GROWTH RATE AND BODY SIZE DIFFERENCES IN *RANGIFER*, A STUDY OF CAUSES AND EFFECTS

Forskjeller i vekst og størrelse hos *Rangifer*, en studie over årsaker og virkninger.

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Abstract: The paper discusses growth rate- and body size differences in *Rangifer;* their causes and effects. Growth rates and autumn body weights vary considerably both within and between *Rangifer* subspecies. The variation measured is within limits found in animals of same genetical stock subjected to different environments. Reproductive age, pregnancy rate, calving time and mortality either are or may be functionally related to autumn body weights. The differences in growth rates and body size among *Rangifer* in different areas are caused primarily by differences in environmental factors during the summer, including stress. The quality of the winter pastures has a minor effect on the body size in areas where the summer conditions allow the animals to grow at their maximum rate. In areas where maximum growth rates for various reasons are counteracted, severely overgrazed winter pastures will contribute to reduced body size. Stress in the terms of human disturbance, insects and predators and the effect on *Rangifer* activity pattern and hence on growth rates and body size need to be more thoroughly dealt with.

***Rangifer** 3 (1): 3-15*

REIMERS, E. 1983.
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Sammendrag: Arbeidet diskuterer ärsaker til og virkninger av vekst- og størrelsesforskjeller hos *Rangifer*. Vekst og høstvekter varierer betydelig bäde innen og mellom de enkelte *Rangifer*-underartene. Variasjonene er imidlertid ikke større enn de som er beskrevet i bestander med samme genetiske utgangspunkt og utsatt for ulike miljøforhold. Alder ved kjønnsmodning, drektighetsfrekvens, kalvingstid og dødelighet er eller synes ä være relatert til høstvektene. Vekst- og størrelsesforskjeller hos rein og caribou i ulike områder skyldes i første rekke forskjeller i miljøfaktorene om sommeren, stress inkludert. Kvaliteten av vinterbeitene har liten effekt pä kroppsstørrelse i områder hvor forholdene sommerstid tillater maksimal veksthastighet. I områder hvor dette av forskjellige grunner ikke skjer, vil sterkt overbeitede vinterbeiter bidra til reduserte kroppsvekter. Stress i form av menneskelige forstyrrelser, insekter og rovdyr og effekten pä reinens/caribouens aktivitetsbudsjett og derigjennom pä vekst og kroppsvekt har krav pä større forskningsinteresse.

***Rangifer** 3 (1): 3-15*

REIMERS, E. 1983. Rangiferin kasvun ja suuruuden eroavaisuuksia. Tutkielma syistä ja vaikutuksista.

Yhteenveto: Työ käsittelee syitä ja vaikutuksia Rangiferin kasvu - ja suuruuseroavaisuuksista. Kasvu ja syyspainot vaihtelevat huomattavasti sekä yksittäisissä Rangifer - alalajeissa että lajien kesken. Vaihtelu ei ole kuitenkaan suurempi kuin se mitä on kerrottu laumoista, joilla on sama perinnöllinen lähtökohta ja jotka ovat joutuneet erilaisten ympäristötekijöiden vaikuttamiksi. Sukukypsyysikä, tiinehtyvyystaajuus, vasonta-aika ja kuolleisuus on tai näyttää olevan suhteessa syyspainoihin. Syy kasvu - ja suuruuseroavaisuuksiin poroilla ja karibulla eri seuduilla näyttää ensi sijassa olevan ympäristötekijöiden eroavaisuudet kesällä, stressi mukaanluettuna.

Talvilaitumien laadulla on pieni vaikutus ruumiin suuruuteen seuduilla, joissa olosuhteet kesäaikaan sallivat enimmäiskasvunopeuden. Seuduilla, joissa tätä ei tapahdu - eri syistä johtuen, voimakkaasti ylirasitetut talvilaitumet vaikuttavat alentuneisiin ruumiinpainoihin. Stressi, inhimillisten häiriöden muodossa, hyönteiset ja petoeläimet ja poron/karibun vaikutus toimintaan sekä siten kasvuun ja ruumiinpainoon ovat seikkoja, jotka vaativat suurempaa tutkimuskiinnostusta.

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INTRODUCTION

A pattern of cyclic growth, with the rapid growth in summer and slow growth or weight loss in winter, seems typical for free ranging caribou and reindeer, both belonging to the genus *Rangifer* (Dauphiné 1976, Skjenneberg and Slagsvold 1968, Reimers et al. 1983.) Northern cervids in general share this cyclicity, it is still evident in animals fed to appetite *(ad libitum)* and the food intake and fasting/resting metabolic rate declines in winter (Wood et al. 1962, McEwan 1968, Nordan et al. 1968, Silver et al. 1969, Wandeler and Huber 1969, Bandy et al. 1970, McEwan and Whitehead 1970, Nordan et al. 1970, Gasaway and Coady 1975, Pollock 1974, Simpson 1976 and Nilssen et al. 1982).

This pattern of growth, food intake and metabolic rate has been interpreted as an adaptation for survival of herbivores in northern areas where food also exhibits a cyclic pattern in availability and quality. Due to differences in growth rates, populations of reindeer reach different body size in different areas (Movinkel and Prestbakmo 1969, Reimers et al. 1983). This and the resulting area-specific differences in sustainable yield in terms of harvestable animals and meat, are well established in wild and domestic reindeer management. The further implications that populations enjoying large body size, also enjoy higher calf production, earlier calving time and lower mortality, than populations where animal body size is small - is suspected - but generally poorly documented. Also the causal factors behind area-differences in animal growth pattern are largely unknown and speculative.

Gaare and Skogland (1980), suggest that the body size and reproductive performance in reindeer relate to lichen biomass of the winter pastures. Klein (1968) on the other hand, has proposed that the summer range quantity and quality determine the body size and reproductive success. Finally, Reimers (1980), has suggested that the animals activity budget, particularly in summer, as determined by harassment factors (such as climate, insects, predators and humans) are the major determinant for growth and fattening in *Rangifer*.

I believe that some of the frustration in the cause and effect discussion presently going on, may simply be that the available data have not been pulled together and critically analyzed.
The following is an attempt to do that and discuss:

1. Body weights and growth rates of *Rangifer*
2. The relationship of body weight to -
   a) pregnancy rates
   b) calving time
   c) mortality
3. Causal factors behind body weights differences.

METHODS

In the references body weight were given either as total body weights or carcass weights (total body weight minus viscera, head, skin and lower legs). In this paper body weights are total body weights, and growth rates are based upon this measurement.

Total body weight was calculated from carcass weight x 1.92 (carcass weight = 52% of the total body weight). Growth rates were calculated (when not stated) from body weight differences divided by the number of days between weighing dates.

BODY WEIGHTS

Genetic factors set the limit for growth rate and ultimate body size. Environmental factors control the growth rate and size attained. Maximum body weights at the end of the growth season are quite variable (Fig. 1). Domestic reindeer from USSR, wild reindeer from North Ottadalen in southern Norway and wild and penned caribou in North America attain maximum weights. Lowest weights are found among domestic reindeer in northern Norway and wild reindeer in Hardangervidda in southern Norway.

There are reasons to believe that the body size variation at least within a region, but possibly also between regions, are dominantly influenced by the environment (Fig. 2). The environmental factors include quality and quantity of the pastures in spring, summer, autumn and winter - and factors influencing activity like predators, insects, man and climate.

