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Aspects of a two-pasture – herbivore model

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Abstract: Pastures for reindeer can be divided into green pastures (mainly herbs and grasses) of summer time and more or less snow-covered lichen pastures of winter. Fall and spring pastures have a composition in-between these extremes, but for model purposes bisection is sufficient. For the animals the green-pasture season is an anabolic phase with a physiological building-up of protein reserves, while winter is a catabolic phase where food-intake is reduced and the animals to a considerable extent survive on the accumulated reserves from summer. While protein reserves are stored from summer to winter, lichen pastures are stored from year to year. Grasses and herbs not being grazed are wilting by the end of the growing season, while lichens not grazed can live for many years. This corresponds with fundamental differences in both growth pattern and resilience. The implications of the different features, and their interconnections, are not easy to survey without formal modeling. The point of departure is a simple pasture-herbivore model, well known from the literature building on a set of differential equations. A new two-pasture-herbivore model is developed. The model includes as basic elements the Klein (1968) hypothesis and that a residual lichen biomass is kept ungrazed due to snow-cover protection. Further the annual cycle is divided into four stylized seasons with herd rates of winter survival, spring calving, summer physiological growth and fall slaughtering. Isoclines are derived for summer pasture, winter pasture and herbivores. Stability properties are discussed in relation to various situations of seasonal pasture balance. Empirical examples, particularly that of changes in pasture balance and vegetation cover in Western Finnmark, Norway, are discussed. The article finds that the two-pasture model provides important features of reality, such as the stability aspects of pasture balance, which cannot be displayed by a one-pasture model. It is suggested that this type of modeling can be used as a basis for further research, *e.g.* implications of climate change.

Key words: Enrichment paradox, Finnmark, lichen pastures, overgrazing, pasture balance, vegetation changes.

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Introduction

Pastures for reindeer can broadly be divided into green pastures (mainly herbs and grasses) of summer time and more or less snow-covered lichen pastures of winter. Fall and spring pastures have a composition in-between these extremes, but for model purposes bisection is sufficient. For the animals the green-pasture season is an anabolic phase with a physiological building-up of protein reserves, while winter is a catabolic phase where food-intake is reduced and the animals to a considerable extent survive on the accumulated reserves from summer. While protein reserves are stored from summer to winter, lichen pastures are stored from year to year. Grasses and herbs not being grazed are wilting by the end of the growing season, while lichens not grazed can live for many

years. This corresponds with fundamental differences in both growth pattern and resilience.

The implications of the different features, and their interconnections, are not easy to survey without formal modeling. However, it is difficult to keep formal models simple enough to handle them analytically without losing too much realism still having explanatory interest. We try to meet this challenge by a step-wise approach. First, we investigate a standard pasture herbivore model (Rosenzweig & Mac Arthur, 1963). Next we present a new two-pasture – herbivore model (Riseth, 2000). This model is built around the Klein (1968) hypothesis of winter survival and summer growth of northern ungulates. Further we bring in some empirical examples from contemporary reindeer management, focusing Western Finnmark,

Northern Norway, and finally we evaluate the achievement of the two-pasture herbivore model.

One-pasture herbivore model

Models describing pasture-herbivore relations can be expressed as either differential or difference equations. The use of differential equations assumes effectively continuous processes, whereas use of difference equations means implicit that we include growth and breeding seasons etc. As no such system is truly continuous, the use of the differential option is a simplification for convenience. Factors and parameters for a simple basic model are provided in Table 1.

Table 1. Factors and parameter in a one-pasture herbivore model.

Vegetation		Herbivores	
V	Vegetation biomass	H	Herbivore biomass
G	Vegetation growth rate	r	Herbivore growth rate
		m	Herbivore mortality rate
D	Vegetation self saturation coefficient	c	Herbivore consumption rate

The two basic assumptions of the model are: Change in vegetation biomass is vegetation growth minus herbivore consumption (eq. 1), and change in herbivore biomass is herbivore growth minus herbivore mortality² (eq. 2).

$$(1) \quad dV/dt = Vg(1-V) - c[(V/(V+D))]H$$

$$(2) \quad dH/dt = H[rV/(V+D) - m]$$

Isoclines are demarcation curves indicating constant biomass for the trophic level in question. Inserting $dV/dt = 0$ into (1) and $dH/dt=0$ into (2) produce the vegetation isocline (3), and the herbivore isocline (4), respectively:

$$(3) \quad H = g/c (1-V)(V+D)$$

$$(4) \quad V = mD/(r-m)$$

The system of the isoclines, the equations (3,4), is depicted in Fig. 1.

The *vegetation isocline*, $dV/dt=0$ in the figure (eq. 3), represents the herbivore biomass (in practice: herd size), which exactly keeps the vegetation biomass constant. The intersection of the V-axis, 1, is the vegetation maximum carrying capacity. At this point the vegetation produce no new growth and the herbivores thus would be extinct. At the

intersection of the H-axis $H=gD/c$ for $V=0$, i.e. there is a positive plant biomass growth consumed by a number of herbivores. A possible interpretation is that the growth gD is sprouting from plant roots, that means V must be interpreted as the accessible over-ground level vegetation, which would be compatible for the growth pattern of perennials. Herd sizes over the isocline represent overgrazing, while herd sizes under the isocline represent undergrazing.

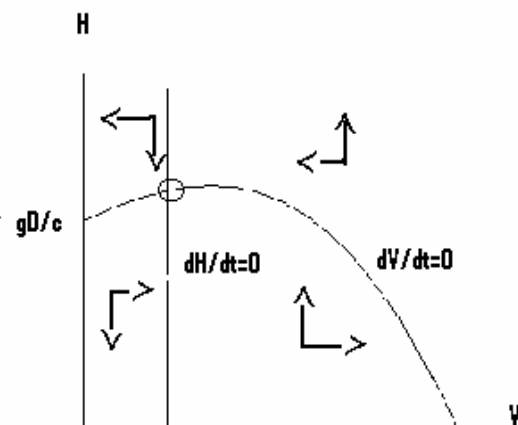


Fig. 1. The Isoclines of Vegetation and Herbivores. The arrows are vectors and indicate movement directions.

The *herbivore isocline*, $dH/dt=0$ in the figure (eq. 4), represents the vegetation biomass exactly sufficient to sustain a stable herd size. All parameters being positive numbers; V is positive when growth is greater than mortality ($r>m$). The graph of this isocline, made up of parameters all being constants, can be depicted as a vertical straight line from one value at the V-axis. Vegetation levels to the right of the herbivore isocline imply an increase in herd size, while vegetation levels to the left of the herbivore isocline lead to reduction in herd size. Depending on the magnitude of V in equation 4, the intersection between the two isoclines can be placed for any nonnegative value of V . The two isoclines create four sectors with particular movements each. The arrows represent the direction of movement for both trophic levels. The intersection of the two isoclines represents the adaptation where both plant and herbivore biomass is sustained and is marked with a circle.

The stability of our system depends of where the intersection of the isoclines is placed in relation to V_{MSY} (the maximum point of the vegetation isocline). According to Maynard Smith (1973): (1) If the $dH/dt=0$ crosses the $dV/dt=0$ curve to the left of V_{MSY} , both vegetation and herbivore will perform temporary oscillations with constant

amplitude. (2) If the equilibrium is to the right of the maximum point, the system will perform dampened oscillations, and the number of both trophic levels will stabilize over time³. Considering the growth rates, we note that increasing g will lift the vegetation isocline, but not influence V_{MSY} . Increasing the herbivore intrinsic growth rate, r , will move the herbivore isocline over to the left and be synonymous with increased instability. Increasing the mortality, m , will on the contrary have a stabilizing effect by moving the herbivore isocline to the right. That is, increasing the herbivore net growth rate, $r-m$, will have a destabilizing effect on the system.

