**-**H3**).

H1: Spatial heterogeneity in resources might weaken the effects of weather and density on population growth of large herbivores by improving nutrition of individuals. Variation in topography causes plants to mature at different times. Large herbivores move to track this topographically induced variation in plant phenology, thereby extending the interval of time when plants can be consumed at peak nutritional quality. Therefore, spatial variation in resources may mitigate resource shortages and attenuate the effects of weather and density on vital rates of their populations.

H2: *Background*: The North Atlantic Oscillation (NAO) is used as an integrating interface between local climate and large spatial climate, which influences the dynamics of populations. However, it is well known that the NAO and SO explain the variability of local climates in different areas to various degrees.
Hypothesis: We hypothesized that large spatial scale climate must work through local, proximate climatic environments to influence the performance of organisms and populations. Responses of ungulate populations to large spatial climatic phenomena might be site- or regional specific.

H3: Fowler's hypothesis states that large mammals exhibit density dependence regulation at high densities near the carrying capacity, and variability of population sizes was inversely related to the strength of density dependence. The Fowler hypothesis predicts that the value of the parameter θ of the theta logistic model (Eqn. 3, Appendix A) will be greater than 1.0 and is inversely related to the CV in population sizes. McCullough hypothesized that the parameter θ in the theta-logistic model is positively related to spatial heterogeneity.

Modeling approach for testing H1 was to fit subsets of the global model, the autoregressive Gompertz model (Eqn. 1, Appendix A) including the direct and indirect density dependence terms to 23 time series of counts of ungulate populations in North America and Europe. The fitting was done with the empirical Bayesian SSM method. Model selection using the Akaike weight was used to select the best approximating model for each time series. The strength of direct density dependence was measured with the magnitude ($|b|$) of coefficient b. Linear regressions were used to establish statistical relationships between the strength of density dependence and spatial variability of topography (standard deviation of elevations within a 25-km radium from the center of a study site) and latitudes of study sites.

The modeling approach for testing H2 was to add the NAO index and the first principle components of local climate variables, and mean temperature and precipitation of growing and dormant seasons, as an explanatory variable in the best approximating model identified in the analysis of density dependence. Inferences on the effects of local and large scale spatial climate were made with the Akaike weight and bootstrapped 95% CI of the coefficient for the climate variable.

The modeling approach for testing H3 was to fit the theta-logistic model (Eqn. 3) cast in the form of the nonlinear SSM model to 30 time series, spanning 20-75 years in length, of ungulate counts or estimates of densities, to estimate the key parameter θ and variance of environmental stochasticity. The fitting was done using the Gibbs sampler and adaptive Metropolis algorithm. The chain was initialized with the unscented Kalman filter. The convergence of the chain was diagnosed using the Geweke statistic. We used the Bayes factor (Eqn. 4 a,b) to assess the weight of evidence in favor of the theta-logistic model against the exponential model and the Ricker model against the exponential model, respectively. Inferences on θ were based on the final model selected and the posterior distribution of θ that the MCMC simulations constructed with Eqn. 3. The value of θ is 1.0 in the Ricker model and zero in the exponential model.

Research Objective 12: SAVANNA-PHEWS Complexity-Fragmentation Experiments
Objective: *Model effects of fragmentation on ecosystems and people.*

In early 2004, we judged that the African SAVANNA-PHEWS applications could not represent effects of fragmentation in other continents well. We began an application of SAVANNA-PHEWS to the part of Kazakhstan south of Lake Balkhash, northwest of Alamty. Development of that application has continued.

We (Boone, BurnSilver, and Thornton) are conducting analyses related to subdivision under leveraged funds supported by the Belgian Ministry of Foreign Affairs, Foreign Trade, and International Co-operation in a grant to the International Livestock Research Institute, Nairobi (Reid, PI). Maasai of Imbirikani Group Ranch, Kajiado District, Kenya, are building a water pipeline that extends from a large pipeline running through the center of their ranch into the Chyulu Hills. We are using SAVANNA-PHEWS to quantify potential changes in wildlife and livestock stocking and pattern due to these additional resources. We are also modeling how planned and structured subdivision of group ranches will affect pastoral resources. The modeled subdivision will emulate, to the degree possible, the staged grazing pattern Maasai use throughout the year (i.e., small parcels for permanent households, larger communally held grazing areas for the dry season). PHEWS is being modified to better represent Maasai decision making in the region, as reviewed under RO9.

Research Objective 13: Complexity and Fragmentation in Theoretical Ecosystems
Objectives: *Study general responses of ASAL ecosystems to fragmentation.*

Research under Objective 13 has been particularly active this year. Manuscripts written in late 2004 were revised and are now 'In press,' and results were disseminated through presentations. A significant research effort was undertaken that will explore how rainfall quantity and variability relate to changes in herbivore populations under landscape fragmentation.

Research Findings

Research Objective 1: Case Study Synthesis and Comparisons

Work in ongoing on writing/editing book chapters for the SCALE synthesis book. The chapters in this book will summarize the findings related to SCALE case studies and synthesis chapters discussing what we know about the drivers of fragmentation, and the nature of fragmented landscapes and how ecosystems and people respond to those changes.

Research Objective 2: Complexity Framework and Analysis

Analyses for the summary chapter by Boone and BurnSilver in the upcoming SCALE volume have continued; the chapter will be completed when case study chapters can be reviewed. We have computed a series of metrics for each of the SCALE sites, including simple measures of heterogeneity such as the deviation in elevation and type counts in vegetation maps. Normalized Difference Vegetation Indices derived from satellite images from more than 20 years have been summarized, yielding integrated estimates of NDVI and coefficients of variation, a useful measure of year-to-year variation in the SCALE sites. Our herbivore-centric metric of landscape complexity, where the greenness herbivores can access as they are allowed to move more freely across a landscape has been calculated for all sites (Table 1). Example variograms, where distance is related to greenness accessed based on Landsat NDVI, are shown for the two most extreme responses in Figure 1. We have worked with R. Kruska and R. Reid of the International Livestock Research Institute and others to define and calculate metrics that represent socioeconomic complexity or fragmentation. Examples include human population density, road density, infrastructure indices, and annual per capita income calculated or assigned for selected SCALE sites. We have also been in contact with SCALE collaborator C. Stokes in Australia, who is conducting analyses of landscape complexity.

Graduate students BurnSilver and Worden, with Boone, continue to analyze how landscape heterogeneity in southern Kajiado District relates to livestock movements Maasai make, responsive to both RO2 and RO4. Boone wrote a tool that allows BurnSilver and Worden to analyze landscape surfaces (e.g., elevation, slope, NDVI images) using their movement data, without requiring them to use GIS commands. Analyses have focused on quantifying how livestock movements may increase access to integrated NDVI. The technique of taking mobile pastoralists and simulating them being sedentary has been particularly effective. For example, in 2000, mobile residents in the Eselenkei, Emeshinani, Lenkism ($P < 0.05$), and North Imbirikani

($P < 0.001$) regions accessed significantly more greenness than they would have had they been sedentarized.

Analyses of the effects of spatial and temporal variability on large herbivores have been revised and accepted for publication in *Ecology* (Wang et al., In press). Analyses are ongoing that expand on that work, correlating variability in weather patterns and the standard deviation of elevation with the strength of density dependence in large herbivores. Those analyses include more than 20 sites across the globe.

K. Price of the Kansas Applied Remote Sensing, University of Kansas, has led graduate student J. Thayn in analyses that correlate integrated NDVI in western US counties and the spatial heterogeneity of the counties to the numbers of livestock each supports. They have shown that more spatially complex counties support more livestock, all else being equal. Thayn has disseminated those results through presentations.

Boone built upon earlier innovations using evolutionary programming techniques to model Serengeti wildebeest migration, devising a two step method that included an evolutionary and a learning phase of modeling. Wildebeest in the Serengeti Ecosystem migrate in essentially a triangular pattern, moving from Maasai Mara National Reserve in the north in the dry season, through the Western Corridor in the transitional periods, and into the southern Serengeti and Ngorongoro in the wet season, then reversing the pattern. The objective function in the model used rainfall estimates derived from satellite images, and 1 km^2 resolution NDVI images from the Spot VEGETATION sensor. Twelve averaged monthly images of rainfall and NDVI were used in an initial stage of modeling, where the general migratory pattern of wildebeest was evolved. Five years of images (180 surfaces from 1998 to 2004) were then used to evolve migratory pathways specific to years. The evolved migratory pathways (Figure 2) mirror reasonably well the migratory pathways of real wildebeest. A manuscript summarizing the results is under review.

Research Objective 3: Herbivore Selection at the Paddock Scale

Preliminary indications from the dietary analysis work were presented in last year’s report (and are not added to here). We will probably continue collecting samples until the end of 2005, after which we will begin a more rigorous analysis of the data, testing for relationships between diet quality and complexity of the landscape areas within which livestock can select forage.

One aspect of landscape complexity that is likely to be of functional significance is asynchronicity in resource availability. Spatially asynchronous resource availability affords humans and herbivores the opportunity to enhance their utilization of landscapes by moving to new areas when resources become locally scarce, provided landscapes are not fragmented (Figure 3).

We have applied correlograms as a method for quantifying the spatial structure of synchronicity in resources in landscapes and have implemented this within a database to allow scaling to large spatial time series data sets. In landscapes where asynchronicity increases rapidly with distance, it would be expected that:

a) there is a strong reward for exploring and exploiting landscape heterogeneity;
b) human cultures and herbivore populations that evolved in these landscapes would likely have developed nomadic/transhumanant/migratory behavior in response to this incentive;
c) fragmenting such landscapes would likely disrupt social and ecological processes related to b);
d) in landscapes that have already been fragmented there would be a strong incentive to restore social and ecological connectivity so that spatial asynchronicity can be exploited (e.g., through carefully-structured enterprise consolidation, agistment arrangements and/or social networks).

