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 list of papers presented at the workshop is below. These papers will also be published in the African Journal of Range and Forage Science. After the workshop we developed a book outline and it was reviewed and accepted by Kluwer Academic Publishers in June 2004. We are currently working on book chapters and plan to have chapters to the publisher by March 2005. The title of the book is: Fragmentation in Semi-arid and Arid Landscapes: Consequences for Human and Natural Systems.

Fragmentation of Rangelands: Ecological and Economic Implications
A Tribute to Jim Ellis
(2003 International Rangeland Congress session)

Galvin, Kathleen A. and N. Thompson Hobbs. Introduction to the Special Theme: A Tribute to Jim Ellis

Coughenour, Michael. The Ellis Paradigm: Humans, Herbivores, and Rangeland Systems

Galvin, Kathleen A., Philip K. Thornton, Randall B. Boone, and Jennifer Sunderland. Climate Variability and Impacts on East African Livestock Herders


Reid, RS, PK Thornton, and RL Kruska. Loss and Fragmentation of Habitat for Pastoral People and Wildlife in East Africa: Concepts and Issues

Kerven, Carol, Ilya Ilych Alimaev, Roy Behnke, Grant Davidson, Leen Franchois, Nurlan Malmakov, Erik Mathijs, Aidos Smailov, Sayat Temirbekov, and Iiain Wright. Retraction and Expansion of Flock Mobility in Central Asia: Costs and Consequences


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 this objective have been diverse. To support a book chapter (Boone and BurnSilver, In prep.) that compares the landscape and socioeconomic heterogeneity of SCALE sites, the boundaries of the 23 sites were finalized. Additional remotely sensed data available globally have been identified. Software was written that automates calculations of changes in greenup dates, season lengths, etc., based on remotely sensed images such as Normalized Difference Vegetation Indices (NDVI). The method developed under SCALE to calculate metrics of vegetation heterogeneity for mobile herbivores was applied to several sites. K. Price of Kansas Applied Remote Sensing, University of Kansas, completed a set of seamless NDVI satellite images of vegetation greenness for East Africa at 1 km resolution, 1989 to 2003. Price has undertaken analyses that will relate satellite greenness, productivity, and heterogeneity to livestock stocking. Boone has used similar data to model wildebeest migratory patterns in the SCALE site Serengeti National Park, using evolutionary programming techniques. Detailed analyses by Hobbs, Wang, and Boone have related large herbivore population dynamics from counts at SCALE sites and others to the variability in climate and forage productivity. Lastly, a presentation was made and manuscript prepared and revised (Boone et al., In press) for a chapter in a volume entitled Resource Ecology, edited by F. van Langevelde and H.H.T. Prins of Wageningen University.

**Research Objective 3: Herbivore Selection at the Paddock Scale**

**Objective:** Determine the effects of pasture size on animal diet quality and performance.

The 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.

To address this question we are using near infra-red spectroscopy (NIRS) analysis of fecal samples to quantify seasonal variation of diet quality in paddocks of differing size and vegetation complexity in the Dalrymple Shire, northeast Queensland, Australia. Initially, in September 2002, we recruited 18 pastoralists from the shire to collect fecal samples for analysis at two-monthly intervals from a total of 35 carefully-selected paddocks. In December 2003 we added an additional 30 paddocks to fill in gaps in the sample design across the set of selection attributes (paddock size, geology type, landscape complexity) and to allow for the loss of some paddocks from the study (e.g., because of destocking, changes in fencing or discontinued/irregular provision of fecal samples from collaborators).

We are currently developing measures of landscape complexity (spatial and temporal) from MODIS satellite imagery and weather data. Landscape heterogeneity indices for each paddock in the study area will then be compared with fecal data and used to explore which elements of complexity in landscapes could be beneficial for animal diet selectivity.

**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 2003 to 2004:

1. 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. Assessment of the effects of landscape fragmentation on predator populations in the Mara ecosystem (partially funded by the NSF SCALE grant),
3. Analysis of the effects of pastoralism and protection on the spatial distribution of wildlife around water points in the Mara ecosystem (partially funded by the NSF SCALE grant), and
4. Completion of a synthesis paper of state of knowledge on fragmentation in East African pastoral systems (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.

Kazakhstan: Jambul district, Almaty region and Moinkum district, Jambul region

Livestock productivity in Kazakhstan is directly affected by whether animals are moved to seasonal pastures or are grazed all year around settlements. During the DARCA project, sheep and goats were weighed from a sample of 46 households within 6 villages representing a number of ecological zones in southern Kazakhstan. Several thousand animals were weighed every 3 months for 2.5 years (2001-2004). Results show the effect of seasonal movement on sheep weights from winter to spring. Sheep which were moved in each of the four seasons gained on average 5 kg weight over winter, compared to village-based sheep which lost on average 8 kg, being stall fed or foraging on over-grazed ranges within 5 km of villages.

A policy issue is whether small, non-mobile flocks can be as productive as large, mobile flocks. Moving animals to temporary seasonal pastures may produce heavier animals, but at what cost to their owners? Mobile flocks have higher costs per head of animal, due to the need for transport and hired shepherding labor. Are heavier animals more financially rewarding to their owners over the longer term?

The aim of the current research activity is 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. A small number of 12 flocks is being monitored in two distinct ecological regions of southeast Kazakhstan. In each of these areas, the DARCA project team conducted intensive research from 2000-2004. The two areas are described in Alimaev and Behnke (2003):

- Moinkum desert-Betpak Dalla migratory circuit (Jambul administrative region)
- Taukum desert-Ay Darly migratory circuit (Almaty administrative region)
In each region, one village has been selected and within each village, 6 cooperating livestock owners. In each village the selected owners comprise two 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.

A sample of approximately 400 sheep and goats has been eartagged within the 12 flocks. The study is measuring the biological and economic returns to seasonal livestock movement compared to circum-village and sedentary grazing management.

The questions are:
- Differences in live weight of adult female sheep and goats
- Viability of their offspring (lambing/kidding rate, mortality, weight gain to 1 year)
- Long-term flock growth through reproduction
- Costs of seasonal movement (labor, capital equipment, transport)
- Costs of winter supplementary feeding
- Cash income from market sales of live animals, wool and fiber
- Subsistence income from home slaughter and animal by-products
- Quality and quantity of forage at different grazing locations.

The analysis will compare overall biological productivity of moving and non-moving flocks, and then determine the economic returns to each management system. The analysis will consider whether non-moving small flocks are viable in the longer term, and whether they are able to continue providing their owners with an income but not capable of expanding due to high offtake. The longer-term profitability of moving animals will be assessed by comparison.

**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**

Data collection had already been completed for the Kajiado case study. During this year, the data were re-examined and some recalibration of the PHEWS model was carried out via a series of sensitivity analyses. The writing up of the scenario analyses was revised and completed, and re-submitted to a peer-review journal for possible publication.
Kazakhstan

A data collection activity was designed and implemented, to generate the information needed to specify a PHEWS module for Kazakhstan. As part of this effort, notes were drawn up on the information needs for a PHEWS application, and permission to gain access to household data collected by the Desertification and Regeneration: Modeling the impact of market reforms on Central Asian rangelands (DARCA) project was sought and granted. Dr. Carol Kerven, who was heavily involved with the DARCA project, was hired on a short-term consultancy basis to advise on the availability of existing household and secondary information from the study region, suggest a preliminary classification of livestock keeping households, assist in the formulation of hypotheses concerning the dynamics of households and pastoral systems in Kazakhstan, and the likely impacts of changes on resource-poor households, that can be tested using a suite of model-based integrated assessment tools. She also advised on the design and implementation of data protocols and collection procedures, and once model development is underway, she will advise on the formulation of household decision rules (such as resource use, livestock trading, and engagement in non-farm economic activity) for subsequent encoding in the PHEWS model. A list of study design features undertaken by Dr. Kerven include:

- Outline of the priorities for a PHEWS survey in Kazakhstan
- General hypotheses related to SCALE that the PHEWS survey may address
- Suggest the villages and their hinterlands which would be appropriate for the survey, providing information on each village
- Discuss household sampling methods
- Suggest an interview schedule for a CSU student, including logistics, for household surveys
- Outline how DARCA data could contribute to the PHEWS survey analysis
- Comment on and revise the draft questionnaire
- Provide further reading references

Further inputs into the study will be provided by Dr. Kerven for the analysis of the survey data, in 2005.

