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Voles, lemmings and caribou - population cycles revisited?

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Abstract: Although we may be confident that many caribou populations fluctuate, we have not made much progress in linking patterns of fluctuations with their underlying processes. Caribou abundance is relatively synchronized across continents and over decades which points to climatic variation as a causative factor. Progress on describing intrinsic and extrinsic factors for smaller-bodied and larger-bodied mammalian herbivore population dynamics also reveals the role of climatic variation and specifically decadal variations. Based on experience elsewhere, we can expect complex relationships between caribou, climatic variation and their forage rather than simple correlations. Caribou responses to decadal trends in climate likely accumulate through successive cohorts as changes in body mass which, in turn, leads to changes in lifetime reproductive success.

Key words: Rangifer tarandus, abundance, decadal climatic variation, cohort memory.

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Introduction

If there is one thing that those knowledgeable about caribou Rangifer tarandus would agree on, it is that caribou abundance fluctuates over decades. However, agreement is less when it comes to describing the mechanisms underlying those fluctuations. Past North American caribou workshops have featured papers relaying or querying our progress in linking fluctuating abundance with the underlying processes. For example, Bergerud (1996) reviewed caribou population dynamics and Crête & Payette (1990), Valkenburg et al. (1994), and Whitten (1996) offered single herd case histories. Those papers largely relied on retroactively correlating abundance and vital rates (births, recruitment or mortality) with harvest, predation and weather events such as severe winters. This paper takes an alternative approach which is to summarize information on caribou abundance across North America and Greenland over centuries to see if that reveals hints about mechanisms underlying fluctuations in abundance.

This paper also approaches changes in caribou abundance through what can be learnt from other mammalian herbivores. Progress in understanding the mechanisms underlying the cyclic abundance of smaller-bodied arctic and sub–arctic herbivores (voles, lemmings and snowshoe hares (Lepus americanus) may be applicable to understanding caribou fluctuations. This is likely given the universality of scaling laws (fixed mathematical rules about the relationships within and between living organisms). Although there has been debate about the relationship between body size and mechanisms for population regulation, it ignored timescale. As Yoccoz et al. (1998) suggested that if for voles, months are considered equivalent to years, then their population dynamics are similar to larger bodied herbivores. Forage intake scales to body size and body size relates to age at maturity and fecundity. Lemmings and caribou have similar gut turnover times when corrected for metabolic weight (Batzli et al., 1980) and the average lemming cycle periodicity of 4 years scales to 71 years for a caribou of body mass 100 kg when scaled to power of 1/4 (longevity scales as 1/4).

This paper, then, asks four questions and discusses some possible answers: firstly what can be learnt from the fluctuations in caribou abundance at a larger geographic and longer timescale. Secondly and

thirdly, what is to be learnt from the population dynamics of smaller and larger-bodied herbivores, respectively. And fourthly, where does the information take us? Before going further, it is worth quoting what Krebs (1996) wrote when reviewing population cycles: "Population ecology is not a baseball game in which one team wins and another loses. All our ideas will be revised and improved in the long run". In any body of knowledge, the current context is established by the efforts of those who preceded and this paper is no exception. The paper's title is a play on the title of Charles Elton's (1942) classic text 'Voles, mice and lemmings' as an acknowledgement of his pioneering work on cycles in the abundance of northern small mammals.

Terminology

Terminology describing the relationship between abundance and rate of increase is from Caughley (1987). Intrinsic regulation is when population density has an instantaneous effect on rate of increase (animals are doing something to each other for example, territoriality or dispersal). Extrinsic regulation is when the effect of increasing density on the rate of increase is indirect (mediated, for example, through forage supply, predation or parasitism/disease). If the rate of increase is predictable from density, the population trend is density-dependent or density-independent if the rate of increase does not correlate with density. Density-dependence is a correlation between abundance and rate of population change but one which reveals little of the underlying mechanisms. A common trap from the correlation is assuming herbivore abundance is exceeding available forage rather than testing to determine if the decline in forage is caused by the herbivores themselves, an environmental factor or both effects interacting. Intrinsic regulation is sometimes referred to as direct density-dependence and extrinsic regulation as delayed density dependence - the connotation of the delay is that population density acts on the rate of increase of the forage or through the numerical increase of a predator.