Studying the effect of varying the magnitudes of D in the herbivore isocline, low D -values⁴ are consistent with animals being efficient grazers. These will have a less stable adaptation than *inefficient grazers* (high D -values). Increasing the value of the self-saturation coefficient D in an existing system, will both shift the H -isocline to the right and also the level of V_{MSY} to the left, thereby stabilizing the system performance (*cf.* Øye, 1996). Opposite, reducing D will shift the level of V_{MSY} to the right and thereby contribute to system destabilization. This is what Rosenzweig (1971) named *the enrichment paradox*. Obviously the paradox is that increasing accessible pasture capacity means lowered stability. Adding our knowledge about herbivore growth rates, we can sum up that for an existing system in initial balance: (1) *High accessibility of pasture through a low self-saturation coefficient D* and (2) *a high herbivore net growth rate ($r-m$)*, by themselves and in combination, have the potential of implying system destabilization.

Discussing the real world implications of instability in models for ungulates, Caughley (1971:211-215) asserts that no cycling ungulate population has ever been recorded, neither has oscillations of increasing amplitudes been reported for herbivores of any area. Including an investigation of the well-known example of reindeer population eruption and crash at St. Matthew Island (Klein, 1968) he concludes that though limit cycles and unstable equilibria are theoretically possible, they are not a feature of ungulate population dynamics (see also Gunn *et al.*, 2003). Metzgar and Boyd (1988) do not consider stability a general feature of ungulate-forage relations and expect catastrophic vegetation instability in relative simple environments where vegetation is particularly vulnerable to herbivores. They therefore find that persistence of such systems will depend on *herbivore migration*.

Two-pasture model - basic attributes

We note that the theoretical sources of instability seem to be connected to the enrichment paradox, and that in practice herbivore migration might be a stabilizing feature. We now proceed to a two-pasture-herbivore model (Riseth, 2000) in search for somewhat more realistic assumptions. Recalling our initial remarks that continuous time and differential equations can serve as a simplification, we try to combine continuous and discrete time.

The new model is thus based on two differential equations on summer and winter pastures respectively (eq. 5 and 6), as we imagine continuous time in a long-term perspective (between years). In addition, we connect them with a *herd equation* (eq. 9) modeling stylized seasons within the year. For the summer pasture, the basic equation of the one-pasture model (eq.1) is used⁵ (eq. 5). For winter pasture, the growth term is for simplicity a logistic model⁶, like the summer model. For the consumption term a residual lichen biomass, denoted R , is kept ungrazed (*cf.* Gaare & Skogland, 1980) due to snow-cover protection (eq. 6). The pasture equations of motion thus become:

$$(5) \quad dV/dt = f_{su}(V, H_{su}) = g_{su}V(1-V) - c_{su}[V/(V+D)]H_{su}$$

$$(6) \quad dL/dt = f_w(L, H_w) = g_L L(1-L) - \alpha_L (L-R)H_w$$

Inserting $dV/dt = 0$ and $dL/dt = 0$ produces the pasture isoclines:

$$(7) \quad H_{su} = g_{su}/c_{su} (1-V)(V+D)$$

$$(8) \quad H_w = (g_L/\alpha_L) L(1-L)/(L-R)$$

The winter isocline⁷ (eq. 8) is depicted in Fig. 2.

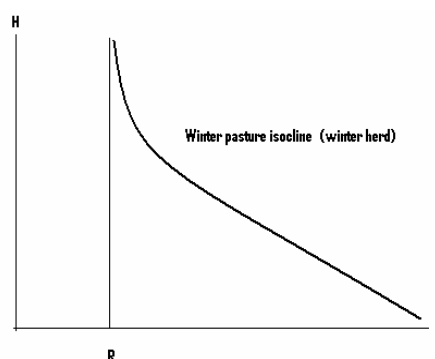


Fig. 2. Winter pasture (lichen) isocline. R = residual (not grazed) lichen biomass.

With lowered lichen biomass L the herd size just grazing the new vegetation is increasing towards a

vertical asymptote⁸ in R. Between 0 and R herd size is negative (not shown), *i.e.* no grazing on lichen.

We now proceed to the discrete time modeling of herd changes within each year. The annual cycle is divided into four stylized seasons with herd rates of winter survival, spring calving, summer physiological growth and fall slaughtering, *cf.* Fig. 3.

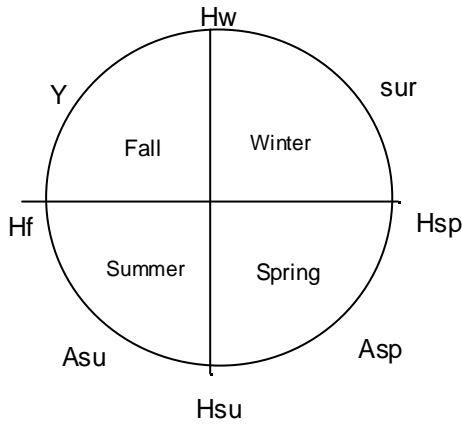


Fig. 3. An annual cycle of herd dynamics. Inspired by Virtala (1992:236).

Two of these seasons, spring and summer, are characterized by herd *increments*, while the two remaining, fall and winter, are characterized by herd *decrease*. For simplicity we thus assume but one event per season; for winter it is *survival*⁹ (*sur*), for spring *calving* (spring accumulation-*A_{Sp}*), for summer *growth*¹⁰ (summer accumulation- *A_{Su}*), and for fall we have *harvest* (*Y*). The three first of these are given by functional relationships being dependent on the relevant pasture biomass (*L* or *V*), while the last one, harvest is a *control variable*, *i.e.* an outcome of human decision. Here we introduce the policy of *long-term steady state winter herd* ($dH_w/dt=0$) and make the overall decision *every year to harvest the natural herd*

increment, defining the output $Y = H_F - H_w$. We now inquire the implications of this policy. Following the circle in Fig. 3 we further define the connections between the seasons:

$$\begin{aligned} \text{Spring herd:} & H_{Sp} = H_w \text{sur} \\ \text{Summer herd:} & H_{Su} = H_{Sp} A_{Sp} = H_w \text{sur} A_{Sp} \\ \text{Fall herd:} & H_F = H_{Su} A_{Su} = H_w \text{sur} A_{Sp} A_{Su} \end{aligned}$$

Combining these definitions by the definition of output $Y = H_F - H_w$, and inserting, we receive the expression:

$$(9a) Y = H_w (\text{sur} A_{Sp} A_{Su} - 1)$$

As this is the condition for $dH_w/dt=0$, it is also the herd-isocline, and thus the third basic equation of our two-pasture-herbivore model. The events, parameters, connections and functional relations for each of the seasons are specified in Table 2.

Winter survival is considered dependent of a mortality rate and increasing with increase in lichen biomass, fastest with small amounts towards an asymptotic level. The biologic rationale is that the effects of increased pasture access are limited when the pasture abundance is relatively high. Calving success (spring accumulation) is governed by a polynomial of degree 3, increasing slowly with low lichen biomass magnitudes, faster for medium ones, and again slower for high ones. The rationale is based on that physiological and nutritional status of the female animals is the most important factor for calving success (Lenvik, 1989). We sum up the functional relationships to winter pasture and the connections between seasonal herd, as functions of lichen biomass, in Fig. 4. The winter herd-isocline (eq. 8) is used as a basis. Winter herd is thus the herd in balance with growth on lichen pasture, spring herd the outcome of winter survival, while summer herd is the outcome of calving and the herd moving into summer pasture. The summer-winter herd connection is given in equation 9b.

Table 2. The events of the herd year connected and specified. All parameters are nonnegative <1.