Example (1) in Fig. 2: The domestic reindeer company Trio tamreinlag A/L, discontinued its activity in 1964. A major part of the animals was slaughtered in September 1964. Some animals were left behind in South Ottadalen and some (402 animals) were moved to North Ottadalen and given the status wild reindeer. Ordinary hunt was opened in 1967. In spite of originating from the same population and hence the same genetic stock, the «wild» male yearlings weighed 23 to 64% more than when weighed as domestic animals. The difference is most likely caused by environmental factors. Stocking rate was higher under herding and herding activity was most intensive during the

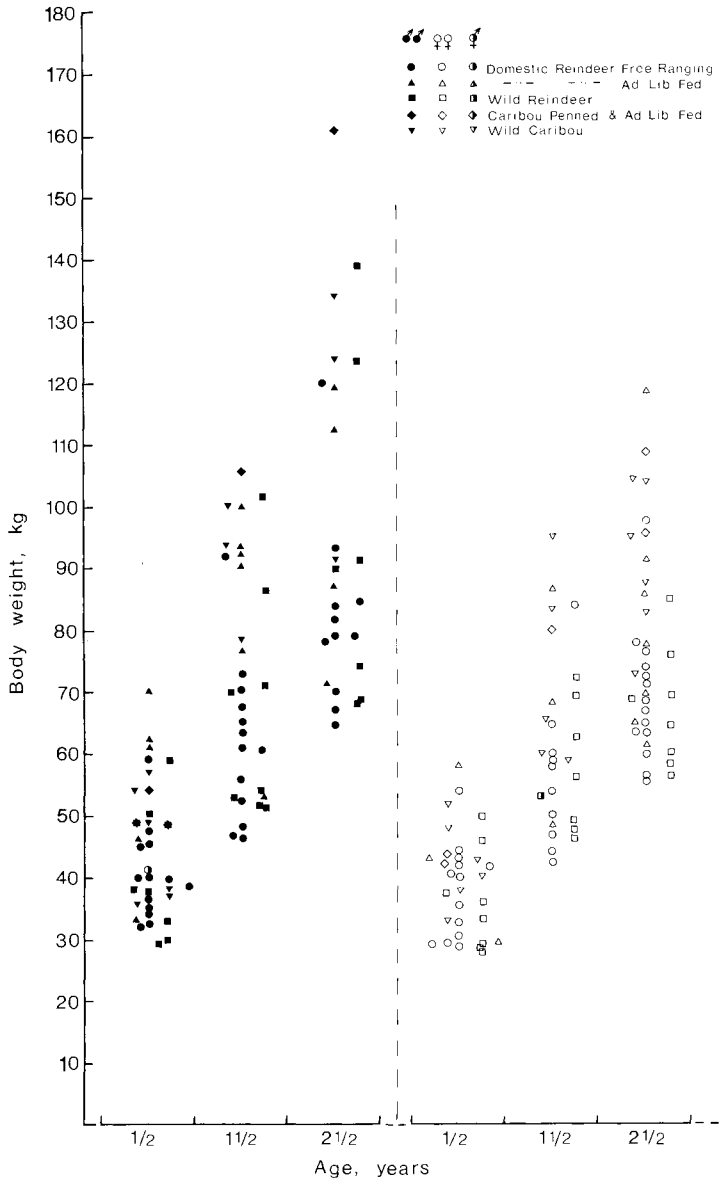

Fig. 1. Total body weights of reindeer and caribou. Data source: Bjarghov et al. (1978), Dauphiné (1976), Druri and Mitjushev (1963), Gultsjak (1954), Holthe in Lassen and Aastrup (1981), Jacobsen (pers. comm 1982), Korak (1972), Krebs and Cowan (1962), Kurkela (1976), Lassen and Aastrup (1981), Leader-Williams and Ricketts (1982), McEwan (1968), McEwan and Whitehead (1971), Movinkel and Prestbakmo (1969), Nieminen (1980), Nieminen et al. (1980), Pavall et al. (1980), Persson (1966), Podkorytov and Stremilov (1975), Reimers and Ringberg (in press), Reimers (unpubl.), Rydberg (1971), Ryg and Jacobsen (1982 a), Skjenneberg and Slagsvold (1968), Skoog (1968), Skuncke in Klein (1968), Varo (1969, 1972), Aarak (1981).

Fig. 1. Totale kroppsvekter hos rein og caribou. Datakilder:

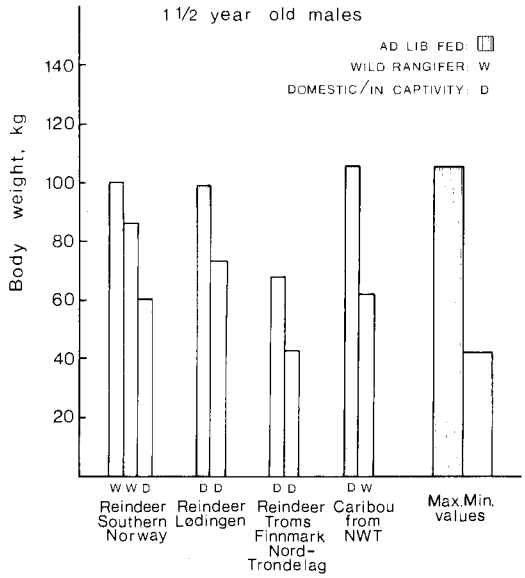

Fig. 2. Total body weights of reindeer and caribou male yearlings. Explanations to the example are given in the text. Data source: Example 1: Reimers (1972). Example 2: Skjenneberg and Slagsvold (1968), E. Jacobsen (pers comm. 1982), Ryg and Jacobsen (1982 a). Example 3: Movinkel and Prestbakmo (1969), Bjarghov et al. (1978), Pavall et al. (1980). Example 4: McEwan (1968).

Fig. 2. Totale kroppsvekter hos årsgamle bukker av rein og caribou. Forklaring til eksemplene er gitt i teksten: Datakilder:

period prior to slaughter (Reimers 1972).

Example (2) in Fig. 2 shows the effect of nutrition. Four months old males from the model herd in Lødingen (The Norwegian Domestic Reindeer Research experimental station) were fed RF-71 (Jacobsen et al. 1977) *ad libitum*. Their body weights as yearlings (16 months old) were nearly twice that of yearlings kept on natural pastures (Skjenneberg and Slagsvold 1968, Ryg and Jacobsen 1982 a, E. Jacobsen pers. comm. 1982).

Example (3) in Fig. 2 gives the maximum and the minimum average body weight of reindeer male yearlings from 23 herds in Nord-Trøndelag, Troms and Finnmark counties in northern Norway (Movinkel and Prestbakmo 1969, Bjarghov et al. 1978, Pavall et al. 1980). The body weight variations are attributable to environmental factors.

Example (4) in Fig. 2 compares body weights of free ranging wild caribou in the northwest territories in Canada and *ad libitum* fed animals from the same herd (McEwan 1968). Lower plane of nutrition and harassment from predators and insects are probably the explanation of the lower body weights of the free ranging caribou.