Population cycles have three phases (increase, decrease and low numbers) with measurable phase-related changes in reproductive rates and survival (Krebs, 1996). Phase-related changes are known for caribou in the increase and decline phase, but available data for the third phase is insufficient to determine if fluctuations in caribou abundance strictly meet this definition of cyclic.

Another term used in this paper is environmental stochasticity which is random and therefore unpredictable variability. Describing how environmental variability (usually climatic) translates as ecological effects is not necessarily simple (Laakso et al., 2001). Complexity also follows when the responses to environmental variability have a time lag.

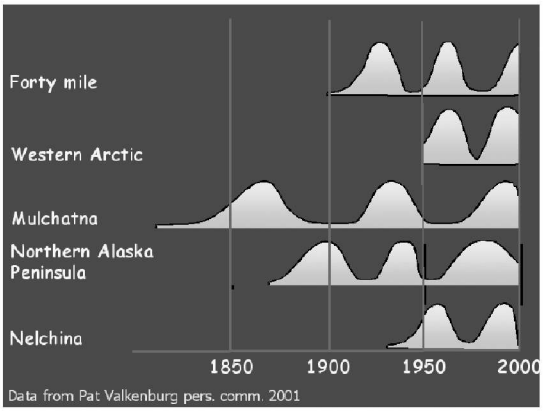
Fluctuating caribou abundance

The first question is whether considering caribou abundance at a larger geographic scale and longer time scale reveals anything about possible underlying mechanisms? Fluctuations in caribou abundance are known from survey data and can be extended back in time using archeological, historic, traditional aboriginal and dendroecological information (for example, Meldgaard, 1986; Ferguson et al., 1998; Morneau & Payette, 2000). The precise timing of the phases of increase, decrease and low numbers is dependent on sampling frequency, which contributes to variation between herds (Gunn & Valkenburg, in prep.). The mean doubling rate for Alaskan (P. Valkenburg unpubl. data) and Canadian barren-ground caribou herds is 10 ± 2.3 SE years and the mean halving rate 7.2 ± 2.6 years (the time taken for population to halve in size calculated from the exponential rate of increase: Caughley, 1977). Herds that increase slowly also are the herds that decrease slowly. The phase of low numbers is the most variable in duration (similar to smaller herbivores) and the ratio between maximum estimated and minimum size (amplitude) is 11 ± 2.2 years (3-24 range). The spread in amplitude suggests that a few herds such as the Porcupine herd fluctuate in size through a narrow range, which might suggest that they are 'trapped' in the phase of low numbers.

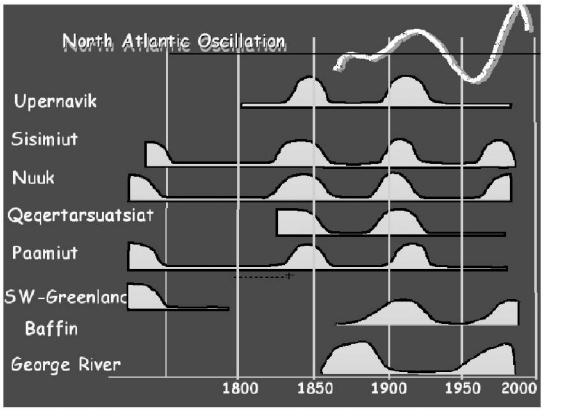
Reducing herds to a standard amplitude smoothes out noise and reveals some synchrony between phases of increase and decrease in western North America herds with most information suggests periodicity of between 40 and 70 years. Western North America (Fig. 1a) and Greenland and eastern North America (Fig. 1b) also have regular fluctuations that operate with a measure of synchrony on a sub-continental scale. The relative spatial synchrony on sub-continental scale suggests an external factor is spatially synchronizing the fluctuations and the most likely candidate is climate. Koenig (2002), for example, reported spatial synchrony in mean annual temperatures and rainfall over large distances which argues for environmental variation rather than dispersal in spatial synchrony.

Smaller herbivore cycles

Turning to the second question, which is what can be learnt from vole, lemming and snowshoe hare cycles?



(a)



(b)

Fig. 1. Standardized fluctuations in caribou abundance in (a) Alaska and (b) Greenland and eastern North America .