SEASON	HERD	Event	PARAMETER	CONNECTIONS AND FUNCTIONAL RELATIONS
Winter	Winter herd (H_w)	Survival rate (<i>sur</i>)	Mortality rate (<i>m</i>)	$H_{Sp} = H_w(1 - m/L)$
Spring	Spring herd (H_{Sp})	Spring accumulation (A_{Sp})	Natality rate (<i>n</i>)	$H_{Su} = H_{Sp}(1+n)(\alpha L^3 + \beta L^2 + \gamma L + \delta)$
Summer	Summer herd (H_{Su})	Summer accumulation (A_{Su})	Growth rate (<i>r</i>)	$H_F = H_{Su}(1+(rV/V+D))$
Fall	Fall herd (H_F)	Harvest (<i>Y</i>)	Harvest rate (<i>x</i>)	$Y = H_w x = H_F - H_w$

$$(9b) H_{Su} = f(H_W, L) = H_W \text{sur} A_{Sp} = (1 - m/L)(1+n)(\alpha L^3 + \beta L^2 + \gamma L + \delta)$$

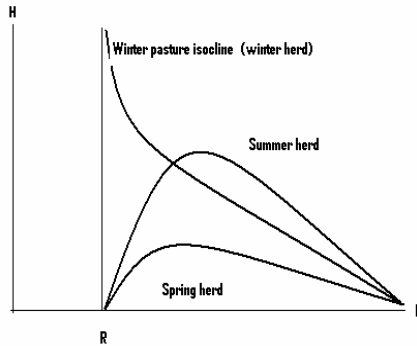


Fig. 4. Winter, spring and summer herds as functions of lichen biomass.

By inserting all the specifications of Table 2 into the herd isocline (eq. 9a), we receive the *specified herd isocline* in eq. 9 c:

$$(9c) Y = f(L, H_W, V) = H_W(\text{sur}A_{Sp}A_{Su}-1) = [(g_L/c_L)L(1-L)/(L-R)][(1-m/L)(1+n)(\alpha L^3 + \beta L^2 + \gamma L + \delta)(1+(rV/V+D))-1]$$

Herd output is basically herd size times total productivity, which is a composite factor of three rates depicted in Fig. 5.

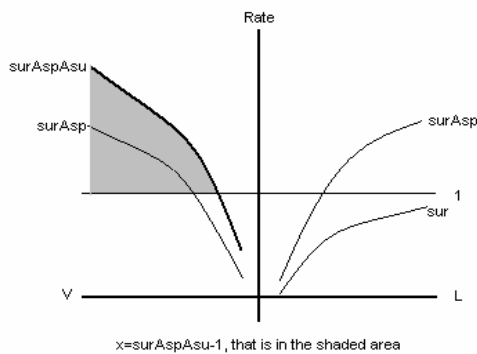


Fig. 5. Herd isocline specified as rates. RHS rates have their mirror image on LHS.

In the figure, the composite factor from survival and calving is transferred by a mirror image from

winter pasture to summer pasture where summer growth is added. The shaded area represents the *equilibrium harvest rate x*. To evaluate *how changes in winter herd size affect output* we take the total derivative of the function $Y = f[L(H_W), H_W, V(H_W)]$, cf. eq. 9, and receive:

$$(10) \quad \frac{\partial Y}{\partial H_W} = \frac{\partial Y}{\partial L} * \frac{\partial L}{\partial H_W} + \frac{\partial Y}{\partial H_W} + \frac{\partial Y}{\partial V} * \frac{\partial V}{\partial H_W}$$

Total effect= (1) Indirect effect winter pasture +(2) Direct effect+(3) Indirect effect summer pasture.

The full expression of eq. (10), as well as a more extensive discussion of the terms, is given in appendix A. The outcome of the discussion of signs, sizes and equilibria for the terms (1), (2), and (3) is given in Table 3.

Analyzing the results we note that both expressions for indirect effects (1) and (3) have maxima of their own, while the direct effect are higher, the higher are the L and V-values. Splitting up the direct effect, we note that *the two elements dependent of L have maxima for intermediate L, while the indirect effect of winter pasture have maxima for intermediate or lower L*. That is, *the effects connected to winter pastures imply a definite maximum for intermediate or lower lichen biomass*.

For summer pastures we have two detrimental effects; on the one hand summer accumulation (A_{Su}) and effect of increased summer biomass ($\partial Y/\partial V$) indicate *higher output with higher summer vegetation biomass*, while on the other hand reducing herd size below the vegetation MSY-point $V=(1-D)/2$ will reduce output.

Even though we have not reached a definite overall equilibrium by modeling, the model provides arguments for that an equilibrium L-value is a good candidate as a second best choice of an overall equilibrium. Taking into account real world facts, as the low lichen growth rate, strengthens these. We can make the following inferences about management implications:

- (1) adapt H_W to $\partial L/\partial H_W$, sur and A_{Sp} that is an *intermediate or lower value of L*.
- (2) adapt H_s to $V = (1-D)/2$.
- (3) If there is excess V biomass, this will influence output positively.

Table 3. Effects on output, Y, of changes in winter herd, Hw (cf. Appendix A).

Terms	Elements	Sign and size	Term equilibria
Indirect effect winter pasture	$\frac{\partial Y}{\partial L}$ (1a)	Negative for high L. Around zero for intermediate L-values. Positive for small L-values.	Negative for high L Positive for low L Possible zero-values for intermediate and lower values of L=>
$\frac{\partial Y}{\partial L} * \frac{\partial L}{\partial Hw}$ (How output is influenced by changes in lichen biomass)	$\frac{\partial L}{\partial Hw}$ (1b)	Negative for high H and high L, $2L + H > 1$, including all $H > 1$ and all $L > 1/2$. Zero for combinations of L and H, $2L + H = 1$. Positive for combinations of L and H, $2L + H = 1 < 1$, both L and H > 0. <i>I.e. conditioned possible maxima for $L < 1/2$</i>	Possible maxima for intermediate and lower values of L
Direct effect	Sur (2a)	Polynomial in L. Positive and decreasing when L increases from low to intermediate.	Positive when product of sub-elements > 1 (cf. Fig. 5) =>
$\frac{\partial Y}{\partial Hw} =$ ($sur * A_{sp} * A_{su} - 1$) (How output is influenced by changes in herd size)	A_{sp} (2b)	Zero for an intermediate L-value. Negative for high L-values	Positive for relative high values of L and H
	A_{su} (2c)	Positive and increasing with increasing V towards an asymptote	
Indirect effect summer pasture	$\frac{\partial Y}{\partial V}$ (3a)	Positive and increasing with increasing V towards an asymptote	
$\frac{\partial Y}{\partial V} * \frac{\partial V}{\partial Hw}$ (How output is influenced by changes in green pasture biomass)	$\frac{\partial V}{\partial Hw}$ (3b)	Positive for $V < (1-D)/2$ Negative for $V > (1-D)/2$ => Maximum for $V = (1-D)/2$ (cf. V-isocline in Fig. 1)	Definite maximum for $V = (1-D)/2$

Two-pasture model; deviating pasture balance situations

We have now discussed the two-pasture model in a long-term steady state situation where the natural increment is harvested from year to year. In practice we know that deviations from this are common. Following the enrichment paradox logic we can ask *how the balance between the capacities of the two seasonal pastures affects stability*. In principle we can have three different balance situations. (1) We denote the situation where both season pastures and the herd size are stable as a *situation of perfect summer and winter pasture balance* and use this situation as our standard reference situation. In deviating situations either of the seasonal pastures is in minimum; we denote them situations of (2) *summer pasture limitation* and (3) *winter pasture limitation*, respectively, defined in Table 4.

The situation of perfect pasture balance is depicted in Fig. 6. Of the right-hand-side three curves the summer herd one is the crucial, representing herd size entering summer pasture. When this herd size equals the summer vegetation isocline on the left-hand-side, the pasture capacity of each season pasture fits the herd dynamic requirements exactly. That is; the summer herd on the right-hand-side $H_{Su(Y(L)Max)}$ equals the summer herd $H_{Su(Max)}$ on the left-hand-side. This is marked by the summer herd-line in the figure. *The*

adaptation is stable

Next we consider the situations where one of the seasonal pastures is in minimum and thus is a constraint upon possible herd size. That is, adaptations *outside* one of the three isoclines.

Let us first consider the situation of summer-pasture limitation, cf. Fig. 7. On the left-hand side, we note that the summer-pasture isocline is lower than the entering summer herd, *i.e.* standing crop of summer vegetation will be reduced if herd size is not lowered down to a level on the summer pasture isocline.