In terms of a classification or typology of households, this is being approached on the basis of flock size and seasonal flock movements for access to grazing resources. A set of preliminary hypotheses for the modelling work to operate around is listed in Table 1, for contrasting household types.

Survey data were collected from 38 households in two villages in southern Kazakhstan by Shauna deLuca, a masters student, in July 2004, and 20 more households are in the process of being surveyed. These data are being cleaned and entered into a database. Once some preliminary analysis has been done, PHEWS model development can start.

Research Objective 9: PHEWS (Pastoralist Household Economic Welfare Simulator)
Model Assessments
Objective: Determine economic-ecological interactions resulting from alternative land use practices.
Recalibration and subsequent sensitivity analysis of the Kajiado PHEWS model indicated that the model is probably overly sensitive to some key variables. In this context, re-calibration refers to the process of balancing the model, because of the large uncertainty associated with many of the input data. It is clear that in reality, household expenditures generally have to balance household income fairly closely, and the model has to reflect this. In the Kajiado case, this process is made difficult by the large number of household types (eight combinations of economic activity multiplied by three wealth levels of each, giving 24 separate types of households). Serious consideration was given to trying to find ways around this problem for future applications. Two aspects in particular were looked at. One is the prospect of doing away with wealth categories altogether, and making household wealth distributions an output of the model (in essence). This could be done by initiating each household in the landscape with resource levels that are drawn from probability distributions of observed resource levels in the landscape. An advantage of this is that households could move between different wealth categories through time, which is clearly what happens in reality. This kind of approach is moving firmly towards an agent-based modelling approach, where instead of using representative households of different types, a whole distribution of individual households is simulated on the landscape, whose collective characteristics match observed data. This would also have the benefit of making PHEWS spatially explicit (i.e., each household is characterized differently from its neighbors on account of its precise location in the landscape, distance to water or grazing resources, etc).

A second area of investigation during the year was on the prospects of building a generic PHEWS model that could be made more applicable to pastoral systems in general. Currently, PHEWS has to be essentially rewritten for each new application, and there are obvious savings in time that could be made with a more generic model that could be specified more easily for new situations. On the other hand, there is so much variation between pastoral and agro-pastoral systems in different places that it is possible that while the basic structure of PHEWS could be made generic, the rules that operate in various situations may be so different as to preclude the possibility of a truly generic approach.

Neither of these changes to PHEWS is trivial, however. There is still much work to do even for outlining a conceptual framework for a generic household model. Given the difficulties and time involved, the PHEWS application for Kazakstan is likely to be similar to that for Kajiado in some major respects, such as limited spatial explicitness and wealth levels that are “built in” to the model.

Research Objective 11: Spatial Complexity, Temporal Variability and Population Patterns Objective: Develop competing models linking animal populations to spatial complexity.

Studies of large herbivores in temperate environments have shown that internal processes regulating population growth are shaped by variability in external conditions. Temporally variable weather conditions can synchronize population dynamics (Grenfell et al. 1998, Post and Forchhammer 2002, Aanes et al. 2003) and can add to the effects of density dependent feedbacks retarding population growth (Forchhammer et al. 1998, Milner et al. 1999, Coulson et al. 2001,
Elevated population density amplifies the stochastic effects of weather, even when deterministic density dependence is weak (Aanes et al. 2000). In contrast to the emerging understanding of the effects of temporal variability on population dynamics, the effects of spatial variation remain largely unknown.

There is reason to believe that spatial heterogeneity in resources might weaken the effects of weather and density on population growth of large herbivores by improving nutrition of individuals. For example, 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 (Albon and Langvatn 1992, Frank and McNaughton 1992, 1993, Wilmshurst et al. 1999, Mysterud et al. 2001a). Moreover, spatially heterogeneous landscapes often include habitats where food resources are stable in time, remaining available to herbivores in the face of weather conditions that create seasonal or episodic resource shortages over most of the landscape (Hunter 1962, Wallmo et al. 1977, Gordon 1989, Illius and O'Connor 1999). It follows from these examples that spatial variation in resources may allow herbivores to exploit temporally variable pulses in forage resources and mitigate resource shortages, thereby attenuating the effects of weather and density on vital rates of their populations. Here, we show how population trajectories of large, mobile herbivores respond to density-dependent feedbacks and how those feedbacks are shaped by temporal variation in weather and spatial variation in vegetation. We offer evidence that temporal variability in weather conditions and spatial variability in vegetation exert opposing effects on the strength of density dependent control on population growth.

We analyzed time series of data on abundance of 5 populations of ungulates in the Rocky Mountains, USA. The duration of these time series spanned 31-75 years. Variation in abundance \( N_t \) was analyzed for each population using subsets of the global model \( \ln(N_t) = a + (1+b) \ln(N_{t-1}) + c \ln(N_{t-21}) \) where \( a \) is the intrinsic rate of increase, \( b \) represents the effect of direct density dependence and \( c \) is coefficient describing the effects of delayed density dependence. When the sign of \( b \) is negative, increases in its magnitude indicate increasingly strong, direct negative feedback between population density and per capita population growth rate. We examined correlations between the absolute value of \( b \) and indices of temporal variation in weather and spatial variation in vegetation.

Annual counts were obtained for a population of bison (Bison bison) in northern Yellowstone National Park (YNP) (44°72’N, 110°64’W), Wyoming, and populations of elk (Cervus elaphus) in Rocky Mountain National Park (RMNP) (40°39’N, 105°64’W), Colorado, the National Elk Refuge (NER) (44°04’N, 110°63’W), Wyoming, the northern range of Yellowstone National Park (YNP) (44°93’N, 110°54’W), and the Gravelly Mountains, Montana (44°64’N, 111°86’W). Counts were obtained by aerial survey during late winter (Singer et al. 1997, Lubow et al. 2002, Lubow and Smith in press). We chose these populations because they experienced reasonably similar climatic conditions and because each population provided a time series of at least 30 years.

Density independent \( (b = c = 0) \) and autoregressive (AR) models of order \( (p) \) 1 and 2 were fitted to the abundance data. Counts of animals have inherent measurement errors that may bias estimates of the strength of density dependence (Stenseth et al. 2003). To account for
measurement errors, we used the classic Kalman filter (Harvey 1989), a state-space time series model, to analyze the time series of counts \( N_t \). Details of our statistical methods are given in Appendix A.

We used the coefficient of variation (CV) in average annual winter (Oct.-March) temperature as an index of temporal heterogeneity. The mean and coefficient of variation of average in annual winter temperatures coincident with the period of ungulate surveys were calculated for each site.