We have tested this analysis with time series NDVI data (Normalized Difference Vegetation Index for AVHRR and MODIS images) and rainfall station data to quantify various temporal patterns of resource asynchronicity that could potentially be exploited. Initial test runs were conducted with rainfall and MODIS data for the Dalrymple Shire and the Serengeti. We are now in the process of running a more rigorous comparison between the Dalrymple Shire and the transhumanant region of the Sahel (where land use patterns are well-documented) using AVHRR data (which provides a longer time series than MODIS but at a coarser resolution). The methods we are using have been used to study the phenomenon of spatial synchronicity in population dynamics (e.g., masting and the Moran effect), often emphasizing the benefit of synchronized reproduction as a means of reducing predation. However, as far as we know, these techniques have not been applied to the corollary of this: that spatial asynchronicity in resources should provide opportunities for optimizing foraging.

Research Objective 4: Herbivore Movements in Fragmented vs. Intact Ecosystems

1. Assessment of the effects of landscape fragmentation on the movement of pastoral livestock herds in the Kitengela and Mara ecosystems (Kshatriya, Nkedianye, Reid)

This study focuses on the effect of the presence/absence of fencing and the presence/absence of high numbers of wildebeest on the movement patterns of cattle. Here, fragmentation is taken to be one factor limiting access to vegetation.

During this year, we expanded the number of herds under study to capture a wider range of herd sizes and to broaden our spatial coverage of the landscape. Previously each of the four herds was tracked for 10 consecutive days, now each herd is tracked for only five days. This allows us to track an additional four herds during the same time period. In addition to sampling a larger number of herds, the design change allows us to measure the effects of landscape fragmentation on livestock grazing patterns over a wider range of fragmentation circumstances.

In addition, for the Kitengela study site, NDVI values from the Vegetation Spot 5 satellite were collected and analyzed with the grazing pattern data for most sampling periods. The resolution of the data is 1 km x 1 km. Results show that total distance walked decreases with higher NDVI values. The relationship between distance walked and NDVI is weaker in areas that are highly fragmented by fences. Another NDVI data base is being developed using MODIS. The resolution is approximately 250m. This fine scale data may help explain finer movement patterns at the landscape level. A program written in C, which was developed last year to identify the cross-over points in each track, is being using to measure a variety of path characteristics over different sampling times.

2. Initiation of an MSc on the current and historical livestock movements at local and regional scales in response to fragmentation in the Athi-Kaputiei ecosystem, Kenya

Kiros Lekarsia, a pastoral MSc student, began a region-wide study to assess the historical and current changes in movement patterns of pastoral people and their livestock in response to drought, comparing sites with different levels of fragmentation. Kiros completed his coursework at the University of Nairobi in July 2005. He will soon start to collect information on livestock herd movements at sites with different histories of fragmentation by interviewing about 50 herders at each site. Herders will be asked to recount seasonal herd movements starting in the 1940s up to the present in response to the droughts of 1961, 1973, 1984, 1991, and 1999. They will be asked why they moved, where they moved and how their decisions on movement are affected by fragmentation. Herders will be asked to compare drought year movements with 'wet' year movements close to the time of each of these droughts. This information will be related to historical data on NDVI, when it is available. Kiros will complete his MSc in September 2006.

3. Completion of a book chapter on fragmentation processes and effects on wildlife and pastoral livelihoods in the Athi-Kaputiei ecosystem (partially funded by the NSF SCALE grant).

In January 2005, we submitted a book chapter entitled: Fragmentation of a peri-urban savanna, Athi-Kaputiei Plains, Kenya, by Robin S. Reid, Helen Gichohi, Mohammed Y. Said, David Nkedianye, Joseph O. Ogutu, Mrigesh Kshatriya, Patti Kristjanson, Shem C. Kifugo, Jasphat L. Agatsiva, Samuel A. Adanje and Richard Bagine. This synthesizes what we know about the process of fragmentation in this ecosystem and its consequences for wildlife populations and people. The following summarizes the findings in this book chapter.

The Athi-Kaputiei Plains (part of which is called the Kitengela) is in southern Kenya and includes Nairobi National Park and the extensive rangelands to the south. It still supports a large and long distance wildlife migration, which is particularly unusual because it sits next to Kenya's capital of Nairobi, currently a city of just over 2 million people. The Athi-Kaputiei is exceptional in East Africa, but it also represents other processes that are globally universal: urbanization, rapid in-migration, expansion of land-use with little planning, high poverty rates, and land tenure change. At the end of the 1800's, some observers claimed that this ecosystem supported the 'most spectacular concentration of wildlife in all of East Africa' (Simon 1962). Over the last century, the Athi-Kaputiei pastoral-wildlife system became progressively compressed, bounded and fragmented. The process of fragmentation included the establishment of the city of Nairobi in the early 1900's, expansion of European and African settlement, establishment of Nairobi National Park in the dry season grazing reserve of both herders and wildlife, formation of group ranches in the 1970's and privatization of land in 1986. In 2004, we measured 6471 fencelines in this 450 km^2 ecosystem, representing enclosure of 14% of the ecosystem. These fences are clustered principally near roads and towns, and cut across several important wildlife corridors.

Our analysis of aerial survey data shows that from 1977-2002, wildlife populations fell precipitously by 72%, or an average of 5% per year, in the three triangles outside Nairobi National Park (Gichohi et al. in prep., Ogutu et al. in prep), nearly identical to the rate of loss of resident wildlife in the Mara ecosystem over a similar time period (Ottichilo, de Leeuw et al. 2000). More than 90% of the eland, giraffe and wildebeest disappeared over this 25-year period, twice the average wildlife loss. Impala and Thomson's gazelle declined by 78% overall, while Grant's gazelle populations halved. Much of these changes are probably due to mortality of animals, but some could be due to movement of animals out of the ecosystem.

With declining wildlife populations, one might expect livestock populations to rise in the pastoral part of the ecosystem, as more forage and water become available, and wildlife-livestock disease transmission presumably decreases. Remarkably, sheep and goat populations dropped by 63% in the last 25 years, at the same rate as the small-bodied wildlife (Gichohi et al. in prep). Donkeys nearly disappeared altogether. Cattle populations were stable except for heavy declines during the more recent droughts, between the periods 1994-96 and 1998-2000 (Gichohi et al. in prep).

We expected fewer losses of wildlife inside Nairobi National Park than in the three triangles outside the park, because of differences in land use. Our data support this. While total wildlife biomass dropped strongly outside the park, there was no perceptible change, over the same period, inside the park (1977-2002, Ogutu et al. in prep.). Poaching and loss and fragmentation of habitat by fencing are the primary causes of the wildlife decline.

Research Objective 5: Typology of Actual Land Use Patterns
Research Objective 7: Factors Driving Contemporary Trends in Land Use Change

Preliminary results from the fall 2004 and spring 2005 animal weighing surveys indicate that the sheep that moved seasonally to graze on the most distant and most productive pastures did not lose weight over winter. Pastures in the winter grazing grounds yielded two to three times the dry matter of peri-village pastures. Sheep grazed around the villages in three seasons and housed over winter with supplementary feed lost between 4 to 6.5 kg between November 2004 and May 2005. Moreover, village-based sheep weighed considerably less – by 6 to 14 kg - going into winter, compared to sheep of the same breeds that were moved each season in 2004 to distant pastures.

Being analyzed are the results of the spring 2005 lambing season, spring 2005 pasture measurements and fall 2004 household economic surveys.

Research Objective 8: Economic Surveys and Analysis

The coupled models created under this RO were used to quantify some of the effects of subdivision and land fragmentation on household livestock numbers and on food security in Kajiado. For the group ranches simulated, model outputs indicated that subdivision results in substantial reductions in livestock numbers, partially because households have to sell more animals to generate the cash needed, with serious long-term consequences on herd sizes and food security. If subdivision occurs, even to parcels as large as 196 km^2, livelihood strategies may need to be modified to maintain current levels of household well-being.

Research Objective 9: PHEWS (Pastoralist Household Economic Welfare Simulator) Model Assessments

Based on the current work of developing new coupled model scenarios, findings from this RO are forthcoming.

Research Objective 11: Spatial Complexity, Temporal Variability and Population Patterns

H1:
Ten ungulate populations had sufficient statistical evidence of negative density dependent regulation. Among the 10 ungulate populations, the strength of density dependence, measured with $|\hat{b}|$, was inversely related to the standard deviation of elevations (Figure 4a). The regression slope was negative and significant (β = - 0.0005, P = 0.019) in the least squares regression of the term $|\hat{b}|$ against the standard deviation of elevations. The regression slope is positive and significant (β = 0.02, P = 0.013) in the least squares regression of the term $|\hat{b}|$ against the latitudes. Our results suggest that the greater the variation in the topography of habitats, the weaker the negative density dependent feedback in northern ungulate populations. Thus, heterogeneous landscapes weakened the strength of density dependence in northern ungulate populations. On the other hand, the strength of density dependence was positively related to the latitudes where ungulates reside. Ungulate populations living further north underwent stronger density dependence in population growth (Figure 4b).

H2:
The bison population of Yellowstone National Park (YNP), Wyoming, and the elk population of National Elk Refuge, Wyoming, and Rocky Mountain National Park, Colorado, showed sufficient statistical evidence suggesting that these ungulate populations primarily responded to local climate variability, and the influence of the NAO was minimal and was not detected through model selection. However, we found that the elk population of YNP, Wyoming, the red deer population of the Rhum Island, United Kingdom (UK), the soay sheep population of the St. Kilda Island, UK, the bison population of Alberta, Canada, the elk population of the Gravelly Mountain, Montana, and the sika deer and red deer populations of New Forest, UK, were related to both local climate and the NAO. The responses of ungulate populations to the North Atlantic Oscillation were population- and site-specific.

In the Gran Paradiso National Park, Italy, the NAO can only explain about 25% of variability in annual average snow depth (Figure 5a). The effects of snow cover were dominant over the effects of the NAO. The Akaike weight was 0.94 for the model including the direct density dependence and snow cover, and 0.04 for the model having the direct density dependence and the NAO index (Figure 5b).

