THE EFFECTS OF FOOD AND MATERNAL CONDITIONS ON FETAL GROWTH AND SIZE IN WILD REINDEER

Effekter av ernæring og simlas kondisjon på vekst og størrelse av foster hos villrein.

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Abstract: Fetal growth rates and birth weights were studied in four wild reindeer areas in Southern Norway (Hardangervidda, Hallingskarvet, Knutshø, Forelhogna), representing high and low density populations, with a 5-fold difference in mean lichen winter-food availability. Fetal growth was depressed by 42% in the high-density Hardangervidda population, and mean birth weights were 3.7 vs. 6.2 kg, with a 10 days difference in mean birth dates. Fetal size was better correlated with maternal weight, than age. Maternal weights increased until 5 yrs. of age and then decreased in the high-density Hardangervidda population (but not so in the low density Knutshø-Forelhogna populations). 55% of the offspring died before weaning in the Hardangervidda herd, but no significant calf losses were found amont the large-sized does in the food-abundant areas.

Key words: Wild reindeer, *Rangifer tarandus tarandus* L, food- limitation, growth, mortality.

Rangifer, 4 (2): 39 - 46

SKOGLAND, T. 1984. Effekter av ernæring og simlas kondisjon på vekst og størrelse av foster hos villrein.

Sammendrag: Fostervekst og fødselsvekter ble undersøkt i fire villreinomräder i Sør-Norge (Hardangervidda, Hallingskarvet, Knutshø og Forelhogna) som representerer høg- og lägtetthetsstammer, med en 5-foldig forskjell i gjennomsnittlig lavbeite-tilgang om vinteren. Fosterveksten ble nedsatt med 42% i høgtetthetsstammen pä Hardangervidda og fødselsvektene var i gjennomsnitt 3,7 kg, mot 6,2 kg i det beste omrädet, og med en 10 dagers forsinkelse i midlere fødselsdato. Fosterets størrelse var korrelert med morens vekt, som igjen var avhengig av hennes alder. Hos de minste simlene i det därligste omrädet økte vektene til 5-ärs alder, for deretter ä avta for hvert gjenlevende är. Hos simlene i det beste omrädet økte vektene til 10-ärs alder, og var da dobbelt sä tunge som fra det därligste omrädet. 55% av avkommet døde før de var avvent med diing hos Hardangervidda-simlene, mens det ikke var noen statistisk mälbar dødelighet hos kalvene i Knutshø-Forelhogna.

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SKOGLAND, T. 1984. Ravinnon vaikutus ja naarasporon kunto porosikiön kasvuun ja suuruuteen.

Yhteenveto: Etelä-Norjan neljällä peura-alueella, jotka ovat Hardangervidda, Hallingskarvet, Knutshö ja Forelhogna, tutkittiin porosikiön kasvua ja syntymäpainoja. Alueet edustavat ylintä ja alinta tiheyskantaa ja löytyy 5-kertainen eroavaisuus keskimäärin jäkälälaiduntaan talvisaikaan. Sikiön kasvu aleni 42% ylemmässä tiheyskannassa Hardangervidda-alueella ja syntymäpainot olivat keskimäärin 3,7 kg mutta 6,2 kg parhaimmalla alueella, ja 10 päivän myöhästyminen keskimääräisestä syntymäpäiväyksestä. Sikiön suuruus oli vastaavuussuhteessa emon painoon, joka oli taas riippuvainen sen iästä. Huonoimmalla alueella pieninpien naaraiden painot lisääntyivät 5-ikävuoteen asti, vähetäkseen sen jälkeen jokaista jäljelläolevaa elovuotta kohden. Parhaimmalla alueella naaraiden painot lisääntyivät 10-ikävuoteen asti, ja oli silloin kaksi kertaa niin raskaita kuin huonoimman alueen naarasporot. 55% jälkeläisistä kuoli ennenkuin ne olivat vierottuneet Hardangervidda-naarasporoista. Sitävastoin ei ollut mitään tilastollisesti mitattavissa olevaa Knutshö - Forelhogna-alueiden vasakuolevaisuudesta.

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INTRODUCTION

It has long been known that nutrition affects fetal growth in a number of ungulates, both wild and domestic (Sadleir 1969).

