The Tenth Arctic Ungulate Conference,
9–13 August 1999, Tromsø, Norway.

Equilibrium and non-equilibrium models of livestock population dynamics in pastoral Africa: their relevance to Arctic grazing systems

R. H. Behnke

Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB15 8QH, Great Britain
(r.behnke@mluri.sari.ac.uk).

Abstract: Equilibrium grazing systems are characterised by climatic stability that results in predictable primary production. Non-equilibrium grazing systems receive low and erratic rainfall that produces unpredictable fluctuations in forage supplies. In semi-arid Africa, these two types of environment present livestock owners with very different management problems. Identifying and maintaining optimal stocking rates is useful in equilibrium systems because livestock reproduce and produce at a rate determined by the availability of feed, which is an inverse function of stock density. The only problem is to determine what stocking rate is optimal. The correct stocking rate for a grazing system will vary depending on the production strategy and the social and economic circumstances of the rangeland user - there is no single, biologically predetermined optimum density. Variable rainfall complicates the picture in non-equilibrium systems. Set stocking rates of any kind have little value if fluctuation in rainfall has a stronger effect than animal numbers on the abundance of forage. More useful in such an environment is the ability to adjust stocking rates rapidly to track sudden changes in feed availability. In semi-arid Africa, the distinction between equilibrium and non-equilibrium systems hinges on the reliability of rainfall. In northern latitudes, at least three primary variables important for plant growth and the survival of herbivores must be considered: rainfall, snow cover and temperature. It is probably not useful to consider arctic grazing systems as equilibrium systems; on the other hand, the non-equilibrium models developed in hot semi-arid environments do not capture the range of complexity which may be an inherent feature of plant-herbivore dynamics on the mountain and tundra pastures where reindeer are herded or hunted.

Key words: caribou, carrying capacity, drought, overgrazing, *Rangifer*, reindeer, semi-arid rangelands.

Rangifer, 20 (2–3): 141–152

Introduction

Like many of the applied agricultural sciences, range management was developed to meet the needs of commercial producers in temperate climates. In the 1960s international aid agencies began to spend large amounts of money to transfer the new technologies to the open ranges of semi-arid Africa. The transplant did not work and - by the early 1980s when enthusiasm for the endeavour had worn off - sub-Saharan range management projects earned a justified reputation as failures (Simpson & Sullivan, 1984; Swift, 1991; Baxter, 1994). In retrospect, it is clear that range management in Africa had been deprived of several of the prerequisites for its success in industrial countries: large-scale commercial producers, private land ownership and a temperate climate. Classical range management had packed its standard conceptual tool bag, migrated south to equatorial latitudes but failed to take note of the particular socio-economic and ecological circumstances that confronted it there.

Like the tropics, the Arctic is a potential consumer of temperate notions of rational livestock production and resource management. A decade ago Beach (1990) identified a standard package of policies promoted by Scandinavian governments to rationalize traditional forms of reindeer herding. The package included the introduction of novel culling practices, selective breeding, grazing rotation and destocking - proven ingredients in the success of commercial livestock husbandry in most of Europe and North America. These techniques were either heavily modified or abandoned when they were applied to small holders in pastoral Africa;

whether they will work in the Arctic is far from certain.

There has been little sustained communication by tesearchers across the latitudinal gradient that separates the tropics and the Arctic and sub-Arctic. This paper contributes to such a dialogue. It recounts a tale of lessons learned the hard way over the course of several decades in equatorial Africa and speculates briefly about the convergence of arctic and tropical range and livestock policy. My treatment of the arctic material is, at best, impressionistic. Real dialogue takes partners, but pastoral studies are still regionally compartmentalized and we have yet systematically to exploit the comparison between temperate, tropical and arctic forms of extensive livestock production.

The standard interpretation and alternative hypotheses

Many African rangelands are heavily stocked with domestic animals and have been for some time (Sandford, 1983). In a dry year, or after a run of dry years, the animals often yield very little output in terms of secondary production and occasionally die in large numbers (McCabe, 1987; Moris, 1988; Bernus, 1988; Fratkin, 1991; Scoones, 1992). The causes and consequences of such fluctuations have been poorly understood. The most common interpretation has been that the rangelands were overstocked, that they were used unproductively and that their long-term productivity declined with each crisis (reviewed in Sandford, 1983; Shackleton, 1993; Turner, 1993; Dahlberg, 1996). Inefficient land use practices were seen to be the problem and destocking was commonly recommended as the remedy (Brown, 1971; Lamprey, 1983; Jarvis, 1991).

In the last ten years this standard interpretation has been challenged by a number of alternative hypotheses about how grazing systems function in semi-arid environments. Central to these arguments is a distinction between equilibrium grazing systems, in which annual rainfall is relatively high and reliable from year to year, and non-equilibrium systems in which it is low and erratic. These two kinds of environments present herd owners with different kinds of management problems and environmental risks.

Equilibrium grazing systems are characterized by relatively high climatic stability resulting in predictable primary production. In this setting, 'fine tuning' for optimal output is possible because livestock renew themselves - reproduce, grow and produce meat and milk - at a rate determined by the availability of feed, which is an inverse function of stock density. Provided with a reliable feed supply, livestock populations can grow to the point where they have considerable impact on the species composition and density of the vegetation on which they depend.

Rangelands that receive low and erratic rainfall present a different picture. In these areas, annual fluctuations in rainfall may have a much stronger effect on the abundance of forage than animal numbers. Productivity levels will therefore be determined by abiotic perturbations - droughts in particular - which the manager cannot predict and which he is unable to control. If droughts and livestock die-offs are severe and frequent, these grazing systems cannot sustain livestock populations at or near long-term ecological carrying capacity. In non-equilibrium systems like this, the potential impact of the livestock on their forage resources is reduced. Rather than providing evidence of mismanagement, periodic livestock population crashes represent one of the mechanisms that promote the persistence of such systems despite the instability and harshness of the environments in which they operate (see references in Ellis & Swift, 1988 and Little & Leslie, 1997 for an analysis of this process among the Turkana of northern Kenya, probably the best studied pastoral system in sub-Saharan Africa).

