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The Ellis paradigm — humans, herbivores and rangeland systems

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The scientific and conceptual contributions Jim Ellis made throughout the course of his career reveal a logical progression towards increased understanding of pastoral ecosystems worldwide. Research in wildlife, large herbivores, systems ecology and energy flows through grazing ecosystems formed the basis of his approach. A leader of the South Turkana Ecosytem Project (STEP), he showed the adaptive basis for opportunistic and spatially extensive resource use in temporally and spatially variable environments. After the STEP, he examined pastoral ecosystems in northern and central Asia and elsewhere in Africa. Spatial extensivity, or scale, emerged as being critically important to pastoral ecosystem function. Livestock development schemes based upon inappropriate ecological and economic assumptions are all too often ecologically and economically unsustainable. However, a new paradigm of pastoral ecology and development is emerging. The paradigm is derived from basic, but comprehensive, understanding of the ecologically adaptive features of pastoral resource utilisation strategies, and the ecological processes and constraints that determine energy flows from plants to livestock and humans in spatially and temporally variable environments. Jim Ellis contributed greatly to improved understanding of the importance of mobility and opportunism in these ecosystems. This understanding could benefit humans, ecosystems and wildlife over a vast portion of the earth's surface.

Keywords: development, ecosystems, livestock, pastoralism, spatial scale

Introduction

Jim Ellis was a pioneer in the development of significant new paradigms about humans, herbivores, and rangeland systems. He was something of a scientific revolutionary (Kuhn 1962). Although he carried out excellent research and refined theories developed within existing frameworks, he also developed entirely new conceptualisations to explain phenomena that were fundamentally inconsistent with the prevailing conceptual framework; that is, the prevailing paradigm.

Long-time associates have made cogent remarks about Jim's scientific contributions:

- His pre-eminent work on understanding the interplay between people and natural processes in arid ecosystems set a global standard for novel research spanning scientific disciplines. He applied integrated interdisciplinary approaches to understanding pastoral ecosystem ecology throughout the world. His work played a fundamental role in supporting wise management and policy in the developing world (Swift 2002).
- Jim's scientific vision was broad and integrated and brought a perspective to range systems that made a major contribution to the understanding of pastoral systems. His work was critical to the development community in a number of ways (Demment 2002).
- First, it provided logical reasons for the failures of past livestock development projects. Second, his work demonstrated the role of research in the development process. Third, his work clearly illustrated the role of spatial scale in unpredictable environments (Demment 2002).

He was a systems ecologist specialising in ecosystems dominated by large mammalian herbivores. His roots were in wildlife ecology and he was well versed in ecological theory. He sought to understand how native herbivore ecosystems functioned and maintained themselves without human interference. However, he also had a decidedly practical orientation, and the majority of his career was devoted to the implications of ecological processes for humans. He was originally educated in animal husbandry and wildlife management. He started to focus on livestock-based ecosystems in the 1970s, which immediately led to human ecology as part of a total systems approach. He saw adaptive value in traditional pastoral ecosystems that had persisted for centuries prior to economic development interventions. He devoted much of his career to understanding the root causes of desertification, degradation, sustainability and ecological integrity of pastoral ecosystems. In a proximate sense, he sought to understand the ecological processes underlying pastoral ecosystem persistence. Ultimately, however, he aimed to develop more enlightened and ecologically sound approaches to improving the human condition in arid and semi-arid ecosystems.

The South Turkana Ecosystem Project (STEP) was clearly his most significant accomplishment as a principle investigator. It occupied over a decade of his career (1980–1992), and it was the project in which he developed and tested many of his most important ideas. The foundations for STEP and post-STEP ideas were laid down earlier, in basic research on systems ecology, large herbivore ecology, and energy flows in grazing ecosystems. The post-STEP period (1992–2001) was a period of expansion into new regions around the globe, applying and further refining lessons learned in the STEP. In 2001, the inception of the SCALE (Scale and Complexity in Arid Land Ecosystems) project arguably marked the beginning of a fourth period — one of synthesis, and further generalisation of earlier ideas to ecosystems around the globe.

Pre-STEP

Jim's approach to ecosystem science evolved out of key academic and scientific experiences in the late 1960s and 1970s. His PhD research at the University of California, Davis in the late 1960s was the nucleus for subsequent research in systems ecology and large herbivore ecology. There, he obtained a National Institute of Health (NIH) research assistantship in systems ecology with one of the early pioneers of the field, Kenneth Watt (Watt 1968). Jim later told me he did not particularly aspire to become a systems ecologist at first, and certainly did not consider himself a mathematician or a computer scientist. However he seized the opportunity, and learned quickly that systems ecology was a powerful approach. He chose as his research topic a computer analysis of fawn survival in pronghorn (Ellis 1970). Computer modelling proved to be an essential tool for predicting the complex chain of processes lying between ungulate foraging ecology and population dynamics. The more important lessons were no doubt about things like system dynamics, feedbacks, interacting processes, emergent properties and the integration of knowledge of the parts to understand the whole.

