## SCALE Annual Report – 2005-2006

#### **Research and Education Activities**

#### **Research Objective 1: Case Study Synthesis and Comparisons**

**Objective:** *Develop a state-of-knowledge publication on complexity, scale, and fragmentation.* 

We are very close to submitting our book, Fragmentation in Semi-arid and Arid Landscapes: Consequences for Human and Natural Systems. The synthesis chapters are being written and reviewed. We will have the book indexed and professionally proofread shortly so the book will be completed in Fall 2006. The team (Hobbs, Galvin, Boone, Lackett, Thornton, Reid, Ash and Stokes) met in Jackson Hole, Wyoming, July 3-7, 2006 to write a synthesis paper on the project. A draft of the manuscript is currently being edited by team members.

## **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 focused on the completion of a synthesis chapter for an upcoming volume from the SCALE project, and on the preparation and revision of manuscripts. BurnSilver and Boone, along with collaborator Russ Kruska of the International Livestock Research Institute of Nairobi, have focused on calculating metrics for selected SCALE sites that reflect infrastructure and opportunities for people that inhabit the sites.

## **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.

The main activity over the past year has involved collecting and analyzing faecal material from selected paddocks in the Dalrymple Shire to compare cattle diet quality to paddock characteristics. The final two-monthly samples were collected in December 2005 and we have since generated a set of metrics of landscape complexity for each of the paddocks from which dung was collected.

We have also continued work that allows us to quantify spatial patterns of asynchronicity in resource availability across landscapes. This aspect of landscape complexity should have practical benefits for human and herbivore access to heterogeneous resources. We have

developed this into a new project that will allow pastoralists to exploit spatial patterns in landscapes to offset the risks associated with (temporal) climatic variation.

# **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 2005 to 2006:

- 1. Completion of field data collection and analysis of data for the study on the effects of landscape fragmentation on the movement of pastoral livestock herds in the Athi-Kapitiei and Mara ecosystems (fully funded by the NSF SCALE grant),
- 2. Completion of fieldwork for 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),
- 3. Completion of an assessment of the efficiency of different techniques for sampling the numbers and diversity of livestock and wildlife populations (partially funded by the NSF SCALE grant), and
- 4. Completion of a draft of a synthesis paper on the causes and consequences of fragmentation for ecosystems and pastoral societies at the SCALE study sites across the world (partially fully 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.* 

Activities under these two research objectives mostly include writing up results in manuscripts.

1. A manuscript 'Free distributions, property rights and fragmentation: the exploitation of natural resources in mobile pastoral systems' was written this year. This was a candidate for a chapter in the SCALE book but Behnke decided that the paper was flawed and is not looking to publish it now, at least in this form.

2. Work is on-going on the Behnke synthesis chapter for the SCALE book. The section on eastern Africa has been sent to the three East African case study authors; the section on southern Africa will be completed and circulated shortly.

3. R. Behnke, G. Davidson, A. Jabbar, and M. Coughenour. Human and natural factors that influence livestock distributions and rangeland desertification in Turkmenistan. To appear in R. Behnke, L. Alibekov and I. Alimaev (eds.) The Socioeconomic Causes and Consequences of Desertification in Central Asia. Springer, scheduled to be published in 2007. This was aready presented at a NATO-financed conference (with same title as the forthcoming book) in Bishkek, Kyrgyzstan in May-June of 2006.

4. Publication of the Nomadic Peoples article included in the journal publications section.

## **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 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 modeling to be carried out in tandem with the Savanna ecosystem model. Scenario analyses are then undertaken to look at the interactions between ecological complexity and household well-being in case-study environments.

During the year, data collected from a total of 58 households in two villages in Kazakstan were analyzed. The villages are Ay Daly in the Almaty Oblast and Sary Ozek in the Zhambyl Oblast. Survey data were summarized on the basis of a simple typology of households based on the size of household flocks. Calculations were done on key household descriptors such as inputs used and outputs produced, rules for cropping were defined, and information was assembled on the timing and nature of livestock sales through the year.

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

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

Work started during the year on specifying the PHEWS module for the Kazakstan case study, using the data collected under RO8. This will be completed in the coming months, and then the module will be linked to the Savanna modeling application for Kazakstan, and various scenarios will be run, analyzed, and written up.

Two sets of Savanna-PHEWS analyses for Kajiado were carried out during the year. One set looked at a series of four scenarios: the ecological and social effects of enhanced livestock breeds; adding water sources in Imbirikani Group Ranch; exploring different pathways to subdivision in Imbirikani and Eselenkei Group Ranches; and exploring different livelihood options that increase societal well-being in southern Kajiado. Results of these are reported elsewhere.

A second set of simulations was run to explore the scope for introducing a "payments for ecosystem services" scheme to compensate pastoralists for spillover benefits associated with forms of land use that are compatible with wildlife conservation (traditional grazing lands in Kajiado are being converted to cropland, with deleterious impacts on wildlife corridors.) Briefly, the results indicate that such a scheme probably would enhance global welfare, but at the risk of encouraging overstocking during droughts.

A paper was written up, involving some new model runs, which sought to synthesize some of the lessons learned from the case studies undertaken in East and southern Africa concerning coping strategies in livestock-dependent households. In addition, inputs were made to book chapters on the case studies in Ngorongoro Conservation Area (NCA) and Northwest Province, Republic of South Africa.

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

Virtually all studies of the factors regulating population dynamics have focused on temporal variation in conditions affecting population growth. The modifying effect of spatial variation on the operation of endogenous and exogenous controls remains largely unstudied. Population dynamics play out in a spatial context, and it remains largely unknown how spatial variation influences the temporal dynamics of population growth. Emerging evidence (Illius and O'Connor 2000, Wang et al. 2006) suggests that spatial heterogeneity in resources may attenuate the effects of density dependent feedbacks on population growth rates of large herbivores. A plausible mechanism for this attenuating effect is that spatial heterogeneity in resources allows animals to be selective for resources that vary over space, and in so doing, may allow them to compensate for resources that vary in time.