Spatial heterogeneity was indexed using Normalized Difference Vegetation Indices (NDVI), which reflect vegetation biomass (Paruelo et al. 1997) and are correlated with ungulate stocking rates (Oesterheld et al. 1998). We acquired 183 NDVI images for each study area, for April 1998 to April 2003. For each image, we calculated the CV in NDVI across all 1 km² pixels within a 25 km radius of the centroid of each study area. For each study site, we averaged the CV across all images to represent spatial heterogeneity in vegetation. We verified that the estimate of the CV was largely independent of scale by showing that the estimate of the CV with the 25 km radius did not depend on the resolution of the analysis, that is, the pixel size.

**Research Objective 12: SAVANNA-PHEWS Complexity-Fragmentation Experiments**

**Objective:** Model effects of fragmentation on ecosystems and people.

Progress using SAVANNA and PHEWS in modeling has again focused on southern Kajiado District, Kenya. Manuscripts were written based upon analyses done in 2002-2003, and additional analyses were conducted. A new SAVANNA/PHEWS application has been initiated for Almaty Oblast, Kazakhstan. Results from analyses in South Africa that were precursors to South Africa SCALE analyses and the generic SAVANNA application (see Research Objective 13) were published.

**Research Objective 13: Complexity and Fragmentation in Theoretical Ecosystems**

**Objectives:** Study general responses of ASAL ecosystems to fragmentation.

A generic application of the SAVANNA Modeling System was used in detailed analyses to explore vegetation responses to fragmentation. Animals confined to smaller and smaller parcels will graze upon vegetation more intensively; detailed vegetation responses were explored.

**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**

The 23 SCALE study sites (Figure 1) include six areas defined by political boundaries (Figure 1, numbers 1,2,3,8,10,17), five conservation areas, parks, or otherwise controlled areas with clear boundaries (9,12,13,14,20), four sites were defined by their minimum and maximum coordinates (4,5,6,7), four defined by farm or paddock boundaries (15,16,21,22), one study area bounded by rivers (11), and two areas defined by the boundaries of large herbivores (18,19). The sites are variable in area, from the site within the Central Plains Experimental Range at less than 100 km², where graduate student Heather Blackburn is working, to the aimags of Mongolia (1000s km²).

Extremely useful spatial data were added to our SCALE GIS this year. High resolution 1 km² NDVI images for East Africa were provided by the Kansas Applied Remote Sensing laboratory. These images were calculated for every 10 day period from February through September of each year, 1989 to 2003. The laboratory holds, and have agreed to make available, similar series of high resolution NDVI for our study areas in Asia and North America. These images join coarser resolution bi-weekly images from 1981 to 2003 provided to us by the NASA Global Inventory Monitoring and Mapping program, plus European Spot-VEGETATION 1 km NDVI data. The Shuttle Radar Topography Mission from 2000 has released finalized digital elevation models for some of our sites, and preliminary data for all sites. These data are more than an order of magnitude higher in resolution than previously available elevation data for most international sites (90 m shuttle data versus 1000 m HYDRO1K data), a dramatic improvement. Other data sets, such as those from the Global Land Cover Characterization project, were put in-place earlier in the project.

Metrics have been calculated to allow comparisons of basic ecological properties across SCALE sites. These include deviations in elevation, season lengths based upon forage production, net primary productivity indices, and the coefficient of variation in NDVI across time, a measure of variability in rangeland resources measured in a uniform way across the globe. For some sites, we have calculated measures akin to a variogram used in spatial statistics – herbivores attempted to maximize their access to NDVI, reflecting forage availability, as their mobility increased from 0.5 to 30 km (Figure 2). A flat line indicates that forage availability in an area is relatively homogeneous through space, whereas a steeply sloping line suggests a heterogeneous forage base. Biological implications are evident in the slope and intercepts of the lines calculated. For example, the slope, reflecting vegetative heterogeneity, for Serengeti National Park is relatively low, whereas neighboring Ngorongoro Conservation Area has a steep slope. Serengeti is dominated by migratory herbivore species, whereas Ngorongoro includes many resident animals able to meet their needs throughout the year without migrating.

Regional migratory patterns of wildebeest within Serengeti National Park have been modeled reasonably well using remotely sensed NDVI images and an evolutionary programming approach. In short, animals that approached typical migratory patterns survived, and those that did not were removed from the population. The surviving wildebeest produced offspring with related, but mutated, migratory pathways. After thousands of simulation cycles, the migratory
pathways of wildebeest reflected the observed pattern, with animals in the south during the wet season, in the north in the dry season, and moving through the western corridor and Loliondo regions during a transitional period.

NREL scientist G. Wang, Hobbs, and Boone have been working with participants in a National Center for Ecological Analysis and Synthesis (Santa Barbara, CA) workshop, such as N. Owen-Smith, on SCALE related issues of large herbivore dynamics. A manuscript (Wang et al., In revision) reports that the strength of density dependence of herbivores in five North American conservation areas is related to weather, and resource availability as reflected in remotely sensed images. The strength of density dependence was positively correlated ($P = 0.02, r^2 = 0.87$) with temporal variation in average annual winter temperature and was negatively correlated ($P = 0.02, r^2 = 0.89$) with spatial variation in resources estimated by NDVI images.

A chapter (Boone et al., In press) prepared for a volume edited by Van Langevelde and Prins reviewed transhumant behavior by pastoralists, using examples from Mongolia, central South America, and Kenya. More detailed results were provided for the Maasai of Kajiado, Kenya. We described how livestock move about the landscape in intact and subdivided landscapes, and quantified differences in benefit associated with different animal mobility. For example, residents of northern Imbirikani Group Ranch in Kajiado District, Kenya accessed more green vegetation the more they moved ($r^2 = 0.59, P < 0.001$), whereas those in the subdivided portion of Imbirikani to the south did not access more green vegetation with their limited movements.

**Research Objective 3: Herbivore Selection at the Paddock Scale**

There are some indications from a simple summary of our data collected so far (Figure 3), that diet quality of cattle in smaller paddocks may be worse than that in larger paddocks, particularly in the dry season, when diet qualities fall below maintenance levels (ca. 5% protein). But these results are only indicative, and do not yet take into account the paddock attributes that were used to stratify sampling (e.g., paddocks are generally smaller on the most productive landscape/geology type).

We duplicated the analysis of spatio-temporal vegetation variation that had been conducted for the Serengeti SCALE site for our Dalrymple Shire site. The method involved plotting the seasonal variation in normalized difference vegetation index (NDVI, from MODIS imagery) values for all 0.5 km x 0.5 km pixels contained within each of two paddocks (Figure 4). These plots indicate the potential restriction on foraging choice for animals enclosed in small, homogenous paddocks relative to accessible variation in vegetation available in large complex paddocks. A variogram of NDVI describes the scale-dependence of access to vegetation heterogeneity more broadly over the whole shire (Figure 5). Even for such a simple measure of vegetation heterogeneity as NDVI, animals exploiting landscapes at the scales of typical paddock sizes for the shire (5,000 – 50,000 ha) only have access to 50 – 75% of the variation that they would have access to, were they free to roam more broadly (over a 50 km radius).

**Research Objective 4: Herbivore Movements in Fragmented vs. Intact Ecosystems**
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 some factor limiting access to vegetation.