If overgrazing of summer pastures is chosen as a policy, this implies *instability and temporary oscillations in V and herd size* (cf. p. 66-67). This instability is not dampened by winter pasture capacity since it is higher than summer pasture capacity. Moreover, the situation of inadequate summer pasturage may, in settings where this is possible, lead to *grazing out of season* in winter pastures, which may lead to winter pasture overgrazing much faster than normal winter grazing.

Next we consider the option of winter-pasture-limitation, depicted in Fig. 8. On the left-hand-side, winter-pasture-limitation is equivalent with excess summer-pasture capacity. Observing the summer herd-line we note that it crosses the summer-pasture

isocline at two points corresponding to the vegetation biomass values, $V_{High} > V_{MSY}$ and $V_{Low} < V_{MSY}$, i.e. two possible adaptations¹¹. Here the combined effect of winter mortality and natality through spring accumulation will dampen the oscillations also for the $V_{Low} < V_{MSY}$ option meaning that *winter pasture limitation is a balanced situation*¹².

Turning our attention to output for the deviating situations Fig. 9 compares the harvest rates of winter-pasture-limitation and summer-pasture limitation with the standard situation of perfect summer and winter pasture balance.

Using subscripts PPB for perfect (summer and winter) pasture balance, SPL for summer pasture limitation and WPL for winter pasture limitation,

the figure building on Fig. 5 demonstrating that the balance harvest rates; $x_{WPL} > x_{PPB} > x_{SPL}$ for the same value of V . For the same winter herd, H_W , all three situations, this implies that $Y_{WPL} > Y_{PPB} > Y_{SPL}$, when compared for the same value of V , i.e., the relatively higher $H_{Su(Max)}$ is, compared to $H_{Su(Y(L)Max)}$, the higher becomes V , when staying on the summer pasture isocline and thus harvest rate and output. Recalling our discussion on management implications (cf. p. 69), this is in line with WPL being the more productive adaptation. Considering output as a function of winter herd size, we have depicted various functional forms for all three pasture-balance situations in Fig. 10.

Table 4. Situations of seasonal pasture capacity relations.

	Entering summer herd	Summer pasture capacity
Perfect summer and winter pasture balance	$H_{Su(Y(L)Max)} = H_{S(Max)}$	
Summer pasture limitation	$H_{Su(Y(L)Max)} > H_{S(Max)}$	
Winter pasture limitation	$H_{Su(Y(L)Max)} < H_{S(Max)}$	

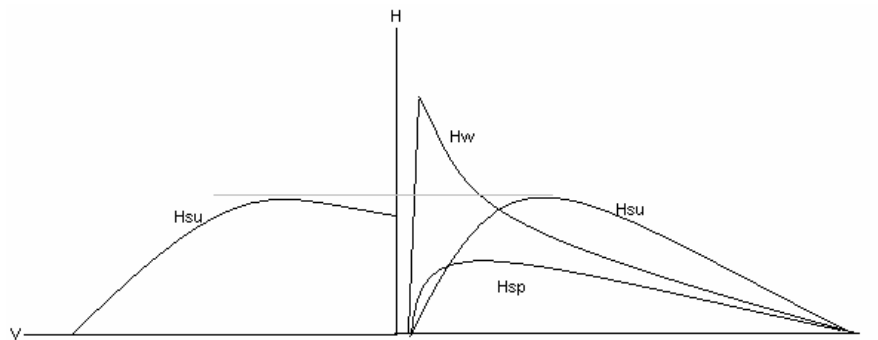


Fig. 6. The situation of perfect summer and winter pasture balance.

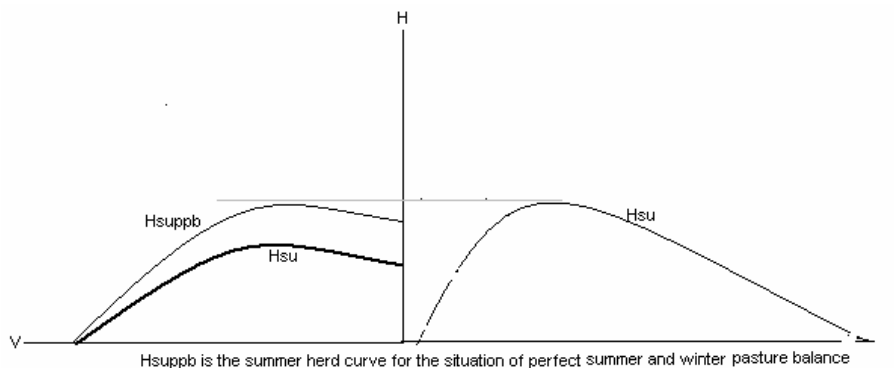


Fig. 7. The situation of summer-pasture limitation.

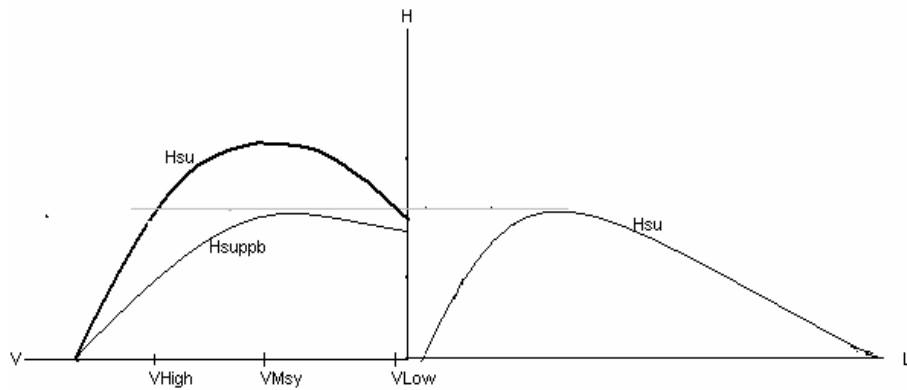
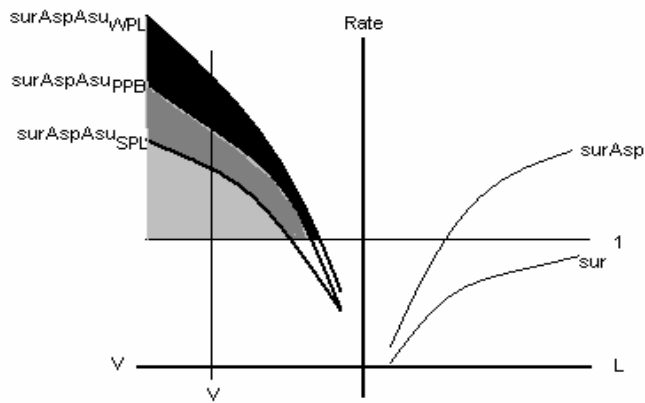


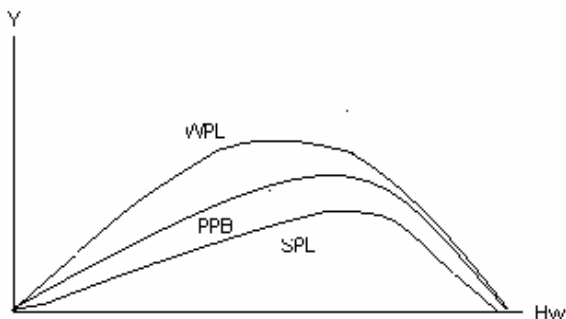
Fig. 8. The situation of winter-pasture limitation.



$surAspAsu_{wPL}$ is total growth rate for the situation of winter pasture limitation
 $surAspAsu_{ppB}$ is total growth rate for the situation of perfect pasture balance
 $surAspAsu_{sPL}$ is total growth rate for the situation of summer pasture limitation

The harvest rates for any optional value of summer vegetation biomass V are $x=surAspAsu-1$; which is the fraction of the vertical line from V passing through the light grey area for summer pasture limitation, the light grey plus the dark grey area for perfect pasture balance and both these areas and the black area for winter pasture limitation

Fig. 9. Harvest rates, x , as functions of summer pasture capacity, V , for the situations of perfect (summer and winter) pasture balance (PPB), summer pasture limitation (SPL), and winter pasture limitation (WPL), when winter herd is given.



