

Expanded abstract

The dynamics of caribou and muskoxen foraging in arctic ecosystems

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Forage system characteristics

Numbers of caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) in the Northwest Territories, Canada have changed rapidly in the last few decades (e.g. Gunn *et al.* 1991). Our ability to respond to questions raised by those rapid changes is, however, compromised by our ignorance of the dynamics of the relationship between arctic ungulates and their forage which in turn inhibits our understanding of the population dynamics.

The arctic ecosystem is relatively simple in terms of species diversity and herbivore numbers fluctuate against a background of unpredictably variable weather: a simple and changeable system is more easily stripped down to its essential components to describe their interactions. Arctic ecosystems have three dominant attributes which are the salient points in my conceptual model proposed here to unravel the population dynamics of arctic herbivores. (a) Plant productivity is restricted to brief annual pulses; (b) the weather is highly unpredictable and (c) most of the biomass is below ground locked into a slow cycle of decomposition.

The nutrient input in tundra ecosystems is low and mostly slowly cycled through soil organic matter at the characteristic cool ambient temperatures. Plants depend heavily on the internal recycling of nutrients from storage tissue

below ground. The tie-up of plant nutrients in detritus opens an accelerating role for herbivory in nutrient recycling – animal fecal material breaks down and releases nutrients to the plants more rapidly than the overall detritus pool (Dowding *et al.* 1981). Muskoxen which forage in herds, graze intensively and deposit large amounts of dung *in situ*, will have a larger role in nutrient recycling than caribou within the plant communities where they forage. Caribou forage in smaller groups and graze extensively while walking.

Arctic plants have a pulse of growth restricted by temperatures to a brief season. The onset of plant growth varies by weeks (Svoboda 1977, Muc 1977). Most plants are conservative and complete their growing season within a fixed period despite annual variations in the duration of the potential growing season. Flowering varies between years and is depressed by as much as 80% following a late cool season but productivity of green plant biomass in meadows is less responsive to summer temperature (Muc 1977, Svoboda 1977).

Unpredictability of arctic weather

Weather is unpredictable between years and the effects of the variations are different for forage supplies firstly, during the growing season and then secondly, for the availability of forage in

the winter. Some effects of the unpredictability in the weather on the herbivores are buffered by the conservatism of the plants. Nevertheless, herbivores cope with wide annual variation in the beginning and end of the growing season.

Arctic herbivore population dynamics

The conventional view of muskoxen population dynamics stresses surges in recruitment mediated by high annual variation in winter calf survival, leading to "boom and bust" population growth. Less frequently, but sometimes catastrophically, severe winter weather reduces calf production and adult survival. This portrait of muskox population dynamics is unsettling: firstly, most of the earlier descriptions of muskox ecology and population dynamics came from extremes of muskox ranges – the High Arctic Islands. Secondly, our acquaintance with muskoxen is tantalizingly brief: data are few and are sporadic in time and place. The sharp declines followed the unregulated commercial hunting in the late 1800s imposed an artificial synchronization of decrease and then increase in populations across mainland Canada. Furthermore, the commercial harvesting emptied large tracts of muskox range and the muskoxen's subsequent recolonization of those regions is a feature of current population dynamics.

The data on muskoxen, especially from the arctic islands suggest that despite the artificial synchronization imposed by the commercial hunting, the population dynamics are different from those of caribou. More is known of fluctuations in caribou numbers but little progress is apparent in understanding of the causes. Proposed explanations have emphasised predation rather than food shortage.

The unpredictability of weather and its driving effects on plants and herbivores in arctic ecosystem has parallels with semi-arid ecosystems elsewhere. In the arid regions of Australia the growth of annual grasses follows the marked and unpredictable swings in annual rainfall.

Foraging dynamics

Kangaroo (*Macropus*) populations did not fluctuate uncontrollably in response to surges in annual plant growth following unpredictable rainfall (Caughley 1987). Instead, the system's dynamics remained centripetal by virtue of a

feedback loop between the numbers of kangaroos and the biomass of their forage. I suggest that the feedback loop in arctic ecosystems is a short-circuiting of the nutrient recycling. Instead of the turnover of the nutrients available to the plants being 8–10 years, the breakdown of dung releases nutrients within 2–3 years (Dowding *et al.* 1981). Attributing a role for herbivory in short-circuiting of the nutrient cycle in arctic ecosystems is not new (Dowding *et al.* 1981, Henry and Svoboda 1989) but the postulation of it as the feedback loop dampening the fluctuations of herbivore populations is.

Plant communities used by muskoxen and caribou differ in their resilience to fluctuations in weather or grazing. Muskoxen select moist graminoid communities during the plant growing season which are characterised by relative high levels of biomass and productivity. Those habitats have larger plants closely packed together which favours a high rate of forage intake. Caribou on the arctic islands select more mesic communities with lower biomass and a lower density of individual plants. The dominant plants in those communities (evergreen dwarf shrubs as *Dryas*) allocate and mobilize nutrients in different patterns than graminoids and deciduous shrubs (Chapin *et al.* 1980). Fluctuations in weather have greater effects on the productivity of the more mesic communities. On the arctic mainland, caribou and muskoxen forage in communities of more comparable density of plants and biomass during the summer. But although the plant communities are more productive than on the arctic islands, the trade-off to the caribou is the energetic loss to insect harassment which is strongly influenced by the weather.