GROWTH RATES

There is a wide variation in growth rates among free ranging reindeer and caribou, both in summer and in winter (Fig. 3). The animals gain weight in summer in most situations, they loose weight in winter. In summer growth rate was highest in calves up to 2 months of age and lowest at an age of 3 to 5 months (Fig. 4). Considering the entire growth period from birth to 4-5 months of age, the average growth rates range from about 200 g/day

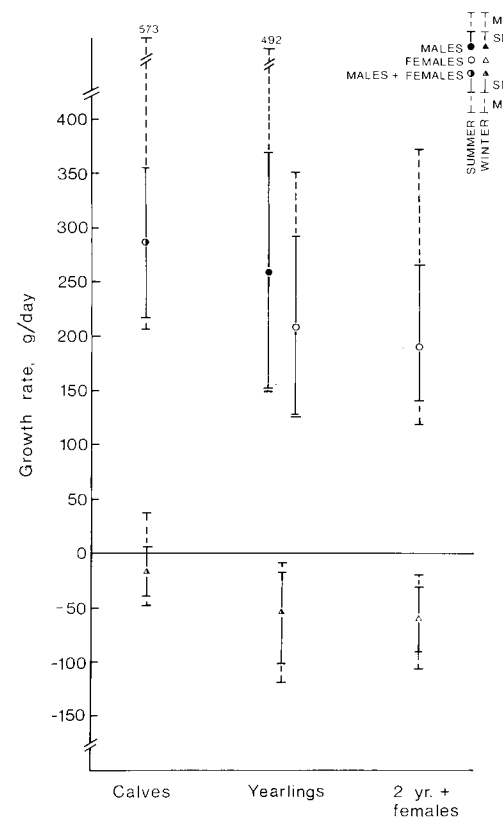

Fig. 3. Average growth rates (g/day) ± SD and maximum and minimum values among free ranging reindeer and caribou on natural pastures. Data source: See Figs. 4 and 5.

Fig. 3. Gjennomsnittlig veksthastighet (g/dag) ± SD og høyeste og laveste verdier blant fritt streifende rein og caribou på naturlig beite. Datakilder: Se Fig. 4 & 5.

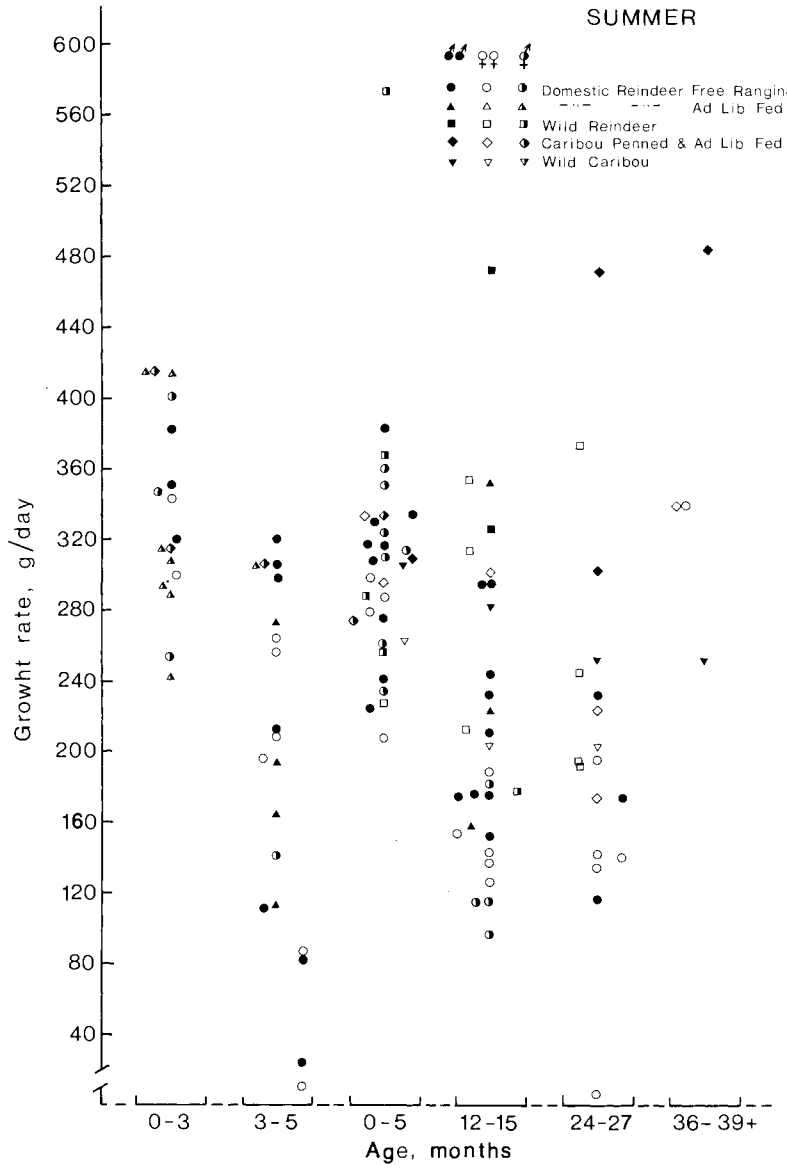

Fig. 4. Summer growth rates (g/day) among reindeer and caribou. Data source: Dauphiné (1976), Druri and Mitjushev (1963), Espmark (1980), Gultsjak (1954), Jacobsen and Skjenneberg (1975, 1981), Jacobsen et al. (1977, 1981), Jacobsen (pers comm. 1982), Krebs and Cowan (1962), Leader-Williams and Ricketts (1982), McEwan (1968), McEwan et al. (1965), McEwan and Wood (1965), McEwan and Whitehead (1969, 1971), Nergård Nyre (1976), Nieminen (1980), Podkorytov and Stremilov (1975), Preobrazhenskii (1961), Reimers et al. (1983), Reimers and Ringberg (in press), Ringberg et al. (1981), Ryg and Jacobsen (1982 a, b), Skjenneberg and Slagsvold (1968), Varo (1972), Aarak (1981).

Fig. 4. Veksthastigheten om sommeren (g/dag) hos rein og caribou. Datakilder:

in free ranging reindeer on overutilized summer pastures to 572 g/day among wild reindeer.

Summer growth rates in older animals are lower, ranging from 90 g/day in domestic reindeer yearlings in Finnmark to 470 g/day in yearling males from North Ottadalen and caribou yearling

males fed to appetite at the University of British Columbia.

In winter, wild or freely ranging domestic *Rangifer* show, with few exceptions, a negative rate of growth from 140 g/day in Svalbard adult females to 6 g/day in wild reindeer calves in Hardangervidda (Fig. 5). Reindeer calves and adult females fed lichens to appetite (protein = 3.2%) either alone or together with minerals and barley, did not do much better and suffered a weight loss of 20 to 60 g/day (Jacobsen et al. 1978, 1981). Increasing the dietary crude protein content to 13.7% Ryg and Jacobsen (1982 b) showed that reindeer calves during winter increased their body weights at a maximum rate of 266 g/day; from 46 kg to 75 kg body weight. But also older animals may increase in weight during winter when fed a diet with a high protein content (Jacobsen et al. 1981, Ryg and Jacobsen 1982 b, Rognmo et al. 1982). It may be speculated that rapid growth through winter is possible only in those situations when maximum growth the preceeding summer for various reasons has been arrested.