WPL is winter pasture limitation, PPB is perfect pasture balance, SPL is summer pasture limitation

Fig. 10. Output as a function of winter herd for various pasture-balance situations.

For the situation of winter pasture limitation *the output is consistently higher than the output for the standard situation* (perfect summer and winter pasture balance). A WPL pasture area also has its output maximum at a lower herd size than the standard situation. The stronger is the winter pasture limitation, the clearer are these features. Thus a winter pasture limited area can support a *smaller* herd than the standard situation, but *each animal will be more productive*. The situation of summer-pasture limitation will, on the contrary, tend to have a lower output than the standard situation for all herd sizes. The maximum output is also found for a relatively higher herd size than the standard situation. Thus a SPL area can support a *large herd, but with low productivity per animal*.

Above we found that the situation of summer pasture limitation could promote grazing out of season and lichen pasture overgrazing to depletion. Whether this is feasible, depends on factors including landscape structure. As *landscapes without natural borders* require the most intensive herding, the tendency for grazing out of season will also be higher in such landscapes than *landscapes with natural borders*. Imagine the case of a summer pasture limited area hosting a relatively large herd with low productivity. In a landscape without natural borders between summer and winter pastures adjacent pastures could be used out of season, thus removing the limitation set by the capacity of each of the seasonal pastures. The potential adaptation of *keeping a large herd on insufficient summer pasture while compensating by using winter pastures out of season* provides a possibility of increased output in the short run, but grazing lichen pastures not protected by snow-cover drops R, and may thus lead to *resource depletion and herd reduction* in the long run.

Empirical examples

Our model suggests clear connections between possible output (productivity) and pasture balance. Let us see if we can find any such connections in contemporary reindeer management.

In Norway the highest productivity of Sami reindeer management, during a couple of decades, are found in South Sami areas, particularly in the areas of South Trøndelag/Hedmark and North Trøndelag (Riseth, 2000:171), see Fig. 11. Most of these areas are clearly winter-pasture limited (*op.cit.*:185-186). In Northern Norway the highest productivity is found in Eastern Finnmark, particularly in Varanger (see Fig. 11), which also is in lack of sufficient winter pastures. Thus we have

good indications that winter-pasture limitation is stabilizing. However, the situation in the Norwegian regions Troms and Nordland show that too severe winter conditions are detrimental to productivity. These areas have most of their natural winter pastures in the Swedish inland. Due to limitations in the border crossing migration rights in the bilateral Norwegian Swedish border convention as well as encroachments and obstructions from forestry, hydro-electrical power regulations, the herders of Nordland and Troms mainly have to rely on limited coastal winter pastures and uncertain sub-oceanic areas on the Norwegian side. Thus, it seems as *if winter-pasture limitation are to promote productivity, it must be moderate, in the meaning that the winter pastures, though they are limited, must be rather certain*.

Going to the deviating balance situation of summer-pasture limitation (SPL), an important point in our modeling is that lichen pastures are protected by snow-cover in winter. When reindeer stay in lichen areas in (dry) summer period trampling destroys much more lichen than grazing.

For example, two potential problem areas are Härjedalen and northern Torne Lappmark in Sweden, both poor in precipitation¹³, with a high proportion of dry lichen-rich heather vegetation in the sub-alpine and alpine belt Oksanen (1992). One of these areas, Härjedalen, has recently encountered overgrazing problems, while the other has not. The reason is clear, since the erection of a reindeer convention¹⁴ bar fence (in the 1970s), the Härjedalen Sami lost access to mountain summer pastures on the Norwegian side¹⁵. The northern Swedish Sami still has convention summer pastures areas in Troms, and the lichen pastures on Swedish side of the border are neither trampled nor grazed in summer.

An even more striking example is the inland mountains of Finnish Lapland, which has been exposed to summer grazing over decades with the outcome that lichens are eroded on the tops of the landscape, and also has marked vegetation changes on lower landscape levels. As much as this includes areas adjacent to the Norwegian border, the contrast to intact lichen carpets on the Norwegian Finnmarksvidda side of the border bar fence has been very sharp, and served as an illustrative example. However the situation at Finnmarksvidda is changing rather fast, and that will be our main example.

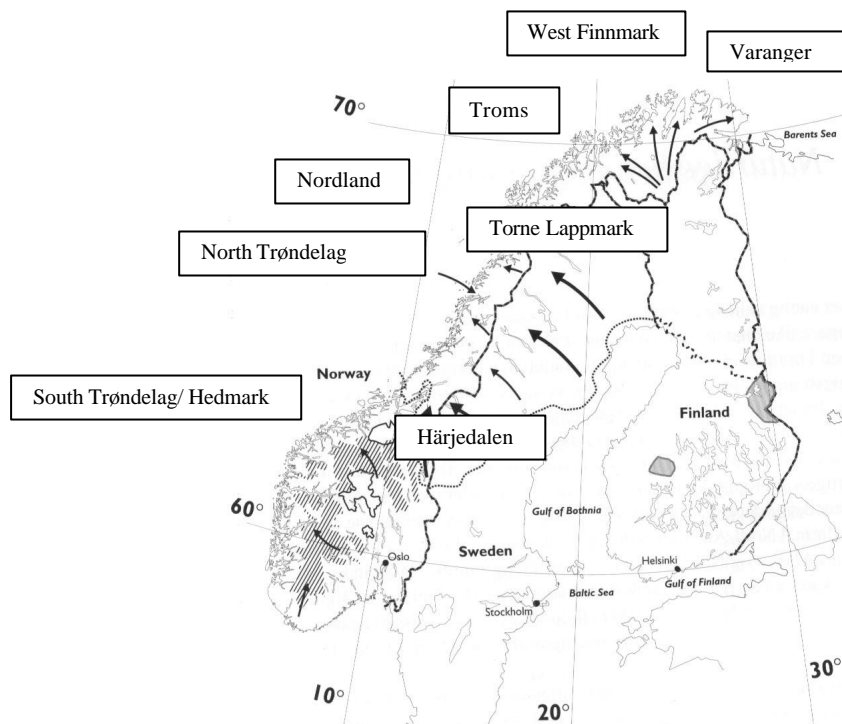


Fig. 11. Reindeer management areas of Fennoscandia. From Gaare (1997:8).

The changes of Finnmarksvidda lichen pastures are particularly interesting and well suited for study by this type of models. From the early 1970s and into the new millennium the lichen biomass at the fall and winter pastures declined dramatically. The dramatic increase in the reindeer population size during the 1980s is regarded as one of the main explanation of the problems faced today. In 1976 the reindeer population in Finnmark was estimated to 90 000 animals. In 1988 the population size had increased to 210 000. On Finnmarksvidda the vegetation types rich in lichen were reduced to half the extent compared to the situation in the beginning of the 1980s (Johansen *et al.*, 1995; Johansen & Karlsen 1998; 2000; Riseth & Vatn, 1998). Damages to the vegetation surface, visible as erosion flats or erosion ridges, are reported at several localities within the spring and fall areas (Evans 1993; Johansen *et al.*, 1996). Concerning current data on reindeer body-weights, reproduction rates, and mortality describes an even more discouraging picture of the today's herding. By comparing reindeer body-weights from early 1960s (Movinkel & Prestbakmo, 1968) with corresponding weights from the period 1998-2000 (RA-1998, 1999, 2000), a significant decrease is observed. In addition to the low body-weights, a

high rate of mortality and low calving success are reported for several districts (RA-1998, 1999, 2000). The overall situation in Finnmark reindeer pastoralism presents as an archetypal example of the «tragedy of the commons» (Sara 1993; Riseth 2000; Riseth 2001). Much of a similar situation is reported both in Finland (Helle & Kojola 1993; Käyhkö & Pellikka 1994; Kumpula *et al.*, 2000) and Sweden (Bergstedt *et al.*, 1999).