We used the spectral analysis to detect the periodicity of the population dynamics of the short-tailed shrew (*Blarina brevicauda*) in central eastern Illinois, using 296 months of data (May 1972 – December 1996). The smoothed periodogram plot shows a peak at the frequency of 1/12 cycles per month for the short-tailed shrew, suggesting seasonal fluctuation. The AICc values of the random walk trend model, the random walk + slope model, and the random walk + random slope + seasonal component model fit to the monthly NAO index were -471.34, -436.24, and -433.65, respectively. The AICc values did not suggest that the NAO fluctuated seasonally. Furthermore, the Pearson correlation coefficients between seasonal fluctuations (extracted using the basic structure model) of temperatures and shrew abundance were significant (0.257 with mean temperature, 0.255 with minimum temperature, and 0.261 with maximum temperature, $P < 0.01$). However, the correlation coefficients between seasonal fluctuations of shrew abundance and the monthly NAO index were not significant (correlation coefficient -0.06, $P = 0.26$). Therefore, spatial scales of climate are important for modeling seasonal population dynamics for small sized animals.

H3: This part of the work is still ongoing. However, we had a number of cases where the value of the parameter θ of the theta logistic model was not greater than 1.0 as the Fowler hypothesis predicts for large mammals.

The Bayes factor (BF) has positive support for the theta-logistic model (BF = 5.3) and the Ricker model (BF) = 4.8) against the exponential model for the bison population in Yellowstone National Park. The density of the posterior distribution of the parameter θ indicates that the 95% credible interval of θ includes 1.0 (right panel, Figure 6). However, the 95% credible interval of term b of the Ricker model (Eqn. 1, Appendix B) ranged from 0.00003 to 0.00005. Therefore, we conclude that the value of θ was 1.0 for the YNP bison. This result did not support the prediction of the Fowler hypothesis.

The Bayes factor (BF) shows positive support of the Ricker model (BF = 3.8) for the alpine ibex (*Capra ibex*) of the Gran Paradiso National Park, Italy, but no support for the theta-logistic model against the exponential model. The 95% credible interval of *b* was 0.00004 to 0.000057 (right panel, Figure 7). In the Ricker model, the value of θ was 1.0. In this case we did not find sufficient support for the Fowler hypothesis.

Research Objective 12: SAVANNA-PHEWS Complexity-Fragmentation Experiments

Climate data for the Balkhash region of Kazakhstan are in place. Landsat GeoCover satellite images from ca. 2000 were placed in our spatial database. Vegetation and land cover was acquired, provided courtesy of the DARCA Project of Macaulay Institute, Aberdeen. A digital elevation model was acquired from the Shuttle Radar Topography Mission program, and from that, slope and aspect calculated. Soils have been scanned from maps purchased from the Soils Ministry of Kazakhstan, and digitizing is ongoing. Topographic maps at 1:200,000 scale were scanned and merged, and along with the other spatial data layers, georectified to overlay the Landsat image. From the topographic layers, information such as distance to water sources can be extracted. Vegetation traits, animal stocking rates, weather data (e.g., snow depth, solar radiation), etc. are being parsed from sources acquired during travels to Kazakhstan in 2004. The Balkhash application will be completed and merged with PHEWS in 2006.

Modeling under the leveraged Belgian project is ongoing, with data gathering still continuing. However, we anticipate highlighting both the advantages of adding water sources to areas, and the costs, such as a loss of grazing reserves. In the subdivision analyses, we will judge how the planned fragmentation will affect wildlife, livestock, and the pastoral people. PHEWS has been modified to more closely approach an agent-based model, and modification will continue.

Research Objective 13: Complexity and Fragmentation in Theoretical Ecosystems

We now have three African SAVANNA ecosystem model applications that have each supported one or more publications, one from Ngorongoro Conservation Area, Tanzania (e.g., Boone et al. 2002; Thornton et al. 2003; Galvin et al., In press), the Vryburg area of South Africa (Boone et al. 2004; Thornton et al. 2004), and southern Kajiado District, Kenya (Boone et al., In press; Thornton et al., In press). Further, a theoretical application derived from the South African SAVANNA effort has proven useful in research (Boone and Hobbs 2004; Boone 2005; Boone et al., In press). These peer-reviewed applications are now forming the foundation for a significant research effort to quantify how variation in the amount and timing of rainfall affects the number of livestock that can be supported on lands under different levels of fragmentation.

In SCALE-supported research in southern Kajiado District, Kenya, we have demonstrated that site productivity is an important determinate in the effects of landscape fragmentation on the number of livestock that can be supported on group ranches (Boone et al., In press). However, those analyses included only four group ranches, and actual recorded rainfall patterns. In the current analyses, the role of productivity on effects of fragmentation will be squarely addressed. Further, variation in rainfall over time will be included, allowing us to speak to the long-standing arguments regarding rangeland equilibrium and disequilibrium dynamics (Vetter 2004).

For each of the three SAVANNA applications, a 1000 km^2 area within the study sites was selected, and the application adjusted to represent that area alone. To ease interpretation, the herbivore components in the models were each simplified to represent only cattle (as in Boone and Hobbs 2004; Boone 2005); the vegetative modeling was not altered. For each of the areas, maps were created that divided the 1000 km^2 area into successively smaller and smaller parcels (Figure 8), down to 100 ten km^2 parcels (1 parcel at 1000 km^2, 2 at 500 km^2, 3 at 333.3, … 50 at 20, 75 at 13.3, 100 at 10 km^2). The weather histories available for each area span 30 or more years. We sought to alter the rainfall amount, and the inter-annual coefficient of variation (CV; year-to-year differences in total rainfall, in percentages). Without careful consideration, it is easy to incorrectly altered seasonality in rainfall when adjusting the CV. Here, a method was developed and programmed that altered rainfall amounts and CVs while retaining seasonality. For each of the three sites, rainfall was altered (Figures 9, 10) to span from 100 to 1000 mm per year (100, 200, 300 … 800, 900, 1000) and CVs from 0 to 60 percent (0%, 5, 10 … 50, 55, 60%).

Conducting analyses for this massive design entails simulations for 394 parcels (i.e., the total shown in Figure 8), each with 10 rainfall levels and 13 levels of CV, for three study areas. These total more than 150,000 simulations. Areas modeled in each simulation were modified to speed analyses, so that only the smallest areas possible are modeled in each case. Winsock TCP/IP host and client programs were written that allow multiple machines to conduct analyses, with the host program tracking and graphically displaying modeling progress. Client programs (including one running on the machine that runs the host program) may join in modeling or be removed from modeling smoothly. Currently, two machines are involved in modeling, which will continue for several weeks.

When modeling is complete, analyses will proceed along two pathways, yielding two manuscripts. First, for each of the areas, analyses will have been run for the observed rainfall, or some close value (mean rainfall and CV for each area are about: Ngorongoro – 800 mm, 20%; South Africa – 400 mm, 35%; Kajiado District – 500 mm, 30%). Analyses will also have been run for the same rainfall amounts, with CVs from 0% to 60%. The strength of density dependence in cattle populations will be quantified, and changes in vegetation dynamics summarized. We will test if non-equilibrium dynamics dominate rangeland dynamics at CVs above 30%, as has been theorized (Ellis 1995), and will quantify how that relates to fragmentation. Second, a large matrix will be created that reflects the changes in livestock that can be supported on 1000 km^2 as rainfall and CV change, under increasing fragmentation. Regression analyses will yield formulas that summarize how rainfall amount, related to productivity, and rainfall CV relate to effects of fragmentation on herbivore stocking. In addition, we will be able to explore interactions between precipitation amount and CV as it relates to rangeland dynamics, which has not been done.

Opportunities for Training and Development

A MSc student working on RO4 in Kenya is being supported on this project.

A young Kazakh pasture scientist at the Kazakh Scientific Centre for Livestock and Veterinary Research has received short training courses in English language and IT skills, Almaty, Kazakhstan.

Galvin, KA. 2005. Scale and Stewardship: From the Local to the Global and Back. Presentation given at the Seminar Series, Department of Forest, Rangeland, and Watershed Stewardship.

Project results and data were used in Tom Hobbs' class, NR75, Systems Ecology.

Boone conducted modeling with Mr. Victor Runyoro, Principal Ecologist of Ngorongoro Conservation Area and doctoral graduate student of Sokoine University of Agriculture, Morogoro, Tanzania, from Nov 18 to Dec 12, 2004. Boone conferred with Thornton during modeling to determine the usefulness of PHEWS in Runyoro's work. In general, the research dealt with how much Maasai would need to be reimbursed monetarily, to offset losses if they stopped cultivating within Ngorongoro. The results were submitted as part of Runyoro's Ph.D. dissertation.

Outreach

At the Australian sites, the participation of local pastoralists in this research activity provides the opportunity for regular feedback on the objectives, developments and findings of the project.

A companion project, funded by the Belgian government, focuses on making sure the information that is generated by this NSF grant reaches the people who need it the most: pastoral community members, wildlife managers, scientists, and policy makers. This project supports four community facilitators that identify community and policy maker needs for research and provide the needed information to the appropriate groups. The team holds community and policy maker meetings every 1-2 months. The team also produces posters, policy briefs and website updates of new research results.

Feb 22 2005. Roy Behnke lecture to MSc students, School of Geography and Environment, University of Oxford: Non-equilibrium theories of rangeland dynamics: the evidence after fifteen years.

March 28 2005. Roy Behnke lecture to School of Geography and Environment, University of Oxford: Free distributions and property rights: resource use in mobile pastoral systems.

Presentations

Boone, R.B., N.T. Hobbs, K.A. Galvin, R.H. Behnke, R.S. Reid, P.K. Thornton, A.J. Ash, C. Kerven, K.P. Price, M.B. Coughenour, and S.J. Tavener. 2005. Biocomplexity, scale, and fragmentation: implications for arid and semi-arid landscapes (SCALE). Biocomplexity in the Environment Awardee Meeting, Washington, DC, Mar 21-23 (Poster presentation)

Boone, R.B. 2005. Land subdivision, heterogeneity, and declining food security for African pastoralists. International Grasslands Congress, Dublin, Ireland, Jun 30. (Poster presentation)

Boone, R.B. 2004. Quantifying effects of patch isolation on large herbivores. NREL Fall Seminar Series, Oct 8 (Invited oral presentation)

Boone, R.B. 2004. Approaches to understanding animal mobility using remotely sensed images. Monitoring Science and Technology Symposium, Denver, Colorado, Sep 22. (Invited oral presentation)

Boone, R.B. 2005. Balancing land uses in East African pastoral areas. NREL Fall Seminar Series, Sep 2 (Invited oral presentation)

Galvin, K.A., M. Betsill, D. Ojima, P.K. Thornton, M. Fernandez-Gimenez and R. Boone. 2005. Factors affecting household decision-making: concepts for understanding change under uncertainty. Paper for presentation at the 6th Open Meeting of the Human Dimensions of Global Environmental Change, 9-13 October 2005, University of Bonn, Germany. (Oral presentation)

Hobbs, N.T., R.B. Boone, and G. Wang. 2005. Spatial and temporal heterogeneity exert opposing effects on density dependence in populations of large herbivores. Sapporo, Japan, Aug. 1 (Invited oral presentation)

McAllister RRJ, Gross JE & Stokes CJ. 2005. Rangeland consolidation patterns in Australia: An agent-based modelling approach. (CABM-HEMA-SMAGET: Bourg-Saint-Maurice.)