During a post-doctoral fellowship with JH Crook in Bristol, England 1970–1971, he worked on the integration of mammalian social systems and ecology (Crook *et al.* 1976). This experience was probably significant on a number of counts. It was his first international foray, and the experience no doubt opened new doorways of perception, leading ultimately to the internationalism and diplomacy that later became hallmarks of his career. More important scientifically, deep thinking on the ecological basis of mammalian social systems was groundwork for later ideas about pastoral subsistence strategies and human-ecosystem interactions in general. This research examined how environmental variables and species parameters interact to determine social variables. The conceptual framework that was developed explicitly considered different ways that mammals use space in relationship to environmental resource concentration and variability. Environmental variables affecting social organisation included resource density, resource temporal distribution, resource spatial distribution and predator distributions. For example, spatial resource distributions were hypothesized to affect social groupings in the following manner. When resources are dense, predictable and clumped, exclusive and territorially defended ranges may evolve. In an environment with clumped resources that are widely spaced and occur irregularly, exclusive ranges are uneconomical and foraging behaviour becomes more opportunistic. If resources are extremely dispersed and unpredictable, nomadic behaviour is the most adaptive response.

In his position as a research ecologist with the Grassland Biome Study of the International Biological Program (IBP) at Colorado State University 1971–1976, he carried out several studies of the trophic ecologies of large herbivores (Rice *et al.* 1974, Dean *et al.* 1975, Ellis and Travis 1975). This area of research was central to his later more integrative studies of wildlife and domestic herbivore systems. A basic understanding of foraging, diet selection, and energy and nutrient transfers from plants to animals was the basis for understanding why and how herbivores persist in a given environment, and how many can be supported. Herbivore trophic ecology was the research topic of most of the early students with whom he interacted as they studied feeding ecology and niche separation (Schwartz and Ellis 1981), plant-animal interactions (Coppock *et al.* 1983), and nutritional ecology (Rowland *et al.* 1983). In the 1970s he also teamed up with Dave Swift, a ruminant ecologist (and hunting partner), and Tom Hobbs, then his PhD student, to assess the nutritional basis of elk carrying capacity in Rocky Mountain National Park (Hobbs *et al.* 1979, 1982).

Systems ecology and computer modelling were extremely important in the IBP (Innis 1978, Breymeyer and Van Dyne 1980). Accordingly, Jim collaborated with other ecologists to devise a model of herbivore dietary selection (Ellis *et al.* 1976). The primary strength of this study, as well as the earlier study by Crook *et al.* (1976), was conceptual modelling. The conceptual approach involved carefully and logically thinking through system interactions and their emergent outcomes. While it was important to eventually formalise the conceptual model mathematically or as a computer program, the first and arguably more important step was to clearly conceptualise the way the system functions. The conceptualist approach to systems ecology served him well throughout his career:

> His greatest strength was his ability to conceptualise large, complex scientific problems as whole systems, to sketch their interactions among significant components, and to develop ways to understand their dynamics (Swift 2002).

The IBP was an arena of 'big biology'. Ecosystem level research was carried out by interdisciplinary teams within the frameworks of large, well-structured projects (Van Dyne 1969). Team members had clearly defined roles and linkages with other team members. As one of the lead 'integrators', Jim no doubt developed a strong appreciation for project organisation — the importance of having the 'big picture', and the importance of synergies and complementarities among project components. A team of interacting researchers is, after all, but another example of a complex system. Thus, his conceptualist systems approach also proved valuable in designing effective research projects. Those who worked with Jim can recall many examples of his project diagrams, really conceptual models showing how subprojects and scientists fit together to produce emergent outcomes. The ability to organise and lead a large team of interdisciplinary researchers proved to be one of Jim's greatest strengths and talents: Coppock *et al.* (2002) comment:

> He was a master at putting together interdisciplinary teams of people to work on complex problems. He recognised the individual qualities that would result in a team working well together, not just as individuals working side by side.

As the IBP was ending in 1976, some of the scientists decided to remain at the Natural Resource Ecology Laboratory (NREL) at Colorado State University and carry on using grants and contracts. Jim led one of the first post-IBP projects in 1977 (Parton *et al.* 1978). This project entailed the development of a new version of the Grassland Biome's ELM model, which came to be known as 'Strip-ELM'. The interdisciplinary team consisted of Jim, a biogeochemical modeller (W Parton), a herbivore modeller (D Swift), a plant modeller (J Detling) and myself (I simultaneously used Strip-ELM in my separately funded PhD research). The approach of conducting team research projects and exploiting synergies between projects proved to be a key element for the viability of the NREL in the following years (www.nrel.colostate.edu). Jim and other IBP stalwarts (V Cole, D Coleman, J Detling, J Dodd, W Lauenroth, J Gibson, W Parton, D Swift, R Woodmansee) were the founders of the NREL as we know it today. Jim served as NREL Associate or Acting Director several times between 1978–1991.