Five cattle herds have been tracked in the Kitengela area starting from March 2003 to the present. The five herds range in size between 45-200 head of cattle. Up to October 2004 a total of 10 data sessions have been completed, each of 10 days in duration. See our report from last year for detailed methods. The only modification was that the location point where the data was downloaded was changed. Before, each GPS unit was taken into town for downloading on a desktop computer and then returned back before the next day for data collection. This incurred high transportation cost and was not considered safe for the person collecting and redistributing the GPS units because he had to drive in the dark and under poor driving conditions. As a result, the download procedure was modified by employing a Pocket PC which could be easily carried by the driver. The driver and the herd followers were trained to use this new unit for downloading the data from the GPS units. For three data sessions, data on body condition index of the livestock was collected for all the five herds. The herders were trained to use a nine-point scoring system on their herds. Such a score helps to quantify the extent to which cattle are affected by nutrition, disease or other environmental factors, especially when large fluctuations in the quantity and quality of available forage occur. We expect all of these factors to be modified by landscape fragmentation. Statistical analysis of the condition index and other data on the grazing pattern is ongoing.

In addition, for the Kitengela study site the NDVI values from Vegetation Spot 5 satellite data have been downloaded for 7 of the 10 data sessions. Data for the remaining three sessions will be downloaded as they become freely available. The analysis of the NDVI data will help to determine if these data are good predictors of the geometry of the grazing orbit. The grazing orbits are quantified using several measures. One of these measures is fractal dimension and the second is the number of times the grazing paths cross each other. The fractal dimension of the grazing orbit is determined using the VFractal computer program (Nams 1996). This program, written in C, identifies the cross-over points of each track. Path characteristics, using such measures, are being analyzed to see if they correlate with fragmentation levels in the landscape due to the presence of fencing in the study area and due to range conditions as indicated by the NDVI values.

Fractal analysis shows that the grazing orbits are highly convoluted and crossover more frequently in areas where fencing limits access to vegetation. In such areas the velocity at which the herd moves over the landscape is much faster than in areas that are more open and less restrictive to where the animals can move. We also find that the total distance covered by the herd decreases at the onset of the rains, when rangelands conditions begin to improve in both fragmented and un-fragmented areas.

The study area in the Maasai Mara ecosystem sees an annual increase in wildebeest numbers during the mass migration of wildebeest from the Serengeti ecosystem in mid-August. This large perturbation causes the vegetation to become patchy or fragmented due to selective and heavy
grazing by these herbivores. At the Mara study site we are documenting the effect of the wildebeest-induced vegetation changes on the grazing patterns of cattle before and during the migration. We collected data on grazing orbits of eight herds before and during the migration. The results show that herding practices change in response to the migration. The grazing orbits were longer and the velocity of movement faster in cattle herds where wildebeest reduced the abundance of the vegetation. The primary grazing area for cattle changed from open grassland before the migration to riverine habitat after the migration. The grazing orbit data will help to quantify how much time is spent in this habitat, which appears to be a feeding refuge area for cattle during the time of the wildebeest migration. In some tracks, the time spent grazing within a riverine habitat (from 0-200 m from a river) increased from 25% prior to the wildebeest migration to 56% in the presence of wildebeest.

Finally, a pastoral MSc student was recruited to begin 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. Information on livestock herd movements will be obtained at all sites by interviewing herders. Interviews with ~50 herders will be conducted at each site. Herders will be asked to recount seasonal herd movements starting in the 1940’s up to the present in response to the droughts of 1961, 1973, 1984, 1991, and 1999. Herders will be asked to compare drought year movements with ‘wet’ year movements close to the time of each of these droughts.

2. Assessment of the effects of pastoralism on the density and distribution of carnivores and their prey in the Mara Area of Kenya (Ogutu, Reid)

The results of this research were reported in last year’s report. This year, the paper was submitted, revised and accepted for publication in the Journal of Zoology.

3. Analysis of the effects of pastoralism and protection on the spatial distribution of wildlife around water points in the Mara ecosystem

This analysis built on the census of people, livestock and wildlife reported last year for this project. The objective of this analysis was to determine how different species of wildlife distribute themselves around water, and to then discover how people and livestock in pastoral areas affect this distribution compared with the nearby Mara Reserve. We used fine-resolution data on the location water points, vegetation, livestock, wildlife and settlements over the 2200 km² ecosystem, collected in 1999 and 2002.

This analysis shows that the distributions of 18 wildlife and 4 livestock species from water followed either the humped or the exponentially decreasing patterns, were mostly consistent between years and did not clearly reflect functional categories, such as feeding guilds. The distributions are consistent with constrained foraging and suggest an optimality model in which herbivores concentrate neither too close to water because food gets depleted there, nor too far from water because of walking costs. This leads to a humped distribution depending on the specific tradeoff between food gains and movement expenditures. We also show that species segregated along the distance-to-water gradient presumably to minimize interspecific competition through resource partitioning. The sequential ordering of species along the distance-to-water gradient varied between landscapes and years, with species more tightly distributed
about their distance-to-water ‘niches’ in the pastoral areas than in the reserve. Range contraction and expansion and shifts in spatial aggregation of several species were also evident and reflected variation in water and forage availability. Pastoral land use modified both the distributions and densities of most wildlife species from water in the ranches relative to the reserve. Wildlife species likely to engender greater conflicts with pastoralists were less abundant whereas those likely to cause fewer conflicts were more abundant in the ranches than in the reserve.

4. Completion of a synthesis paper of state of knowledge on fragmentation in East African pastoral systems (Reid, Thornton, Kruska)

We reported on the results in this report last year. This year, the paper was submitted to a peer-reviewed journal and is now in press.

**Research Objective 5: Typology of Actual Land Use Patterns**

**Research Objective 7: Factors Driving Contemporary Trends in Land Use Change**

Current results from the DARCA surveys are equivocal (Kerven et al. 2003): animals that are moved gain more weight over winter, but their owners have higher management costs per head. On the other hand, sedentary flocks that lose weight over winter bring higher annual economic returns per head to their owners. It is likely that this higher annual per head income in sedentary flocks reflects a greater offtake rate for home consumption and sales, due to the poverty of non-moving households who have much smaller flocks.

Results of the first round of weighing are shown in Table 2. Sheep in flocks that move each season are on average about 8 kg heavier in springtime, compared to sheep in sedentary flocks. Goats, on the other hand, do not seem to be affected by differences in forage and feeding regimes.

Results are currently being analyzed from the autumn (October 2004) round of animal weighing and surveys of livestock owners.

**Research Objective 8: Economic Surveys and Analysis**

Scenario analyses are ongoing to look at the interactions between ecological complexity and household well-being in case-study environments (Kajiado, Kenya and Kazakstan). For the Kazakstan site, the new data from this year are being cleaned and entered into a database. The preliminary analyses are being done now, and then PHEWS model development will start. More findings will be available next year.

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

*Kajiado*

Some of the Kajiado runs were redone using the recalibrated model, but the basic results reported previously did not change: for the baseline run, most households need some external calories at some stage, but for most households, the call on these is at specific times of the year, rather than
a constant requirement, and is fairly low. About 80% of households have to do other things in addition to keeping livestock, as herd sizes are generally not large enough to sustain the large numbers of people per household. As before, model results indicate that, generally speaking, the more diversified the household, the better off the household is.

**Kazakhstan**

Development of PHEWS for Kazakhstan has not started yet, pending analysis of the survey data that is currently being undertaken.

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

Rates of population growth declined as population density increased in four of the five populations (Figure 6) providing evidence consistent with density dependent feedback to survival and or reproduction. Best approximating models of population growth showed no effect of density in one population, direct feedback from density to population growth rate in three populations and direct and delayed density dependence in one population. The means and 97.5% posterior percentiles of \(1+b\) were less than 1.0 for all but one of populations studied.