Reid, R.S., Said, M.Y. and Nkedianye, D. 2005. Integrating different levels of scale in science, management and policy to sustain pastoral – wildlife ecosystems of East Africa. Invited symposium paper presented at the annual meeting of the Ecological Society of America, Montreal, Canada, 7-10 August, 2005.

Reid, R.S. 2004. Are synergies between people and wildlife possible? Keynote speech at the 10^{th} Anniversary conference at the University of Groningen, Netherlands, 10-12 Sept, 2004.

Reid, R.S. 2004. Sustainability and policy options for wildlife-rich rangelands in East Africa. Invited symposium paper presented at the annual meeting of the Ecological Society of America, Portland, Oregon, 1-6 August, 2004.

Stringer R, Boone R, Damania R and Bulte E. 2005. Paying for elephant conservation in Amboseli, Kenya. Presentation by Erwin Bulte at FAO, Rome, 29 May 2005.

Thayn, J.B., K.P. Price, and R.B. Boone. 2005. Rangeland fragmentation and cattle stocking rates in Kansas. Association of American Geographers Annual Meeting, Denver CO, April 5-9. (Oral presentation)

Thornton, P.K., K.A. Galvin, R.B. Boone, S.B. BurnSilver, M. Waithaka, and M. Herrero. 2005. Risk impacts on households in agropastoral and mixed systems in East and southern Africa. Paper for presentation at the 6th Open Meeting of the Human Dimensions of Global Environmental Change, 9-13 October 2005, University of Bonn, Germany. (Oral presentation)

Journal Publications

Behnke, R.H., Jabbar, A., Budanov, A. and Davidson, G. C. 2005. The administration and practice of leasehold pastoralism in Turkmenistan. *Nomadic Peoples* vol. 9. 1. In press. (acknowledges SCALE)

Boone, R.B., S.B. BurnSilver, P.K. Thornton, J.S. Worden and K.A. Galvin. In press. Quantifying declines in livestock due to land subdivision in Kajiado District, Kenya. Rangeland Ecology & Management (*Acknowledges SCALE with grant number*)

Boone, R.B. 2005. Quantifying changes in vegetation in shrinking grazing areas in Africa. Conservation and Society 3:150-173. (*Acknowledges SCALE with grant number*)

Boone, R.B. and N.T. Hobbs. 2004. Lines around fragments: effects of fencing on large herbivores. African Journal of Range & Forage Science 21:147-158. (*Acknowledges SCALE with grant number*)

Boone, R.B. In review. Evolving Serengeti wildebeest migratory patterns. Ecology. (*Acknowledges SCALE with grant number*)

Galvin, K.A., P.K. Thornton, J. Roque de Pinho, J. Sunderland, and R.B. Boone. In press. Integrated modeling and assessment for resolving conflicts between wildlife and people in the rangelands of East Africa. Human Ecology. (will acknowledge SCALE)

Galvin, K.A., Thornton, P.K., R.B. Boone, and J. Sunderland. 2004. Climate variability and impacts on East African livestock herders: the Maasai of Ngorongoro Conservation Area, Tanzania. African Journal of Range & Forage Science 21:183-189. *(no SCALE acknowledgement*)

Kerven, C., Alimaev, I., Behnke, R..H., Davidson, G.C**.**, Smailov, A., Temirbekov, S., Wright, I.A. 2004. Fragmenting pastoral mobility: Changing grazing patterns in post-Soviet Kazakstan. African Journal of Range and Forage Science 21(3): 159–169. (no SCALE acknowledgement)

McAllister, Ryan R.J., Iain J. Gordon, Marco A. Janssen, and Nick Abel. In press. Pastoralists' responses to variation of rangeland resources in time and space. Ecological Applications. (will acknowledge SCALE)

Ogutu J.O., Bhola, N. and Reid, R.S. 2005. The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Journal of Zoology of London* 265:281-293 (this grant is acknowledged in the paper)

Reid, R.S., Thornton, P.K. and Kruska, R.L. 2004. Loss and fragmentation of habitat for pastoral people and wildlife in East Africa: concepts and issues. *African Journal of Range and Forage Sciences* 21(3):171-181. (this grant is acknowledged in the paper)

Stokes CJ, McAllister RRJ & Ash AJ. In review. Fragmentation of Australian rangelands: risks and trade-offs for land management. The Rangeland Journal. (acknowledges SCALE with grant number)

Thornton, P.K., S.B. BurnSilver, R.B. Boone, and K.A. Galvin. In press. Modelling the impacts of group ranch subdivision on households in Kajiado, Kenya. Agricultural Systems (*Acknowledges SCALE with grant number*)

Wang, G., N.T. Hobbs, R.B. Boone, A.W. Illius, I.J. Gordon, J.E. Gross, and K.L. Hamlin. In press. Spatial and temporal variability exert opposing effects on density dependence in populations of large herbivores. Ecology. (*Acknowledges SCALE with grant number*)

Other Publications

Alimaev, Ilya I. and R. H. Behnke. Submitted. Ideology, land tenure and livestock mobility in Kazakhstan. In: Galvin, K.A., Reid, R.S., Behnke, R.H. and Hobbs, N.T. (eds), Fragmentation in Semi-arid and Arid Landscapes: Consequences for Human and Natural Systems. Kluwer Academic, Dordrecht. (Acknowledges SCALE with grant number)

Behnke, R.H, and G. C. Davidson**.** 2005. Range-based livestock production in Turkmenistan. In J. Milne (ed) *Pastoral Systems in Marginal Environments*. Proceedings of a satellite workshop of the XXth International Grasslands Congress, July 2005, Glasgow. Wageningen Academic Publishers, Netherlands, pp. 91-102. (does not acknowledge SCALE)

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Reid, R.S., H. Gichohi, M.Y. Said, D. Nkedianye, J.O. Ogutu, M. Kshatriya, P. Kristjanson, S.C. Kifugo, J.L. Agatsiva, S.A. Adanje and R. Bagine. Submitted. Fragmentation of a peri-urban savanna, Athi-Kaputiei Plains, Kenya. In: Galvin, K.A., Reid, R.S., Behnke, R.H. and Hobbs, N.T. (eds), Fragmentation in Semi-arid and Arid Landscapes: Consequences for Human and Natural Systems. Kluwer Academic, Dordrecht. (does not acknowledge SCALE)

Stokes CJ, McAllister RRJ, Ash AJ & Gross, JE. Changing patterns of land use and tenure in the Dalrymple Shire, Australia. In: Fragmentation in semi-arid and arid landscapes: consequences for human and natural systems. (Eds K. A. Galvin, R. Reid, R. H. Behnke, and N. T. Hobbs) (Kluwer: Amsterdam.) Submitted. (Acknowledges SCALE with grant number)

Other Products and Activities

Modeling conducted by Boone on the CoGRID grid computing system, and supported by SCALE, entailed simulating wildebeest migration. The model was used by CoGRID developers in a presentation entitled "Grant Report – Colorado GRID Computing Initiative" to the Colorado Institute of Technology, a Colorado government initiated organization that facilitates private and academic technological issues.

Findings Significant to the Discipline

Our results offer the first empirical evidence that spatial and temporal heterogeneity exert opposing effects on density dependence in populations of large herbivores. These results are important because they suggest that restricting access of large herbivores to spatial heterogeneity in resources, for example by fragmenting habitats, may reduce herbivore abundance even if the total amount of resources remains constant.

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Wang, G., N.T. Hobbs, R.B. Boone, A.W. Illius, I.J. Gordon, J.E. Gross, and K.L. Hamlin. In press. Spatial and temporal variability exert opposing effects on density dependence in populations of large herbivores. Ecology.

Appendix A

Eqn. 1

$\ln(N_t) = a + (1+b)\ln(N_{t-1}) + c\ln\left(N_{t-2}\right)$, where N_t, is population size at time t, *a* is the intrinsic rate of increase, *b* represents the effect of direct density dependence, and *c* is a coefficient describing the effects of delayed density dependence.

Eqn. 2

$\ln(N_t) = a + (1+b)\ln(N_{t-1}) + c\ln\left(N_{t-2}\right) + \mathrm{dZ_t}$, where N_t, *a*, *b*, *c* are the same as Eqn.1, Zt is a climatic variable, and d is the coefficient for the climatic variable.

Eqn. 3

$N_t = N_{t-1}\exp\left(r_0 1 - \left(\frac{N_{t-1}}{K}\right)^{\theta}\right)$, where r_0 is the intrinsic rate of increase, *K* is the carrying capacity, N_t is the population size at time t, and θ measures the curvature of population growth rates and strength of density dependent regulation.

Eqn. 4a

$B_{12} = \frac{p\left(\mathrm{data}\middle|H_2\right)}{p\left(\mathrm{data}\middle|H_1\right)}$, where B_{12} is the weight of evidence in favor of hypothesis H_2 against hypothesis H_1. $p\left(\mathrm{data}\middle|H_.\right)$ is the harmonic mean of the likelihood ($p\left[\mathrm{data}\middle|\theta^i, H_.\right]$) of the data output by the MCMC simulation.

Eqn 4b

$\hat{p}\left(\mathrm{data}\middle|H_.\right) = \left\{\frac{1}{m}\sum_{i=1}^{m} p\left[\mathrm{data}\middle|\theta^i, H_.\right]^{-1}\right\}^{-1}$, where *m* is the number of iterations in the MCMC simulation, θ^i is the sampled parameter value in the ith iteration, and $p\left[\mathrm{data}\middle|\theta^i, H_.\right]$ is the likelihood value given data, hypothesis H. and parameters.