Voles and lemming abundance cycles over 3-5 years with a low phase of 1-3 years and amplitudes can reach 200:1 (Krebs, 1996). Snowshoe hare abundance in boreal forest cycles at 8-13 years with a mean of 9-10 years. The amplitude is 50-180 depending on latitude. The variability in the cycle length is largely the duration of the low numbers phase. An additional characteristic is that spatial synchrony of peak abundance is regional (voles) or continental (snowshoe hares) (Krebs et al., 2002).

The generalized conclusion is that cycling in voles and lemmings is the consequence of extrinsic factors of predation interacting with food as well as intrinsic factors (Krebs, 1996). Earlier hypotheses and research concentrated on factors intrinsic to the animals themselves which were observable as phase-dependent qualitative changes. And although some ideas such as stress caused by crowding and the hereditability of spacing behavior did not stand the test of field data, other ideas were valid. For example, Lambin & Yoccoz (1998) determined that pup survival was higher in related family groups.

Predation appears to be more important in snowshoe hare cycles and snowshoe hares also differ from voles and lemmings if nothing else because they do not have spacing behavior or socially related survival. However, other forms of intrinsic mechanism are possible such as maternal effects that are the carry-over from early life (Krebs, 1996).

Environmental (climate) variability is also being advanced as a factor in population cycles and to explain their spatial synchrony (Sinclair et al., 1993; Yoccoz & Ims, 1999; Krebs et al., 2002). Population modeling is suggesting a case for stochasticity as a driving force in cycles as log-linear models mimic many of attributes of wild populations although without specifying the mechanisms (Stenseth et al., 1998). This is, in a sense, a reversion to earlier investigation which emphasized how winter and spring snow conditions modified predation levels. For example in Alaska, brown lemming Lemmus trimucronatus cycled 1949-1965 but then the populations fluctuated at low levels for 7 years partly due to unpredictable weather interacting with predation (Pitelka, 1973).

Larger herbivore population dynamics

Turning to the paper's third question which is what can we learn from the population dynamics of larger-bodied herbivores. The role of climatic variation is being increasingly acknowledged (Gaillard et al., 2000). Weather interacts with density dependence through directly and indirectly affecting forage availability and subsequently both fecundity and mortality (Saether, 1997) especially at higher herbivore densities. Grenfell et al. (1998) modeled the interaction between environmental noise and sheep Ovis aries density. The best-fit-model was non-linear with a density-dependent threshold below which population increased exponentially and noisily and above which environmental conditions determined whether numbers increased, stabilized or declined. Experimental evidence for the interaction of density-dependence and independence is, however, scarce. An exception is Portier et al. (1998) who experimentally tripled ewe density to examine interactions between density dependent and density independent factors for bighorn sheep Ovis canadensis.

Further evidence for the role of climatic variability is apparent from examining the relationships between decadal fluctuations in climatic variability and body mass and growth early in life. Climate variability occurs as repeatable patterns caused by teleconnections which are recurring and persistent, large-scale pressure and circulation anomalies on a

sub-continental scale and over oceans (Hurrell, 1995; Brown & Braaten, 1998). The Pacific North American (PNA) teleconnection influences western North America and the Arctic Oscillation/North Atlantic Oscillation (NAO) influences eastern North America, Greenland and east to Europe. Characteristically, those teleconnections oscillate over decades switching from one mode to another.

In eastern North America, western Greenland and Europe, the North Atlantic Oscillation is the dominating feature as variation between Atlantic high and low pressure centers flips between two states. The positive NAO index is when Iceland low is enhanced which strengthens flow of northerly colder and drier airflow toward western Greenland reducing precipitation. When NAO is negative, more snow falls (NOA explains 59% of the annual variation in snowfall). The snow accumulation for 350 years has been indexed from ice cores which reveal that there are also trends imposed on the decadal oscillations. Since 1980, the index has tended to be positive and more variable but in the 1960s, it was frequently negative (Appenzeller et al., 1998).