Thus, spatial and temporal heterogeneity may influence population dynamics in different ways. We sought to understand how the strength of density dependence in ungulate populations responds to variation in climate conditions occurring over a gradient of latitude  $(40 - 70^{\circ} \text{ N})$  and to spatial variation in resources created by variation in altitude. We analyzed 23 time series of estimates of abundance of northern ungulate populations in Europe and North America (latitude range of  $40^{\circ}$ - $70^{\circ} \text{ N}$ ) using autocorrelative Gompertz models.

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

Our application of the SAVANNA-PHEWS model to the Balkhash Basin of Kazakhstan is continuing. Analyses applicable to RO 12 were conducted by Boone and BurnSilver under leveraged work related to the SCALE project, rather than directly funded by SCALE. That work is now almost complete. Boone also collaborated with Erwin Bulte, Tilburg University, The Netherlands and Randy Stringer, at the time with the Food and Agriculture Organization, Rome, Italy, on analyses that quantified possible effects of removal of cultivation and other reductions in fragmentation on elephant populations.

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

The bulk of SCALE modeling efforts have been to address advanced hypotheses related to Research Objective 13. Under both RO 12 and RO 13, in past work we had quantified how sensitive landscapes were to fragmentation, here defined as the decline in the number of ungulates that can be supported on a given landscape as the landscape is fragmented into small parcels. In those analyses, we had used observed weather patterns, or weather created by

randomized draws from the observed weather patterns. The effects of fragmentation under variable climates had not been quantified. In simulations started in 2005 and written-up in manuscripts in 2006, Boone varied rainfall in simulations conducted for three areas (North-West Province, South Africa, southern Kajiado, Kenya, Ngorongoro Conservation Area, Tanzania) from 100 to 1000 mm per year, and inter-annual coefficients of variation from 0 to 60%. For each of the areas, a 1000 km<sup>2</sup> area was subdivided into progressively smaller and smaller parcels, until the area was composed of 100 parcels each 10 km<sup>2</sup>. Simulations were conducted for each parcel, with each climatic pattern, including over 150,000 simulations. A local-area network of computers was constructed, with one computer storing simulation results, and several computers running simulations, to complete analyses in a timely way.

## **Research Findings**

## **Research Objective 1: Case Study Synthesis and Comparisons**

Work in ongoing on writing/editing book chapters for the SCALE synthesis book. The book will be submitted this fall.

## **Research Objective 2: Complexity Framework and Analysis**

The synthesis chapter will be forwarded to external reviewers shortly. In the chapter, metrics are presented for each of the 22 SCALE study sites that reflect how sensitive the landscapes are likely to be to fragmentation. The metrics include standard deviations in elevation, autocorrelation within Landsat satellite images, and a novel metric summarizing access to forage resources by mobile ungulates, reported in our previous annual report. We have calculated metrics representing infrastructure within 5 of the SCALE study regions (i.e., Northern Great Plains, USA; Kajiado District, Kenya; North-West Province, South Africa; Northern Queensland paddocks and Victoria River District sites, Australia; and Moinkum Desert and Balkhash Basin, Kazakhstan. Metrics include road density, human population density, and infrastructure represented by nighttime lights as shown in satellite images.

Students Worden and BurnSilver continue to explore how landscape heterogeneity in southern Kajiado District, Kenya affects movements of wildlife, livestock, and people, as described in RO2 and RO4. Worden has been using a tool written by Boone that plots changes in normalized difference vegetation indices (i.e., greenness measures from satellite images) for areas within the district. Worden hypothesizes that pastoralists may not be moving to areas of high average greenness, but rather to small patches of maximum greenness, sometimes imbedded in less productive landscapes. Ongoing analyses are exploring that possibility.

Analyses that summarize the relationships between population dynamics in northern hemisphere ungulates and temperature and elevation variability are complete, and have been submitted to *Ecology* for review (Wang et al., In review). In that work, we have demonstrated that temperature extremes can increase density dependence in animal populations, as others have found (our showing that the relationship ceases in very high latitude populations is unique). Most importantly, we showed that variation in elevation, reflecting variation in vegetation and

the heterogeneity of forage availability, related inversely to density dependence – areas that are most diverse allowed animals to find enough forage to avoid strong density dependent feedbacks. These results relate directly to the goals of the SCALE project, and the potential for harmful effects from fragmenting landscapes.

A publication Boone had reported on in the last annual report, which featured evolutionary programming used to model migratory wildebeest migration in Serengeti wildebeest, was revised. Boone worked with S. Thirgood, G. Hopcraft, and others to gather observed animal movement data to compare with the modeled distributions (Figure 1). The revised manuscript was published in *Ecology*.

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

Paddocks from which cattle dung samples had been collected were characterized by the following metrics: Paddock area (ha); Topographic variation (standard deviation of elevation, and the number of elevation classes (10m height intervals)); Vegetation diversity (Shannon diversity index for an isoclass unsupervised classification of a Landsat TM image of the Dalrymple Shire); Average distance from permanent water; Number of soil types in the paddock; and Stocking rate (number of stock grazing days ha<sup>-1</sup> yr<sup>-1</sup>)

The study paddocks covered three different underlying geological formations that differed in productivity: Basalt (most productive, 18 paddocks), Igneous (16 paddocks) and Canozoic (least productive, 16 paddocks). Sampling and analysis was therefore stratified by geology type. For each geology type, paddocks that were larger than the median for that geology type were classified as 'large' and the remainder as 'small'. Binary classifications of each of the other paddock metrics were conducted in the same manner.