We will here focus the region West Finnmark where the overgrazing is connected to an extraordinarily increase in herd size; reindeer numbers more than doubled from about 1975 to 1990. This was followed by a gradual decrease through the 1990s, reaching the level of the 1970s by 2000. Simultaneously seasonal pasture use was gradually changed. For a further study we need to know the physical organization of seasonal pastures, depicted in Fig. 12. Panel A shows that summer pastures¹⁶ are towards NW; on islands, peninsulas and sub-coastal inlands. The winter pastures with lichen heaths are in the SE towards the Finnish boarder, while the fall and spring pastures are in-between. Panel B details the same map zoning summer pasture districts into inner and outer based on relative position.

The spatial development pattern of overgrazing is

especially interesting. The herd increase is connected to changes in seasonal pasture use. Fig. 13 depicts a time series of satellite images of lichen biomass impact at Finnmarksvidda fall and winter pastures¹⁷. Some of the lines on the map are main roads; the road between Karasjok (East) and Kautokeino (West) indicates the border between fall and winter pastures.

We can note that an increasing grazing pressure starts in the NW, at fall pastures, and gradually spreads towards SE and into the winter pastures. Before 1980 winter pastures are not affected, in 1987 West Finnmark fall pastures are all overgrazed, and by 2000 only a minor part of the winter pastures are fully intact.

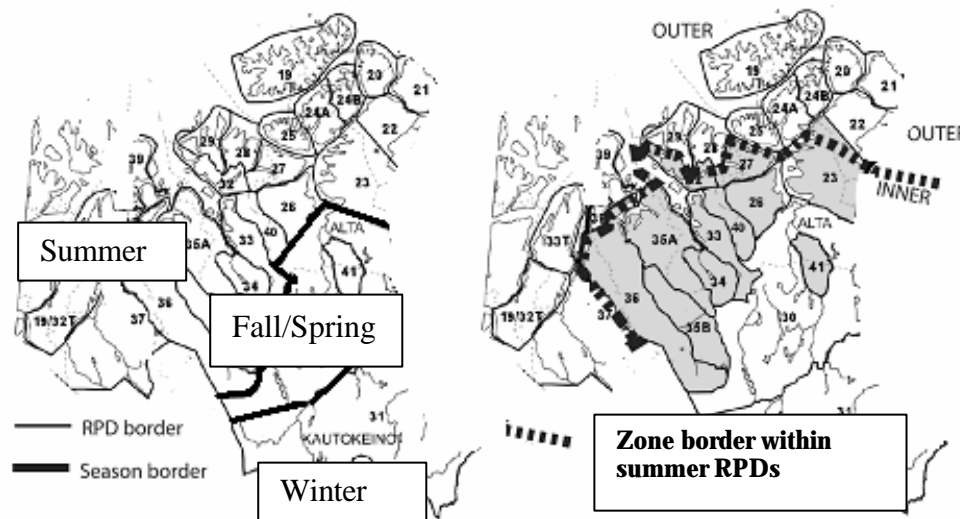


Fig. 12. Panel A. Seasonal pastures (RPDs).

Panel B. Zonation of summer RPDs (Inner vs. outer).

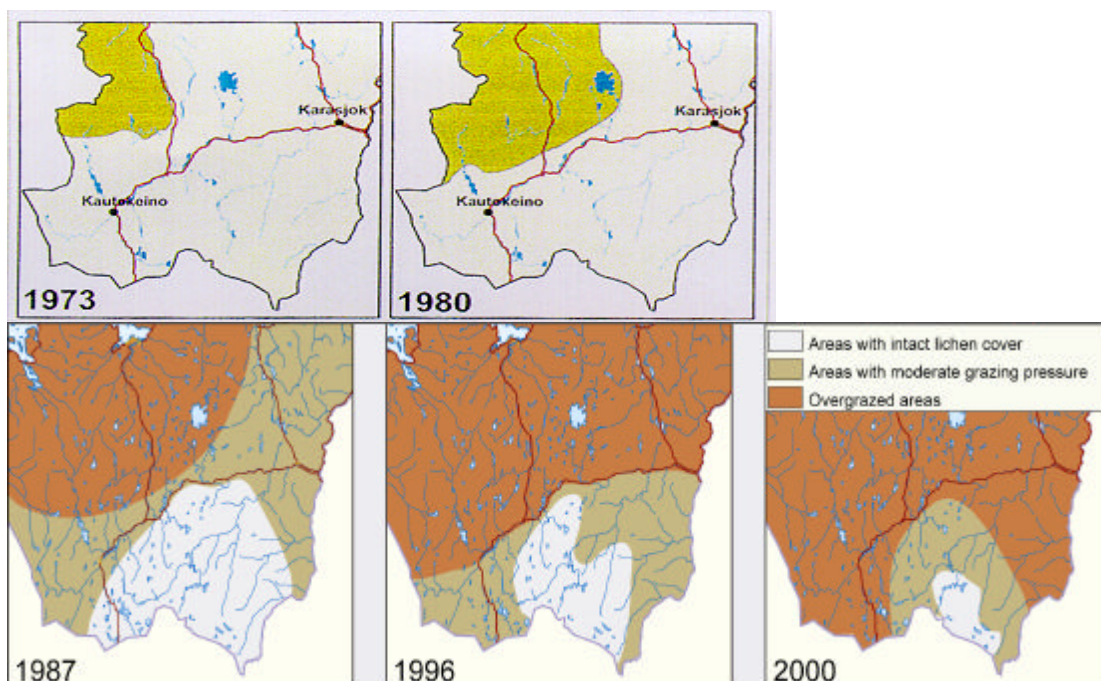


Fig. 13. Time series panel of grazing impact on lichen pastures of Finnmarksvidda 1973-2000. From Johansen, B. & S.R Karlsen (1998, 2002).

Herd size and harvest WF 1980-1995

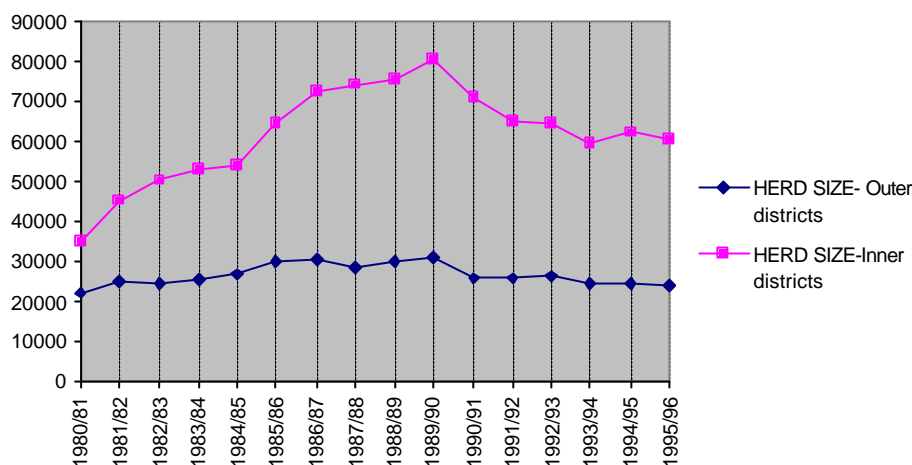


Fig. 14. Herd size development pattern for West Finnmark inner and outer districts 1980 to 1995. Own computation of statistics (Reindriftsadminstrasjonen/Reindriftsforvaltningen 1980-1998).