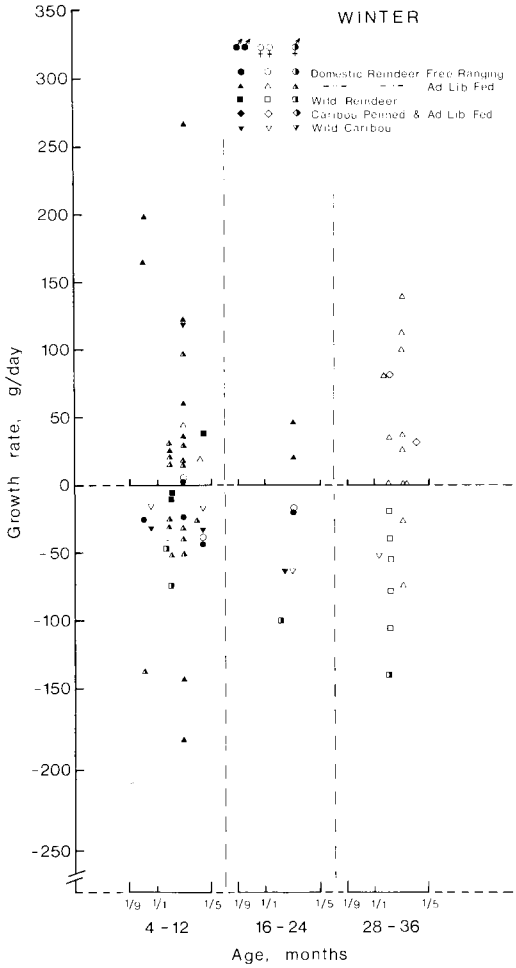

Fig. 5. Winter growth rates (g/day) among reindeer and caribou. Data source: Bøe and Jacobsen (1981), Daphiné (1976), Jacobsen and Skjenneberg (1975, 1977, 1979), Jacobsen et al. (1978, 1980, 1981), Jacobsen (pers. comm. 1982), McEwan and Whitehead (1969, 1971), Persson (1966), Reimers and Ringberg (in press), Reimers (unpubl.), Rognmo et al. (1982), Rydberg (1971), Ryg and Jacobsen (1981, 1982 a), Skjenneberg and Slagsvold (1968), Aarak (1981).

Fig. 5. Veksthastigheter om vinteren (g/dag) hos rein og caribou. Datakilder:

RELATIONSHIP BETWEEN BODY WEIGHTS AND PREGNANCY RATES, CALVING AND MORTALITY

Pregnancy rates

Skjenneberg and Slagsvold (1968) showed that the annual variation in pregnancy rates was profound. They suggested a possible relationship between pregnancy rates, body weights and environmental quality.

Recently Hamilton and Blaxter (1980) for red deer *(Cervus elaphus)*, Lenvik (1981) for domestic reindeer, Thomas (1983) for Peary caribou *(Rangifer tarandus pearyi)* and Reimers (1983) for wild reindeer, have found that reproduction in these species or sub-species is a function of weight rather than age. This means that the pregnancy status of a female may be predicted once her rutting weight is known. In wild reindeer, when a female dressed weight (W) increases from 25 to 30 kg, her probability (P) of being pregnant increases from 0.49 to 0.78 (i.e. 49 to 78%) according to the equation: $P = 1 - e^{[-0.169\,(W-21)]}$ (Reimers 1983). Therefore from knowledge of the weight distribution of females in a population, its pregnancy rate may be calculated.

It is interesting to note that in South and North Ottadalen where female calves have autumn dressed weights at 24 - 26 kg, 75% of the calves killed in winter were pregnant (Reimers 1983). Calves in Rondane, Snøhetta and Hardangervidda, which have dressed weights below 19 kg at the time of the rut, have never been found pregnant in winter or lactating the following summer.

In North and South Ottadalen adult 2 year and older females have rutting dressed weights at 38 kg or higher, and 100% of the females were pregnant. In comparision average female dressed weight in August - September for Hardangervidda, Snøhetta and Rondane ranged between 29 and 36 kg with corresponding pregnancy rates between 75 and 94%. Lenvik (1981) finds a higher pregnancy rate at lower rutting dressed weights among adult females. He also introduces the age and vigour of the breeding males as an additional (to female body weight) determinant for reproductive success among the younger (calves and yearlings) females.

Calving time

Fig. 6 shows a significant relationship between autumn dressed weights of females 2+ year old and the calving time in 8 wild reindeer areas in southern Norway. Whether the relation shown in Fig. 6 is cause and effect, remains to be shown. It may be that early rut and hence early calving is possible only if the female can energetically afford it, i.e. that she is able to enter calving with relatively intact body reserves, which she can draw upon until the green spring vegetations is available.

This imply that she is able to store this surplus energy during the preceding summer and that the winter conditions allow her to retain some of it until spring.

As the period on typical winter diet may last for 4 weeks after calving (May 6) in North Ottadalen, the females suffer a substantial weight loss, from 38 kg dressed weight in April to 28 kg in early June (Reimers et al. 1983).

However, when the calves are 4 weeks old, the milk production is rapidly decreasing (White et al. 1978) and the calf is developing into a true ruminant. Hence, both the mother and the calf are able to utilize the new nutritious green growth for tissue production from the very start of the growing season.

In Rondane and Hardangervidda the females calve later, towards the end of May. As they have access

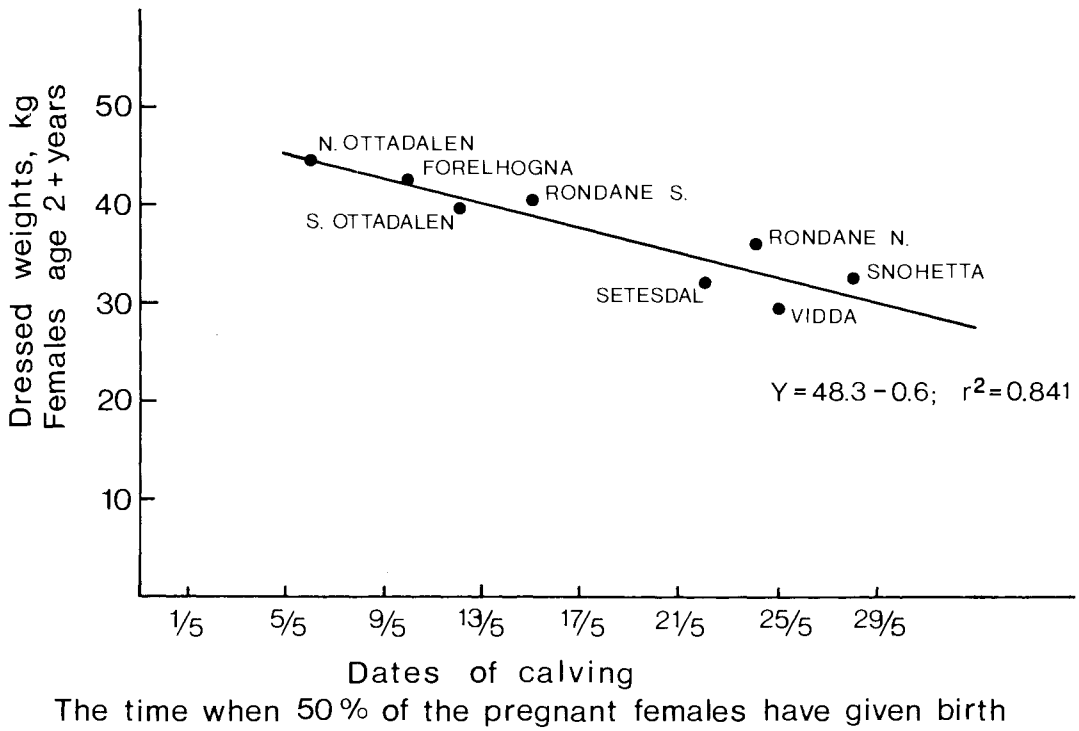

Fig. 6. Adult female dressed weights (kg) and calving dates in different wild reindeer areas in southern Norway. Calving date references are: North and South Ottadalen: Reimers 1969, Holthe 1971; Forelhogna, Setesdal, Rondane North, Hardangervidda and Snøhetta: Reimers et al. 1980; Rondane South: Reimers et al. 1982.