Appendix B

Eqn 1. $N_t = N_{t-1}\exp\left(r_0 - bN_{t-i}\right)$, where r_0 is the intrinsic rate of increase, b is the parameter measuring density dependence, and N_t is the population size at time t.

Table 1. Heterogeneity and other metrics for SCALE study areas.

Study area	Area (km^2)	Elevation $\overline{X}$ (m)	Elevation σ (m)	Int. NDVI[b] ∑ (index)	Int. NDVI[b] CV (%)	Cover types MODIS (n)	Cover types SLCR (n)	Variogram Slope (ind./km)	Landsat Slope (ind./m)
1Dornod Aimag	123,618	818	25.1	1300	9.0	15	55	5.42	-0.209
2Suhbaatar Aimag	82,517	1089	28.6	1439	10.1	9	26	4.69	-0.175
3Moinkum Desert	71,958	456	15.2	824	6.9	13	29	5.60	-0.250
4Balkhash Basin	30,047	1293	135.2	1525	9.7	15	62	9.62	-0.253
5Gokdepe region	13,378	100	7.2	514	7.5	8	26	6.56	-0.159
6Bayramali region	13,298	254	8.1	737	9.6	9	19	7.49	-0.086
7Baiyinxile Farm	3547	1212	33.2	1482	8.6	9	10	5.51	-0.249
8South Turkana study area	8874	785	49.9	1235	12.5	10	30	15.74	-0.151
9Maasai Mara Nat. Res.	1480	1594	31.4	2863	5.6	7	17	7.89	-0.257
10Kitengela region	453	1671	25.8	2171	8.4	6	9	8.25	-0.246
11Southern Kajiado District	10,741	1252	30.5	1850	12.0	14	48	15.68	-0.211
12Loliondo Game Cntrl Area	7269	1676	74.1	2601	4.2	14	41	13.37	-0.245
13Ngorongoro Cons. Area	8240	1883	136.4	2354	4.8	14	52	16.58	-0.143
14Serengeti National Park	13,044	1558	30.5	2820	4.6	12	37	8.82	-0.185
15Lowveld game ranch[a]	75	585	267.3	2601	4.2	2	3	6.51	-0.236
16Vryburg farms	49,222	1174	12.5	1832	7.4	12	29	5.87	-0.296
17Northern Great Plains	10,009	795	19.5	1985	6.5	7	13	5.99	-0.373
18Yellowstone bison range	2050	2438	297.7	1802	4.3	14	32	8.85	-0.358
19National Elk Refuge	6090	2435	158.5	1780	4.9	12	35	12.08	-0.353
20Central Plains Exp. Range[a]	68	1668	136.2	1444	7.8	2	2	4.89	-0.310
21N. Queensland paddocks[a]	1313	394	149.5	2826	6.1	7	11	4.65	-0.284
22Victoria River District[a]	326	167	39.4	1968	8.2	6	2	5.65	-0.297

[a] – Areas or area patches were too small to be sampled (see methods). The elevation and standard deviation of the entire area is reported.

[b] – Int. (Integrated) NDVI indices is based upon long-term (1981-2003) coarse-resolution greenness indices. The metric ∑ is the integrated annual NDVI reflecting productivity, and the interannual coefficient of variation (CV) in integrated NDVI is shown

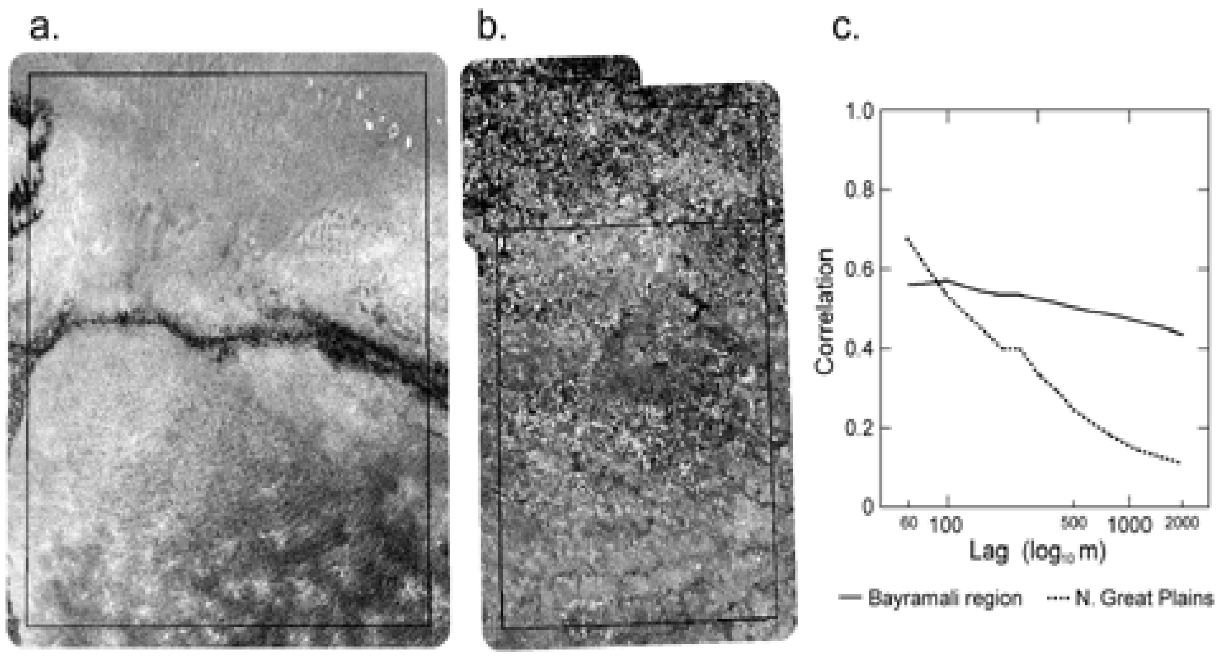

Figure 1. Bayramali region (a) and Northern Great Plains (b) sites, represented by images derived from Landsat ETM+ data. Bayramali has the highest autocorrelation across distances (c) of the SCALE sites, and the Northern Great Plains (c) the lowest.

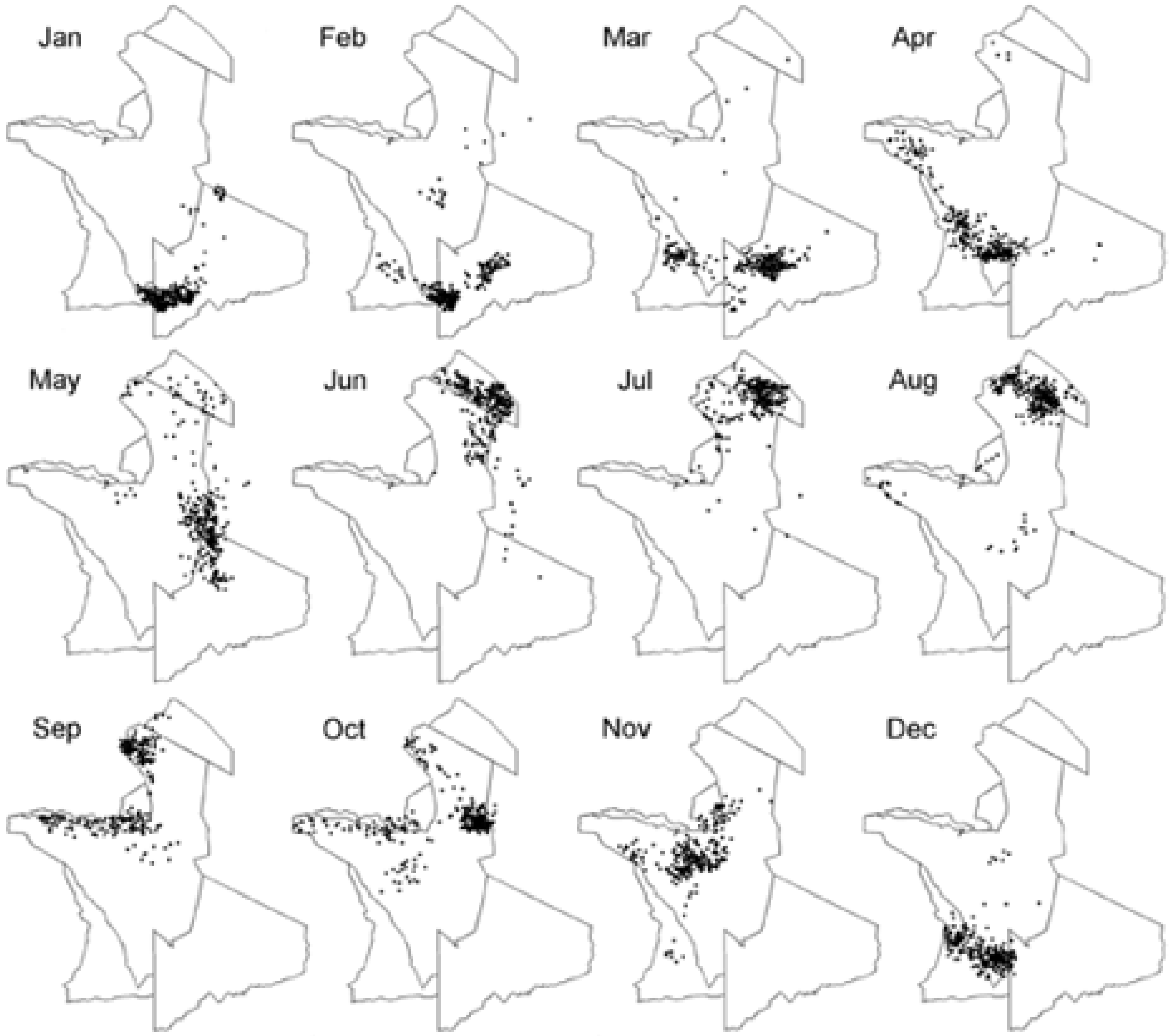

Figure 2. Monthly locations of 300 wildebeest whose migrations were modeled using evolutionary programming, with rainfall and NDVI used in the objective function.