A coefficient of inter-annual rainfall variability (CV) of 33% probably marks the boundary between African livestock systems dominated by stability

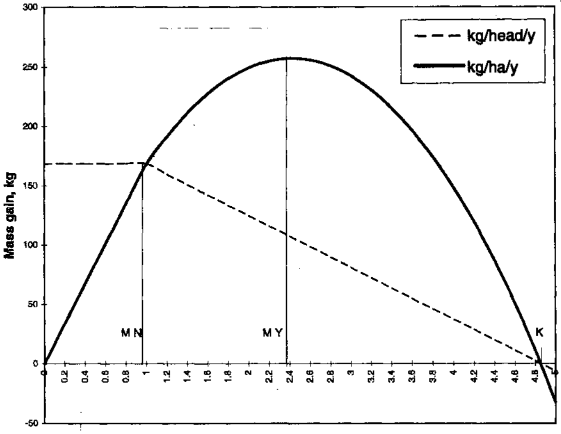

Fig. 1. Stocking rate and beef production (Jones & Sandland, 1974).

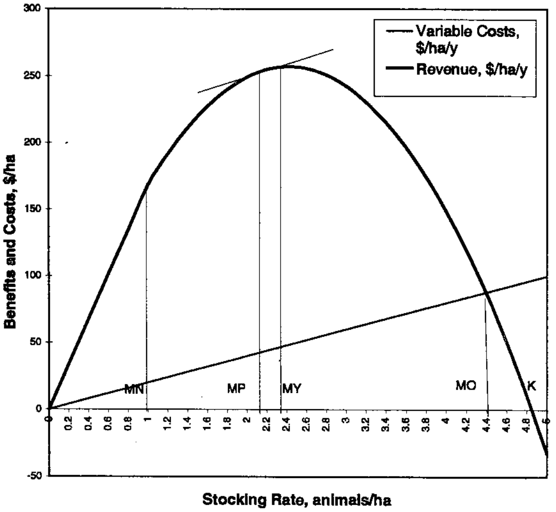

Fig. 2. Economically and biologically optimal stocking rates.

Notes to Fig. 2.

- Beyond *MN*, increases in density entail a progressive decline in livestock nutritional levels, individual animal productivity and overall herd condition (Malechek, 1984).
- *MP* is the most advantageous stocking density for commercial ranchers trying to maximize their profits. The precise location of the commercial optimum is sensitive to changing cost levels and output prices (Workman, 1986; Wilson & Macleod, 1991; Jarvis, 1991).
- *MY*, maximum yield, marks the density at which a herd owner can obtain maximum aggregate output per unit area a consideration important to subsistence-oriented pastoralists who directly consume their own produce and seek to provide food for large human populations (Behnke, 1994).
- Stocking densities in the vicinity of *MO* are possible when herders are free to enter and use a pasture at their own discretion. New operators and theit animals will be attracted to the area until aggregate stocking densities approach *MO* and declining revenues equal rising operational expenses, removing any further incentive for new entrants. This 'open access equilibrium' can occur at high densities which depress yields and is not a desirable stocking target for any group of producers except the very poor.
- *K* is what wildlife and population biologists refer to as 'ecological carrying capacity' - the level at which a herbivore population would naturally stabilize assuming a relatively constant forage supply. Since herds at *K* generate no offtake but simply maintain themselves, this stocking density is not of interest to ownets of domestic stock.
- The expansion of animal numbers beyond *K* can occur in cyclic irruptions or when new herbivore species are introduced into favorable habitats, temporarily releasing normal controls on population growth. The botanical asset stripping which underpins the herbivore irruption has commercial parallels. Assuming that a rangeland cannot maintain pastoral incomes at levels comparable to opportunities elsewhere in the economy, the rapid deplerion of vegetation at *K*+ densities is a feasible commercial proposition. An area is 'mined', abandoned and profits are re-deployed elsewhere.

and instability. CVs of 33% or higher are possible anywhere in Africa with 600 mm or less of rainfall per year and, in southern and eastern Africa, even where rainfall exceeds 1000 mm per year. This means that about half the continent's land area is potentially exposed to the effects of severe climate variability, drought, and non-equilibrium dynamics (Ellis, 1994).

The opening sections of this paper summarize some of the evidence for, and policy implications of, the equilibrium/non-equilibrium dichotomy as it has been applied to semi-arid grazing systems. The last part of the paper discusses the relevance of this dichotomy for management regimes for ungulates in the Arctic and sub-Arctic.

Carrying capacity in equilibrium systems

Figs. 1-3 illustrate the effect of alternative stocking densities on livestock output in equilibrium grazing regimes. Fig. 1 depicts physical product output from a beef ranching system and Fig. 2 examines the economic profitability of such a system. Figs. 1 and 2 summarize the results of numerous experiments carried out under the reasonably stable conditions typical of equilibrium systems (Jones & Sandland, 1974; Butterworth, 1985; Wilson & MacLeod, 1991; Ash & Stafford Smith, 1996). Fig. 3 compares the outputs from commercial ranching versus those from mixed subsistence/market-oriented African husbandry systems.

In Fig. 1 weight gain per animal is constant at very low stocking densities when forage is abundant and does not constrain animal performance (*0-MN*) but decreases as an inverse linear function of stocking density when density exceeds *MN*. Gain per hectare initially increases with increasing stocking rate to a point of maximum yield (*MY*) and then declines quadratically to zero at *K*, the feed-imposed ceiling on further herd growth, often called 'ecological carrying capacity'.

Fig. 2 converts physical outputs in Fig. 1 into cash equivalents and compares the returns with operating costs at different stocking densities. For

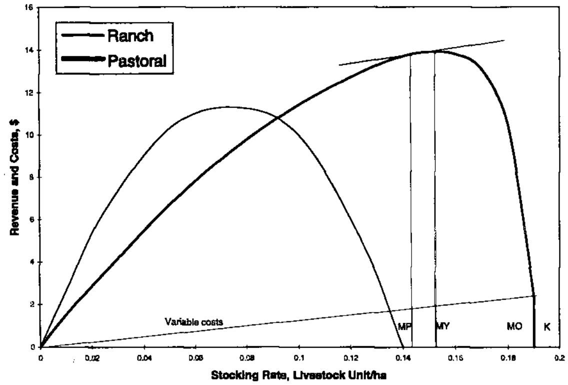

Fig. 3. Ranch and pastoral revenues and costs at various stocking rates.

Notes to Fig. 3.