Models and analyses of energy flow through ecosystems were used as a framework for integrative research in the IBP, in the tradition of H Lindeman and E Odum (Andrews *et al.* 1974, Coleman *et al.*1976). Later, we used the approach in the STEP (Coughenour *et al.* 1985). A comparative energy flow analysis by Ellis *et al.* (1979) was seminal. Energy flow patterns revealed why there were rational, fundamental differences among grazing ecosystems in different environments. They concluded that

> indices can be calculated indicating...the direction of selection acting within the system, toward either 'production systems' or 'biomass maintenance systems'. Other aspects of cattle energetics demonstrate the divergence of grazing strategies used by different peoples...It is evident that cattle play diverse roles in different segments of human society. The Pawnee (Colorado, USA, short-grass steppe) situation can be viewed as a predator-prey relationship...while that in Karamoja (Uganda) can be viewed as a parasite-host relationship …Rational parasitism favours the maintenance of herds with many mature but few young animals, since young animals have a substantial growth requirement and thus cannot withstand a chronic drain on their reserves. Herds with this type of age structure are common in E Africa. (Ellis *et al.* 1979).

It is noteworthy that the study incorporated humans as integral components of the ecosystem.

The South Turkana Ecosystem Project (STEP)

The seeds for the STEP were sown as early as 1976, when Jim and Mike Little met during the IBP. Mike was a professor of physical anthropology at the State University of New York, Binghamton who had been conducting research on the human ecology of the Quechua in the Andes under the Human Adaptability Component of the IBP. Also at Binghamton was Neville Dyson-Hudson, a social anthropologist who had previously conducted field research on the Karamojong in Karamoja District, Uganda, and who had made contacts with the Turkana in neighbouring Turkana District of northwest Kenya when he was member of the Royal Geographic Society's South Turkana Expedition. Jim and Mike saw a natural opportunity to carry out a research project in Turkana, in which human ecological studies were fully integrated with traditional soil, plant and animal ecology studies, in an undisturbed traditional pastoral ecosystem. Ideas were formed in 1978 during informal planning meetings amongst the three, Dave Swift and others. A pilot project was developed, the Ecosystems Studies and Anthropology Programs of the National Science Foundation provided joint funding and the first research team entered the field in 1980 (Coppock *et al.* 2002).

The 1980–1981 pilot study proved that it was logistically feasible to carry out research in this remote, undeveloped and not entirely secure location but, more importantly, Jim and the other investigators drew the following conclusions. Despite a three year drought, there was no evidence of widespread overgrazing or human malnutrition. The pastoral system demonstrated that it could withstand major climatic variation, but how? Their observations suggested a structurally complex ecosystem and a diverse set of human exploitation pathways. They surmised that the temporal and spatial patterns of nutrient and energy distribution and flows are probably critical elements in maintaining the ecosystem.

In their subsequent full proposal in 1982, Ellis and Swift began by pointing out that 'the conventional wisdom states that pastoralists, for socio-political and other reasons, strive to accumulate large herds of livestock which then overgraze their environments...The drought in the Sahel in the late 1960's and early 1970s refocused attention on this view.' However, based upon their pilot research and some deep thinking, they noted that 'it is not entirely clear that subsistence pastoralism leads to degradation' (Ellis and Swift 1982).

Then, they developed a conceptual model of the functioning of this pastoral ecosystem based upon ecosystem energy flows. They posited there are two axes of energy flow through the system which converge at the human trophic level. First, there is a 'maximum gain' pathway based on surface moisture and rapid, but short-lasting, herbaceous plant production. This pathway is exploited by grazers, especially cattle. Second, there is a 'pulse attenuation' pathway based on deep water and longer lasting production by woody plants. This pathway is exploited by browsers, especially goats and camels. This conceptualisation was a logical successor to previous work on energy flows in grazing systems, ideas of Noy-Meir about the pulsed nature of desert ecosystems (Noy-Meir 1973) and knowledge of large herbivore ecology. They hypothesised that these energy flow pathways were a result of the spatial redistribution of water and nutrients on the landscape, thus linking ecosystem function to structure. Specifically, they proposed that woody plants, particularly large trees, tended to be located along ephemeral drainages where runoff water would concentrate, infiltrate to deeper depths and last longer into the dry season. They also hypothesised that the nomadic pastoralists often located their temporary livestock corrals (*anok* is the Turkana word for these corrals, pronounced *a-nook*) along these drainage channels and that livestock deposited dung and urine there in large concentrations. Together, enhanced water and nutrient concentrations would promote an attenuated pulse of woody vegetation growth and thus support the energy flow pathway that was critical for pastoral subsistence in dry seasons and years.

The studies required to support this ecosystem level conceptual framework were many, and from several different disciplines. It required studies of soil water and soil nutrients; studies of herbaceous and woody plant productivities and spatial distributions and studies of five species of livestock, including their seasonal diets, forage intake rates, movements, habitat utilisation, and nutritional balances. It required modelling efforts to synthesize the results to make predictions of energy flow to humans based upon the interaction of all of these processes.