Dung samples were analyzed using Near Infrared Spectroscopy to estimate the dry matter digestibility (DMD) and crude protein (CP) content of cattle diets. The ratio of CP:DMD was used as a combined indicator of diet quality. On occasions dung samples were not available either because cattle had been withdrawn from paddocks or because participants were unable to collect samples. To address the problem of missing samples, we focused on the three collection dates in the dry season (June, August and October) where diet quality was lowest and most static and took the average diet quality for this period each year in each paddock. T-tests showed that cattle in paddocks with high vegetation diversity were better able to maintain their diets through the dry season than cattle in low diversity paddocks (Figure 2). Neither paddock size nor any of the other metrics of landscape complexity was found to have a significant influence on cattle diet quality.

This result supports the hypothesis that landscape complexity can be exploited by herbivores by providing a greater variety of resources from which they can select their diets, allowing them to maintain a more nutritious diet through the dry season than is possible in more homogenous

paddocks. While this may be a benefit to animals / livestock production, there may be environmental trade-offs that need to be considered if diet selectivity in diverse paddocks is accompanied by localized overgrazing of preferred vegetation types.

## **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 Athi-Kaputiei and Mara ecosystems (Kshatriya, Nkedianye, Reid)

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

We completed all data collection in December 2005. In total, we followed the daily grazing orbits for 14 sampling sessions, which included tracking the movement of 4-5 livestock herds for a 5-10 day period at the Athi-Kaputiei site. In addition, a pilot study on livestock herd movements in response to wildebeest grazing in the Mara site was completed.

In 2006, data collected over the last 2 years was prepared for analysis and analysis began. The preliminary data analysis suggests the following results:

- a. Grazing orbit paths become more convoluted in areas that restrict movement due to fences.
- b. Energetic requirements may be higher in more fragmented areas in terms of total time grazing.
- c. Speed of movement is much slower in open areas, which are less restricted to grazing.
- 2. Completion of fieldwork for 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 in late 2004. Kiros completed his coursework at the Dept of Land Resource Management and Agricultural Technology (LARMAT), College of Agriculture and Veterinary Sciences, University of Nairobi in July 2005. He presented his MSc research proposal to his academic department in November 2005; the proposal was approved by the department. It was then approved in July 2006 by the Board of Postgraduate Studies (BPS).

Kiros and Mrigesh Kshatriya then designed a questionnaire to collect information on historical herder and livestock movements, as far back in time as possible. The questionnaire attempts to obtain the following information from herders: where the Maasai pastoralists moved their livestock in response to drought, why they moved, which species moved, whether or not the whole cattle herd moved, whether or not individual heads of household moved alone or with others, and whether or not fencing or fragmentation affected movement decisions. Herders were also asked about their movements during the year preceding each of the droughts. They were

asked whether or not they anticipated the droughts and what they did if they foresaw them. In addition, herders were asked what they did to cope with droughts in the past fifteen years, comparing the coping mechanisms with what they do at present. The questionnaire was designed in English and then pre-tested and translated with enumerators into ki-Maa in May, 2006. The enumerators began interviews in June 2006.

During the pre-testing, it was clear that respondents had difficulty recalling what they did during specific droughts that occurred before the 1960s. They also had a hard time differentiating the 1940s from the 1950s. So Kiros decided to use the 1940s as the earliest dates instead of the 1950s since 1940 was when the Nyangusi age set had their *Eunoto* (graduation to elderhood) ceremony, which was easier for them to recall.

Interviewees were selected from two areas that have had different histories of fragmentation in terms of the time of onset of subdivision, as well as its present extent and level of fencing. These were the Olturoto/Olkinos area and Olooloitikoshi in the Athi-Kapitiei site. The former (Olturoto/Olkinos) had been fenced much earlier and currently has one of the highest fence densities. On the other hand, Olooloitikoshi is one of the least fenced areas. Fifty individuals were randomly selected from each of the two areas (n=100 total) using the random-select feature of SPSS software using a list (sampling frame) of all pastoral households in those areas identified in previous socioeconomic research done by ILRI.

For every interview, an attempt was made to secure the presence of two or three other family members since movement decisions are usually made collectively as a family unit. Data collection was completed in July and data entry by August, 2006. In September, the data entry team mapped all the movement data. Kiros will now start data analysis and writing of his MSc thesis.

3. Completion of an assessment of the efficiency of different techniques for sampling the numbers and diversity of livestock and wildlife populations

This work was completed in the Mara site in 2005 and a paper was published from the work in the Journal of Zoology in 2006. This following is the abstract of the work that appears in the article: 'Effective management and conservation of wildlife populations require reliable estimates of population size, which can be difficult and costly to obtain. We evaluated how precision in estimates of herd size and abundance varies with sample size and strip width using two field surveys and bootstrap re-sampling of the field data. We also examined precision under distance sampling and evaluated the cost-effectiveness of both survey techniques. Precision in estimates of abundance increased with increasing sample size and varied with strip width independently of sample size. The hazard rate key function was best for five species in two surveys with contrasting visibility conditions. Precision in density was more sensitive to the number of herds sighted than to variation in herd size and effective strip width for distance sampling. Strip counts produced lower abundance estimates but higher precision than distance sampling. We estimated that distance sampling would cost about US\$3.1 km<sup>-1</sup> of transect. Strip counts deserve serious consideration for surveys of species that occur at high densities and form large, loose agglomerations but distance methods are suitable for species occurring at moderate to low densities in areas where visibility varies substantially. Distance sampling may thus need

to be supplemented by strip counts to efficiently estimate densities of rare, abundant and highly clustered multi-species assemblages of African savanna mammals. In small areas, it may often prove necessary to conduct several surveys to obtain adequate sample sizes for distance models.' The citation for this paper appears in the section on journal articles below.