- At low stocking densities pastoral output is probably lower than ranch output. Under favorable nutritional conditions, indigenous African cattle can match neither the absolute level of output per animal nor the efficiency of the rate of feed conversion into livestock product achieved by commercial breeds (Richardson, 1994).
- In pastoral systems both maximum yield (*MY*) and maximum herd size (*K*) occur at higher stocking densities compared to ranching systems, reflecting the capacity of pastoral stock to withstand nutritional stress. African cattle breeds can survive, produce and reproduce under nutritional conditions that are inadequate by the standards of commercial breeds in temperate climates.
- In pastoral systems, herd output falls precipitately from the point of *MY* to zero yield at ecological carrying capacity, reflecting a non-linear relationship between stocking density and live animal outputs such as fibre, milk or manure. If production and reproduction can continue during periods of weight loss, stocking rates that maximize live animal outputs will be higher than those that maximize meat output (Donnelly *et al.*, 1983; Donnelly *et al.*, 1985; Behnke & Abel, 1996)
- Pastoralists can obtain over 2.5 times more energy from combined meat and milk production than from meat production alone, because of the greater efficiency of conversion of both feed energy and nutrients - principally nitrogen - from pasture into milk (Western, 1982; Western & Finch, 1986; Blaxter, 1962; King, 1983; Spedding, 1971).
- Operating costs for inputs other than labour are very low for many subsistence-oriented herders, giving a gently sloping variable cost curve. When variable costs are minimal, *MP*, the stocking rate that maximizes net revenue, shifts to the right, effectively eliminating for subsistence-oriented systems the distinction between those stocking rates that optimize economic profits (*MP*) versus gross output (*MY*) (Tapson, 1990).

commercial ranchers, the economically optimal stocking density – *MP* or maximum profit - is the stocking rate which maximizes the differential between total revenue and variable costs. This economic optimum can be identified by inspection; it occurs at the point of greatest vertical distance between the revenue and variable cost curves. Finally, *MO* – the density beyond which rising costs exceed revenue - represents the outer margin of viable economic operation on the rangeland in question. Beyond *MO* net revenue is nil, rendering insolvent any unsubsidized herd owner who persistently operates at these densities.

In Figs. 1 and 2, livestock and plant populations are closely coupled by density-dependent negative feedback - more livestock result in more pasture eaten, therefore less pasture available and consequently fewer livestock (Caughley, 1987: 168). Stable densities of plants and herbivores and predictable levels of herd output are made possible by this feedback and because these systems are not unduly buffeted by the vagaries of climate. It only remains for the manager to decide what level and what kind of output is required from the system and what densities of plants and animals will deliver this output.

Fig. 2 addresses this issue. It identifies at least six distinct management objectives and associated stocking densities at which different observers - or producers - might conclude that the system contained the correct number of animals: optimal individual animal performance (*MN*), profit maximization (*MP*), yield maximization (*MY*), maximization of the number of herding operations supported by the resource (*MO*) and, finally, the maximum total number of livestock which could be supported on a permanent (*K*) or temporary basis (*K*+, not shown in Fig. 2). With the exception of *K*+ all these stocking densities are potential equilibria at which the rate of growth of plants equals the rate at which plants are consumed by herbivores. With the exception of *K*, all these potential optima are managed equilibria sustained by alternative culling rates. Although all are technically feasible, each of these different 'equilibrium' densities is appropriate to a particular management and production system or is advocated by different sets of professional observers.

In contrast to large-scale market-oriented ranching, however, open-range African herding is characterized by different livestock breeds, species and product combinations, variable levels of market involvement and different systems of land tenure.

Fig. 3 presents hypothetical revenue or physical product curves for fenced beef ranching systems and subsistence-oriented African husbandry systems using communal rangelands. These curves illustrate some of the principal differences between commercial and pastoral productivity and the likely impact of these differences on stocking policy. The altered shape of the pastoral output curve combined with a 'flat' variable cost curve for subsistence producers minimizes the difference between *MP, MY, MO* and *K;* it also positions these thresholds at very high stocking densities compared to commercial ranching. Maximum yield at *MY.* is higher in the pastotal system than in the ranch system as a result of the combined effects of a broader product mix, exploitation of live rather than terminal animal products, and the greater physiological resilience of indigenous breeds. These factors help explain why African pastoral producers can achieve their production goals at stocking rates near ecological carrying capacity.

Figs. 1-3 also illustrate why carrying capacity has proved such a slippery concept. Within the limits of what is biologically feasible, the correct stocking rate for a grazing system must be determined in relation to the production strategy and the social and economic circumstances of the rangeland user. There is no single, biologically predetermined optimum equilibrium density and, hence, little point in simply characterizing an area as 'overstocked'.

This analysis explains why outside observers commonly perceive African rangelands as chronically overstocked. Due to the historical association of range management with commercial beef ranching, many of the standard botanical indicators used to assess 'carrying capacity' have actually been implicitly derived to identify economically profitable stocking rates for commercial ranchers which is shown as the density *MP.* in Fig. 2. Subsistence producers are likely to target an alternative density, *MY,* situated along an entirely separate production function depicted in Fig. 3. Here we have an explanation of how livestock numbets in some parts of Africa have continued to grow, in some instances for decades, beyond the purported limits of carrying capacity. What was being estimated were not ecological but economic carrying capacity levels and, moreover, economic carrying capacity levels for kinds of production systems that did not exist in the areas being assessed (Behnke & Scoones, 1993)

Fig. 3 also demonstrates why the controversy over pastoral overstocking has been so intractable in semi-arid regions of Africa. Mixed-product output per hectare from subsistence-oriented pastoralism is routinely several orders of magnitude higher than beef output from commercial ranching in comparable environments (Prins, 1989; Behnke & Abel, 1996). In climatically stable environments these economic benefits are achieved at the cost of lowered plant density and destocking would immediately make many people poorer (Abel, 1993).

That subsistence-oriented producers can meet their production targets at much higher stocking rates than commercial producers does not mean that the land they occupy is more resilient (Stafford Smith, 1996). On the contrary, it implies that there are strong incentives for African herd owners to stock heavily for their immediate benefit but with potentially disastrous long-term environmental consequences. This is not, unfortunately, a problem that most stocking experiments are equipped to examine because they rarely continue long enough to pick up the lagged effect of high stocking densities on output levels (Ash & Stafford Smith, 1996). For African husbandry systems, reliable data on the long tetm sustainability of highly productive and highly stocked systems are virtually non-existent.

The population dynamics of non-equilibrium systems

Semi-arid grazing systems are arrayed along a continuum ranging from non-equilibrium to equilibrium, with most African grazing systems probably lying somewhere between the extremes (Wiens, 1984; Ellis & Swift, 1988; Coppock, 1993; Scoones, 1993). For purposes of comparison, the following account ignores the intermediate forms and presents a simplified picture of several important features of strongly non-equilibrium grazing systems.