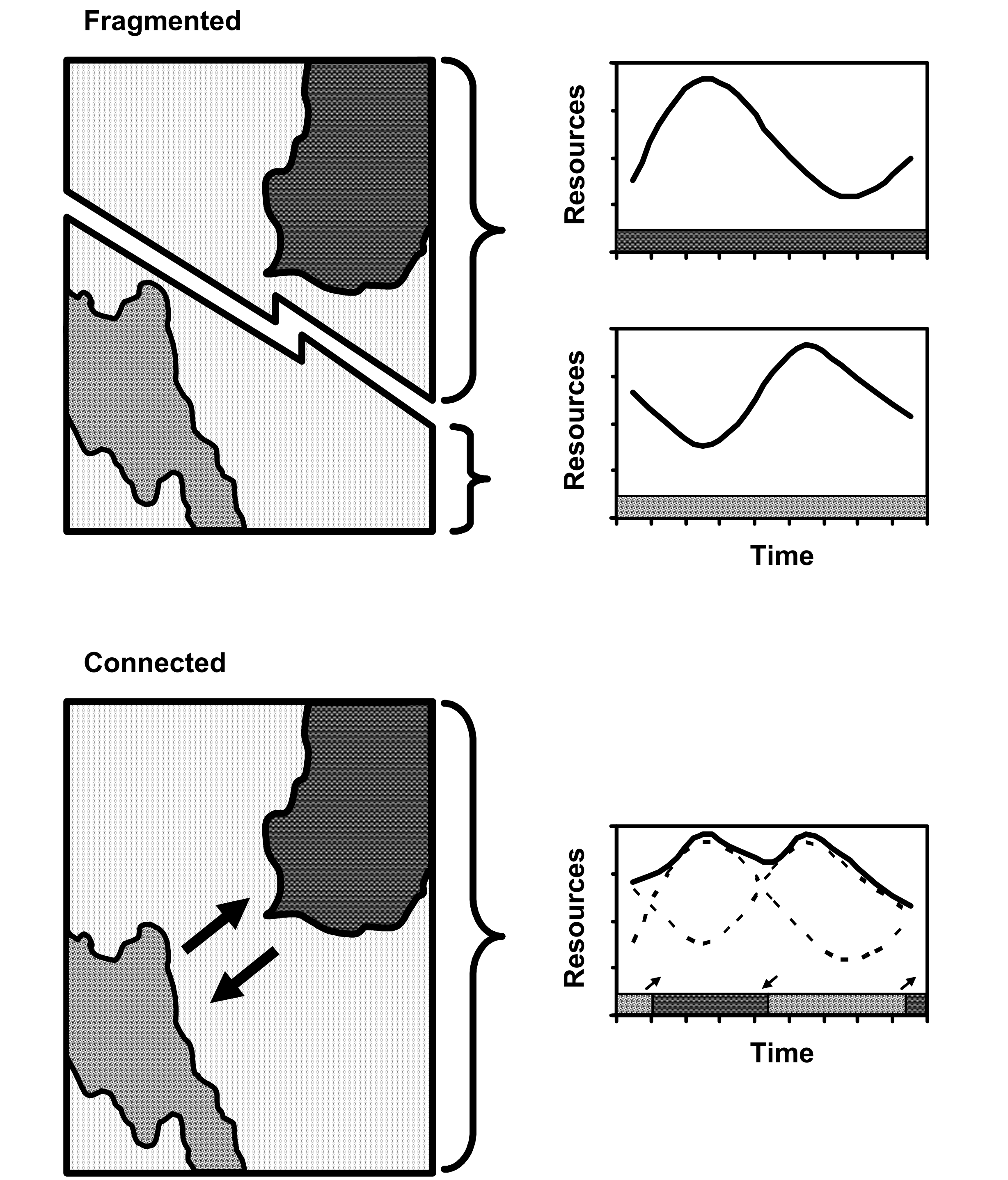

Figure 3. Spatial buffering is provided in unfragmented landscapes where there is asynchronous variation in the availability of resources between connected patches. By moving between patches over time according to peaks in resource abundance, utilisation of resources is enhanced relative to fragmented landscapes.

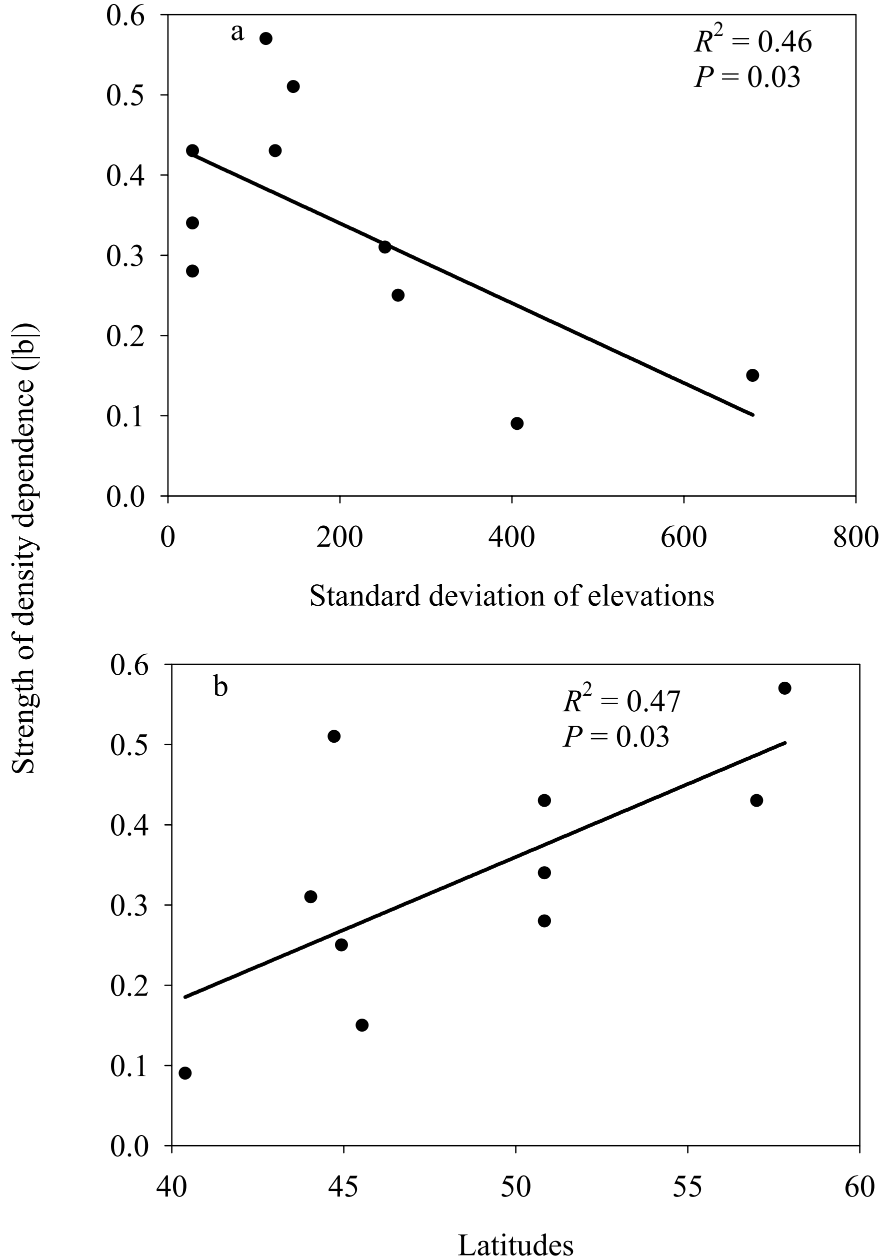

Figure 4. Relationships between the strength of density dependence of northern ungulate populations, spatial heterogeneity of habitat (a), and latitudes of study sites (b).

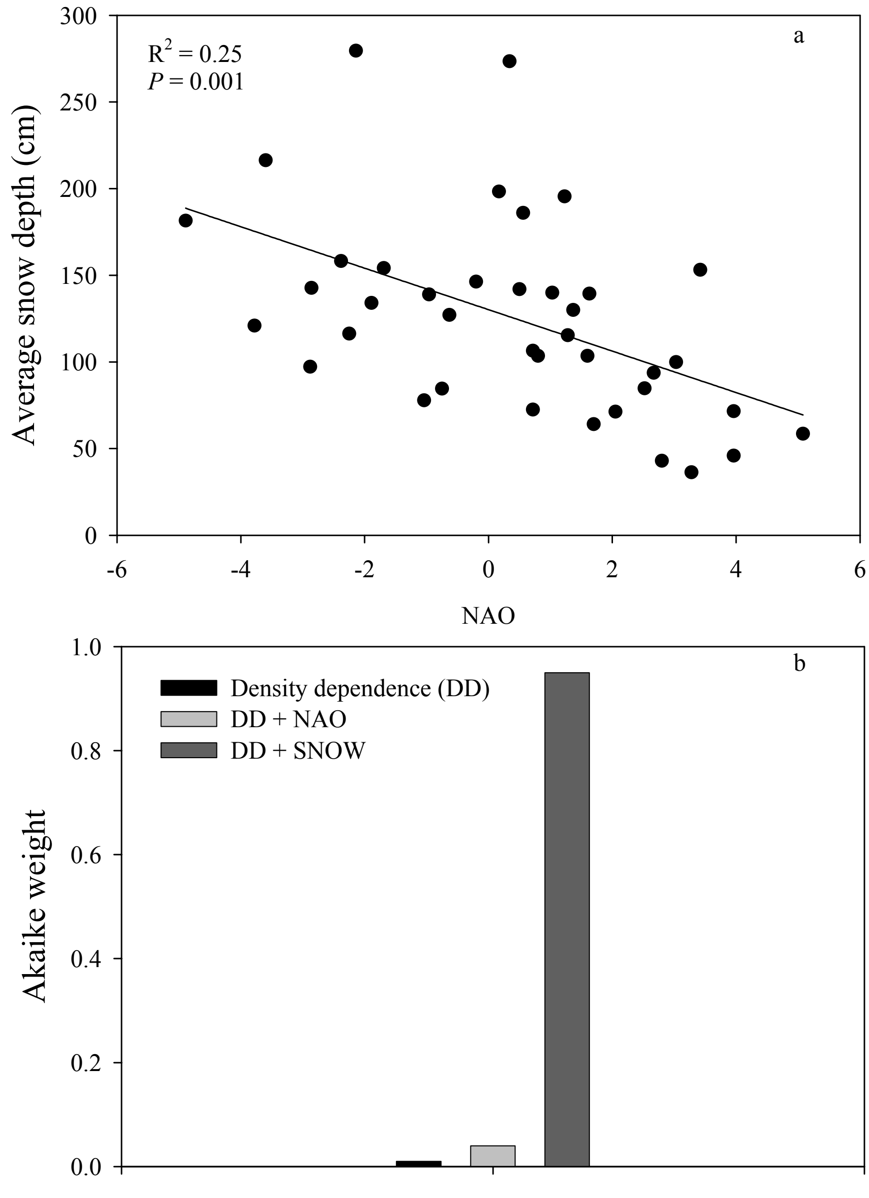

Figure 5. Inverse relationship between average snow depth in the Gran Paradiso National Park, Italy, and the north Atlantic oscillation index (NAO) (a) and model selection (b) for the effects of north Atlantic oscillation and winter snow cover on the population dynamics of alpine ibex (*Capra ibex*) in the Gran Paradiso National Park, Italy.