4. Completion of a draft of a synthesis paper on the causes and consequences of fragmentation for ecosystems and pastoral societies at the SCALE study sites across the world

In July 2006, the project team members, including Robin Reid, met for a week and wrote a draft article for publication, synthesizing the results from this project. Reid contributed the section on the policy implications of this project. The paper will be submitted to *BioScience* and the team proposed a policy forum piece to the journal, *Science*.

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

Findings are included in manuscripts and in the SCALE book being completed.

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

The household typology is shown in Table 1, together with a few household characteristics. Households are classified as small, medium, large or very large, depending on the number of TLUs owned by the household. These data, together with a large amount of secondary information, are being used to specify a PHEWS module for Kazakstan, that will be linked to the Savanna application for the case study area.

Work on the Kajiado case study continued during the year, although no further socio-economic information was collected. Further analyses were carried out with the linked Savanna-PHEWS model, and these are outlined under RO 9 below.

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

The synthesis study sought to pull together results from three case studies in East and southern Africa: pastoralist communities in NCA, northern Tanzania, agro-pastoralists in Kajiado, southern Kenya, and communal and commercial ranchers in South Africa. The synthesis study also included some integrated assessment work done in the mixed crop-livestock systems in western Kenya as a comparison. The object was to test the hypothesis that households' capacity to adapt in the face of increasing external stresses is governed by flexibility in livelihood options.

In all the systems studied, there are options related to the management of natural resources that can help households at least partially overcome the effects of increasing stresses to the system caused by population growth, changes in climate and weather variability, and land fragmentation. There are costs involved, however, in terms of impacts either on natural resources and other stakeholder groups or on the variability of household income. In NCA, for example, poorer households can partially offset increasing population pressure by increasing size of cultivated plots, although this is ultimately limited by conservation status. There are only small impacts on simulated wildlife numbers, but the impacts on tourism of such increased areas of cultivation may be more substantial and negative. In southern Kajiado, poorer households can also partially offset impacts of subdivision by increasing size of cultivated plots, and they may also do this through diversification of livelihood options, such as engaging in a business or other off-farm activity. Model results show that wildlife numbers are relatively sensitive to increases in cultivated areas in Kajiado, however. In the Northwest Province of RSA, commercial ranchers can partially offset impacts of increased rainfall variability through stocking and destocking decisions, at the risk of increasing the year-to-year variability of income. In addition, there may be longer-term ecological impacts on grasslands of over-stocking. In the already highlyfragmented landscapes of western Kenya, on the other hand, the process of continual decline in size of land holdings can be partially offset only through intensification or diversification, although long-term impacts on soil fertility may be negative with insufficient use of inputs. In all the case studies addressed in the synthesis, households can offset increased stresses through the management of natural resources only up to a point. Eventually some threshold is reached, beyond which this offsetting is simply not possible through internal manipulation of the system.

The synthesis has shown that integrated assessments have a key role to play in quantifying tradeoffs and in identifying what is both desirable and feasible in highly complex systems. The models and tools used have several limitations, which further research may be expected to address. Even so, they can contribute substantially to identifying the limits within which natural resource management can reasonably be expected to contribute to improving and sustaining the livelihoods of resource-poor people who keep livestock.

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

#### Density dependence in ungulate population growth

We were unable to detect an effect of population density on per capita population growth rate for any of the eight populations of ungulates that occupied habitats north of 59 degrees latitude (Table 2). The Akaike weights of the density independent model for these populations exceeded 0.6, indicating that although density dependence cannot be ruled out, evidence for these feedbacks was weak. South of this latitude, ten of 15 populations showed evidence of density dependence, e.g. (1 + b) < 1, and a larger value for the Akaike weight for the AR(1) or AR(2) models (Table 2). Direct density dependence was found in nine populations (AR[1] models, Table 2), while bison population dynamics in Yellowstone National Park were best approximated by an AR(2) model, providing evidence for direct as well as delayed density dependence. Considerable variation in the strength of density dependence existed among the populations (Table 2).

Spatial factors influencing the strength of density dependence

Broken stick regression identified two possible breaking points for  $\left|\tilde{b}\right|$  of 0.06 (for SD in elevation) and 0.09 (for latitude). We selected a breaking point at  $\left|\tilde{b}\right| = 0.09$  (Figure 3) based on AIC<sub>c</sub> and the observation that all the populations showing strong evidence of density

independent growth had values of  $\left| \tilde{\vec{b}} \right|$  less than or equal to 0.09. The breaking point divided the 23 pairs of latitude and  $\left| \tilde{\vec{b}} \right|$  into two groups.

For populations that showed density dependence (Akaike weight > 0.6 for AR[1] or AR[2] model and  $\left| \tilde{b} \right| > 0.09$ ), the strength of feedbacks on per capita population growth (measured with  $\left| \tilde{b} \right|$ ) were inversely related to the standard deviation of elevation (Figure 4a) and positively related to latitude (Figure 4b). The slope was negative and significant ( $\beta = -0.0005$ ,  $w_i = 0.74$ , P = 0.07) in the regression of the model-averaged estimates of *b* with the standard deviation of elevation, and positive and significant ( $\beta = 0.02$ ,  $w_i = 0.86$ , P = 0.04) in the regression of the model-averaged estimate of *b* with latitude.

In summary, ungulate populations located above 59° N latitude exhibited density independent growth; below this latitude, populations showed negative feedback from population density to population growth rate. The strength of this feedback increased with increasing habitat latitude and declined with heterogeneity in habitat elevation. We conclude that the effects of increasing population density are shaped by spatial variation in both weather and resources. Density dependence appears to be amplified by increasing severity of weather along a latitudinal gradient until a threshold is reached where density independent forcing prevails. Where density dependence occurs, it is attenuated by spatial heterogeneity in altitude, which we interpret as an index to heterogeneity in resources.