At low rainfall levels, semi-arid grazing systems are driven by one dominant input - water - which arrives in discontinuous pulses some of which are large enough to send waves of biological activity cascading through the system (Noy-Meir, 1973). Biotic activity is regulated by a sporadic aboitic variable. In these environments, predictable seasonal fluctuations in rainfall are compounded by stochastic annual variations. Since annual variability in rainfall is inversely correlated with mean annual rainfall levels, the supply of water becomes more erratic as the total amount declines (Nicholson *et al.,* 1986; Nicholls & Wong, 1990). This combination of a harsh and unstable climate has several consequences for the relationship between livestock and vegetation:

- *Seasonality.* In semi-arid areas livestock populations are commonly limited by the abundance and quality of forage in the dry season. It may be difficult to maintain livestock in sufficiently high numbers through the dry season to challenge the vegetation in the wet season when it is growing, vulnerable to damage but abundant relative to feed requirements. Conversely, when grazing pressure is high - i.e. in dry seasons or during droughts when demand for feed often outstrips supply - the plants are relatively impervious to abuse, the living bits having retreated behind thorns, inside woody structures, below ground or been stored in seeds.
- *Stochastic disturbance.* Seasonal fluctuations in food supply are compounded by stochastic annual variations. Plants and herbivores respond to and recover from droughts at different rates (Caughley, 1987; Ellis & Swift, 1988). If droughts are frequent and severe enough, differential die-back and recovery rates will ensure that livestock populations will be almost continuously out of synchronization with their food supply in a particular year. In extreme instances, the herbivores are 'ambushed when at high density by a drought that cuts the food from under them, and ... trapped inappropriately at low density when a burst of pasture growth provides enough food to maintain a hundred times their number' (Caughley, 1987: 179, referring to kangaroos). In these systems, any equilibrium between the supply and demand of feed is largely coincidental - a fortuitous match between forage production and rainfall in one year and livestock population levels generated by rainfall and forage production in past years (Ellis & Swift, 1988).
- *Weak habitat saturation.* If herds die off in droughts more quickly than they tecover in good years, mean stocking rates in environments subject to stochastic rainfall variation will be lower than they would be under comparable but constant conditions (Caughley, 1987; Scoones, 1993). If livestock densities that are in theory sustainable under stable conditions are equated with 'carrying capacity', then these systems will maintain mean stocking densities below carrying capacity (Ellis & Swift, 1988; McLeod, 1997; Hary *et al.*, 1997).
- *Density independence.* Shortfalls in feed supply are a consequence of periods of plant senescence that result in declines in the quality and quantity of forage. If forage quality routinely declines below maintenance levels as the vegetation cures, most animals begin to starve at the start of the dry season (Coppock *et al.*, 1986 a; b). The rate at which animals die will depend more on the length of the dry period than on the number of animals subjected to it. To an extent that is remarkably independent of their density, livestock in semi-arid Africa lose weight in normal dry seasons, recruitment and reproduction suffer in poor years and adult animals die in severe multi-year droughts (Coughenour *et al.*, 1985; McCabe, 1987; Homewood & Rodgers, 1991).
- *Spatial heterogeneity.* Despite the loose overall coupling between livestock populations and their feed resources, there may be intense, density-dependent competition for the limited amount of high quality forage that is available to livestock in key resource areas in the dry season (Scoones, 1993; 1995).

In general, we might expect the impact of livestock on vegetation to diminish with increased distance from water and key resource areas, during the wet season, and in the early years of post-drought herd recovery when livestock populations are low. There is ample evidence that the reverse also holds true: that livestock impacts on vegetation can be intense in 'sacrifice' areas around watering points and in riparian areas that are key dry-season grazing resources (references in Illius & O'Connor, in press).

It is also possible that droughts may 'focus the impact of animals on the vegetation into intense episodes' thereby precipitating sudden, discontinuous changes in plant species composition over wider areas (Illius & O'Connor, in press). The extent to which this happens or is likely to happen is unknown. Numerous experiments show that the species composition of vegetation in semi-arid areas changes in response to constant high grazing pressure. But these results are not pertinent to non-equilibrium dynamics, which are characterized by alternating periods of high and low stocking densities and recurrent imbalances in the supply and demand for forage. Field studies that document the negative consequences of pastoral land use are more compelling but are contradicted by case material that suggests little widespread rangeland degradation even in the Sahel, long presumed to be the locus classicus of desertification (Tucket *et al.*, 1991; Hiernaux, 1996).

The relevance of the equilibrium/non-equilibrium dichotomy for arctic ungulates

In their comparison of kangaroos and caribou, Caughley & Gunn (1993) noted parallels between semi-arid and arctic grazing systems in terms of structural simplicity, exposure to uncertain weather extremes and the instability of herbivore populations. Their analysis suggests that non-equilibrium grazing systems comparable to those in the semi-arid tropics may exist in the Arctic. In both settings the 'components of climate that determine plant growth...vary prodigiously from year to year' (Caughley & Gunn, 1993: 52), forage availability rather than herbivore density drives changes in herbivore populations and does so quickly: 'Populations of both red kangaroos and caribou appear to be buffeted, and occasionally hammered, by changes in the availability of food mediated entirely by capricious weather' (Caughley & Gunn, 1993: 53, 54). As Caughley (1987) showed for kangaroos, major changes in herbivore population size can be generated simply by compounding frequent but less extreme perturbations. Long term fluctuations in caribou/reindeer populations could therefore be 'essentially a mathematical artifact of year-to-year fluctuations in weather...even when the weather has no time trend' (Caughley & Gunn 1993: 54).