Fig. 6. Slaktevekter (kg) hos voksne simler samt kalvingsdata i forskjellige villreinområder i Syd-Norge. Referanser for kalvingsdta er:

to the spring vegetation after 1-2 weeks, they suffer a smaller weight drop. On the other hand, the female continues to lactate, and milk is the major food for the calf through the first part of the vegetation period. Hence, both the female and the calf get a shorter period for tissue growth on the very nutritious sprouting green vegetation.

Mortality

The mortality relevant in this context relates to the physical condition of the animals and includes before-birth (prenatal) mortality and mortality of calves up to 2 months of age (neonatal mortality). The third type, winter mortality, apply to all animals.

Prenatal mortality

This is largely unknown, but results from Dauphiné (1976) and Reimers (1983) working with caribou and wild reindeer respectively, indicate that this mortality is low, regardless of the autumn body weights or the winter grazing conditions.

Neonatal mortality

This is found to occur in situations where the pregnant females are offered restricted feed, during the latter part of the pregnancy. Jacobsen et al. (1981) and Rognmo et al. (1982) found that calves from undernourished mothers were born smaller and somewhat later than the calves in the control group fed to appetite. The mortality was higher among calves from the restricted group, partly because of their smaller size, lower milk intake due to reduced milk production and poorer mother care. Correspondingly, T. Skogland (pers. comm.) reports a greater loss of calves from calving time to midsummer in areas where female autumn body weights are low and where the winter pastures are severely overgrazed.

Winter mortality

One would expect that animals with small body weights and hence small body reserves both in terms of lean and fat tissue have a poorer chance of survival during severe winters than animals with large body weights and reserves. The high winter mortality figures reported for domestic reindeer (Rehbinder 1976) and caribou (Bergerud 1980) are caused by a mixture of factors including adverse climate, poor grazing conditions, predators, diseases, parasites, and occasional exhaustive migrations from the winter to the spring pastures. A critical analyses of the «pure» relationship between different autumn body weights and starvation mortality has so far not been carried out.

Conclusion

- Growth rates and autumn body weights vary considerably both within and between *Rangifer* subspecies.
- The variation measured is within limits found in animals of same genetical stock subjected to different environments.
- Reproductive age, pregnancy rate, calving time and mortality either are or may be functionally related to autumn body weights.

Thus it becomes not only biologically interesting but also economically important to discriminate between the environmental factors that control autumn body weights in reindeer and caribou.

CAUSAL FACTORS BEHIND BODY WEIGHT DIFFERENCES

The strategy behind the cyclic growth is a build-up of body reserves in times of plenty for use in times of need. The reasons why animals in most areas fail to reach maximum mature body weights may be:

1. The growth set back or weight drop in winter is too great to be compensated for in summer.
2. Growth rate in summer is lower than maximum due to environmental factors, including range quality and/or harassment by insects, predators and man. The effect of those factors are likely to vary in the areas.

Weight loss during winter and weight increase during summer

Body weight loss in winter seems to be the rule among freely grazing *Rangifer*. The maximum weight loss on continental ranges was 65 g/day in calves, 70 g/day in yearlings and 110 g/day in adult females (Fig. 5). Assuming that the animals enter a negative energy and nutrient balance in the period January 1 to June 1, maximum weight loss in calves, yearlings and adult females amount to 9.8, 10.5 and 16.5 kg, respectively. Even a moderate growth rate of 200 g/day in summer (see Fig. 4) results in a body weight increase of 18 kg during a 90 days summer.

Compensatory growth

Compensatory growth is well documented in domestic live-stock as reviewed by Wilson and Osbourn (1960) and Allden (1970). The conclusion from the numerous studies on temporary food

restriction is that the food restricted animals upon realimentation are able to reach similar body size and body composition as the unrestricted animals.

Compensatory growth in domestic reindeer

Three growth studies from Lødingen confirm compensatory growth in reindeer. Jacobsen et al. (1977) showed that calves on natural winter pastures lost 64-65 g/day in contrast to a gain of 87-166 g/day in calves fed to appetite on RF-71, leaving the former with lower total body weight at start of the growth season in April. Daily average body weight increase from April till September was 114-180 g/day in the low plane winter group versus 96-114 g/day in the group fed to appetite.

The highest growth rates and autumn body weights were measured in animals which spent the summer on an island in Troms and lower values in those which spent the summer in the interior of Finmark confirming the important effect of the summer-grazing situation. On the island the animals which were kept on a low plane winter diet reached higher body weights than did the animals fed RF-71 to appetite during the winter.

In another short term study Ryg and Jacobsen (1982 a) showed that male calves fed RF-71 to appetite through winter had an average growth rate of 209 g/day vs. 352 g/day among animals kept on a restricted diet through the winter; both groups being fed RF-71 to appetite through the summer.

In a third experiment Espmark (1980) fed one group of adult pregnant females a restricted diet from April 13 to May 16, while the other group was fed RF-71 to appetite. When offered RF-71 to appetite and later natural pastures until September 9, the growth rate of the restricted group was 194 g/day vs. 134 g/day in the group offered to appetite feed throughout the study.

Growth rate in wild reindeer

During summer growth rates in male yearlings and lactating females were highest in North Ottadalen, intermediate in Rondane and lowest in Hardangervidda (Table 1).

All of these rates were considerably higher than found in domestic reindeer on natural pastures. Only among lactating females on Hardangervidda, the growth rate was as low as that of domestic reindeer; and Hardangervidda reindeer hold the lowest body weights among wild reindeer in Norway. The maximum growth rate measured in domestic reindeer fed to appetite or wild reindeer in North Ottadalen is sufficient to compensate any weight loss during winter. And yet, the maximum growth rates are not met by wild reindeer in Rondane and Hardangervidda or apparently not by any domestic reindeer herd in northern Norway (Movinkel and Prestbakmo 1969). This suggests that there is something limiting during summer in all of these herds. This «something» relates to range

Table 1. Summer growth rates in wild and domestic Norwegian reindeer.
Tabell 1. Veksthastighet om sommeren hos norsk vill og tam rein.

Area	Status		Growth rates, g/day	
			Male yearlings	Lactating females 2 yr+
Område	*Status*		*Tilvekst, g/dag*	
			Bukker, 1 år.	*Melkende simler, 2 år+*
North Ottadalen[1]	Wild reindeer	Natural pastures	470	372
Rondane[1]	Wild reindeer	Natural pastures	324	244
Hardangervidda[1]	Wild reindeer	Natural pastures	242	190
Lødingen[2]	Domestic reindeer	Natural pastures	96 - 180	
Lødingen[3]	Domestic reindeer	Fed ad lib.	350	
Lødingen[4]	Domestic reindeer	Natural Pastures		134 - 194
Svalbard[5]	Wild reindeer	Natural pastures	333 - 373	293 - 456

[1] Reimers et al (1983).
[2] Jacobsen et al. (1977). (The authors have included April in the summer growth period).
[3] Ryg and Jacobsen (1982 a).
[4] Espmark (1980).
[5] Reimers and Ringberg (in press).

quality and to harassment. Among the two, quality of ranges as causal factor has received the most attention in the past, while harassment factors only recently have been emphasized.