The human components of the project were no less important (Little *et al.* 1982, *Little et al.* 1990, Little and Leslie 1999). The anthropologists proposed complementary studies that would assess human biological adaptations to the physical environment; growth, morphology, and body composition; dietary intake and nutritional status; health status and disease prevalence; physical activity levels and physiological work capacity; demographic structure and population dynamics; decision-making; herd management; grazing orbits; mental maps; and human labour.

An ecosystem energy flow analysis was used to integrate the findings (Coughenour *et al.* 1985). The integration of our team's research findings clearly showed a diversity of energy flow pathways from plants to humans, including the two primary pathways (pulse attenuation and maximum gain) as originally proposed. Using a simple geographic information system (GIS) with spatial data on precipitation, soils, vegetation type, and herd movements, we calculated spatial totals of forage production and offtake integrated over the entire study area. Although dynamics were not quantified, a partitioning of energy flows between the herbaceous and woody pathways was evident. Using elements of energy flow analysis techniques that I had learned from an earlier mentor (B Hanon, University of Illinois), we calculated fractions of energy flows to humans attributable to different plant types, via plant-livestock-human energy flow pathways. The analysis successfully traced energy flows to humans back through different species of livestock, and different types of plants, to the heterogeneous distributions of resources on the landscape. Could this diversity of energy flow pathways lead to ecosystem stability? Could ecosystem stability therefore be linked to landscape heterogeneity and nomadic exploitation strategies?

Pastoral subsistence strategies were therefore congruent with the structure and function of the landscape ecosystem (Swift *et al.* 1996). Other studies showed ecological adaptiveness in plants (Coughenour *et al.* 1990), livestock (Coppock *et al.* 1986a, 1986b), pastoral land use (McCabe and Ellis 1987), human food procurement (Galvin 1992), and human biology (Little and Leslie 1999).

Moreover, we found evidence that pastoralists had certain positive effects on their resource base. While the resource-exploitation activities of subsistence pastoral people were often related to environmental degradation, the Turkana and their livestock were apparently responsible for enhancing the regeneration of an important tree, *Acacia tortilis*. In an unpublished but favourite paper of Jim's, affectionately known as the '*anok'* paper, we showed the degree of nutrient enhancement by livestock deposition, the positive outcomes of *A. tortilis* seed pod consumption by goats and camels, and subsequent seed deposition into the nutrient rich seed beds (Ellis *et al.* 1985). Trees regenerated there and the pastoralists could readily point out corrals 10–20 years old with maturing trees. The cumulative result of repeated movements and corral construction over time could be shown to have a significant positive effect on tree cover, despite simultaneous offtake by pastoralists for corral and dwelling construction (Reid and Ellis 1995).

The 1982–1985 STEP project demonstrated ecosystem characteristics that allow Turkana pastoralists to persist in an arid and unpredictable environment. Turkana was shown to be a structurally diverse environment comprised of different vegetation life-forms varying in their phenological and drought response patterns (Coughenour and Ellis 1993). This forms the basis of a complex set of trophic pathways which extend through five species of livestock to humans. Pathways emanating from woody plants tend to be more resistant while herbaceous based pathways tend to be more resilient. Combined, these pathways yield low production efficiency and high maintenance costs, but stable flows of energy to humans.

Building upon these findings, the basic rationale for the STEP renewal proposal in 1985 was the idea that pastoralism is not inherently destructive. The long-term viability of traditional systems strongly suggests that they are adaptive. However, disruptions of traditional systems lead to the breakdown of their original adaptive mechanisms through spatial reconfiguration, socio-economic modernisation and other changes, and land use intensification beyond safe limits. We (Ellis, Swift, Coughenour) proposed that 'the results of our past work present a very different picture than conventional perceptions of African pastoral ecosystems' (Ellis *et al.* STEP 1985 unpublished). Pastoralism has been blamed for drought, wholesale environmental degradation, and human famine. While the 1984 drought had serious effects in other parts of Africa, the Ngisonyoka Turkana were adversely affected, but recovered rapidly and without incidence of famine or environmental degradation, suggesting that their resource exploitation strategies are adaptive and rational.

We began to question the existing paradigm of equilibrial ecology. As was earlier observed in deserts, environmental variability in Turkana was so high from year to year that negative feedback relationships never have the opportunity to develop (Noy-Meir 1979/1980). Our earlier energy flow analysis showed that livestock were well below a theoretical carrying capacity based on mean annual rainfall. We proposed that grass-grazer (cattle) interactions were only loosely coupled due to strong density independent drought bottleneck effects. Long-term trends in cattle density depended instead on drought frequency and severity. In contrast, camels were hypothesised to be tightly coupled to browse resources, and would follow long-term trends in browse production. The resistance, resilience, and thus the persistence of the Ngisonyoka Turkana ecosystem were hypothesised to be due to a high degree of vegetation structural heterogeneity providing a resource base with a variety of patterns of production, phenology, and stress response, and diverse stress response patterns within livestock and human communities. When coupled to heterogeneous vegetation resources these yield 'multiple trophic pathways which…enhance the continuity of ecosystem energy flow during and after stress periods' (Ellis *et al.* STEP 1985 unpublished). Consequently, interdependent livestock and human populations exist at levels that do not exceed the long-term support capacities of the ecosystem and their activities have positive effects on ecosystem structure, dynamics, and resistance and resilience. In sum, the overarching goals of the 1985 project were to:

a) improve understanding of the flows of energy and materials through ecosystems that result in reliable food production at the human trophic level,
b) improve understanding the mechanisms of pastoral ecosystem persistence in variable and stressful environments,
c) develop a deeper appreciation and awareness of the adaptive features of traditional pastoralism and,
d) contribute to ecologically informed economic development and policy-making in the grazing ecosystems of the world.