Subsequent to the publication of Caughley & Gunn (1993) there has accumulated additional evidence that sustains their interpretation, as follows:

- More complete data have been assembled on population trends for the major barren-ground caribou herds in Northwest Territories, Canada, and this material makes an even stronger case for population instability than the data initially summarized by Caughley & Gunn (Gunn, 1998: Fig. 13.2, and Fig. 13.3 for Peary caribou on Bathurst Island, Northwest Territories, Canada).
- Additional evidence has emerged that insular caribou populations are 'loosely regulated by food at low populations density' due to 'the impact of frequent density independent factors', a conclusion that could be sustained despite the possibility that the index of winter severity used in the study was 'too simplistic' and that one of the study islands had no weather station (Ouellet *et al.*, 1996; see also Nagy *et al.*, 1996 for Peary caribou on Banks Island; Tyler *et al.*, 1999 for Svalbard reindeer).
- Whitten's (1996) analysis of the demography of the Porcupine caribou herd in Alaska has moved on from a presentation of census results (Fancy *et al.*, 1994) to an analysis of the mechanisms of population regulation, summarized as follows:

  > The Porcupine Herd undergoes population fluctuations of variable amplitude and period because weather setbacks come at irregular intervals. Recovery rates under normally prevailing conditions are slow enough and weathet setbacks occur frequently enough that the population tends to stay within a fairly narrow range of densities and seldom, if ever, reaches levels where there would be population regulation through food competition if access to forage were never restricted. There is no true equilibrium in this system.
- Similar conclusions apply to the population dynamics of a mountainous caribou herd in the Alaskan interior: 'The size of a caribou herd in a given year is likely to be largely a function of its size during the previous population low and the number of years of favorable weather in the interim' (Valkenburg *et al.*, 1996).

There are, however, also likely to be consistent differences in the way semi-arid tropical and arctic climates stress animals, differences that complicate simple comparison between unstable, weather-driven population dynamics in these two types of systems. In semi-arid Africa and Australia weather affects livestock viability in a remarkably simple way: either it rains or it does not. Plant growth and senescence, livestock malnutrition and recovery all hinge on the presence or absence of a single physical input. No other climatic factor comes close to having the importance of rainfall, which can be exceedingly unstable in areas where it is scarce. This means that the character of an entire year is established by rainfall in the preceding wet seasons.

The situation is more complex at higher latitudes where fluctuations in both temperature and precipitation influence both the growth and the availability of forage in summer or winter, respectively. At northern latitudes, one set of weather variables - such as rainfall or the timing of the onset of warmer weather in spring - may cause fluctuations in the quality and quantity of feed production, while a second set of weather factors - such the prevalence of ground ice or the depth of snow cover - determine how much of total primary production is accessible to herbivores in winter (Mech *et al.*, 1987; Tyler 1987; McRoberts *et al.*, 1995; Langvatn *et al.*, 1996; Post *et al.*, 1997; Forchhammer *et al.*, 1998). With multiple factors determining the outcome, weatherinduced stress is a function of the impact of individual factors, their correlation, and their additive or offsetting consequences. Multiple confounding factors could dampen or exacerbate climatic instability. Caughley & Gunn (1993) documented high coefficients of variation for important individual climate factors. How this variability is 'packaged' in individual years will present analytical problems and is likely to have impacts on herbivore dynamics that are not apparent in semi-arid grazing systems.

The picture is further complicated by the way different kinds of arctic vegetation respond to weather and to grazing. Herbaceous vegetation in semi-arid Africa and Australia responds quickly to rainfall. In the arctic green biomass production may also react rapidly to fluctuating weather stimuli, but at least one kind of forage - lichens - does not. Lichen recovery from fire or heavy grazing is measured in decades (Thomas *et al.,* 1995; Arseneault *et al.,* 1997). Depending on the relative availability of winter and summer ranges in an area, reindeer/caribou populations may be constrained by vegetation resources that fluctuate either annually or across decades. Because they are grazed in different seasons, these feed sources may also influence different vital rates (Sæther, 1997) with different levels of variance and elasticity (Walsh *et al.,* 1995; Gaillard *et al.,* 1997). Just this sort of complexity is suggested by the dynamics of the George River caribou herd which may be regulated by winter or summer feed availability, or both (Messier *et al.,* 1988; Crête & Huot, 1993; Manseau *et al.,* 1996; Arseneault *et al.,* 1997). What initially looked like a simple system now looks rather complicated.

Constrained by forage resources that respond to grazing pressure on different time scales and influence different vital rates, reindeer/caribou grazing systems appear to exhibit locally specific patterns of population regulation depending on the relative abundance of winter and summer forage in an area. For example, marked yearly fluctuations in herd size are not apparent in the data on Norwegian wild reindeer summarized by Skogland (1990) who emphasized density-dependent population regulation and attributed large crashes to over-hunting:

> The primary factor in population regulation of wild reindeer herds is density-dependent food limitation in winter, and...density-independent effects are most likely to be a contributory factor only at high population density (Skogland, 1985).

On the other hand, Adamczewski *et al.* (1986) and Tyler (1987) describe island grazing systems in which seasonal and inter-annual fluctuations in feed availability create intriguing parallels with semi-arid Africa grazing systems. Reindeer/caribou are not limited by summer nutrition and populations can be severely reduced by icing; winter nutrition is limited and stocking rates may be maintained below summer carrying capacity. Substitute 'dry season' for 'winter', 'wet season' for 'summer' and 'drought' for 'ice' and we could be talking about African livestock-vegetation interactions rather than island reindeer/caribou. Non-equilibrium dynamics caused by stochastic disturbance may represent an appropriate model.

Policy implications for reindeer management

Two decades ago Ingold (1980: 27, 47, 211) argued that reindeer pastoralism destabilised arctic grazing systems by encouraging violent oscillations in ungulate numbers and pasture availability in a 'vicious circle' in which 'impoverishment results from a cultural failure to impose effective limits to [herd] growth, just as the impetus for growth derives from the prospect of impoverishment'. For Ingold, reindeer pastoralism destroyed natural balances or exacerbated natural imbalances. In the semi-arid tropics, remarkably similar arguments were part of what Sandford (1983) has called the 'Mainstream view' - the assertion that contemporary pastoralism upset natural homeostasis, degraded the environment and impoverished those who practiced it. The work summarized in the first two sections of this paper was an attempt to dismantle parts of the ecological rationale that underpinned Mainstream perceptions of semi-arid Africa. A similar debate is underway in the Arctic, with some scholars arguing that the flexibility and opportunism characteristic of indigenous production systems are appropriate responses to an erratic and harsh environment (Beach, 1990; Krupnik, 1993; Fox, 1998; Tyler, 1999) while others take the opposite point of view (Riseth & Vatn, 1998; Skonhoft, 1998; Karlstad, 1998).