For the understanding of the development pattern, it is interesting to know that in the late 1960s West Finnmark as a region was evaluated as clearly summer-pasture-limited, *i.e.* with winter pastures in excess. Both registrations and accounts document that there were ample space between winter siidas up to the mid 1970s. The further development can be traced by annual administration reports. In the early 1970s some of the inner districts, *cf.* Fig. 12B, had started to graze at fall and spring during the summer. This practice expanded during the 1980s. Technological change, the introduction and spread of all-terrain vehicles (ATVs) promoted¹⁸ this by increased potential of herd control. Reports during the 1980s assert that (1) the capacity of the summer pastures are too limited, that (2) several siidas use the spring and fall pastures far more than the given pasture time, and that (3) competition is very great at spring/fall and winter. The irregular grazing in the spring/autumn pastures particularly harms siidas belonging to outer RPDs, being behind in the queue. From the early 1980s reports express that the northern part of the winter pastures is heavily exploited causing the siidas having their pasture in these parts to move out early. From 1985 the reports express that the winter pastures now are used several times during the winter (probably still so) and that the total herd size were all to great in relation to the winter pasture capacity. From 1988 one of the western and inner districts changed their pasture use pattern by a rapid fall migration through a wide area of the winter pasture of several other siidas. The reports clearly indicate that inner districts are the more

expansive, due to their strategic advantage of being nearest to the fall pastures (Riseth, 2000). This is also reflected in the herd size development patterns, *cf.* Fig. 14.

It is remarkable that the sum increase for the outer districts is less than 50% while the inner districts more than double their total number from 1980 to 1990. On average inner districts had both higher gross and net growth rates than the inner ones, *cf.* Table 5.

Table 5. Average growth rates for total populations 1980-1990.

	Gross growth rate	Harvest rate	Net growth rate
Inner RPDs	35.9	29.6	6.3
Outer RPDs	28.0	26.4	1.6
West Finnmark	33.2	28.5	4.7

Net growth rate (annual herd increment) = Gross growth rate – Harvest rate (Riseth, 2000).

These numbers and the administrative reports clearly indicate that inner district actors govern the development pattern, and that these actors pursue expanding strategies. Recalling Fig. 9 we note that the relative high growth rates for inner districts deviates from what we would expect for a SPL situation. The explanation seems to be that these districts undermine the limitation by expanding into fall and winter pasture areas belonging to others.

Paine (1994:115-130) found that these siidas (in 1962) before the technological revolution did not have the possibility to realize their full expansion potential. Our analysis is that in the 1990s they utilized the new possibilities (*cf.* Riseth 2000:124).

Data on district/siida¹⁹ level can clarify to what extent these siidas expanded at the cost of others. Comparisons of different siidas relative share of the winter pasture area reveal that some of the inner districts have expanded their relative share of the winter pasture very clearly, *cf.* Table 6.

Table 6. West Finnmark Summer RPDs. Relative share of winter pasture areas (RPD31) 1957 -1997. For location see Fig. 12, Panel B.

RPDs	Relative share of winter pasture (in percent)			Relative change
	1957	1997	Change	Percent
23	6.4	8.2	+1.8	+28
34	7.5	11.0	+3.5	+46.7
35A/35B	11.8	12.2	+0.4	+3.4
36	2.9	8.2	+5.3	+182.8
40/41	5.8	7.2	1.4	+24.1

From Riseth (2000).

The RPDs/siidas in Table 6 are the major inner districts, which to a large extent dominate the development of West Finnmark in the period. In Fig. 15 we can see that the relative change of lichen biomass is not uniform for this group. Particularly D40 and one of the siidas in D 41 have good pastures up to the year 2000, as they are located rather far SE (*cf.* Fig. 13).

Another feature of SPL adaptation in our model is low growth per animal. Slaughter weights are good indicators of that, *cf.* Table 7.

Table 7. Average slaughter weights 1997-2000. Chosen inner RPDs and WF average.

RPD#	Calves	Males >2yrs	Males 1-2yrs	Females >2yrs	Females 1-2yrs
23	14,3	36,0	23,4	27,2	19,9
33	13,4	34,8	20,8	24,6	18,5
34	15,6	35,0	22,1	25,2	19,8
35A	14,1	44,0	22,1	27,1	18,2
36	18,3		21,6	24,0	19,0
40	13,1	35,2	21,1	23,9	17,7
41	13,2	34,8	20,8	24,6	18,5
WF average	15,6	42,1	23,0	26,1	19,1

From Reindriftsforvaltningen (2002).

We note that almost all numbers in Table 7 is well below the West Finnmark average. Further the major inner districts also differ to some extent in herd size development, *cf.* Fig. 16. We note that 35A/B, 23 and 40/41 have the clearest raise and fall development in the middle of the period. We still have data only for a preliminary analysis, but both their absolute size and the fact that all three groups were included in early out-of-season grazing seem to have some explanatory power. Thus, we have clear indications that the expanding strategy has been successful only so far there were more areas to expand into. During the late 1990s the expansive inner siidas, which earlier expanded in herd size and area, now face low slaughter weights and low lichen biomass at winter pastures.

Relative change lichen covered ground on winter pastures

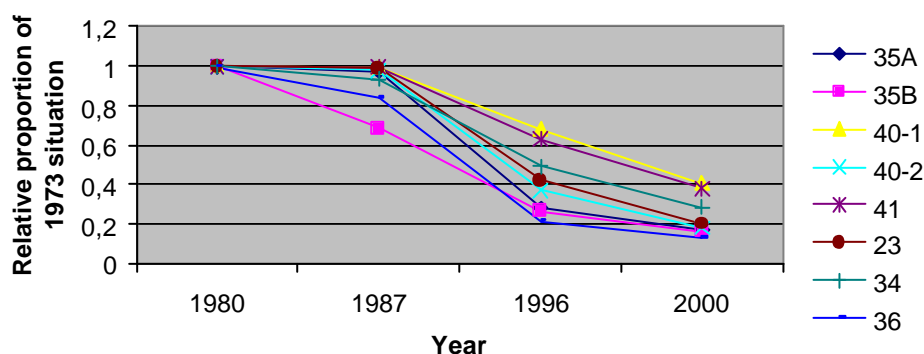


Fig. 15. Relative change in lichen covered ground on winter pastures for chosen inner RPDs/siidas. Own computations based on satellite data.

Reindeer numbers chosen inner RPDs 1980-2002

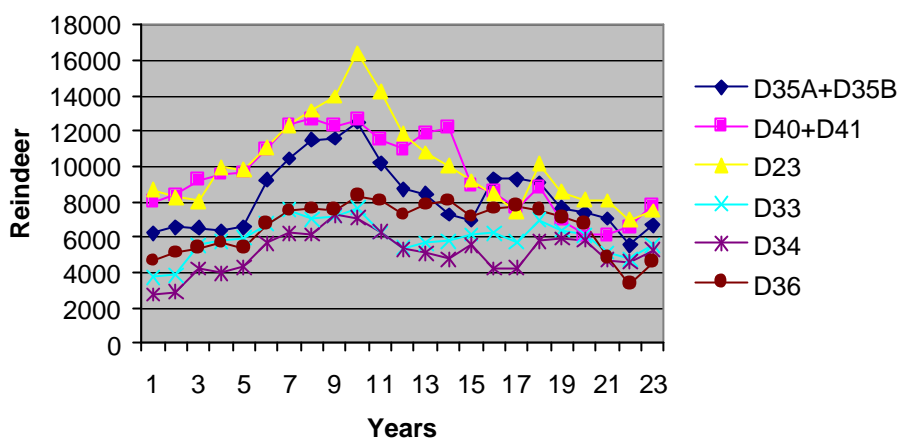


Fig. 16. Herd size development in major inner RPDs. Own computations based on Ims (2002).

Discussion

We started this contribution with discussing a standard one-pasture model, finding the enrichment paradox to be a challenge to stability in pasture-ungulate relations. Through the two-pasture model we deepened the discussion of stability finding that *pasture balance* is a major concern. In our empirical examples we have found examples suggesting both connections between winter-pasture limitation and high productivity as well as summer-pasture limitation and low productivity.

We have focused our investigation on one problem area, West Finnmark, and particularly the siidas having taking advantage of their strategic position to graze out-of-season in fall and winter pastures. We have tracked the development of expansive inner siidas using their strategic position to change their land-use. In herd size both inner siidas as a group, and three leading ones, display a typical rise and fall pattern. Our interpretation is that these siidas have expanded out of the pasture limitation both by season and original areas, but during the late 1990s they also met the limitations by eroding lichen pastures. We find that the two-pasture model has provided us with good analytic tools to understand this particular development.