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

Parameterizing the Kazakhstan application of SAVANNA continues. Most of the spatial model inputs (e.g., maps of elevation, soils, vegetation, slope, distance-to-water) are in place, as is livestock information. Parameterizing files that describe the nine plant functional groups is continuing. Sayat Temirbekov, now with our laboratory but previously working in the region being modeled, has been extremely helpful in this effort. SAVANNA modeling in the region will be completed in the coming months, then PHEWS will be parameterized by Thornton and Galvin using household data gathered for this purpose.

Our leveraged work (Boone, BurnSilver, and Thornton) includes four general scenarios, two of which are closely associated with the ideas behind SCALE. In one scenario, we explore the most appropriate means of subdividing Imbirikani and Eselenkei Group Ranches. Most people agree that subdivision is inevitable. We are using integrated assessment techniques to contribute to the discussions on the best pathways to subdivision. We explored the cost of fully subdividing the group ranches (Figure 5), versus providing 5 ac (2 ha) parcels for each ranch member and leaving much of the ranches as communal lands, and allowing herders to move animals within 5 km of their settled parcels for part of the year, and using communal lands for other periods (Figure 5). The 5 ac parcels themselves were not adequate to support the livestock of the area, but if the animals move beyond the limits of the subdivided area during the wet season, the population can be supported reasonably. In the other analysis, a pipeline is being constructed in

Imbirikani Group Ranch that will provide water to what is now a grazing reserve (Figure 6). We demonstrated that, as may be predicted, a water source in a grazing reserve leads to declines in animal numbers as the forage held in reserve is mined. More importantly, we demonstrated that in simulations, if the new water sources were only used if the previous three months had been unusually dry (< 75 mm rainfall), livestock populations in the group ranch actually increased, relative to what was supported in the past.

Simulations in Kajiado where we used payment for ecosystem services demonstrated that paying Maasai to stop cultivating (and reduce landscape fragmentation) was feasible, and would increase the elephant population in the Amboseli Basin. A manuscript by Bulte, Boone, Singer, and Thornton has been reviewed favorably by *Environment and Development Economics*. A chapter summarizing our work has been included in a book by the FAO.

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

Two manuscripts are now in review that summarize findings from these analyses. In one, by Boone and Wang, we analyzed how equilibrium/non-equilibrium dynamics related to climatic variation. We used density dependence/density independence to place populations on the equilibrium/non-equilibrium gradient. Rules of thumb have been given that suggest livestock in arid lands will be non-equilibrial if the coefficient of variation in precipitation (CV) is greater than 30% or 33%. However, our results showed population dynamics can be extremely variable. For two of our sites (Kajiado and the North-West Province) (Figure 7, a,c), density independent responses increased as CV increased, as we had hypothesized. In the third site (Ngorongoro), a weaker but opposite pattern was seen. In that site, a biocomplex response was seen, where in some simulations, tree density increased dramatically, and increased the likelihood of density dependent responses (Figure 7, b). The manuscript is being considered by the *Journal of Arid Environments*.

The other manuscript directly tests SCALE queries. The manuscript, by Boone, summarizes the sensitivity of the three landscapes to fragmentation. Three large figures summarize the results for the sites; Figure 8 is an example from the North-West Province, South Africa. At 100 mm annual precipitation, the landscape was not sensitive to fragmentation, as hypothesized. The population increased to peak at about 300 to 400 mm per year, then declined as density dependent responses increased and shrub cover increased. Sensitivity to fragmentation declined as inter-annual CV increased, as hypothesized, but only above the peak populations (e.g., 500 to 600 mm, Figure 8). The pattern was opposite below the peak populations (300 mm, Figure 8). The messages for policy makers, land managers, extinction specialists, and others, which follow from this work are that: different landscapes have different sensitivities to fragmentation; fragmentation in sensitive landscapes will require more intensive inputs (e.g., rotational grazing, supplemental feeding) to offset declines in forage access; and changes in the severity of extreme weather events associated with climate change will alter the sensitivity of landscapes to fragmentation. The manuscript is being considered by the journal *Landscape Ecology*.

## **Opportunities for Training and Development**

A MSc student working on RO4 in Kenya is being supported on this project. Kiros Lekarsia completed fieldwork for an MSc on the current and historical livestock movements at local and regional scales in response to fragmentation in the Athi-Kaputiei ecosystem, Kenya.

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

## Outreach

The participation of local pastoralists in Australia in this research activity provides the opportunity for regular feedback on the objectives, developments and findings of the project. Results of this research are currently being reported back to participants.

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 held over 350 meetings in 2005-2006 to discuss research implications with community groups and policy makers. The team also produced 12 posters and 5 policy briefs describing the implication of the results for community action and policy on conservation and development.

#### Presentations

Behnke, R., G. Davidson, A. Jabbar, and M. Coughenour. Human and natural factors that influence livestock distributions and rangeland desertification in Turkmenistan. A presentation at a NATO-financed conference entitled Human and natural factors that influence livestock distributions and rangeland desertification in Turkmenistan in Bishkek, Kyrgyzstan in May-June, 2006.

Boone, R.B. Balancing land uses in East African pastoral areas. Talk presented at the Fall 2005 Natural Resource Ecology Laboratory Seminar Series. September 2, 2005.

Brown, J.C., W. Jepson, and K.P. Price. 2005. Modern agriculture on tropical frontiers: Rethinking methods for land-change research. Open meeting of Human Dimensions of Global Change Research Community. Bonn, Germany. October 9-13. (Oral)

Brown, J.C., W. Jepson, and K.P. Price. 2005. Modern agriculture on tropical frontiers: Rethinking methods for land-change research. Association of American Geographers Annual Meetings, Denver CO, April 5-9. (Oral)

Galvin K A, Betsill M, Ojima D, Thornton P K, Fernandez-Gimenez M and Boone R B (2005). Factors affecting household decision-making: Concepts for understanding change under

uncertainty. Paper for the 6th Open Meeting of the Human Dimensions of Global Environmental Change, 9-13 October 2005, University of Bonn, Germany.