Jim's most important syntheses of STEP findings were his contributions to the paper he co-authored with Dave Swift in the Journal of Range Management (JRM) in 1988 (Ellis and Swift 1988). Dave Swift (2002) recounted that after working in Turkana for some years, they realised that variability and lack of predictability in rainfall was one of the most important features of the system and the average annual rainfall was but a statistic that was rarely realised. The system was inherently non-equilibrial and viewing it that way would be more useful than trying to characterise its mean state. Jim later proposed that when the coefficient of variation (CV) in rainfall exceeds a certain level, the variance explains more about system dynamics than the mean (Ellis *et al.* 1993, Ellis 1994a, 1994b). Such an outcome was observed by Caughley *et al.* (1987) in Australian kangaroo systems, where high CVs led to displacements of mean kangaroo densities, i.e. the centre of centripitality of the vegetation-herbivore system, to values where herbivore density is lower and vegetation biomass is higher than the theoretical 'equilibrium point'. This is largely due to the fact that dry periods reduce herbivore numbers rapidly, while moist periods result in a slower rate of recovery. This is exactly the dynamic that Ellis and Swift (1988) described in Figure 6 of their paper. A 30% or 33% CV threshold has often been cited based upon Jim's interpretation of the Caughley *et al.* (1987) research, but these CV thresholds were merely simplifications to make the point that there is a level of variation beyond which the concept of equilibration with a mean has little or no utility.

The policy implications of non-equilibrial (or disequilibrial) dynamics are that:

- appropriate policies and technical interventions can be applied only if the fundamental dynamics of the target systems are clearly understood...Unless pastoral ecosystem dynamics are considered and used as guidelines for development policies, interventions are likely to be random activities which comprise development by trial and error (Ellis and Swift 1988).
- Development procedures which may be useful and appropriate in equilibrial systems will often be counterproductive and destabilising in non-equilibrial systems...Such destabilising practices would include those which limit the pastoralist's ability to obtain external resources (when needed), for example, by confining pastoralists to relatively small ranches or other such schemes (Ellis *et al.* 1993).

The Ellis and Swift (1988) JRM paper provided a unifying concept for ecologists and social scientists working with pastoral people, development, or desertification, that incorporated climatic variability, rather than equilibrium tendencies, as a central driving force. It also changed the way that desertification is viewed, with a lot less blame being placed on pastoralists. Jim later reflected that partly as a result of the ideas presented in this paper, pastoralists are no longer viewed as pariahs, and livestock is on the development agenda once again (Swift 2002).

Coppock *et al.* (2002) put it well: 'The STEP was a landmark effort in ecosystem science, particularly with regards to the inclusion of humans in an integrative ecological framework.' It was unique it its interdisciplinarity, spanning the spectrum from soils and plants through human societies. It was unique in that it was funded by two NSF Divisions. It spanned a significant time period (1980–1992) and several funding cycles, each requiring peer review and renewal based upon a fresh set of excellent ideas. It was an early precursor for 'human dimensions', 'humans as components of ecosystems', and 'coupled human-natural systems' research agendas that are highly topical today.

Post-STEP

Before the STEP project had ended, Jim was setting his sights on grazing lands in other parts of the world. In 1988–1990 he and Gerald Ward, a long-time colleague at Colorado State University with experience in Asia, obtained an NSF grant to conduct a systems analysis of grazing lands in Gansu Province of the People's Republic of China. Dave Swift, and long-time associate Jerry Dodd from the IBP, were also on board. Together, the team made a lengthy visit to Gansu in 1988, where they familiarised themselves with the ecology and uses of Asian grasslands. They organised an exchange programme with scientists from the Gansu Grassland Ecology Research Institute. After their first visit in 1988, Jim and the others were faced with the paradox that while people had made sustainable use of these grasslands for thousands of years, there was widespread evidence of degradation (Ojima and Chuluun 2002). In 1989, Jim was called upon to serve on an NSF review panel of the US-China Cooperative Science Program, and in 1990 he was asked to chair a US National Academy of Science Panel on the state of grasslands and grassland science in northern China. This involved a fact-finding mission in 1990, a research exchange programme with China and Mongolia in 1991, and National Academy of Science conferences in 1992 and 1993 (Ellis 1992). In 1993, as a consultant on the Project on Alternatives for Livestock Development (MacArthur Foundation, C Humphrey, D Sneath, J Swift and R Mearns, Principle Investigators), he carried out a biological and social survey of pastoral land use in Mongolia. These activities were hugely successful in developing new cross-institutional and international networks and communication channels (Ojima and Chuluun 2002). Jim continued to be highly interested in northern Asia after 1993, but it was not until 1996 that he obtained funding from NSF to carry out a research project of his own there.