The main purpose of this model is analytic, and we consider this work as start of a search for bio-economic models for reindeer management. We think that the strength of this model work is its firm basis in the *enrichment paradox* and the *Klein hypothesis*. However, the model should be refined and worked out as full and coherent mathematical model.

Continued model work should *e.g.* try to find better functional forms than the logistic model for the lichen pasture growth model.

A step into dynamic modelling is taken by, *e.g.* the work of Virtala (1992). However, we think static models could achieve much still. New challenges as climate change could also be an area for bio-economic modelling. Moxnes *et al.* (2003) also have provided important simulation work of reindeer pasture adaptation. Even though simulation is interesting, we think analytic models still have a role to play, by providing increased understanding of how different factors co-work. The empirical implementation on West Finnmark problems shows that the model can be used to catch main features of the development during the latest decades.

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Footnotes

¹In standard models K =vegetation carrying capacity is a factor. To simplify K is omitted in equation 1, assuming that $K=1$.

²Here m is considered to be constant; a more realistic model would consider mortality dependent on pasture biomass.

³The stability pattern is connected to the marginal growth rates of both vegetation and herbivores. Generally low marginal growth rates are stabilizing, and the change to dampened oscillations when the isocline intersection is to the right of V_{MSY} may be an outcome of that the marginal pasture growth rate is negative (Øye, 1996).

⁴We should note that in model where we defined $D=0$ as a possible value this would be compatible with a situation where all plant parts, roots included, were removed. Thus there would be no renewal of vegetation and the herbivores would extinct. This is possible to imagine for efficient grazers as e.g. goats.

⁵Except for the use of subscripts su for summer.

⁶With $K=1/2$ though a more realistic model would have been $K=1/3$ (cf. Andreyev (1977), Kärenlampi (1973), Helle *et al.* (1990).

⁷Inspecting equation (8), we find that H_W is undefined for $L=R$ and zero for $L=0$ and $L=1$. H_W is negative for $0<L<R$ and positive for $R<L<1$. We interpret negative herd size as no grazing on lichen.

⁸Negative part of a hyperbolic function with a vertical

asymptote in R .

⁹We thus assume that all natural mortality takes place in winter.

¹⁰The physiological growth of each animal.

¹¹Recalling the stability properties of the one-pasture model; the option $V_{High}>V_{MSY}$ in that model imply dampened oscillations and stability, while $V_{Low}<V_{MSY}$ imply temporary oscillations and instability.

¹²Independent of whether the actual adaptation is to the right or to the left of V_{MSY} .

¹³The southern area poor in precipitation is situated in an extensive rain shadow created by the South Norwegian high mountains. The northern area poor in precipitation represents both a rain shadow and a transition area from the West European climate rich in precipitation to the Arctic climate poor in precipitation (Oksanen, 1992:7), my translation JÅR.

¹⁴The Norwegian-Swedish reindeer pasture convention of 1972.

¹⁵Storvigelen, Vigelfjella, Skardølsfjella, Sylene (Oksanen, 1992:10).

¹⁶RPD=reindeer pasture district.

¹⁷Also including Karasjok areas East of Kautokeino areas.

¹⁸Inner districts had so far been stuck with very intensive herding through summer (Paine, 1994).

¹⁹District and siida is partly used interchangeably as data is partly on either level.

Appendix A

$$(10) \frac{\partial Y}{\partial Hw} = \frac{\partial Y}{\partial L} * \frac{\partial L}{\partial Hw} + \frac{\partial Y}{\partial Hw} + \frac{\partial Y}{\partial V} * \frac{\partial V}{\partial Hw}$$

(1a) (1b) (2) (3a) (3b)

where:

$$(10-1a) \frac{\partial Y}{\partial L} = H_w * \frac{d(\text{sur}^* A_{sp} * A_{su} - 1)}{dL} + \frac{dH_w}{dL} * (\text{sur}^* A_{sp} * A_{su} - 1)$$

$$= (g_L / \alpha) [L(1-L) / (L-R)] [(1+n)(1+rV) / (V+D)] \{ d[(L-m) (\alpha L^3 + \beta L^2 + \gamma L + \delta) / L] / dL \}$$

$$+ (g_L / \alpha) \{ [-L^2 + 2RL - R] / (L-R)^2 \} \{ [(L-m) / L] (1+n) (\alpha L^3 + \beta L^2 + \gamma L + \delta) [1+rV / (V+D)] - 1 \}$$

$$= [g_L / \alpha (L-R)] \{ [(1+n)(1+rV) / (V+D)] [3\alpha L^4 - 2m\alpha L^3 + (\gamma - m\beta) L^2 + m\beta] [L(1-L)] \}$$

$$+ \{ [-L^2 + 2RL - R] / (L-R) \} \{ [(L-m) / L] (1+n) (\alpha L^3 + \beta L^2 + \gamma L + \delta) [1+rV / (V+D)] - 1 \}$$

$$(10-1b) \frac{\partial L}{\partial Hw} = (\alpha / g_L) (L-R) / (1-2L - H_w)$$

$$(10-2) \frac{\partial Y}{\partial Hw} = (1-m/L) (1+n) (\alpha L^3 + \beta L^2 + \gamma L + \delta) (1+rV / (V+D)) - 1$$

$$(10-3a) \frac{\partial Y}{\partial V} = [g_L L(1-L) / \alpha (L-R)] \{ [(L-m) / L] (1+n) (\alpha L^3 + \beta L^2 + \gamma L + \delta) r \frac{d[V / (V+D)]}{dV} \}$$

$$= \{ [g_L L(1-L) / \alpha (L-R)] \{ [(L-m) / L] (1+n) (\alpha L^3 + \beta L^2 + \gamma L + \delta) \} r D / (V+D)^2 \}$$

$$(10-3b) \frac{\partial V}{\partial Hw} = 1 / (1-2V-D)$$

Equation	V	0		(1-D)/2	1
	L	0	R		1
10-1a	$g_L / \alpha (L-R)$		+++++	+++++	+++++ 0
	$(1+n)(1+rV) / (V+D)$	+++++	+++++	+++++	+++++
	Polynomial in L		+++++	???	0 ???
	$L(1-L)$		+++++	+++++	+++++
	Term 1		+++++	???	0 ???
	$-L^2 + 2RL - R / (L-R)$		-----	-----	-----
	$\text{sur}^* A_{sp} * A_{su} - 1$		-----0	+++++	+++++
	Term 2		+++++0	-----	-----
1a (Term1+ Term 2)		+++++?? ? ? ?	?? ? ? ? ? ?	?? ? ? ? ? ?	
10-1b	$(\alpha / g_L) (L-R)$		+++++	+++++	+++++
	$1-2L - H_w$ ¹⁾		+/-+/-+/-+/-+????	-----	-----
	1b		+/-+/-+/-+/-+????	-----	-----
	Indireff. WP		+/-+/-+/-+/-+????	????? ?	+++
10-2	$(\text{sur}^* A_{sp} * A_{su} - 1)$ by L		-----0	+++++	+++++
	$(\text{sur}^* A_{sp} * A_{su} - 1)$ by V	+++++	+++++	+++++	+++++
	Direct effect		-----0	+++++	+++++
10-3a	$\text{Const}^* rD / (V+D)^2$	+++++	+++++	+++++	+++++
10-3b	$1 / (1-2V-D)$	+++++	+++++	0	-----
	Indir effect SP	+++++	+++++	0	-----

Table note

¹⁾ Sign for low values of L will depend on the relative size between L and H. Positive for combinations of low L and H -values, i.e. $2L+H < 1$. Positive for $L < 1/2$ given that H is not too large in relation to L. For $L < 1/2$, $H < 1$, $L \rightarrow 0$ when $H \rightarrow 1$. Negative if $H > 1$, $L > 1/2$ or combinations of L and H $\Rightarrow 2L+H > 1$.