Price, K.P. 2006. Using Remote Sensing to Measure Vegetation Characteristics in Natural and Agro-ecosystems. Department of Agronomy, Kansas State University, Manhattan, Kansas. October 4, 2006. (Invited speaker, Departmental Commemorative Seminar Series)

Price, K.P. and J.E. Kastens. 2006. Detecting drought and mortality with remote sensed spectral measurements. Drought Impacts on Regional Level Ecosystems (DIREnet), Northern Arizona University, Flagstaff, Arizona. August 16 - 18. (Invited Speaker, oral)

Price, K.P., Yu, F., Kastens, J., Ramspott, M.E., Thayn, J.B., and Houts, M. 2005. Investigating the Potential of Remotely Sensed Data and Spectral Mixing Models for Mapping Juniper and Estimating its Cover. Oral Presentation, Association of American Geographers Annual Meetings, Denver, CO, April 5-9.

Ramspott, M.E., K.P. Price, B.L. Foster., and C. Murphy. 2005. Using Time-Series Airborne Multispectral Imagery To Characterize Grassland Cover And Land Management Practices Influencing Soil Carbon Stocks. Pecora 16 "Global Priorities in Land Remote Sensing." October 23 – 27, 2005 Sioux Falls, South Dakota.

Reid, R.S., Makui, R., Said, M. and Nkedianye, D. 2006. Integrating different levels of scale in science, management and policy to sustain pastoral – wildlife ecosystems of East Africa. Conference on Ecosystem Health, University of Guelph, Guelph, Canada, 4-7 June 2006.

Said, M.Y., Reid, R.S. et al. 2005. Changing land and land use in greater Maasailand, Kenya and Tanzania. 5th TAWIRI conference, Arusha, Tanzania, 1-3 December 2005.

Thayn, J. B., & Price, K. P. (2006,). *Estimating Red Cedar Invasion Rates using Landsat and Spectral Matched Filtering*. Oral paper presented at the Association of American Geographers Annual Meeting, March 7-11, Chicago, Illinois.

Thayn, J.B., Voisey, D., and Price, K.P. 2005. Using ArcMap and High Resolution Imagery to Assess the Accuracy of Linear Unmixture Analysis Results. Oral Presentation, University of Kansas GIS Day, Lawrence KS, November 16.

Thayn, J.B., Price, K.P., and Boone, R.B. 2005. Rangeland Fragmentation and Cattle Stocking Rates in Kansas. Oral Presentation, Association of American Geographers Annual Meetings, Denver CO, April 5-9.

Thayn, J.B., Price, K.P., and Boone, R.B. 2005. Using Land Cover Pattern Metrics to Predict Cattle Stocking Rates in Kansas. Oral Presentation, University of Kansas Geography Department Colloquium Talk, Lawrence KS, March 17.

Thayn, J.B., Price, K.P., and Boone, R.B. 2005. Examining Relationships between Landscape Biocomplexity and Cattle Stocking Rates on the Rangelands of Kansas. Oral Presentation,

Sigma Xi (Chapter 004) Student Research Paper Competition, Lawrence KS, March 8.

Thayn, J.B., K.P. Price, and R.B. Boone. Rangeland biocomplexity and cattle stocking rates in Kansas. Paper presented at the PECORA 16 "Global Priorities in Land Remote Sensing," Sioux Falls, South Dakota. November 28, 2005.

Thornton P K (2005). Farming Futures: The role of improved crop and livestock systems modelling in assessing household-scale impacts of change. Lunchtime seminar, IFPRI, Washington DC, 18 November 2005.

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

Worden, J., Reid, R.S., Coughenour, M., Ellis, J., and Gichohi, H. 2005. The Implications of land-use and land tenure change for livestock and wildlife in the Greater Amboseli Ecosystem, Kenya. 5th TAWIRI conference, Arusha, Tanzania, 1-3 December 2005.

The following is an accepted abstract for the American Anthropological Association meetings, November 2006:

Climate Change and Conservation Policy: Implications for Access to Water in a Unique Region of the Greater Serengeti Ecosystem, Ngorongoro Conservation Area, Tanzania. Kathleen A. Galvin, Colorado State University, <u>Kathleen.Galvin@colostate.edu</u>

The Ngorongoro Conservation Area (NCA), Tanzania, is unique among East Africa's protected areas because of its multiple land-use status. This distinction includes the explicit mandate of conserving wildlife and other natural resources while also serving the needs of the resident Maasai pastoralists and promoting tourism. It is increasingly becoming fragmented from pastoral use through climate and conservation policy. This has implications for access to water resources.

Rainfall seasonality affects forage availability, livestock production, availability of water, and ultimately the livelihoods of pastoralists. Data from Serengeti National Park shows that annual and wet season rainfall has declined significantly since the 1960s despite the fact that dry season rainfall increased slowly throughout the 20<sup>th</sup> century. These factors create a forecast of unpredictability. In addition, restricted grazing, and the tourism industry affect water availability to local residents and wildlife. It is likely that with climate change and constrained water availability, conflict over access to resources will occur.

Such variability in climate and conservation policy will make fundamental changes to ecosystem structure and function. These in turn will affect human land-use and livelihoods. For NCA pastoralists freedom to engage in transhumance in order to access various sources of water and patches of rangeland across the landscape are crucial for adaptability to and resilience within the projected changes.