The 1996–1999 project involved field, modelling and remote sensing research primarily focused on Inner Mongolia, northern China. Ellis *et al.* (2002) argued that grassland degradation in northern China was due to an interaction between abiotic factors and land use intensification. Coarse textured (sandy) soils were clearly the most vulnerable to intense grazing. Remote sensing data indicated that different parts of the region were exhibiting delayed or earlier green-ups (Lee *et al.* 2002), possibly due to climatic change or interactions between climate and land use change. Climatic variations coupled with changes in land use could push grazing ecosystems beyond a threshold, resulting in fundamental state changes. Rapid socio-economic changes promoted overstocking in northern China, but the areas that were most heavily overstocked were agricultural communities, and the evidence suggested that while pure pastoralism could cause degradation, the cause was more often sedentarisation and the most serious cases of desertification were associated with cultivation or agropastoralism. Ecosystem modelling suggested that steppe grasslands should be resilient to moderate grazing intensities, but degradation could occur under abnormally high livestock densities, especially when coupled with climatic change (Christensen *et al.* 2003, 2004). Elevated livestock densities would be much more likely to occur when livestock are confined to small-scale grazing areas, particularly within matrices of cultivation where livestock could be subsidised with fodder.

Ellis and Galvin (1994) made a number of astute observations about climatic patterns and land use changes in pastoral ecosystems. Drawing upon indigenous knowledge, they noted that Turkana pastoralists ranked years with moderate, but with rainfall spread out in time as good years, while years with above average annual rainfall but with rainfall concentrated in time, were poor. The Turkana knew quite well that the seasonal distribution of rainfall is as important, if not more important, than the annual total. One year the 'rainy season' basically failed, but there were small rains during what might, on average, be considered the 'dry season'. This provided a small but continued supply of forage for livestock. Ellis and Galvin (1994) applied the same logic to a comparison between rainfall patterns in east and west Africa. In equatorial east Africa rainfall is bimodal due to the northerly and southerly passages of the intertropical convergence zone. This results in a lengthened growing season, and continued forage availability and milk production in most years. However, in west Africa, the unimodal rainfall pattern results in a pulse of annual grass production followed by a long and stressful dry season. Multi-year droughts also appeared to be longer in west Africa. For a given amount of rainfall, a single larger pulse of rainfall is more favourable for crop production. Consequently, pastoralism in west Africa is riskier, and there is increased reliance on crop-based agriculture. Here again, Jim made the point that strategies for economic intervention or development must be informed by a fundamental understanding of climate/ecosystem/land-use interactions.

Jim described how maladaptive political and economic forces could lead to rangeland degradation and a massive breakdown in pastoral ecosystems in Kazakhstan (Ellis and Lee 2003). Jim collaborated with Roy Behnke and Carol Kerven on research on their project called 'Desertification and Regeneration: Modelling the impact of market reforms on Central Asian rangelands' (DARCA). The former Soviet countries in Central Asia have introduced market economies and dissolved state collective farms, resulting in altered patterns of rangeland use, degradation and recovery (Kerven 2003). He integrated analyses of precipitation and NDVI, a satellite-based index of green vegetation biomass, to assess fundamental changes in the vegetation-livestock system. Results suggested that prior to the late 1980s, a less variable climate and the availability of fodder at low state-subsidised cost may have led to long-term overstocking, overgrazing, and rangeland degradation. When fodder became scarce and expensive after decollectivisation, it became apparent that the system had become more vulnerable and less resilient. Increased climatic variation and reduced forage production likely resulted in the dramatic decline in livestock numbers that occurred there in the 1990s.

SCALE precursors

Jim's last major scientific endeavour was to lead the ambitious SCALE (Scale and Complexity in Arid Land Ecosystems) project (2001–2006), funded by the Biocomplexity in the Environment Program of US National Science Foundation. To address the biocomplexity theme, Jim and his co-investigators suggested the central thesis that landscapes function as complex, integrated systems. From the SCALE proposal: 'The movements of herbivores, materials, humans, and money, among different landscape elements result in many emergent properties at the ecosystem level of organisation'. 'Landscape elements become connected by virtue of movement-mediated interactions' (Ellis *et al.* STEP 1985 unpublished). We hypothesised that this connectivity is important for ecosystem viability, but modern land tenure systems tend to fragment arid and semiarid land grazing ecosystems into small parcels. 'This fragmentation reduces biocomplexity and simplifies ecosystems by disconnecting the interdependent spatial units into separate entities, thus compartmentalising important components of ecosystem function into isolated tracts' (Ellis *et al.* STEP 1985 unpublished).