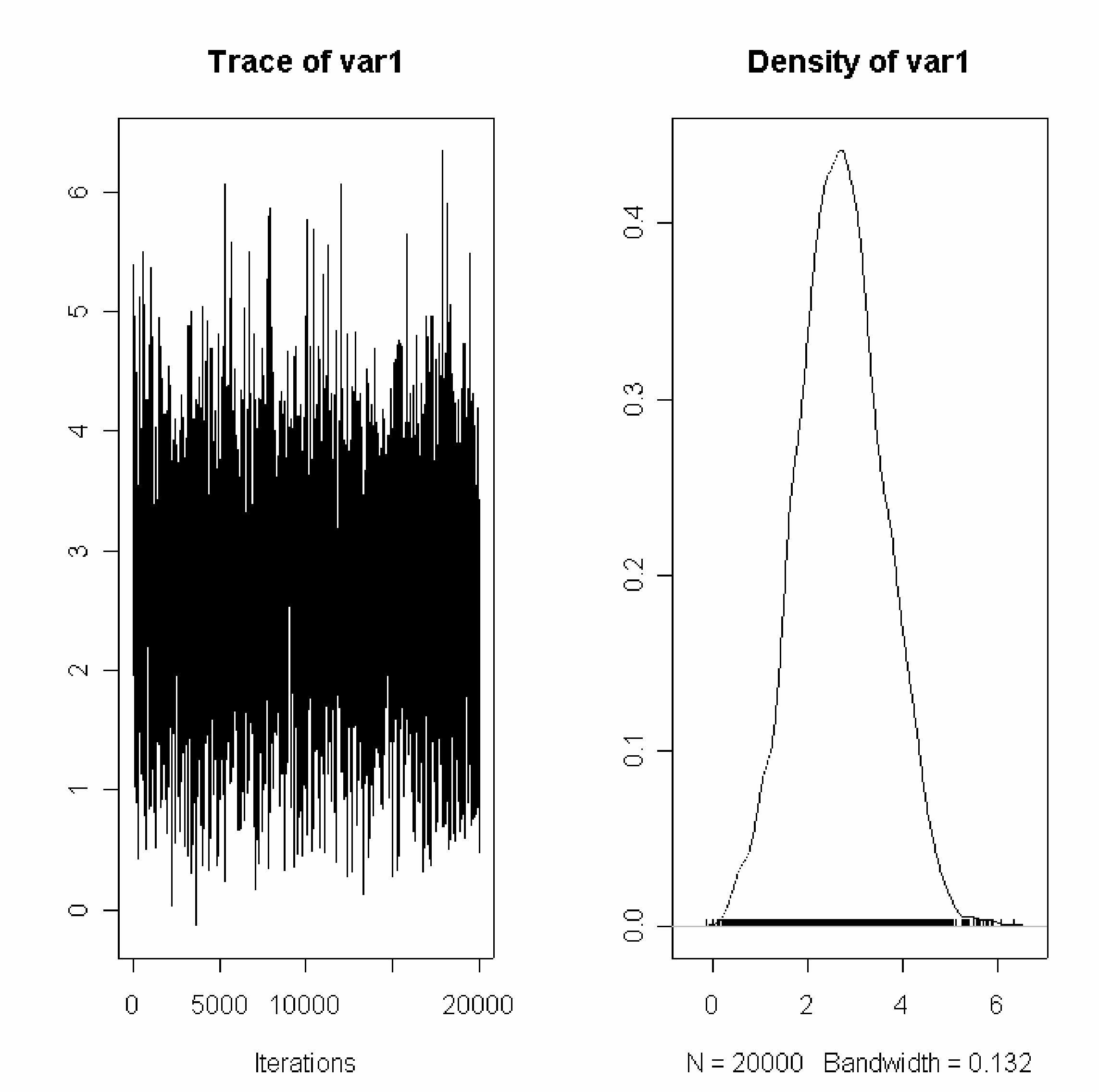

Figure 6. Trace plot (left panel) and density (right panel) of the posterior distribution of the parameter θ of the theta logistic model fit to time series data on annual counts of the bison in Yellowstone National Park, Wyoming. The posterior distribution of the parameter θ was estimated using the Markov chain Monte Carlo simulations with 20,000 iterations and a burn-in period of 300,000 iterations.

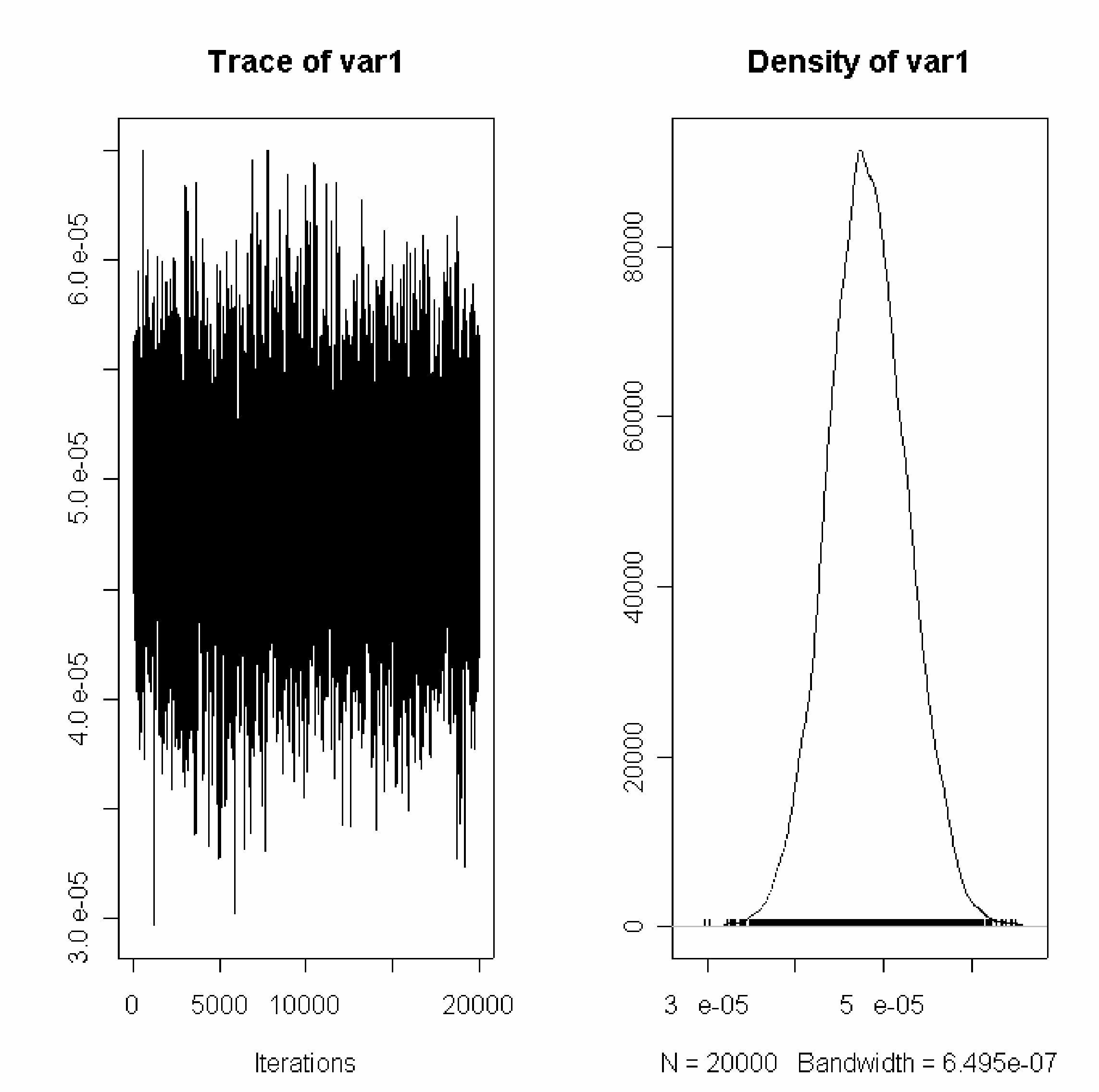

Figure 7. Trace plot (left panel) and density (right panel) of the posterior distribution of the parameter *b* of the Ricker model fit to time series data on annual counts of the alpine ibex (*Capra ibex)* in the Gran Paradiso National Park, Italy. The posterior distribution of the parameter θ was estimated using the Markov chain Monte Carlo simulations with 20,000 iterations and a burn-in period of 300,000 iterations.