The coefficient of variation in average annual winter temperatures was positively related to the strength of model averaged estimate of density dependence (Figure 7a), indicating that increasing variability in winter severity also strengthened the effect of density (Akaike weight = 0.94, \(r^2 = 0.72\)). In contrast, the strength of density dependence was inversely related to spatial heterogeneity in vegetation (Fig. 2b, Akaike weight = 0.88, \(r^2 = 0.53\)) suggesting that access to heterogeneous vegetation attenuated feedbacks between population density and per capita growth rate (Table 3).

These results are based on small samples because estimating \(\tilde{b}\) requires relatively long time series of observations of population size. Thus, although our final results are based on \(n = 5\), this sample is composed of 205 individual census observations. Long time series of census data for large herbivores are relatively rare within any single region. We avoided combining data across regions because of inherent differences in the expression of spatial heterogeneity among them. The independent variables represent similarly synthetic quantities, drawing on many observations to produce a single index of heterogeneity. Our Bayesian hierarchical modeling borrows strength from each of five time series. Thus, although our sample size is statistically small, the observation set that was distilled to create the statistical analysis was large.

Our findings offer the first empirical evidence that heterogeneities in space and time exert fundamentally different effects on population dynamics of mammals. We show that the magnitude of the effect of density on population growth rate depends on variation winter weather over time. This interaction is plausible because severe weather likely reduces the carrying capacity of habitats by increasing food requirements of animals and by reducing food supplies available to meet those requirements (Wallmo et al. 1977, Hobbs 1989). It is plausible, in turn, that these reductions in carrying capacity amplify the intensity of feedback from population density to individual survival and or reproduction. This amplification is manifest in changes in the slope of the relationship between per capita growth rate and population density. In a
In contrast to the effect of temporal heterogeneity, spatial heterogeneity appeared to weaken the effect of density dependence. We propose that this effect is mediated by the ability of herbivores to exploit spatial heterogeneity by selective feeding (Senft et al. 1987, Hobbs 1996, 1999, Illius and Gordon 1999). Selective feeding allows herbivores to cope with food resources containing concentrations of nutrients that vary over time. However, some type of spatial variation is a necessary condition for selectivity (Senft et al. 1987, Bailey et al. 1996); in an environment where resources are homogeneous across all spatial scales, selectivity is impossible. Reductions in spatial heterogeneity in resources can compress the options available to herbivores, and this compression may harm the ability of herbivores to respond to temporal heterogeneity by selective use of space. The implications of spatial heterogeneity for density dependent feedbacks have been explored via simulation, yielding results similar to ours—increasing spatial variation in resources reduced the impacts of increasing population density on population growth (Illius and O’Connor 2000). Other simulations (Underwood 2004) have shown that spatial heterogeneity can amplify or dampen the effect of density on population growth rate. The direction and magnitude of this effect depended on the strength of the relationship between the intrinsic rate of population growth and carrying capacity, and the absolute magnitude of carrying capacity.

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.

**Research Objective 12: SAVANNA-PHEWS Complexity-Fragmentation Experiments**

*Southern Kajiado District, Kenya*

In the late 1960s and early 1970s, the Kenyan government cooperated with international organizations in subdividing Kajiado District into what are now 52 group ranches, averaging about 31,000 ha. That process continues today, with group ranch councils voting to subdivide entire ranches into small parcels of perhaps 40 ha (100 ac) to be dispersed among group ranch members. Pastoralists use movement strategies to access variable green forage and water, and those movement may be prevented in subdivided lands. In that light, in 2002-2003 we quantified the loss in livestock production and effects on households due to subdivision, and to quantify effects of parcel sharing through grazing associations.

In 2003-2004, we prepared manuscripts from those results, including some additional analyses (Boone et al., In review; Thornton et al., In review, with findings cited under Research Objective
9). Esequi, a ranch of low but heterogeneous productivity, showed a steady decline in capacity under subdivision, until 25% fewer livestock could be supported on the ranch composed of 1 km² parcels relative to the intact ranch. Olguoluli Group Ranch, with both low productivity and heterogeneity, supported 20% fewer livestock relative to the intact ranch when parcels were still 10 km². The most productive ranch studied, Osilalei, saw small population changes with subdivision. Participation in grazing associations was helpful to herders in Esequi, but was not helpful in relatively homogeneous Olguoluli Group Ranch, or productive Osilalei.

Subdivision of Kajiado lands may be inevitable, but results show the relative benefits if land owners and policy makers act to maintain open or flexible access to individually held parcels.

In 2003-2004, Boone extended these analyses to focus on vegetation (Boone, In review). Counter to what may be intuitive, group ranches in which livestock populations declined under subdivision showed increases in herbaceous biomass, whereas the ranch where livestock populations that did not change under subdivision had less herbaceous biomass (Figure 8). Livestock within small parcels were food stressed in the dry season and their populations declined so that vegetation increased beyond what could be eaten in the wet season (Figure 9). The vegetation changes modeled led to, or reflect, significant declines in livestock. Whether the focus is upon changes in livestock or vegetation, stakeholders are encouraged to retain open access to subdivided lands to reduce losses.

Western Almaty, Kazakhstan

SCALE project personnel recognized that PHEWS applications to regions other than East Africa may yield unique insights, but to date, PHEWS has only been used in Tanzania and Kenya. Household surveys under SCALE to support this effort are reported in Research Objective 9. Boone has begun putting in-place a relatively straightforward application of the ecosystem model SAVANNA to an area in Almaty Oblast, Kazakhstan, south of Lake Balkash and extending from north of Aidaly Town south to the foothills. Using travel funds from SCALE and leveraged funds from a Global Livestock CRSP (Univ. California, Davis) project, Boone gathered ecological and spatial data for the study site. Boone acquired relatively detailed (1:200,000) topographic maps for the area, soils maps, a more general map of Almaty, vegetation information, livestock population data, land cover data mapped by the DARCA Project of Macaulay Institute (Aberdeen, United Kingdom), and climate data for a 20 year period from nine weather stations. The detailed maps have been scanned, and will be merged and georectified to agree with Landsat ETM+ that is now in-place. The resulting maps will yield important data for use in SAVANNA, such as distance to water.

Research Objective 13: Complexity and Fragmentation in Theoretical Ecosystems

Our generic application was used for these analyses. The application was based upon an existing application of SAVANNA to the Vryburg area in the North-West Province of South Africa. A 300 km² block (20 x 15 km) within Vryburg 1 Township was used in modeling. All geographic data were generalized to 1 x 1 km resolution cells.

Analyses used a suite of fenced parcels, with parcels ranging from the entire 300 km² block modeled, to 30 parcels each 10 km². The model was run separately for each of the parcels, with
cattle able to move about freely or confined to the parcel in question. Each simulation was run for 30 years, and average stocking in the last 15 years of the simulation was the response of interest. Stocking rates were summed across parcels, so that in each case, the measure of interest was the number of cattle that could be supported on 300 km². Weather history affects stocking strongly in this arid region, so weather was kept the same for each analyses of the set parcels (i.e., 300 km² to 10 km²), but the entire set was modeled 12 times, using a different randomly generated weather pattern for each set.

Prior analyses had demonstrated that if the 300 km² block was subdivided into thirty 10 km² parcels, there as a 19% decline in livestock (stocking = 3583 + 2.858 * parcel area in km², df = 106, r² = 0.41, P < 0.001) that could be supported (Boone and Hobbs, In press). Such declines could confound interpretation of changes in vegetation. In these analyses, livestock populations present on each parcel were calculated, with the livestock allowed to move throughout the entire 300 km² block. These populations were then used in a second large set of analyses, where livestock were confined to each focal parcel. This approach allowed analyses to be done where the only difference between simulations was the mobility of livestock. Given these closely paired analyses, the results for a variable of interest (e.g., biomass) with animals confined to parcels was subtracted from the result with animals able to move about freely, then the difference was integrated across time to summarize changes due to subdivision.