The destructive power of harassment is described through an observation by Robert A. Dieterich on Baldwin Peninsula in Alaska (Boertje 1981): In a fenced reindeer population several reindeer starved to death and all animals were in extremely poor condition during mid July. Starvation resulted from a dramatic increase in energy expenditure and time spent on non-foraging activities which occurred primarily as a result of prior herding of the animals and high levels of insect harassment. Overgrazing was not observed. But no detailed range study was carried out.

Preliminary conclusion

Based on the previous discussion I suggest as a preliminary conclusion that body weight differences in various areas are related to differences in environmental factors in summers, and not by pasture quality or quantity in winters.

This conclusion is possibly challenged by three reindeer studies, and a red deer study (Sutti 1980). In two of the reindeer studies (Espmark 1980, Jacobsen et al. 1981) 2 groups of each 10 pregnant females were fed either a restricted diet (lichens) or an unrestricted diet (lichen and TF-69 or RF-71 concentrates) during late pregnancy. In both studies the restricted group lost body weight while the unrestricted group gained weight. When fed to appetite during summer the restricted group in Espmark's (1980) study showed compensatory growth which left them with almost the same body weight as the unrestricted group in the autumn.

Jacobsen et al. (1981) measured milk production and showed that the composition of the milk was similar in the two groups. The milk volume produced by the unrestricted group was, however, twice that of the restricted group.

In both studies the calves from the unrestricted mothers had a more rapid growth rate than those from the restricted group. Male calves have a faster growth rate than female calves and, as pointed out by Espmark (1980), the faster growth rate among calves from the unrestricted mothers may be the result of more males (7:2) in that group and more females (7:2) among the calves from the restricted mothers. Jacobsen et al. (1981) do not reveal the calf sex distribution in their study.

When kept on a restricted diet through the winter Ryg and Jacobsen (1982a) showed that male calves/yearlings, in spite of fast compensatory growth (350 g/day) the following summer, did reach lower body weights than the unrestricted controls.

Limited winter nutrition during several years

Alternating restricted and unrestricted feeding, simulating winter and summer nutritional regimes, have not been carried out for longer periods of time. Hence, the influence on body size and composition of several subsequent food restricted periods are unknown for domestic livestock as well as for wild ruminants.

Body weight development may follow two patterns when summer food is unrestricted for both groups and winter nutrition is restricted for one group (Fig. 7).

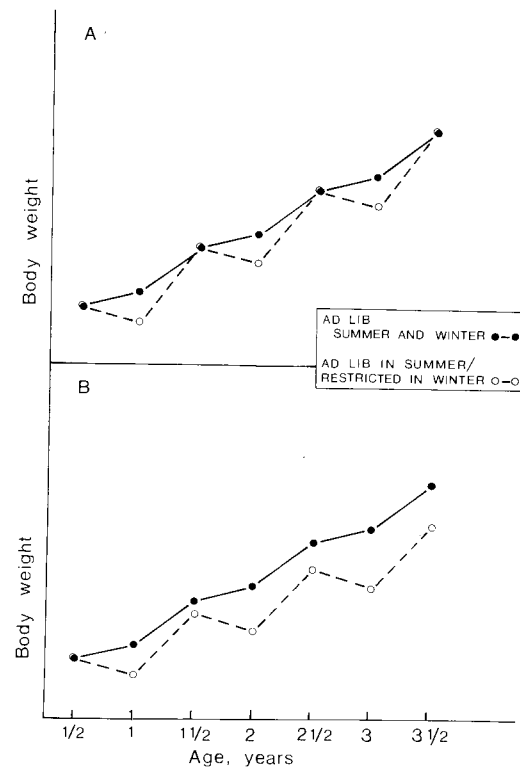

Fig. 7. Compensatory growth. Explanation in the text.
Fig. 7. Kompensatorisk vekst. Forklaring i teksten.

In example A, body weights of both groups end up similar at the end of the growth season. In example B, the restricted group is unable to completely compensate the winter growth set-back

and autumn body weight difference between the two groups increases year by year. The referred study by Ryg and Jacobsen (1982 b) and the red deer study by Sutti (1980) appear to support the B-development. Sutti (1980) provided data from the only long term study on seasonal food restriction and resulting compensatory growth in wild ruminants. In a study lasting 115 weeks he fed one group of red deer stags a pelleted barley diet to appetite while the other group was food restricted during the winters of 1978 and 1979. Both groups were freely grazing during the summers. The growth rate during the first 5 months was 333 g/day. The second and the third summer, the growth rate of the group fed to appetite was 189-194 g/day vs. 284-349 g/day in the restricted group. As a measure of skeletal growth Sutti measured hind foot length and found that the restricted males reached a length 7-8 mm shorter than among the unrestricted males. Although exhibiting compensatory growth, the restricted group was not able to catch up to the body weight or the hind foot length reached by the unrestricted group. Sutti concludes that the poor and prolonged winter nutrition prevents stags from reaching their genetic potential size.

I have three critical comments to his conclusions:

1) The growth rates calculated from Sutti's figures are surprisingly low compared to reindeer or caribou fed to appetite. This indicates that neither the *ad libitum* feed nor the natural summer pastures meet the animals growth capacity.
2) The study terminated after 115 weeks in the middle of the third summer growth period. As males continue to grow until they have passed their fourth or fifth summer, Sutti's conclusion is drawn to early.
3) A difference of 7-8 mm in the hind foot length on basis of lengths close to 400 mm, seems too small to justify the conclusion that the restricted group has a smaller skeleton frame to build upon during periods of better nutrition.

CONCLUSION

The available data indicate that the observed differences in growth rates and body size among *Rangifer* in different areas are caused primarily by differences in environmental factors during summer, including stress. The quality of the winter pastures has a minor effect on the body size in areas where the summer conditions allow the animals to grow at their maximum rate. In areas where maximum growth rates for various reasons are counteracted, severely overgrazed winter pastures will contribute to reduced body size.

A final settlement of this important biological question requires a 4-5 yr study similar to Sutti's (1980) work, in which one group of reindeer is fed to appetite throughout the study, and the other group is fed a restricted diet in winter and *ad libitum* in summer.

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REFERENCES

ALLDEN, W.G. 1970. The effect of nutritional deprivation on the subsequent productivity of sheep and cattle. - Nutr. Abs. Revs. 40: 1167-1184.

BANDY, P.J., COWAN, I. McT., WOOD, A.J. 1970. Comparative growth in four races of black-tailed deer *(Odocoileus hemionus)*. Part I. Growth in body weight. - Can. J. Zool. 48: 1401-1410.

BERGERUD, A.T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. - Proc. 2nd Int. Reindeer/Caribou Symp., Norway, 1979: 556-581.