The signals of the climatic oscillations are far-reaching: for example, their signature is detectable in plant growth (Post & Stenseth, 1999; Aanes et al., 2002), tree-growth and the timing of freeze-up and break-up (Robertson et al., 2000). The oscillations also coincide with changes in caribou abundance. The NAO index, when positive, coincided in the early 1900s and late 1900s with peak caribou abundance in western Greenland (Post & Forchammer 2002), Baffin Island and northeast Canadian mainland (Fig. 1b). Describing the effects of the decadal trends in climate variation is complex as for example, elevation can confound generalities (Loison et al., 1999). Elevation differences are greater among the ranges of the caribou herds in Alaska which may be why the Pacific North American teleconnection does not correlate closely with fluctuations in abundance.

The relationships between climate variability, forage and body mass are characterized by non-linear and reversed relationships (Mysterud et al., 2001). Body mass subsequently influences survival, age for reproductive maturity, adult body size and lifetime reproductive success. Complexity is increased by time lags: the effects of climate variability on intrauterine growth may be compensated and if not, persist into adulthood leading to inter-cohort variation in body size and reproductive success (Post et al., 1997a). In Norwegian red deer, the effect of the North Atlantic Oscillation partially lagged at least 1 year. The effect of winter weather on fetal growth and birth mass was not fully compensated during calf's summer feeding and weather during gestation explained 13% variability in winter calf body mass (Loison et al., 1999). Subsequently, in the Norwegian red deer, the cohort differences persisted only for 2 and 3-year olds after which they were able to compensate and calve every year. In contrast, cohort effects persisted and reproduction paused in alternate years on the Island of Rum where deer abundance affects forage availability (Albon et al., 1987).

To summarize progress in population dynamics, in smaller-bodied herbivores, the interaction between forage and predation is relatively well described and there is evidence for intrinsic processes. The mechanisms for the role of environmental variation is less secure which is in contrast to larger-bodied mammalian herbivores, where the relationships are better understood. However, in the latter, relatively little has been studied about intrinsic factors or how predation interacts with foraging. In voles and snowshoe hares, it is the interaction between predation and forage rather than either alone or intrinsic factors (spacing and dispersal) also have a role. In both the smaller and larger bodied herbivores including caribou, the cycles or fluctuating abundance are spatially synchronized on a regional to sub-continental scale that suggests a pervasive factor and the most likely is climatic variation (the geographic scale and genetic distinctness of herds (K. Zittlau, unpubl. data) argues against dispersal as the main process for temporal and spatial synchrony in caribou fluctuations). The climatic variation is patterned into decadal trends and the ecological consequences of those decadal trends is beginning to be understood in large–bodied herbivore population dynamics.

Conceptual model for caribou fluctuations

We can propose a conceptual model for how caribou abundance responds to decadal patterns of climatic variation. Simple relationships between caribou abundance and weather are only likely during particularly severe events (shocks) and on the edge of the range. Elsewhere, relationships will be complex given for example, the functional and numerical relationship of caribou to forage plants which in their turn are dancing to the environmental variability (for example, Aanes et al., 2002).

Mechanisms for the relationship between climate and caribou abundance will operate through how variability in weather affects fecundity, mortality and dispersal. A key component is the tightly coupled relationships between forage intake, body mass, pregnancy and calf survival (Cameron, 1994; Russell et al., 1996; Griffith et al., 2002). The role of climatic variation does not preclude but adds complexity to the roles of predation and probably as well,

parasitism. For example, Post et al. (1997b) detected the signature of the North Atlantic Oscillation in predator prey relationships and Stenseth et al. (1999) correlated regional synchrony in lynx (Lynx canadensis) with regional climates including NAO.

Trends in weather likely accumulate as cohort effects on body mass (cohort memory). Within the decadal timescale and at a regional scale, when weather trends are favorable, the caribou are in the increasing phase of abundance and are resilient with abundant forage readily available (high indices of condition and fecundity; high calf and adult survival). Calves during summer will be able to compensate any reductions in intra-uterine growth caused by variations in winter weather and buffer the annual variation in weather. Predator numerical response is also lagging.