Significant declines in annual net primary productivity and root biomass were recorded as the 300 km² block of land was subdivided into parcels 10 km². Under subdivision, high palatability grasses declined significantly, as did moderately palatable grasses (Figure 10a). In contrast, low palatability biomass measures generally increased, as did acacia shrubs (Figure 10a). High palatability grass root biomass declined under subdivision, but increased for moderate and low palatability grasses (Figure 10b). In general, woody plant populations increased (Figure 11a), nitrogen content declined for high palatability grasses (Figure 11b), surface litter declined and slowly decomposing organic matter increased (Figure 11c). The decline in surface litter is associated with a decline in vegetation producing dead material, and an increase in livestock feeding upon standing dead vegetation. Increased woody plant populations caused the slowly decomposing woody organic matter to increase.

**Opportunities for Training and Development**

Training activities were similar to last year for RO4. It supports 3 Ph.D. students and 3 MSc students that contribute directly to the subject of the SCALE grant.

Boone and Coughenour trained Simon Bisrat, an Instructor at the University of Eritrea and a graduate student with Utah State University, in modeling techniques he may use to understand the ecology of African wild ass in Eritrea. Issues of scale in the ecology of the animal and pastoralists were discussed.

The fieldwork and analysis for RO5 and 7 is being conducted in collaboration with two Kazak research organizations within the Kazak Scientific Institute for Livestock and Veterinary Research (Ministry of Agriculture).

- Department of Pasture and Fodder
Institute of Sheep Breeding
These organizations are providing several young Kazak scientists for the study, who carry out field measurements of animal weights and pasture production as well as economic surveys of livestock-owners on management costs and returns. Field costs for the scientists are covered by the study budget. The study is sponsoring one of the young scientists to learn English and computer IT skills in part-time courses. This scientist is also being trained in the field to conduct interviews with livestock owners, and to weigh livestock in the monitored flocks.

In May 2004 a program of instruction in the English language and a computer training program were started for a graduate in the Kazak Scientific Institute for Livestock and Veterinary Research who is working with SCALE. A program of statistical data collection covering the period from 1960-2005 was also drawn up, and work has begun collecting material from libraries and archives in Kazakstan. The information being sought includes data on sheep, goat, cattle, horse and camel populations at provincial and district levels as well as livestock performance indicators such as lambing and calving rates, slaughter weights and wool production for all the SCALE study sites.

Data collection for RO8 was undertaken by Shauna de Luca, a masters student at Colorado State University, who was trained to write questionnaires and to collect household survey data. Survey data were collected from 38 households in two villages in July 2004.

Outreach

The participation of local pastoralists in the Dalrymple Shire, Northeast Queensland in RO3 provides the opportunity for regular feedback on the objectives, developments and findings of the project.

A companion project in Kenya, 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.

Presentations


**Journal Publications**

Boone, R.B. In review. Quantifying changes in vegetation in shrinking grazing areas. Conservation and Society (Invited) *Acknowledges SCALE with grant number*


Ogutu, J. Reid, R.S., Rainy, M.J., Kruska, R.L., Nyabenge, M., Worden, J.S., and Piefo, H.-P. In review. Wildlife and livestock distributions from water show evidence for constrained foraging, spatial segregation, range contraction and expansion in East Africa. *Ecological Applications.* (Acknowledges SCALE)


**Other Publications**

Behnke, R.H. In preparation. *Free distributions and property rights: the exploitation and ownership of natural resources in mobile pastoral systems* (21 pages), submitted (for review by Galvin, Hobbs and Reid) as a possible chapter to the upcoming SCALE book.


**Other Products and Activities**

Boone has received preliminary approval to use leveraged funds from a grant to the International Livestock Research Institute, Nairobi (Reid, PI) by the Belgian Ministry of Foreign Affairs,
Foreign Trade, and International Co-operation to advance research related to SCALE. Boone will calculate detailed responses of Kajiado District, Kenya landscapes to subdivision, quantifying changes in livestock capacity and Maasai food security. BurnSilver and Boone will then disseminate the results to Maasai within the district.

The DARCA study data set for Kazakhstan has been shared with several other researchers on the SCALE project: Kathy Galvin, Philip Thornton, Randy Boone and Mike Coughenour.

One of the SCALE project partners in Kazakhstan, Ilya Alimaev, head of the Dept. of Pasture and Fodder, prepared a set of time-series data from 1990 to 2002 for Tom Hobbs, the project team leader. This data was collected from a research experiment station in the semi-desert zone of southern Kazakhstan. The data were from a long-term study (starting in 1971) to determine the impact of different stocking rates on individual development of semi-shrubs, soil, animals and long-term productivity and preservation of pastures. The objective was to define how it is better and cheaper to preserve long-term productivity of sandy semi-desert pastures and get maximum output from pastures. The data set comprised sheep weights, pasture productivity, precipitation, temperature and soil analysis.

**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.


Appendix A

In the state space model (SSM), a true state variable \( X_t \) is unobservable; however, the observation of the true density \( Y_t (= \ln N_t) \) is the true state \( (X_t) \) plus a random measurement error \( (u_t) \), i.e., \( Y_t = X_t + u_t \). Therefore, the structural form of the AR(p) Gompertz model (Royama 1992) is:

\[
X_t = a + (1 + b) X_{t-1} + c_2 X_{t-2} + \ldots + c_p X_{t-p} + e_t, \tag{1}
\]
\[
Y_t = X_t + u_t. \tag{2}
\]

Error terms \( e_t \) and \( u_t \) are assumed normal and independent of each other and independent over time, i.e., \( e_t \sim N(0, \sigma_e^2), u_t \sim N(0, \sigma_u^2), \ Corr(e_t, u_t) = 0 \). Given these assumptions, the AR(p) Gompertz model was arranged as

\[
X_t = F_t X_{t-1} + w_t, \tag{3}
\]
\[
Y_t = H_t X_t + \varepsilon_t, \tag{4}
\]

\[
\begin{bmatrix}
    w_t \\
    \varepsilon_t
\end{bmatrix} \sim \mathcal{N} \left( \begin{bmatrix}
    0 \\
    0
\end{bmatrix}, \begin{bmatrix}
    Q_t & 0 \\
    0 & R_t
\end{bmatrix} \right) \]

where \( Q_t \) is the variance-covariance matrix of \( w_t \), and \( R_t \) is the variance-covariance matrix of measurement errors \( \varepsilon_t \). At \( p = 2 \), we have

\[
X_t = \begin{bmatrix}
    a \\
    X_t \\
    X_{t-1}
\end{bmatrix}, \tag{6}
\]
\[
F_t = \begin{bmatrix}
    1 & 0 & 0 \\
    1 & 1+b & c \\
    0 & 1 & 0
\end{bmatrix}, \tag{7}
\]
\[
H_t = \begin{bmatrix}
    0 & 1 & 0
\end{bmatrix}. \tag{8}
\]