BJARGHOV, R.S., JACOBSEN, E., MÆHLE, H., SKJENNEBERG, S., WAAGE, S. 1978. Slaktevekter fra Kautokeino reinslakteri ordnet etter sommerbeitedistrikt. - Statens reinforsøk. Forsøksrapport nr. 9. 15 pp.

BOERTJE, R.D. 1981. Nutritional ecology of the Denali caribou herd. - M. Sci. Thesis, University of Alaska. 294 pp.

BØE, U.-B., JACOBSEN, E. 1981. Fôringsforsøk med ulike typer fôr til rein. - Rangifer 1 (1): 39-43.

DAUPHINÉ, T.C. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4. Growth, reproduction and energy reserves. - Can. Wildl. Serv. Rept. Ser. No 38. 71 pp.

DRURI, I., MITJUSHEV, P. 1963. Alenevadstvo. - Izdatelstvo selskohozjaistvennoi literatury, zhurnalob i plakatob. Moskva, Leningrad. 243 pp.

ESPMARK, Y. 1980. Effects of maternal pre-partum undernutrition on early mother-calf relationship. - Proc. 2nd Int. Reindeer/Caribou Symp., Norway, 1979: 485-496.

GASAWAY, W.A., COADY, J.W. 1974. Review of energy requirements and rumen fermentation in moose and other ruminants. - Nat. Can. (Ottawa), 101; 227-262.

GULTSJAK, F.Y. 1954. Reindrift i de nordlige strøk. - Statens forlag for landbrukslitteratur, Moskva. I utdrag av russisk litteratur om tamreindrift. Oversatt fra russisk for Landbruksdepartementet 1963.

GAARE, E., SKOGLAND, T. 1980. Lichen-reindeer studied in a simple case-model. - Proc. 2nd Int. Reindeer/Caribou Symp., Norway, 1979; 47-56.

JACOBSEN, E., SKJENNEBERG, S. 1975. Some results from feeding experiments with reindeer. - Proc. First Int. Reindeer/Caribou Symp., Fairbanks, Alaska, 1972. Biol. Pap. Univ. Alaska. Spec. Rept. 1: 95-107.

JACOBSEN, E., BJARGHOV, R.S., SKJENNEBERG, S. 1977. Nutritional effects on weight gain and winter survival of reindeer calves (*Rangifer tarandus tarandus*). - Meldinger fra Norges landbrukshøgskole, 56 (8): 12 pp.

JACOBSEN, E., SKJENNEBERG, S. 1977. Fordøyelighet av lav til rein. - Forskning og forsøk i Landbruket. 28: 63-67.

JACOBSEN, E., LYSNES, H., NYMOEN, L., SKJENNEBERG, S. 1978. Energi-, protein- og mineraltilskudd til reinsdyrkalver fôret med lav. - Meldinger fra Norges landbrukshøgskole 57 (2): 22 pp.

JACOBSEN, E., SKJENNEBERG, S. 1979. Forsøk med ulike fôrblandinger til rein. - Meldinger fra Norges landbrukshøgskole 58 (34): 11 pp.

JACOBSEN, E., BJARGHOV, R.S., SKJENNEBERG, S. 1980. The ability of reindeer (*Rangifer tarandus*) calves to gain weight in the winter. - Meldinger fra Norges landbrukshøgskole 59 (32): 7 pp.

JACOBSEN, E., HOVE, K., BJARGHOV, R.S., SKJENNEBERG, S. 1981. Supplementary feeding of female reindeer on a lichen diet during the last part of pregnancy. - Acta. Agric. Scand. 31: 81-86.

JACOBSEN, E., SKJENNEBERG, S. 1981. Oppfôring av reinkalver for slakting om høsten. - Rangifer 1 (1): 44-48.

JACOBSEN, E. Pers Comm. 20. sept. 1982.

HAMILTON, W.J., BLAXTER, K.L. 1980. Reproduction in farmed red deer. 1. Hind and stag fertility. - J. Agric. Sei. 95: 261-273.

HOLTHE, V. 1975. Calving season in different populations of wild reindeer in South Norway. - Proc. First Int. Reindeer/Caribou Symp., Fairbanks, Alaska, 1972. Biol. Pap. Univ. Alaska, Spec. Rept. 1: 194-198.

HOLTHE,V. unpublished data referred in Lassen and Aastrup (1981).

KLEIN, D.R. 1968. The introduction, increase and crash of reindeer on St. Matthew Island. - J. Wildl. Manage. 32: 350-367.

KORAK, H. 1972. Renhjordens sammansättning - rennäringens viktigaste planeringsfråga. - Rennäringsnytt 6 (2): 6-11.

KREBS, C.T., COWAN, I. McT. 1962. Growth studies of reindeer fawns. - Can. J. Zool 40 (4): 863-869.

KURKELA, P. 1976. Prospects for reindeer husbandry based on grass and silage feeding. - Acta Vet. Scand. Suppl. 60: 75 pp.

LASSEN, P., AASTRUP, P. 1981. Undersøgelser over tamrenbestanden (*Rangifer tarandus tarandus* L.) ved Itivnera, Vestgrønland. - Danske vildtundersøgelser 35, Vildtbiologisk Station, 36 pp.

LEADER-WILLIAMS, N., RICKETTS, C. 1982. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. - Oikos 38: 27-39.

LENVIK, D. 1981. Momenter til diskusjon omkring individmerking av rein. - Ordförande - konferens i Aktuella rennäringsfrågor, Arvidsjaur 1981. 22 pp.

McEWAN, E.H., WOOD, A.J. 1965. Growth and development of the barren-ground caribou. 1. Hearth girth, hind foot length and body weight relationships. - Can. J. Zool. 44: 401-411.

McEWAN, E.H., WOOD, A.J., NORDAN, H.C. 1965. Body temperature of barren - ground caribou. - Can. J. Zool. 43: 683-687.

McEWAN, E.H. 1968. Growth and development of the barren-ground caribou. II. Postnatal growth rates. - Can. J. Zool. 46: 1023-1029.

McEWAN, E.H., WHITEHEAD, P.E. 1969. Changes in the blood constituents of reindeer and caribou occuring with age. - Can. J. Zool. 47: 557-562.

McEWAN, E.H., WHITEHEAD, P.E. 1970. Seasonal changes in the energy and nitrogen intake in reindeer and caribou. - Can. J. Zool. 48: 905-913.

McEWAN, E.H., WHITEHEAD, P.E. 1971. Measurements of the milk intake of reindeer and caribou calves using tritiated water. - Can. J. Zool. 49 (4): 443-447.

MOVINKEL, M., PRESTBAKMO, H. 1969. Variasjon i slaktevekter hos rein i en del sommerbeitedistrikter i Finnmark og Troms. - Meldinger fra Norges landbrukshøgskole 48 (21) 26 pp.

NORDAN, H.C., COWAN, I. McT., WOOD, A.J. 1968. Nutritional requirements and growth of black-tailed deer, *Odocoileus hemionus columbianus*, in captivity. - Symp. Zool. Soc., London, 21: 89-96.

NORDAN, H.C., COWAN, I. McT., WOOD, A.J. 1970. The feed intake and heat production of the young black-tailed deer (*Odocoileus hemionus columbianus*). - Can. J. Zool. 48: 275-282.

NIEMINEN, M. 1980. The composition of reindeer blood in respect to age, season, calving and nutrition. - Acta Universitatis Ouluensis, Series D, Medica No 54. 67 pp.