#### **Journal Publications**

Behnke, R.H., A. Jabbar, A. Budanov and G. Davidson. 2005. The administration and practice of leasehold pastoralism in Turkmenistan. Nomadic Peoples 9(1):147-169. (*Acknowledges SCALE with grant number*)

Boone R B, Galvin K A, Thornton P K, Swift D M and Coughenour M B (2006). Cultivation and conservation in Ngorongoro Conservation Area, Tanzania. *Human Ecology* 34, DOI 0.1007/s10745-006-9031-3 (*does not acknowledge SCALE*)

Boone, R.B., S.J. Thirgood, and J.G.C. Hopcraft. 2006. Evolving Serengeti wildebeest migratory patterns. Ecology 87:1987-1994. (*Acknowledges SCALE with grant number*)

Boone, R.B. and G. Wang. In review. Cattle dynamics in African grazing systems under variable climates. Journal of Arid Environments. (*Acknowledges SCALE with grant number*)

Boone, R.B. In review. Effects of fragmentation on ungulates in African savannas under variable climates. Landscape Ecology. (*Acknowledges SCALE with grant number*)

Boone, R.B., S.B. BurnSilver, P.K. Thornton, J.S. Worden and K.A. Galvin. 2005. Quantifying declines in livestock due to land subdivision in Kajiado District, Kenya. Rangeland Ecology & Management 58(5):523-532. (*Acknowledges SCALE with grant number*)

Bulte E H, Boone R B, Stringer R and Thornton P K (2006). Elephants or onions? Paying for nature in Amboseli, Kenya. *Environment and Development Economics* (submitted). (does not acknowledge SCALE)

Galvin K A, Thornton P K, de Pinho J, Sutherland J and Boone R B (2006). Integrated modeling and its potential for resolving conflicts between conservation and people in the rangelands of East Africa. *Human Ecology* 34 (2), 155-183. (*does not acknowledge SCALE*)

Hobbs, N.T., K.A. Galvin, A. Ash, R. Boone, J. Lackett, R. Reid, C. Stokes, and P. Thornton. Causes, processes and consequences of fragmentation of dry rangelands for people, livestock, and ecosystems. BioScience. In preparation.

McAllister, Ryan R.J., Iain J. Gordon, Marco A. Janssen, and Nick Abel. 2006. Pastoralists' responses to variation of rangeland resources in time and space. Ecological Applications 16(2):572-583. (*Acknowledges SCALE with grant number*)

Ogutu J.O., Bhola, N., Piepho, H.-P, and Reid, R.S. 2006. Efficiency of strip and line transect surveys of African savanna mammals. *Journal of Zoology*. 269: 149-160. (*Acknowledges SCALE with grant number*)

Stokes CJ, McAllister RRJ & Ash AJ (2006) Fragmentation of Australian rangelands: risks and trade-offs for land management. The Rangeland Journal 28(2): in press. DOI: 10.1071/RJ05026 (*Acknowledges SCALE with grant number*)

Thornton, P.K., S.B. BurnSilver, R.B. Boone, and K.A. Galvin. 2006. Modelling the impacts of group ranch subdivision on agro-pastoral household in Kajiado, Kenya. Agricultural Systems 87:331-356. (*Acknowledges SCALE with grant number*)

Thornton P K, Boone R B, Galvin K A, BurnSilver S B, Waithaka M M, Kuyiah J, Karanja S, González-Estrada E and Herrero M. In review. Coping strategies in livestock-dependent households in East and southern Africa: a synthesis of four case studies. *Human Ecology. (Acknowledges SCALE with grant number)* 

Wang, G., N.T. Hobbs, S. Twombly, R.B. Boone, A.Illius, I. Gordon, and J. Gross. In review. Latitudinal gradients and heterogeneity in elevation modify the strength of density dependence in populations of northern ungulates. Ecology. (*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. 2006. Spatial and temporal variability exert opposing effects on density dependence in populations of large herbivores. Ecology 87(1):95-102. (*Acknowledges SCALE with grant number*)

Wang, G. 2006. On the latent state estimation of nonlinear population dynamics using Bayesian and non-Bayesian methods. Ecological Modelling. (In press) (*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)

Ash, A., Hunt, L., Petty, S., Cowley, R., Fisher, A., Macdonald, N. and Stokes, C. 2006. Intensification of pastoral lands in northern Australia. In: Proceedings of the 14th Biennial Australian Rangeland Society Conference (Ed. P. Erkelenz), pp 43-46. Australian Rangeland Society, Renmark. (does not acknowledge SCALE)

Boone R B, BurnSilver S B and Thornton P K. 2006. Optimising aspects of land-use intensification in southern Kajiado District, Kenya. Research Report, CSU & ILRI. (will acknowledge SCALE)

Bulte E H, Boone R B, Stringer R and Thornton P K (2006). Wildlife conservation in Amboseli, Kenya: Paying for nonuse values. FAO publication. (does not acknowledge SCALE)

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)

## **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.

#### **Literature Cited**

- Illius, A.W., and T. G. O'Connor. 2000. Resource heterogeneity and ungulate population dynamics. Oikos 89:283-294.
- Wang, G. M., N. T. Hobbs, R. B. Boone, A. W. Illius, I. J. Gordon, J. E. Gross, and K. L. Hamlin. 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. Ecology 87:95-102.



Figure 1. Observed pathways of wildebeest marked with VHF radio collars (a) and GPS satellite collars (b) are compared to pathways modeled using evolutionary programming, rainfall, and new vegetation data (c).



Figure 2: Comparison of seasonal variation in diet quality for paddocks with high and low vegetation diversity. "\*" indicate significant differences for marked dates or dry seasons (June – October) (t-tests).