These ideas are the ends of threads woven deeply and pervasively throughout Jim's career. Crook *et al.* (1976)

examined the influence of resource abundance and spatial distribution determined on mammalian social organisation. 'In free ranging species…since the animals have to locate food and water continually, individuals utilising heterogeneous resources have to range over an area large enough to contain available resources…This might necessitate huge ranges in some highly mobile species'. Crook *et al.* (1976) showed that mammals have a rich variety of behavioural adaptations and resource exploitation strategies for surviving in environments having different spatio-temporal resource distributions. When resources are unpredictable and sparsely distributed, it is critical for animals to be able to move opportunistically.

Research on the STEP necessarily addressed questions involving spatial heterogeneity and scale, given we were working with highly mobile nomadic pastoralists. We asked, does vegetation heterogeneity contribute to temporal continuity of energy flow on a regional scale? At what spatial scale does temporal continuity of green biomass reach a maximum level? We saw that nomadic pastoralists and their livestock integrated landscape heterogeneity through their movements, and their persistence depended upon large-scale patterns of resource exploitation. In their JRM paper Ellis and Swift (1988) noted that '…persistence (under destabilising perturbations) may be maintained by increasing the spatial scale of the model ecosystem' (e.g. DeAngelis and Waterhouse 1987). Similarly, they pointed out that the scale of exploitation by the Turkana expanded as a means for coping with multi-year drought. They noted that in Turkana:

> as stress increases, herds are divided into smaller and more dispersed units, thereby spreading risk; the fact that there is unused space to move into during drought due to being stocked well below carrying capacity… is a critically important feature…buying time for pastoralists in the form of an ungrazed reserve.

I never had the opportunity to work with Jim on a paper specifically linking spatial scale to ecosystem function. However, the STEP certainly stimulated my interest in this area. I started the development of a spatially explicit ecosystem model beginning in 1984 while working on the STEP (Coughenour 1989, 1992, Ellis and Coughenour 1998). I conducted spatial modelling studies in 1986 examining the consequences of herbivore movement for plant animal-interactions in the Serengeti and Turkana (Coughenour 1986). In 1991 I used the 'SAVANNA Landscape Model' to study the effects of spatial heterogeneity and scale of livestock movements on stabilising energy flows to the Turkana. About the same time, I had the opportunity to write a synthetic article on the importance of spatial heterogeneity and movement for stabilising plant-herbivore systems (Coughenour 1991), drawing heavily from lessons learned on the STEP. I thank Jim for these opportunities.

In 1995–1996 Jim was the Leader for the Program for Resource Conservation and Rural Development at Wits Rural Facility, University of the Witwatersrand, South Africa, which is located in the low-veld near Kruger National Park. During this time he began to think specifically about the consequences of reduced spatial scale for wildlife communities. Lands outside of the National Park had long ago been carved up into individual holdings, mostly used for ranching. Some of these have since been converted to private game reserves which are small in comparison to expansive reserves such as Kruger. Other parks and reserves were created, spanning a range of spatial scales. Accordingly, Jim collaborated with Mike Peel of the Range and Forage Institute in Nelspruit to investigate whether reduced spatial scale constrains wild ungulate community structure in these ecosystems (Ellis and Peel 1995). They pointed out that wildlife biologists have long known that complete ecosystems, including wet and dry season ranges, are often very large-scale systems, especially in arid or semi-arid lands where resources may be patchy and/or sparsely distributed. Landscape parcelisation had potentially defeated those processes. However, they noted a recent trend for consolidation of small reserves into larger conservation blocks, as well as intensive management efforts to overcome detriments of limited scale. The study would have used census data from 20+ game reserves to see if spatial scale affected ungulate biomass density and diversity.

While in South Africa, Jim also prepared a talk called 'Spatial and social dimensions of arid savannas — or small is not beautiful'. The purpose of his talk was to review some examples of the importance of spatial scale in the human exploitation of dryland ecosystems. He used the example of Turkana to illustrate the importance of mobility, and the degradation that could result from sedentarisation in such a system. He compared the dynamics of the tribal subsection we studied in the STEP (Ngisonyoka) with those of another tribal subsection confined to a much smaller area (Ngiboceros), pointing out that the latter were much more susceptible to droughts due to reduced options for movement. He used the example of Mongolia, where a large-scale migratory system was replaced with one having more, but smaller movement systems. He showed that the economic costs of reducing the spatial scale of pastoral exploitation were substantial, being based on subsidised transport and fodder inputs. He cited Andrew Ash's Australian research, then in progress, suggesting that livestock performance was higher in larger paddocks (Ash *et al.* 2004). His conclusion was that 'in drylands large spatial scale plays an important role in human land use by ameliorating risk, by reducing the likelihood of grazing induced degradation, or by enhancing productivity'.