NIEMINEN, M., TIMISJÄRVI, J., LAITINEN, M. 1980. The effects of antiparasitic treatment on the condition of semi-domestic reindeer (*Rangifer tarandus*). - Rep. Kevo Subarctic Res. Stat. 16: 23-26.

NILSSEN, K.J., SUNDSFJORD, J.A., BLIX, A.S. 1982. Energetics of the high Arctic (77-81°NL) Svalbard reindeer. - Abstract Fed. Proc. 41: 1238.

NYRE NERGÅRD, B. 1976. Produksjonsegenskaper hos rein. Statistisk behandling av data fra Statens reinforsøk. - Hovedoppgave Norges landbrukshøgskole. 59 pp.

PAVALL, I.-L., SARA, E.M., JACOBSEN, E., JÅMA, P.N., KOSMO, A. 1980. Slaktevekter på rein i Nord-Trøndelag. - Statens reinforsøk og reindriftsagronomen i Nord-Trøndelag. Forsøksrapport nr. 12: 43 pp.

PERSSON, E. 1966. Renhjordens sammansättning och det praktiska avelsarbetet. - Ekonomisk renskötsel. LTs förlag, Borås, 320 pp.

PODKORYTOV, F.M. STREMILOV, P.I. 1975. (Body conformations of reindeer from the taiga uplands of the Chitinsk region). - Nauchnye Trudy. Nauchno - Issledovatel'skii. Institut Sel'skogo Khozyaistva Krainego Severa. 21: 22-28. (English Abstract).

POLLOCK, A.M. 1974. Seasonal changes in appetite and sexual condition in red deer stags maintained on a six-month photoperiod. - J. Physiol. (London), 244: 95-96.

PREOBRAZHENSKII, B.V. 1961. Management and breeding of reindeer. - In Zhigunov, P.S. (ed), Reindeer Husbandry, Moskva: 78-128.

REHBINDER, C. 1975. Kalvdödligheten i Ångså samebys renhjord. - Nord. Veterinärmedicin 27: 241-252.

REIMERS, E. 1969. Villreinens kondisjon i Snøhettafeltet og Ottadalsområdet. - Jakt- Fiske- Friluftsliv. 98 (8): 386-389.

REIMERS, E. 1972. Growth in domestic and wild reindeer in Norway. - J. Wildl. Manage. 36: 612 - 619.

REIMERS, E. 1980. Activity patterns the major determinant for growth and fattening in *Rangifer*. - Proc. 2nd Int. Reindeer/ Caribou Symp., Norway 1979. 466-474.

REIMERS, E. 1983. Reproduction in wild reindeer in Norway. - Can. J. Zool. 61: 211-217.

REIMERS, E., VILLMO, L., GAARE, E., HOLTHE, V., SKOGLAND, T. 1980. Status of *Rangifer* in Norway including Svalbard. - Proc. 2nd Int. Reindeer/Caribou Symp., Norway 1979. 774-785.

REIMERS, E., HAGELAND, J., WINTHER, E., HEITKØTTER, N., EIDE, G. 1982. Villreinen i Rondane-regionen. - Jakt- Fiske- Friluftsliv. 111: 36-39.

REIMERS, E., KLEIN, D.R., SØRUMGÅRD, R. 1983. Calving time, growth rate and body size of Norwegian reindeer on different ranges. - Arct. Alp. Res. 15 (1): 107-118.

REIMERS, E., RINGBERG, T. (in press). Seasonal changes in body weights of Svalbard reindeer from birth to maturity. - Ann. Zool. Fennici.

RINGBERG, T.M., WHITE, R.G., HOLLEMAN, D.F., LUICK, J.R. 1981. Body growth and carcass composition of lean reindeer (*Rangifer tarandus tarandus* L.) from birth to sexual maturity. - Can. J. Zool. 59: 1040-1044.

ROGNMO, A., MARKUSSEN, K.A., JACOBSEN, E., BLIX, A.S. 1982. Effects of high and low level nutrition of pregnant reindeer *(Rangifer tarandus tarandus)* on calf birth weight, growth and mortality. - Third Int. Theriological Congress, Helsinki, 1982. Abstract: 300.

RYDBERG, A. 1971. Tilväxten hos renar. - Rapport från Norrlands Lantbruksförsöksanstalt, Röbacksdalen, Umeå. Nr. 31. 4 pp.

RYG, M., JACOBSEN, E. 1981. Virkninger av ernæring på serumnivåer av thyroxin og triiodothyronin hos rein *(Rangifer tarandus tarandus)*. - Rangifer 1 (1): 4-9.

RYG, M., JACOBSEN, E. 1982 a. Seasonal changes in growth rate, feed intake, growth hormone and thyroid hormones in young male reindeer *(Rangifer tarandus tarandus)*. - Can. J. Zool. 60: 15-23.

RYG, M., JACOBSEN, E. 1982 b. Effects of castration on growth and food intake cycles in young male reindeer *(Rangifer tarandus tarandus)*. - Can. J. Zool. 60: 942-945.

SILVER, H., COLOVOS, N.F., HOLTER, J. B., HAYES, H.H. 1969. Fasting metabolism of white-tailed deer. - J. Wildl. Manage. 33: 490-498.

SIMPSON, A.M. 1976. A study of the energy metabolism and seasonal cycle of captive red deer. - Ph. D. thesis, The University of Aberdeen, Scotland.

SKJENNEBERG, S., SLAGSVOLD, L. (eds) 1968. Reindriften og dens naturgrunnlag. - Universitetsforlaget, Oslo. 332 pp.

SKOOG, R.O. 1968. Ecology of the caribou *(Rangifer tarandus grantii)* in Alaska. - Ph.D. thesis, University of California, Berkley. 699 pp.

SUTTI, J.M. 1980. Influence of nutrition on growth and sexual maturation of captive red deer stags. - Proc. 2nd Int. Reindeer/Caribou Symp., Norway, 1979: 341-349.

THOMAS, D.C. 1982. The relationship between fertility and fat reserves of Peary caribou. - Can. J. Zool. 60: 597-602.

VARO, M. 1969. Långsiktiga renavelsfrågor. - Samnordisk renforskningskonferens, Gällivare 1969. Kungl. Lantbruksstyrelsen, Meddelanden - Serie B-nr 88: 31-40.

VARO, M. 1972. Investigations of the possibilities of reindeer breeding II. - J. Sci. Agric. Soc. of Finland 44: 234-248.

WANDELER, A., HUBER, W. 1969. Gewichtswachstum und jahreszeitliche gewichtschwankungen bei Reh und Gemse. - Rev. Suisse Zool. 76: 686-696.

WHITE, R.G., THOMSON, B.R., SKOGLAND, T., PERSSON, S.J., RUSSEL, D.E., HOLLEMAN, D.F., LUICK, J.R. 1975. Ecology of caribou at Prudhoe Bay, Alaska. - Ecological Investigations of the Tundra Biome in the Prudhoe Bay Region, Alaska. Biol. Dep. Univ. Alaska, Spec. Rept. 2: 151-201.

WOOD, A.J., COWAN, I. McT., NORDAN, H.C. 1962. Periodicity of growth in ungulates as shown by deer of the genus *Odocoileus*. - Can. J. Zool. 40: 593-603.

AARAK, E., 1981. Statusrapport for Kvaløy-prosjektet - Notat til Reindriftssjefen 9/12 1981. 11 pp.