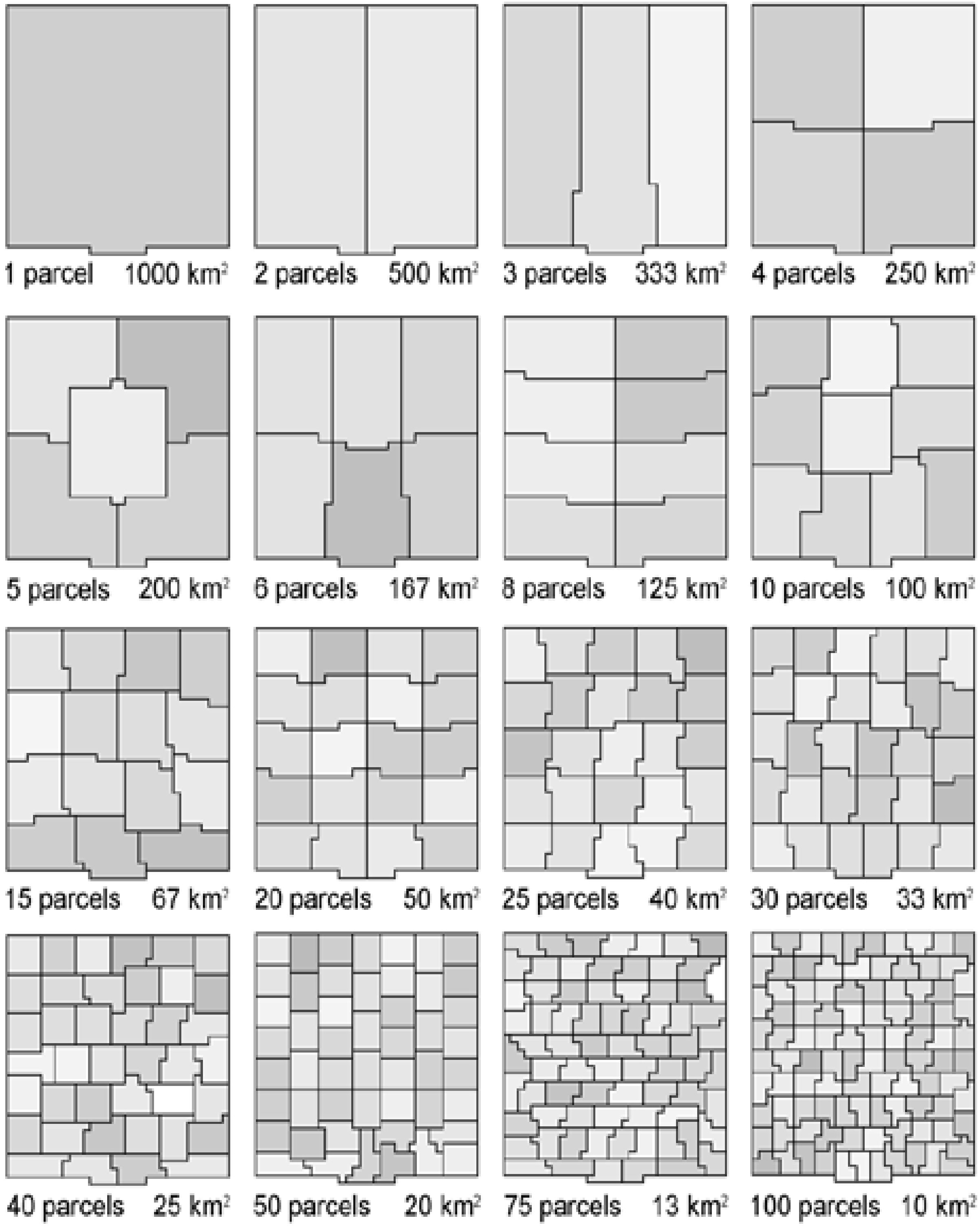

Figure 8. For areas in South Africa, Tanzania, and Kenya, a 1000 km^2 area was fragmented into smaller parcels, with their areas and number shown below each map.

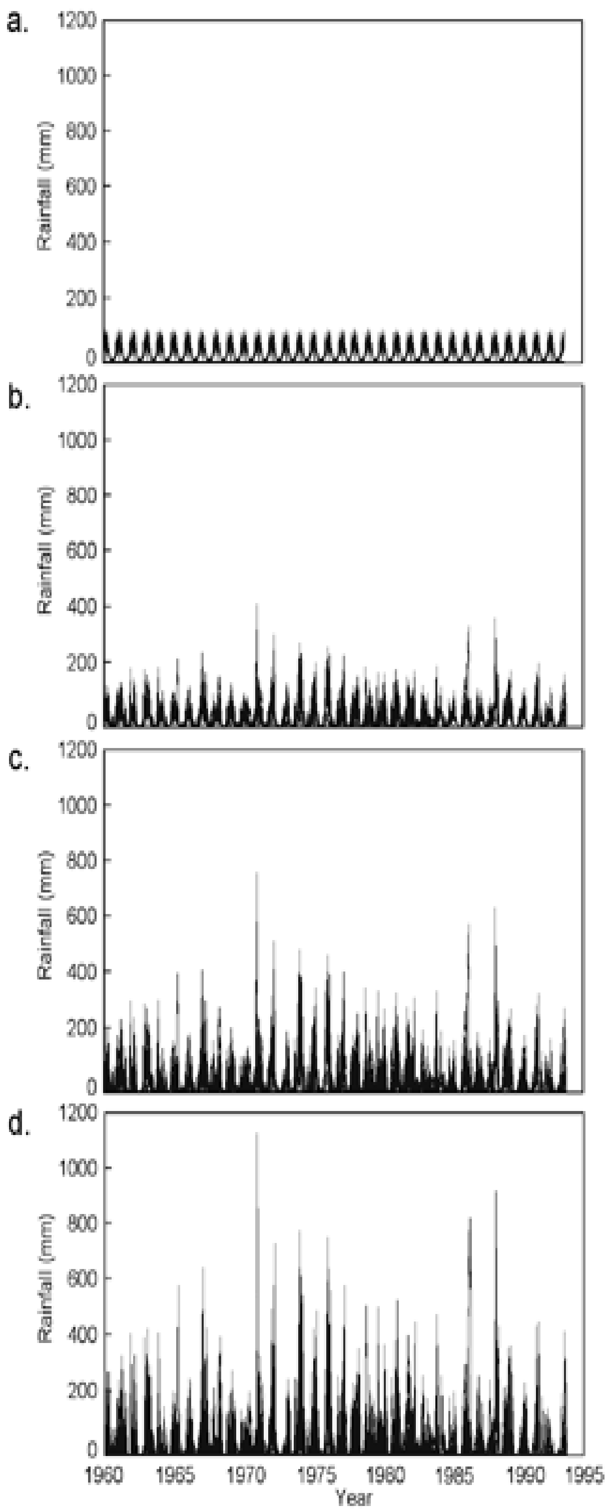

Figure 9. Monthly rainfall totals for the Vryburg area of South Africa from 1960 to 1994, with the coefficient of variation (CV) adjusted from (a) 0%, (b) 20%, (c) 40%, to (d) 60%. In each case, rainfall was 400 mm per year. In actual modeling, CV was altered by 5% increments.

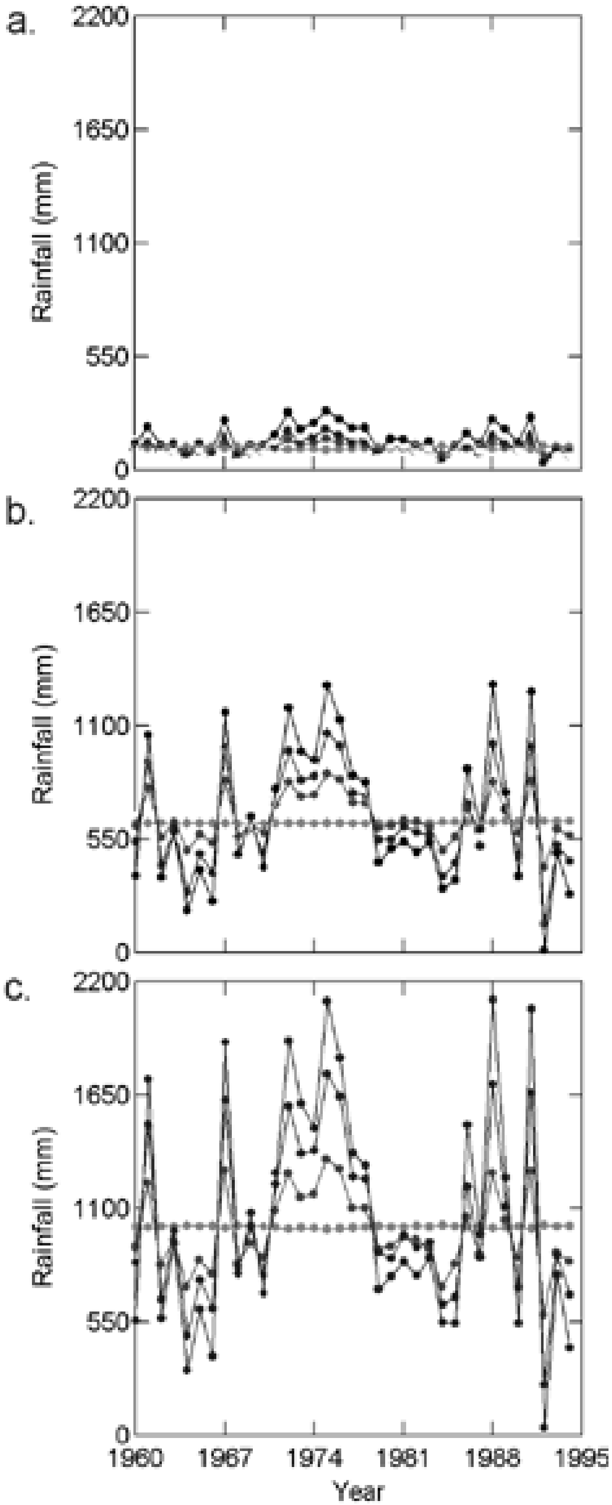

Figure 10. Annual rainfall totals for the Vryburg area of South Africa from 1960 to 1994, with the totals and coefficients of variation (CV) adjusted. Rainfall totals are (a) 1000 mm, (b) 600 mm, and (c) 100 mm. In each case, shading gradates from 0% to 60% CV, in 20% increments. In actual modeling, rainfall was altered by 100 mm increments, and CV by 5% increments.