Spatial scale was identified as an important issue during the formative stages of the 1997–2000 Integrated Modelling and Assessment System (IMAS) project of the USAID Global Livestock Collaborative Research Support Program (GL-CRSP) (Coughenour *et al.* 1997). In the late 1960s the Government of Kenya requested, and the World Bank implemented, the Kenya Livestock Development Program (KDLP), a district-wide project aimed at promoting commercial livestock production among the Maasai herders of Kajiado District. The principal instrument was land adjudication; providing freehold title to groups of Maasai who organised themselves into group ranches. The most prominent effect of group ranch formation was reduction of the spatial scale of grazing land exploitation. Recent government policies are now encouraging subdivision and privatisation of the group ranches, further reducing spatial scale. Jim was the leader of the Kajiado component of the IMAS project, which aimed to investigate the consequences of scale reduction for pastoral persistence, rangeland condition, and livestock-wildlife interactions. The IMAS project also considered effects of limiting pastoral movements in the Ngorongoro Conservation Area, Serengeti region (Boone *et al.* 2002). In 2001, the IMAS project ended, but Jim initiated and led a follow-on GL-CRSP project called Policy Options for Livestock Based Livelihoods and Ecosystem Conservation (POLEYC) (2001–2004). Dave Swift served as the PI of the POLEYC following Jim's death. The original emphasis of the POLEYC project was to try to bring about changes in governmental and developmental policies that undermine ecological and human needs in livestock and wildlife ecosystems. However, the issue of spatial scale was central to the POLEYC project and further assessments of scale reduction in Kajiado were completed, along with studies of effects of land use intensification around Meru National Park in Kenya and Tarangire National Park in Tanzania.

In 1998 Jim gave a keynote address at the GL-CRSP biannual conference in Tarangire National Park, Tanzania called 'Extensive grazing systems: persistence under political stress and environmental risk'. In this presentation, Jim outlined ideas that would later define the SCALE and POLEYC projects. Primarily, he questioned approaches to livestock development over the last century which have sought to eliminate spatial extensiveness and mobility in pastoral ecosystems world-wide. He hypothesised that a major cause of failure of development lies in the SIP model, in which sedentarisation (S) leads to intensification (I) which then leads to increased agricultural production (P). He explored different socio-political contexts that have led to these policies, showing that, in the final analysis, the socialist and capitalistic approaches both sought the same thing — intensification. In the Asian socialist model, seen in former Soviet systems as well as northern China, the approach was state-planned, sedentarised collective farms. In the African capitalist or ranching approach as seen in Kajiado, sedentarisation would be achieved through privatisation, assuming free markets would respond with sufficient demand. Neither of these SIP-based approaches was very successful, because the SIP assumption itself is all too often inappropriate — it often defies the fundamental principles and properties of spatially extensive grazing systems. Jim proposed that the ecological 'deck' is stacked against SIP because the economic benefits usually do not offset the costs imposed by aridity, seasonality, and climatic variability. Collective farms worked as long as there were state subsidies. Private ranches did not work because markets could not bear the high costs required to replace extensive systems with intensive systems in these environments. He used each of the examples to illustrate his point: Turkana, Kazakhstan, Mongolia, northern China, Kajiado, Australia, and South African low-veld ranches. He suggested that a new approach must be developed that considers how grazing systems are constrained by economic and ecological externalities. The approach must use integrated ecological-economic assessments which determine the values of extensive systems, particularly their sustainability, under environmental risk and their effectiveness in exploiting large scale ecological gradients. The assessments must not underestimate the economic costs of sedentarisation, nor overestimate the economic benefits that will flow from intensification.

Synthesis

Jim Ellis was a conceptualist, theorist and pioneer in developing a paradigm of humans, herbivores and rangeland systems. Paradigm shifts do not occur as a result of one person's thinking. Instead, a paradigm is a consensus among scientists about solutions to central problems in their field. Old paradigms are rejected when they cannot explain anomalies, while new paradigms readily accommodate previous anomalies as normal, real phenomena. The old paradigms were based upon human experiences in temperate, relatively productive and predictable environments. They were based upon the concept of an equilibrium as the normative ideal. Anomalies arose mainly as outcomes of human experiences in tropical, relatively unproductive and unpredictable environments. They included examples of mobile pastoral societies persisting for hundreds of years in such environments without causing environmental degradation, and modern development schemes that met with either marginal success or failure.

The paradigm is derived from basic, but comprehensive understanding of the ecologically adaptive features of wildlife and human societies and resource utilisation strategies, and the ecological processes and constraints that determine energy flows from plants to livestock and humans in spatially and temporally variable environments. It is derived from a systems approach which considers how interactions between components lead to emergent outcomes, and in which multidisciplinary teams work together on integrated assessments to balance needs for ecosystem integrity, viable wildlife populations, and human well-being. It is based upon the idea that humans are integral components of ecosystems, depending upon and affecting interactions amongst climate, soils, plants, and herbivores. The implications of understanding the non-equilibrial and spatially extensive nature of arid and semiarid grazing ecosystems, and of understanding the importance of mobility and opportunism in these ecosystems, are tremendous. This understanding could benefit humans, ecosystems, and wildlife over a vast portion of the earth's surface.

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