Figure 3: Identification of the breaking point of the absolute values of model-averaged estimates of *b* for linear relationships between the latitude of the study site and the absolute values of model-averaged estimates of *b* measuring the strength of direct density dependence. The y axis represents corrected Akaike information criterion (AICc); the x axis represents the absolute values of model-averaged estimates of  $b(|\tilde{b}|)$ . The breaking point is determined by broken line regressions and divides the whole data set into two subsets that are fitted by two different regression lines. The search for breaking point iterates through all values of  $|\tilde{b}|$  between 0.01 and 0.45, and the breaking point results in the lowest AICc value for the broken line regressions.



Figure 4: Relationships between the strength of density dependence of northern ungulate populations, spatial heterogeneity of habitat (a), and latitude of study site (b).  $w_i$  is the Akaike weight showing 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 5. Eselenkei Group Ranch fully subdivided into 100 ac (40 ha) parcels (left), 5 ac (2 ha) parcels around developed areas (middle), and 5 ac parcels with 5 km buffers around those parcels (right).



Figure 6. A new water pipeline (with overlaid dots) extends from the western portion of Imbirikani into the Chyulu Hills.



Figure 7. The number of simulations, out of 20, that were (i) density dependent or density independent for the North-West Province (a), Ngorongoro (b), and (c) Kajiado District, Kenya. Other ecosystem responses include tree cover (ii) and shrub cover (iii).



Figure 8. The sensitivity of the North-West Province, South Africa to fragmentation. The number of cattle that can be supported on the landscape when it is fully intact, or subdivided into progressively smaller parcels, is shown for every combination of annual rainfall and inter-annual coefficient of variation tested. The slope of the lines indicate declines in the number of animals that can be supported on the landscape as it is fragmented.

Characteristic	Household type				
	Small	Medium	Large	Very Large	
Tropical Livestock Units per household	< 3	3-10	11-50	> 50	
Number of households	4	17	11	5	
Average age of household members	17.0	15.9	17.4	15.4	
Average age of the household head	48.8	49.6	47.2	47.6	
Average number of household members	5.8	5.4	5.9	4.8	
Number of household members leaving village for employment in the past year	1.7	1.8	1.9	2.0	
Amount of land in crop production (ha)	1.8	2.4	3.1	0.0	
Fate of household-produced dairy products	Home consumption	Home consumption	Home consumption	Home consumption	
Number of sheep/goats slaughtered (for meat) during the year	0.8	4.9	7.4	22.6	

Table 1. Household typology for Kazakstan case study area, based on flock size of household.

Table 2. Result of selection among autoregressive Gompertz population models describing temporal variation in abundance of populations of northern ungulates. In the term (1 + b), *b* is a measure of the strength of density dependence. Estimates of (1 + b) < 1 provide estimates of negative feedback from population density to per capita population growth rate.

Species	Location	1+b	$\Delta AICc^1$	AR order <sup>2</sup>	$w_i^3$	$\left  \tilde{\overline{b}} \right ^4$
Alpine ibex <i>Capra ibex</i>	Italy	0.85	1.49	1	0.56	0.14
Bighorn sheep Ovis canadensis	Ram mountain, Canada	1.0	1.57	Exp	0.69	0.03
Bighorn sheep	Sheep river, Canada	1.0	1.15	Exp	0.62	0.08
Bison Bison bison	Yellowstone National Park, Wyoming	0.49	17.42	2	0.999	0.51
Bison Bison bison	Alberta Canada	1.0	1.94	Exp	0.62	0.05
Caribou Rangifer tarandus	Denali, Alaska	1.0	3.79	Exp	0.85	0
Elk <i>Cervus elaphus</i>	Rocky Mountain National Park, Colorado	0.91	3.94	1	0.81	0.16
Elk Comus alanhus	Jackson	0.69	3.05	1	0.82	0.31
Elk Cervus elaphus	Gravelly Mountains, Montana	1.0	2.31	Exp	0.66	0.06
Elk <i>Cervus elaphus</i>	Yellowstone National Park, Wyoming	0.75	4.7	1	0.91	0.26
Fallow deer Dama dama L.	New forest, UK	0.57	3.84	1	0.85	0.47
Moose Alece alece	Norway	1.0	2.11	Exp	0.65	0.01
Mule deer Odocoileus hemionus	Oregon	1.0	1.36	Exp	0.62	0.04
Muskox Ovibos moschatus	Nunivak island, Alaska	1.0	2.18	Exp	0.72	0
Red deer <i>Cervus elaphus</i>	New forest, UK	0.72	2.98	1	0.81	0.29

Red deer	Rum island, UK	0.57	3.51	1	0.83	0.45
Cervus elaphus						
Reindeer	Alakyla,	1.0	2.76	Exp	0.68	0.06
Rangifer	Finland					
tarandus						
Reindeer	Muotkatunturi,	1.0	2.9	Exp	0.78	0
R. tarandus	Finland					
Reindeer	Palojarvi,	1.0	1.58	Exp	0.64	0.06
R. tarandus	Finland					
Reindeer	Kaldoaivi,	1.0	1.50	Exp	0.64	0.09
R. tarandus	Finland					
Roe deer	New forest, UK	1.0	2.71	Exp	0.78	0.01
Capreolus						
<i>capreolus</i> L.						
Sika deer	New forest, UK	0.66	3.03	1	0.71	0.23
Cervus Nippon						
Soay sheep	St Kilda, UK	0.43	2.32	1	0.76	0.63
Ovis aries						

 $^{1}\Delta$ AICc is the difference in the values of corrected Akaike information criteria (AICc) between the models of the lowest and second lowest AICc values;

<sup>2</sup> AR order – the largest order of autocorrelated terms identified in the model

selection. Exp indicates exponential or density independent population growth;

 ${}^{3}w_{i}$  = the Akaike weight (Burnham and Anderson 2002);

 $\left|\tilde{\vec{b}}\right|^4$  is the model-averaged estimate of b over the three candidate models.