Near peak abundance, fecundity and juvenile survival decline as the caribou are starting to affect their forage and are consequently less resilient to environmental variation. The decadal oscillation changes to a run of less favorable years with greater forage unavailability during winter and lag effects on summer plant growth as summers are cooler and cloudy (Aanes et al., 2002). Population increase slows and halts although exactly why the system switches so abruptly at the peak is unclear. However, the shape and duration of the peak is uncertain as it depends on the frequency of population estimates. The abruptness argues against predation but more that a threshold in resilience is exceeded. Predation increases due to the predator's numerical response but also the increasing vulnerability of prey in poorer body condition and their vulnerability in winters with more snow (cf. Post et al., 1997b). Predation likely accelerates the decline and then possibly maintains the low numbers phase.

One of the few data sets available to examine for cohort variability is from the Beverly caribou herd. March fetal weights annually varied (1980-87) presumably as the cows were facing different foraging conditions (D. C. Thomas, pers. comm. 2001). The variability between years within cohorts changes with age possibly due to growth compensation or 'weeding out' of individuals. Juveniles compensating for intra-uterine conditions are trading off between growth and accumulating body fat which raises interesting speculation about fitness, as body size is a factor in social status. In small social birds, for example, Gosler (1996) determined that social status and predictability of food determined fat reserves. Rate of fattening increased when food was less predictable. Those findings and social interactions of caribou during foraging hint at intrinsic regulation mechanisms.

Because the trends in climate variation are subcontinental they could serve to entrain the noisy dynamics of the caribou abundance and impose a sub-continental spatial and temporal synchrony. The variation between herds and each 'cycle' reflects differing strengths of interactions between factors and for example, dispersal opportunities, hunting levels and alternate prey to mention three levels of detail. The idea that weather, forage and predation are interacting to affect caribou abundance has also been suggested before (Valkenburg et al., 1994; Whitten 1996) but without possible mechanisms. The suggested role for cohort memory could be how more subtle changes accumulate even when the effects of variation in weather are not enough to cause conspicuous effects such as die-offs.

Climatic variation is unpredictable between years and accentuates seasonality but over decades, climatic variation is patterned and at longer time intervals is likely entrained by solar fluctuations. For example, the NAO correlates with sunspot peaks as indicated by strong oxygen isotope lows (proxy for winter temperature from ice core records) during the sunspot highs in the 1930s to 1950s. An example of how oscillating systems may be coupled is Sinclair et al.'s (1993) phase analyses for snowshoe hares cycles. Peak hare numbers correlate with browsing marks on white spruce tree-rings and the white spruce growth correlates with the annual snow accumulation measured from ice cores which has a 10.5 year cycle and 42-46 year cycle. Snow accumulation, tree marks and hare fur records cross correlate with sunspot activity (solar variability influences climate through effects in upper atmosphere). The solar cycles do not cause the hare cycles directly but entrain the different trophic levels including tree–growth and predation.

The likely role of the decadal fluctuations in climatic variability contrasts with Caughley & Gunn's (1993) explanation that the fluctuations were simply a consequence of a randomly variable climate. Even a weak negative feedback between an herbivore and its forage can interact within a randomly variable environment and cause apparently periodic fluctuations in abundance (Caughley & Gunn 1993). The model did not include the decadal fluctuations in climatic variation which may serve to strengthen the fluctuations through the cohort effect. Although the caribou-forage likely is a non-equilibrium grazing system (sensu Behnke, 2000), over the longer-term, the climate variability may be entrained by solar cycles similar to the arguments developed by Sinclair et al. (1993) for snowshoe hares.

The paper's fourth question was where do we go now? Given the status of many herds are at high

abundance, we can focus on what happens at the peak - what halts the increase and what starts the decrease? Then, the question becomes what maintains the phase of low numbers which is when management (meaning regulation of hunting) becomes important. The answers include in measuring cohort differences and their relationship to trends in climatic variability. Monitoring fall calf body mass and survival may be adequate to track 'cohort memory' especially as juveniles likely contribute highly to annual variation in population growth (Gaillard et al., 2000). Measuring trends in climatic variation could include looking at the relationships between plant phenology and biomass data and forage intake which can then be modeled to predict effects on body mass. Consideration has to be given to describing which processes at which scale – from individual forage selection to the sub-continental scale where the coupling effects of stochastic entrainment operate. Hypotheses will have to be devised to start to determine how intrinsic factors including spacing (forage or mating opportunities) and spacing/dispersal strategies (reduce risk predation or parasites vs. forage) will interact with the extrinsic factors.

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