Annual and unpredictable variations in the onset of plant phenology and flowering have more implications for caribou than muskoxen. Milk production of muskoxen peaks 2–3 weeks before greening vegetation is available and body fat supplies the energy for lactation (White *et al.* 1989). Barren-ground caribou peak in lactation the first week after calving (Parker *et al.* 1990) which coincides with the greening of shrubs and early forbs. Calving is the nadir in their annual fat cycle which leaves the cows dependent on the greening vegetation to support lactation. Timing of caribou calving on arctic islands is more variable and the relationship

with plant phenology is likely even tighter. The 1-year lag between summer temperatures and flowering of forbs may contribute to a greater responsiveness to fluctuations in weather.

Measuring food intake in relation to changes in plant biomass (the functional response) is the logical first step to determining the interactions between muskoxen and their food supply. It will require experimentation as well as field observations to account for behavioral and physiological strategies to increase the return of metabolizable energy from the forage – "Multiplier" effects (White 1983).

Understanding the coupling of forage supplies and arctic ungulate populations is necessary and urgent given the questions raised by changes in populations in the N.W.T. in the 1980s. For example, if we assume in the absence of data that after years of protection and limited quotas there are now too many muskoxen on Banks Island (Gunn *et al.* 1991), and removed a large proportion, we could destabilize the system by uncoupling the feedback between muskoxen and their forage supply. Consequences of the swings between protection and overexploitation are strikingly obvious in the management of other large mammals (e.g.: Fay *et al.* 1989). An understanding of the dynamics of the plant-herbivore system is necessary to predicting its behaviour. Without that understanding, it would be only too easy to instigate management interventions that will drive the amplitude or frequency of the fluctuations. Our current management practice of monitoring population parameters (physical and reproductive condition, rate of increase) only conveys information on current or past conditions and does not allow us to predict future trends. The demonstration of feedback loops dampening the swings in the grazing system is testable through experimental study and would lead to verifiable predictions about the systems.

References

- Caughley, G. 1987. Ecological relationships. – In: Caughley, G., N. Shepherd and J. Short (eds.). *Kangaroos: their ecology and management in the sheep rangelands of Australia*. Cambridge: Cambridge University Press, pp. 159–187.
- Chapin, F. S. III, Johnson, D. A. and McKendrick, J. D. 1980. Seasonal movement of nutrients in plants of different growth form in an Alaska tundra ecosystem: implications for herbivory. – *Journal of Ecology* 68: 189–209.
- Dowding, P., Chapin, F. III, Wielgolaski, F. E. and Kilfeather, P. 1981. Nutrients in tundra ecosystems. Pages 647–683. In: L. C. Bliss, W. Heal and J. J. Moore (eds.). *Tundra Ecosystems; a comparative analysis*. Cambridge University Press, 813 pp.
- Fay, F. H., Kelly, B. P. and Sease, J. L. 1989. Managing the exploitation of Pacific walrus: a tragedy of delayed response and poor communication. – *Marine Mammal Science* 5: 1–16.
- Gunn, A., Shank, C. C. and McLean, B. 1991. The history, status and management of muskoxen on Banks island. – *Arctic* 44: 188–195.
- Henry, G. and Svoboda, J. 1989. Comparison of grazed and non-grazed high arctic sedge meadows. – In: *Proceedings of the Second International Muskox Symposium, Saskatoon, Sask., Canada, 1–4 October 1987*. Edited by P. F. Flood. National Research Council of Canada, Ottawa.
- Hubert, B. A. 1977. Estimated productivity of muskoxen in Truelove Lowland. Pages 467–491. – In: L. C. Bliss (ed.). *Truelove Lowland, Devon Island, Canada – a High Arctic Ecosystem*. Univ. Alberta Press pp. 467–491.
- Muc, M. 1977. Ecology and primary production of sedge-moss communities, Truelove Lowland. – In: L. C. Bliss (ed.). *Truelove Lowland, Devon Island, Canada – a High Arctic Ecosystem*. Univ. Alberta Press pp. 157–184.
- Parker, K., White, R. G., Gillingham, M. P. and Holleman, D. F. 1990. Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. – *Canadian Journal of Zoology* 68: 104–114.
- Svoboda, J. 1977. Ecology and primary production of raised beach communities, Truelove Lowland. – In: L. C. Bliss (ed.). *Truelove Lowland, Devon Island, Canada – a High Arctic Ecosystem*. Univ. Alberta Press pp. 185–216.
- White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. – *Oikos* 40: 377–384.
- White, R. G., Holleman, D. F. and Tiplady, B. A. 1989. Seasonal body weight, body condition and lactational trends in muskoxen. – *Canadian Journal of Zoology* 67: 1125–1133.

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