In Africa and I suspect in the Arctic as well, these debates have practical implications for the design of public policy. Our perception of the resource management capacities of local communities, the relationship between rural communities and regulatory authorities and pastoral development priorities all turn on the extent to which grazing systems are naturally homeostatic and subsequently perturbed, or intrinsically non-equilibrial. There are several reasons for suspecting that these questions can be usefully investigated for arctic and sub-arctic pastoral systems. To an extent rare in sub-Saharan Africa, circumpolar real-estate is controlled by powerful industrial states that possess the means to enforce their will. It is unlikely that the official policies promulgated by these states will be so inadequately funded or erratically implemented as to be irrelevant to the daily lives of reindeer herders. Even in their hinterlands, central government policies make a difference, as will any contributions that science makes to the formulation of better policies.

Recent advances in the understanding of semi-arid tropical grazing systems resulted from a re-examination of agricultural problems from an ecological perspective. Ecological analyses provided an alternative to the prescriptive formulae of the applied agricultural sciences, formulae that were better suited for temperate rather than tropical environments and for commercial rather than subsistence producers. The ecological sciences are well qualified to fulfill a similar role with respect to debates on reindeer pastoralism. Because they reside in the industrialized north, reindeer/caribou have been extensively studied. We probably already know more about *Rangifer* than we will ever, unfortunately, be able to discover about the agro-ecology of African cattle breeds managed under subsistence conditions on Africa's open ranges. Domesticated reindeer share both their geographical range and their genetic constitution with caribou which facilitates comparison between the ecology of wild and domesticated populations. Despite the inevitable shortcomings, the empirical record on *Rangifer* ecology is robust enough to enable ecologists usefully to scrutinize the development of grazing management policy. Routine ecological studies, clear synthesis of results and vigorous engagement may contribute a great deal.

Acknowledgements

I would like to thank Nicholas Tylet for introducing me to the literature on arctic ungulate ecology and also, together with Carol Kerven and Cara Kerven, for suggesting improvements to earlier versions of this paper.

References

Abel, N. O. J. 1993. Reducing cattle numbers on Southern African communal range: is it worth it? – *In:* R. Behnke, I. Scoones & C. Kerven (eds.). *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas,* pp. 173–195. London: Overseas Development Institute.

Adamczewski, J. Z., Gates, C. C., Soutar, B. M. & Hudson, R. J. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. – *Canadian Journal of Zoology* 66: 1986–96.

Arseneault, D., Villeneuve, N., Boismenu, C., Leblanc, K. U., & Deshaye, J. 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Quebec: an application of fire history and Landsat data. – *Journal of Applied Ecology* 34: 65–78.

Ash, A. J. & Stafford-Smith, D. M. 1996. Evaluating stocking rate impacts in rangelands: animals don't practice what we preach. – *Rangeland Journal* 18: 216–243.

Baxter, P. T. W. 1994. Pastoralists are people: why development for pastoralists, not the development of pastoralism? – *Rural Extension Bulletin* 4: 3–8. University of Sussex.

Beach, H. 1990. Comparative systems of reindeer herding. – *In:* Galaty, J. G. & Johnson, D. L. (eds.). *The World of Pastoralism,* pp. 255–298. New York: The Guilford Press.

Behnke, R. H. 1994. Natural resource management in pastoral Africa. – *Development Policy Review:* 12: 5–27.

Behnke, R. H. & Able, N. 1996. Revisited: the overstocking controversy in semi-arid Africa. – *World Animal Review* 87 (2): 3–27.

Behnke, R. H. & Scoones, I. 1993. Rethinking range ecology: implications for rangeland management in Africa. – *In:* R. Behnke, I. Scoones & C. Kerven (eds.). *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas,* pp. 1–30. London: Overseas Development Institute.

Behnke, R. H., Scoones, I., & Kerven, C. 1993. *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas.* London: Overseas Development Institute.

Bernus, E. 1988. Seasonality, climatic fluctuations, and food supplies (Sahelian nomadic pastoral societies). – *In:* de Garine, I. & Harrison, G. A. (eds.). *Coping with Uncertainty in Food Supply,* pp. 318–36. Oxford: Oxford University Press.

Blaxter, K. L. 1962. *Energy Metabolism of the Ruminants.* London: Hutchinson.

Brown, L. H. 1971. The biology of pastoral man as a factor in conservation. – *Biological Conservation* 3 (2): 93–100.

Butterworth, M. H. 1985. *Beef Cattle Nutrition and Tropical Pastures.* New York: Longman.

Caughley, G., 1987. Ecological relationships. – *In:* Caughley G., Shepherd, N., & Short, J. (eds.). *Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.* Cambridge: Cambridge University Press.

Caughley, G. & Gunn, A. 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. – *Oikos* 67: 47–55.

Clutton-Brock, T. H., Illius, A. W., Wilson, K., Grenfell, B. T., MacColl, A. D. C. & Albon, S. D. 1997. Stability and instability in ungulate populations: an empirical analysis. – *The American Naturalist* 149: 195–219.

Coppock, D. L. 1993. Vegetation and pastoral dynamics in the southern Ethiopian rangelands: implications for theory and management. – *In:* R. Behnke, I. Scoones & C. Kerven (eds.). *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas,* pp. 42–61. London: Overseas Development Institute.

Coppock, D. L., Ellis, J. E., & Swift, D. M. 1986a. Livestock feeding ecology and resource utilization in a nomadic pastoral ecosystem. – *Journal of Applied Ecology* 23: 573–83.

Coppock, D. L., Swift, D. M. & Ellis, J. E. 1986b. Seasonal nuttitional characteristics of livestock diets in a nomadic pastoral ecosystem. – *Journal of Applied Ecology* 23: 585–95.

Coughenour, M. B., Ellis, J. E., Swift, D. M., Coppock, D. L., Galvin, K., McCabe, T. J. & Hart, T. C. 1985. Energy extraction and use in a nomadic pastotal ecosystem. – *Science* 230: 619–25.

Crête, M. & Huot, J. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. – *Canadian Journal of Zoology* 71: 2291–2296.

Dahlberg, A. C. 1996. *Interpretations of environmental change and diversity: a study from North East District, Botswana.* The Department of Physical Geography, Stockholm University Dissertation Series, Dissertation No. 7.

DeAngelis, D. L. & Waterhouse, J. C. 1987. Equilibrium and nonequilibrium concepts in ecological models. – *Ecological Monographs* 57: 1-21.

Donnelly, J. R., McKinney, G. T. & Morley, F. H. W. 1985. The productivity of breeding ewes grazing on lucerne or grass and clover pastures on the tablelands of southern Australia (IV): lamb growth. – *Australian Journal of Agricultural Research* 36: 469–481.