Model parameters \( a, b, \) and \( c \) and variance \( \sigma_u^2 \) and \( \sigma_e^2 \) were estimated using the maximum likelihood methods. We maximized the complete data log-likelihood function (Shumway and Stoffer 2000) using the expectation-maximization (EM) algorithm (Dempster et al. 1977),

\[
\log L_{X,Y} (\theta) = -\log |\Sigma_0| - (X_0 - \mu_0)^\top \Sigma_0^{-1} (X_0 - \mu_0) \]
\[-\log |Q_t| - \sum_{t=1}^T (X_t - FX_{t-1})^\top Q_t^{-1} (X_t - FX_{t-1}),
\]
\[
\log |R_t| - \sum_{t=1}^T (Y_t - HX_t)^\top R_t^{-1} (Y_t - HX_t),
\]

where \( T \) is the sample size, \( Q_t \) and \( R_t \) are defined as Eq. (5), \( X_t \) is the state vector at time \( t \), \( Y_t \) is the observation at time \( t \), \( F \) is the transition matrix as in Eq. (3), \( H \) is the measurement matrix as in Eq. (4), \( X_0 \) and \( \mu_0 \) are the initials of state vector and its expectation, and \( \Sigma_0 \) is the covariance matrix of \( X_0 \). The EM algorithm is an iterative algorithm. Each iteration \( j \) has two steps, expectation (E step) and maximization (M step). In the E step, the conditional expectation of the complete data likelihood with respects to the state vector \( X_t \),
\[ Q\left( \theta \mid \theta^{(j-1)} \right) = E \left( \log L_{XY} (\theta) \mid Y, \theta^{(j-1)} \right), \]

is evaluated using current estimates of \( \theta \), i.e. \( \theta^{(j-1)} \). In the M step, the estimates of unknown parameters \( \theta \) comprising \( \mu_0, \Sigma_0, F, Q, \) and \( R \) are updated to maximize the conditional expectation of the complete data likelihood. In the linear and normal case, the close form solutions for the updating exist (Shumway 1988, Shumway and Stoffer 2000). To resolve the invertibility of covariance matrix \( Q \) of our AR(2) model, we adopted Wu et al. (1996)’s modified forward filtering and backward smoothing algorithms for the parameter estimations. Wu et al.’s algorithm allows element-wise updating of matrices \( F, Q, \) and \( R \) with some elements of the matrices being restricted as the known (Wu et al. 1996).

The maximized likelihood was used to compute the corrected Akaike information criterion (AICc) and Akaike weights (Burnham and Anderson 2002). Akaike weights were used to obtain model averaged estimates of parameters. For example, the model averaged estimate \( \tilde{b} \) of the parameter \( b \) was obtained as the weighted average of maximum likelihood estimates \( \hat{b}_r \) from each of the 3 models in the candidate set (Burnham and Anderson 2002),

\[ \tilde{b} = \sum_{r=1}^{3} w_r \hat{b}_r, \]

where \( w_r \) is the Akaike weight for model \( r \).

We checked assumptions on model errors following Harvey (1989, p.259). The residuals of the best approximating Kalman filter model were not autocorrelated (Box-Ljung statistic \( Q, P > 0.05, \) Harvey 1989). Inspection of the sample autocorrelation function (ACF) also indicated that the residuals were not serially correlated. Q-Q plots confirmed the assumption of normally distributed residuals.

To examine effects of spatial and temporal heterogeneity on the strength of density dependence, we regressed estimates of the absolute value of the model averaged estimate of \( b \) on indices of temporal variation in weather and spatial variation in plant biomass, i.e., \( |\tilde{b}| = \alpha + \beta x \) where \( x \) is the value of the index of heterogeneity. We used the regression model \( |\tilde{b}| = \alpha \) as a null model and compared the strength of evidence for the single parameter null model relative to model parameters representing effects of heterogeneity, i.e., those including \( \alpha \) and \( \beta \).

We used Bayesian hierarchical modeling (Gelman et al. 2004) to estimate the 95% posterior intervals of \( \alpha \) and \( \beta \). The hierarchical modeling was based on the AR(1) Gompertz models Eq. (3)-(5). We specified the prior distributions of state \( X_{i,t} \) and the likelihood function as,

\[
\begin{align*}
X_{i,t} &\sim N \left( \mu_{X_{i,t}}, \tau_{i,1} \right), \\
\mu_{X_{i,t}} &= a_t + (1 + b_t) X_{i,t-1}, \\
Y_{i,t} &\sim N \left( X_{i,t}, \tau_{i,2} \right), \\
X_{i,0} &\sim N \left( \mu_{X_{i0}}, \tau_{i,1} \right),
\end{align*}
\]
and the prior distribution of the hyper-parameters as follows,

\[ b_i' = (1 + b_i) \sim N(\mu_{b_i}, \tau_{b_i}) \],
\[ \mu_{b_i} = \alpha + \beta X_{env}, \quad \alpha \sim N(0, \tau_{\alpha}), \quad \beta \sim N(0, \tau_{\beta}) \],
\[ \tau_i \sim \text{Gamma}(0.001, 0.001), \quad i = 1, 2, 3, 4, 5 \],

where \( X_{i,t} \) is the logarithm of the true population size of population \( i \) at the time \( t \), \( X_{i,t-1} \) the logarithm of the true population size of population \( i \) at the time \( t-1 \), \( \mu_{X_{it}} \) is the expectation or mean of \( X_{i,t} \), \( \tau_{i,1} \) is the precision of \( X_{i,t} \) - the reciprocal of the process variance of \( X_{i,t} \), \( \tau_{i,2} \) is the reciprocal of measurement variance of \( Y_{i,t} \), \( a_i \) is the intrinsic rate of population growth of population \( i \), \( b_i \) is the strength of direct density dependence in population \( i \), \( X_{env} \) is the CV in winter temperatures or the CV in the NDVI, \( \alpha \) and \( \beta \) are the regression coefficients. Notations \( \sim N(\cdot) \) and \( \sim \text{Gamma}(\cdot) \) stand for being distributed as a normal and the gamma distribution, respectively. In a preliminary run, we specified the intrinsic rate of population growth as a stochastic variable distributed normally. However, the posteriors of \( a_i \) and \( b_i \) were highly correlated. We reparameterized the hierarchical model using the MLE values estimated with the EM algorithm to facilitate the convergence of the chain (Congdon 2001). Our main objective of the hierarchical modeling is to model the relationship between the strength of density dependence and environmental heterogeneity among the five ungulate populations. We used the most recent 30 years of survey data for all five ungulate populations in our hierarchical model. The Monte Carlo Markov chain was run for 10,000 iterations. The first 5,000 iterations were the burn-in period and discarded. The second 5,000 iterations were used to construct the posterior distributions. The model was implemented using WINBUG 1.4.1 (Spiegelhalter et al. 2003). The convergence of the chain was checked by monitoring the trace or trajectories of the posteriors of variances and estimated parameters b, \( \alpha \) and \( \beta \) (Raftery and Lewis 1996).
Table 1. A set of comparative hypotheses for two basic household types that are being addressed by the data collection and PHEWS modelling work in Kazakhstan (Source: C. Kerven, 2004)