Donnelly, J. R., Morley, F. H. W. & McKinney, G. T. 1983. The productivity of breeding ewes grazing on lucerne or grass and clover pastures on the tablelands of southern Australia (II): wool production and ewe weight. – *Australian Journal of Agricultural Research* 34: 537–548.

Ellis, J. E. & Swift, D. M. 1988. Stability of African pastotal ecosystems: alternate paradigms and implications for development. – *Journal of Range Management* 41: 450–459.

Ellis, J. E. 1994. Climate variability and complex ecosystem dynamics: implications for pastoral development. – *In:* Scoones, I. (ed.). *Living with Uncertainty: New Directions in Pastoral Development in Africa,* pp. 37–46 London: Intermediate Technology Publications.

Fancy, S. G., Whitten, K. R. & Russell, D. E. 1994. Demogtaphy of the Porcupine caribou herd, 1983-1992. – *Canadian Journal of Zoology* 72: 840–46.

Forchhammer, M. C., Stenseth, N. C., Post, E. & Langvatn, R. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. – *Proc. R. Soc. Lond.* 265: 341–350.

Fox, J. L. 1998. Finnmarksvidda: reindeer carrying capacity and exploitation in a changing pastoral ecosystem - a range ecology perspective on the reindeer ecosystem in Finnmark. – *In:* Jentoft, S. (ed.). *Commons in a Cold Climate: Coastal Fisheries and Reindeer Pastoralism in North Norway - the Co-management Approach,* pp. 17-39. UNESCO and the Parthenon Publishing Group: Paris and New York.

Fratkin, E. 1991. *Surviving Drought and Development: Ariaal Pastoralists of Northern Kenya.* Boulder: Wesrview Press.

Gaillard, J-M., Festa-Bianchet, M. & Yoccoz, N. G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. – *TREE* 13: 58-63.

Gunn, A. 1998. Caribou and muskox harvesting in the Northwest Territories. – *In:* Milner-Gulland, E.J. & Mace, R. (eds.): *Conservation of Biological Resources,* pp. 314–33. Oxford: Blackwell Science.

Hary, I., Schwartz, H-J., Pielert, V. H. C. & Mosler, C. 1996. Land degradation in African pastoral systems and the destocking controversy. – *Ecological Modelling* 86: 227-33.

Hiernaux, P. 1996. The crisis of Sahelian pastoralism: ecological or economic? – *Pastoral Development Network* Paper 39a. London: Overseas Development Institute.

Homewood, K. M. & Rodgers, W. A. 1991. *Maasailand Ecology: Pastoralist Development and Wildlife Conservation.* Cambridge: Cambridge University Ptess.

Illius, A. W. & O'Connor, T. G. In press. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. – *Ecological Applications.*

Ingold, T. 1980. *Hunters, Pastoralists and Ranchers.* Cambridge: Cambridge University Press.

Jarvis, L. S. 1991. Overgrazing and range degradation: the need for and the scope of government policy to control livestock numbers. – *East African Economic Review* 7: 95–116.

Jones, R. J. & Sandland, R. L. 1974. The relation between animal gain and stocking rate: derivation of the relation from the results of gtazing trials. – *Journal of Agricultural Science* (Cambridge) 83: 335–342.

Karlstad, S. 1998. Institutional theory, co-management and sustainable development in Sami reindeer pasture commons - critical factors for a robust system of local management. – *In:* Jentoft, S. (ed.). *Commons in a Cold Climate: Coastal Fisheries and Reindeer Pastoralism in North Norway - the Co-management Approach.* UNESCO and the Parthenon Publishing Group: Paris and New York.

King, J. M. 1983. Livestock water needs in pastoral Africa in relation to climate and forage. – *ILCA Research Report* No. 7. Addis Ababa: ILCA.

Krupnik, I. 1993. *Arctic Adaptations: Native Whalers and Reindeer Herders of Northern Eurasia.* Hanover and London: University Press of New England.

Lamprey, H. F. 1983. Pastoralism yesterday and today: the overgrazing problem. – *In:* Bourliere, F. (ed.). *Tropical Savannas: Ecosystems of the World,* Vol. 13, pp. 643–666. Amsterdam: Elseviet.

Langvatn, R., Albon, S. D., Burkey, T. & Clutton-Brock, T. H. 1996. Climate, plant phenology and variation in age of first teptoduction in a temperate hetbivore. –*Journal of Animal Ecology* 65: 653–70.

Little, M. A. & Leslie, P. W. (eds.). 1997. *Turkana Pastoral Nomads: Biobehavioral and Ecological Conditions of their Lives.* Oxford: Oxford University Press.

McLeod, S. R. 1997. Is the concept of carrying capacity useful in variable environmenmts? – *Oikos* 79: 529–42.

Malechek, J. C. 1984. Impacts of grazing intensity and specialized grazing systems of livestock response. – *In:* National Research Council, National Academy of sciences (ed.). *Developing Strategies for Rangeland Management.* Boulder, Colorado, and London: Westview Press.

Manseau, M., Huot, J. & Crête, M. 1996. Effecrs of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. –*Journal of Ecology* 84: 503–13.

McCabe, J. T. 1987. Drought and recovery: Livestock dynamics among the Ngisonyoka Turkana of Kenya. – *Human Ecology* 15: 371–89.

McRoberts, R. E., Mech, L. D. & Peterson, R. O. 1995. The cumularive effect of consecutive wintets' snow depth on moose and deer populations: a defense. –*Journal of Animal Ecology* 64: 131–35

Mech, L. D., McRoberts, R. E., Peterson, R. O. & Page, R. E. 1987. Relationship of deer and moose populations to previous winters' snow. – *Journal of Animal Ecology* 56: 615–627.

Messier, F., Huot, J., Le Henaff, D. & Luttich, S. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. – *Arctic* 41: 279–87.

Moris, J. 1988. Failing to cope with drought: The plight of Africa's ex-pastoralists. – *Development Policy Review* 6: 269–94.

Nagy, J. A., Larter, N. C. & Fraser, V. P. 1996. Population demography of Peary caribou and muskox on Banks Island, N.W.T.., 1982-1992. – *Rangifer* Special Issue No. 9: 213–222.

Nicholls, N. & Wong, I. K. 1990. Dependence of rainfall variability on mean rainfall, latitude, and the southern oscillation. –*Journal of Climate* 3: 162–70.

Nicholson, S. E., Kin, J. & Hoopingarner, J. 1986. *Atlas of African Rainfall and its Interannual variability.* Department of Meteorology, Florida State University. Tallahassee, Florida.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. – *Annual Review of Ecology and Systematics,* part 4: 25–51,

Ouellet, J.-P., Heard, D. C., & Mulders, R. 1996. Population ecology of caribou populations without predators: Southampton and Coats Island herds. – *Rangifer* Special Issue No. 9: 17–25.

Post, E., Stenseth, N. C., Langvatn, R. & Fromentin, J-M. 1997. Global climate change and phenotypic variation among red deer cohorts. – *Proc. R. Soc. Lond.* 264: 1317–1324.

Prins, H. H. T. 1989. East African grazing lands: overgrazed or stably degraded. – *In:* Verwey, W. D. (ed.). *Nature Management and Sustainable Development,* pp. 281–306. Amsterdam: IOS.

Richardson, F. D. 1994. *Models for the selection of cow types for extensive meat and milk production in developing areas (III): cow types and biological efficiency of production.* Department of Applied Mathematics, University of Cape Town, South Africa (mimeo).

Riseth, J. A. & Vatn, A. 1998. Adaptive sttategies under technological change - a compatative study of Sami reindeer management regions in Norway, 1960-1990. – *In:* Jentoft, S. (ed.). *Commons in a Cold Climate: Coastal Fisheries and Reindeer Pastoralism in North Norway - the Co-management Approach,* pp. 235–246. UNESCO and the Parthenon Publishing Group: Paris and New York.

Sandford, S. 1983. *Management of Pastoral Development in the Third World.* London: John Wiley & Sons.

Scoones, I. 1992. Coping with drought: responses of herders and livestock in contrasting savanna environments in Zimbabwe. – *Human Ecology* 20 (3): 293–314.

Scoones, I. 1993. Why are there so many animals? Cattle population dynamics in the communal areas of Zimbabwe. – *In:* R. Behnke, I. Scoones & C. Kerven (eds.). *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas,* pp. 62–67. London: Overseas Development Institute.

Scoones, I. 1995. Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. – *Journal of Arid Environments* 29: 221–37.

Shackleton, C. M. 1993. Are the communal grazing lands in need of saving? – *Development Southern Africa* 10: 65–78.

Simpson, J. R. & Sullivan, G. M. 1984 Planning for institutional change in utilization of Sub-Saharan Africa's common property range resources. – *African Studies Review* 27: 61–78.

Skogland, T. 1990. Densiry dependence in a fluctuating wild reindeer herd: maternal vs. offspring effects. – *Oecologia* 84: 442–50.

Skonhoft, A. 1998. Bioeconomic modelling of Sami reindeer pastoralism. – *In:* Jentoft, S. (ed.). *Commons in a Cold Climate: Coastal Fisheries and Reindeer Pastoralism in North Norway - the Co-management Approach,* pp. 41–59. UNESCO and the Parthenon Publishing Group: Paris and New York.

Spedding, C. R. W. 1971. *Grassland ecology.* Oxford: Oxford University Press.

Stafford Smith, M. 1996. Management of rangelands: paradigms at their limits. – *In:* Hodgson, J & Illius, A.W. (eds.). *The Ecology and Management of Grazing Systems,* pp. 325–358. CAB, Wallingford, UK, and New York.

Swift, J. 1991. Local customary institutions as the basis fot natural resource management among Boran pastoralists in Northern Kenya. – *IDS Bulletin* 22 (4): 34–37. Institute of Development Studies, Sussex University.

Sæther, B-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. – *TREE* 12: 143–49.

Tapson, D. R. 1990. *A socio-economic analysis of small-holder cattle producers in Kwazulu.* PhD thesis: Vista University, Pretoria.

Thomas, D. C. 1996. Needed: less counting of catibou and mote ecology. – *Rangifer* Special Issue No. 10: 15–23.

Thomas, D. C., Barry, S. J. & Alaie, G. 1996. Fire - caribou - winter range relationships in northern Canada. – *Rangifer* 16: 57–67.

Tucker, C. J., Dregne, H. & Newcomb, W. 1991. Expansion and contraction of the Sahara Desert from 1980 to 1990. – *Science* 253: 299–301.

Turner, M. 1993. Overstocking the range: a critical analysis of the environmental science of Sahelian pastoralism. – *Econ. Geogr.* 69: 402–21.

Tyler, N. J. C. 1987. *Natural Limitation of the Abundance of the High Arctic Svalbard Reindeer.* PhD thesis, Cambridge University.

Tyler N. J. C. 1999. Reindeer pastutes at disequilibrium. – *In:* Z. Zomborszky (ed.). *Advances in Deer Biology.* (Proceedings of the 4th International Deer Biology Congress, Kaposvar 1998), p. 231. Pannon University of Agriculture, Kaposvár ISBN: 963-9096-53-9.

Tyler, N. J. C., Forchhammer M. C. & Øritsland N. A. 1999. Persistent instability in Svalbard reindeer dynamics: density-dependence in a fluctuating environment. (10th Arcric Ungulate Conference, Tromsø, Norway 9-12th August 1999). – *Rangifer* Report No. 4: 70–71.

Valkenburg, P., Davis, J. L., Ver Hoef, J. M., Boertje,, R. D., McNay, M. E., Eagan, R. M., Reed, D. J., Gardner, C. L., & Tobey, R. W. 1996. Population decline in the Delta caribou herd with reference to other Alaskan herds. – *Rangifer* Special Issue No. 9: 53–62.

Walsh, N. E., Griffith, B. & McCabe, T. R. 1995. Evaluating growth of the Porcupine caribou herd using a stochastic model. –*Journal Wildl. Management* 59: 262–272.

Western, D. 1982. The environment and ecology of pastoralists in arid savannas. – *Development and Change* 13: 183–211.

Western, D. & Finch, V. 1986. Cattle and pastoralism: survival and production in arid lands. – *Human Ecology* 14: 77–94.

Whitten, K. R. 1996. Ecology of the Porcupine caribou herd. – *Rangifer* Special Issue No. 9: 45–51.

Wiens, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. – *In:* Strong, D. R., Simberloff, D., Abele, L. G., & Thistle, A. B. (eds.). *Ecological Communities: Conceptual Issues and the Evidence.* Princeton: Princeton University Press.

Wilson, A. D & Macleod, N. D. 1991. Overgrazing: present or absent? – *Journal of Range Management* 44: 474–482.

Workman, J. P. 1986. *Range Economics.* New York: Macmillan.