<table>
<thead>
<tr>
<th>Hypotheses</th>
<th>Small flocks (1-20 sheep and goats) with no cattle</th>
<th>Medium-large flocks (100-500 sheep/goats) plus cattle, horses and/or camels</th>
</tr>
</thead>
<tbody>
<tr>
<td>•</td>
<td>Small-medium flocks (21-100 sheep/goats) and/or 1-5 cattle, riding horses</td>
<td>• Large flocks (500+ sheep/goats), plus cattle, horses and/or camels</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>A.</th>
<th>Livestock more sedentary around villages (less seasonally mobile), therefore have a reduced scale of land use and sub-optimal nutrition</th>
<th>Livestock more seasonally mobile to distant pastures, make use of ecological complexity (heterogeneity in the landscape) and have better nutrition</th>
</tr>
</thead>
<tbody>
<tr>
<td>B.</td>
<td>Livestock in sedentary flocks are less productive (lower liveweight, reproductive performance, milk and wool; higher lamb/kid mortality). Therefore they provide less output (offspring/meat/milk/wool) per head for consumption</td>
<td>Livestock in mobile flocks are more productive and provide higher output per head. Positive feedback of nutrition+reproduction-lower mortality allows higher flock/herd growth</td>
</tr>
<tr>
<td>C.</td>
<td>Offtake rate of animals slaughtered for home consumption and sold is much higher, depleting flocks and not allowing growth</td>
<td>Offtake rate of animals slaughtered for home consumption and sold is lower, allowing annual flock growth</td>
</tr>
<tr>
<td>D.</td>
<td>Provide more dairy products for home consumption and inter-family distribution, because there is more milk taken from each cow and goat</td>
<td>Provide more dairy products for the market as there is more total milk produced from larger herds (cows, horses, camels)</td>
</tr>
<tr>
<td>E.</td>
<td>Provide a higher proportion of total household food (meat and milk) to their owners</td>
<td>Provide a higher proportion of cash to home consumption income to their owners</td>
</tr>
<tr>
<td>F.</td>
<td>Owners of small flocks convert a greater percentage of their livestock into food goods through the market</td>
<td>Owners of large flocks convert a greater percentage of their livestock into non-food goods through the market</td>
</tr>
<tr>
<td>G.</td>
<td>Owners of small flocks must depend more on non-livestock sources of income – informal employment, pensions, remittances, small-scale irrigated plots, and benefits from wealthier kin</td>
<td>Owners of large flocks are re-investing in their livestock through new inputs (capital equipment, vehicles, new breeds, hired labor) and moving out to distant pastures. They depend less on non-livestock income sources but rely on poorer kin for labor inputs</td>
</tr>
<tr>
<td>H.</td>
<td>Households with very small flocks get insufficient meat to eat and suffer nutritional deficits, especially iron</td>
<td>Households with larger flocks have adequate amounts of animal protein and do not have nutritional deficits.</td>
</tr>
</tbody>
</table>
Table 2: Mean live weights of sheep and goats in flocks according to seasonal movement, May 2004

<table>
<thead>
<tr>
<th>Species</th>
<th>In village, never move</th>
<th>Out of village, never move</th>
<th>Move each season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheep</td>
<td>49.5 kg</td>
<td>48 kg</td>
<td>57.2 kg</td>
</tr>
<tr>
<td>n</td>
<td>50</td>
<td>71</td>
<td>80</td>
</tr>
<tr>
<td>Goats</td>
<td>37.7 kg</td>
<td>41.4 kg</td>
<td>40.1 kg</td>
</tr>
<tr>
<td>n</td>
<td>63</td>
<td>59</td>
<td>83</td>
</tr>
</tbody>
</table>

s.e.d. 1.34 \( P^{***} \)

Table 3. Model selection for the effects of spatial heterogeneity of Normalized Difference Vegetation Indices (NDVI) and temporal variability of winter temperatures on the model-averaged strength of density dependence in five ungulate populations

| Models            | \( |\tilde{b}| = a \) | \( |\tilde{b}| = a + c \cdot NDVICV \) | \( |\tilde{b}| = a + c \cdot TempCV \) |
|-------------------|------------------|---------------------------------|----------------------------------|
| AICc              | 1.9              | -2.8                            | -0.7                             |
| \( w_r \)         | --               | 0.88                            | 0.94                             |

\( |\tilde{b}| \) is the model-averaged estimate of \( |b| \), a measure of density dependence strength; Model \( |\tilde{b}| = a \) serves as a null model; TempCV is the coefficient of variation in winter temperatures, NDVICV the coefficient of variation in NDVI, \( a \) intercept, and \( c \) regression slope. Akaike weights \( (w_r) \) show the strength of evidence for each model including an intercept and a slope relative to the null model containing a single term for the intercept.
Figure 1. SCALE study sites and their geographic locations.
Figure 2. Lines representing vegetation heterogeneity across space and time, with the intercept reflecting productivity, and the slope represents the greatest access to forage an animal moving a given distance can access. Locations are: NGOR – Ngorongoro Conservation Area, Tanzania; Mara – Maasai Mara Natural Reserve, Kenya; RMNP – Rocky Mountain National Park, Colorado; SNP – Serengeti National Park, Tanzania; Kruger – Kruger National Park, South Africa; YNP – Yellowstone National Park, Wyoming, Montana, and Idaho.

Figure 3: Variation in cattle diet quality as estimated from fecal NIRS analysis for paddocks of different sizes in the study. (Large Paddocks > 2200 ha, Small Paddocks < 2200 ha.)
Figure 4: Seasonal variation in normalized difference vegetation index (NDVI) for sets of 0.5 km x 0.5 km pixels within a small and a large study paddock, illustrating constrained access to vegetation variability (red arrows) for cattle in smaller paddocks.

Figure 5: Variogram of wet season normalized difference vegetation index (NDVI) values showing spatial structure of vegetation heterogeneity in the Dalrymple Shire. Access to vegetation heterogeneity is constrained at the scale of paddocks in the shire (5,000 – 50,000 ha).
Figure 6. Relationships between population growth rate and the natural logarithm of population sizes of bison (*Bison bison*) and elk (*Cervus elaphus*) in the Gravelly Mountains, Montana, Rocky Mountain National Park (RMNP), Colorado, National Elk Refuge (NER), Wyoming, USA
Figure 7. Effects of mean winter temperatures, temporal variability in winter temperatures and spatial heterogeneity in vegetation on the model-averaged strength of density dependence in the bison (*Bison bison*) and elk (*Cervus elaphus*) of the Gravelly Mountains, Montana, Rocky Mountain National Park, Colorado, Yellowstone National Park, and National Elk Refuge, Wyoming, USA. Akaike weights ($w_i$) show the strength of evidence for the model including an intercept and a slope relative to the null model containing a single term for the intercept.
Figure 8. Changes in vegetative properties for group ranches in Kajiado District, Kenya, under subdivision. Herbaceous biomass (a) and leaf biomass (b) increased under subdivision, and nitrogen mass of herbaceous plants did not change (c).
Figure 9. In Eselenkei Group Ranch, herbaceous green leaf biomass remained relatively high during the dry season (solid line) when livestock were allowed to move about the entire group ranch, but when confined to individual 1 km$^2$ parcels, livestock grazed intensively and leaf biomass declined to near zero in most years (dotted line).
Figure 10. The difference in green leaf biomass (a) relative to an intact 300 km$^2$ parcel for high palatability grasses (closed circle), moderate palatability grasses (open circles), low palatability grasses (closed squares), and acacia shrubs (open squares). Root biomass (b) of high palatability grasses (closed circle), moderate palatability grasses (open circles), and low palatability grasses (closed squares) are shown. Integrated differences in biomass are shown.
Figure 11. The increase in woody plant populations (a) relative to an intact 300 km² parcel for acacia trees (closed circles) and shrubs (open circles). Average nitrogen mass (b) is shown for high palatability grasses (closed circle), moderately palatability grasses (open circles), low palatability grasses (closed squares), and annual grasses (open squares). Surface litter biomass (c) declined under subdivision (closed circles), whereas soil organic matter that decomposes over long periods increased (open circles). Integrated differences in biomass are shown.