The pattern of fetal growth in reindeer is well known (Roine et al. 1982). The influence of nutrition as well as maternal size and age, or genetic factors on fetal growth are less well understood (Varo 1972, Cothran et al. 1983), but recent work on penned reindeer has shown the nutritional influence of experimental diets on birth weights and post-natal growth and maternal milk supply (Rognmo et al. 1983, White 1983).

Some recent evidence suggests that reproductive effort increases with age in red deer (Clutton-Brock 1984). After hinds began to breed, their body weights, condition, survival and reproductive value declined throughout the rest of their life span. Maternal weight was strongly related to age and calf weights were smallest among young and old hinds. Lenvik and Bo (1983) showed that among a sample of summer slaughtered semi-domestic reindeer, calf weights were correlated with maternal age.

Elswhere I have shown the influence of density-dependent food-limitation on post-natal growth and size in wild reindeer (Skogland 1983). The objective of this paper is to report on the effects of food limitation on fetal growth and birth weights in wild reindeer.

STUDY HERDS

All the four study areas are situated in Southern Norway within the Langfjella-Dovrefjell region. Hardangervidda is the largest with 8000 km^2 and a population of about 20 000 wintering reindeer in 1983, and a population density of 2.5 per km^2. The winter range has been overgrazed (Gaare and Skogland 1979) and the mean lichen biomass on the available «rabb» communities are about 1/5 that on the best ranges in the Forelhogna and Knutsho areas (Skogland 1983). Those two areas are situated adjacent to each other and are about 1600 km^2 each, with a population of 1800 wintering reindeer in Forelhogna and 900 in Knutshø in 1984. The population densities are 1.1 and 0.6 per km^2. All population sizes are based on aerial counts in the years of study.

In the Hallingskarvet area a mixing of wild and semi-domestic reindeer occurred during the last part of the 1970's when the area, situated adjacent to Hardangervidda, was invaded by reindeer from that herd. During the winter of 1981 the remaining semi-domestic stock was slaughtered and a sample from the culling was obtained.

All the four areas are of the typical alpine barren tundra type with fairly similar physiognomy and climate on summer and winter ranges (Skogland 1983, 1984a).

METHODS

189 reindeer were culled during the winters of 1981 in the Hallingskarvet area, 98 in 1983 in the Hardangervidda area, and 57 in 1984 in the Forelhogna and Knutsho areas. Animals were shot by same wardens in February, March and April, but in the Hallingskarvet the sample was collected in February at the slaughter-station of the previous domestic reindeer operation. All shot animal carcasses were dressed in the field and weighed. Fetuses were sexed and weighed. Shot animals were aged by tooth eruption patterns untill the age of 2 years. Older animals were aged by microscopic inspection of annuli in the incisors (Reimers and Nordby 1968).

During the calving seasons live calves were caught and weighed. By watching a parturient doe I approached her by stealth and rushed forward to pick up the calf after the calf had been dry-licked by the mother, usually about 30 min. after birth. The calf was put into a canvas bag and weighed by a spring weight. Thereafter the calf was placed back on the ground and I made a quick retreat. The whole sequence usually took less than a minute. From a distance I watched for the reunion of the mother and its calf. All calves were rejoined by their mother within 10 min. on the average (range 2 min. to 4 hours).

Pregnancy rates were obtained from the shot samples. Calf mortality was estimated by comparing the live calf per female rates obtained during field sampling after birth with the precalving pregnancy rates. Variance on the fetal or calf ratio estimates are based on a binomial sampling distribution. The mean time of births in each of the herds was determined as the date on which 50% of the births had been completed.

DIETS

Lichens constituted the largest part of the winter diet in all areas. Among Hardangervidda females lichens made up 35% of the diet, and in Forelhogna 62% (Gaare and Skogland 1975, Gaare and

Hansson 1975). As population densities doubled lichen content was halved and substituted by alternative plants such as dead grasses, mosses and litter of low quality (Skogland 1984a).

RESULTS

Fetal growth

Fetal development in the three compared herds is shown in Fig. 1. Least squares exponential growth curves were fitted until the time of observed births in each herd. Fetal growth rates did not vary in the three herds between February and April, but during the last period before birth, growth rate (based on the mean values) was depressed in the Hardangervidda herd, i.e. 0.0111 per day, compared to 0.0147-0.0152 in the Forelhogna and Knutshø herds respectively, with a difference of 26% between the resource-limited herd and the two on abundant winter forage.

There was a difference in the time of calving between the three herds. When birth weights and fetal sizes are back-dated from the birth time there is no significant difference in size of the Forelhogna

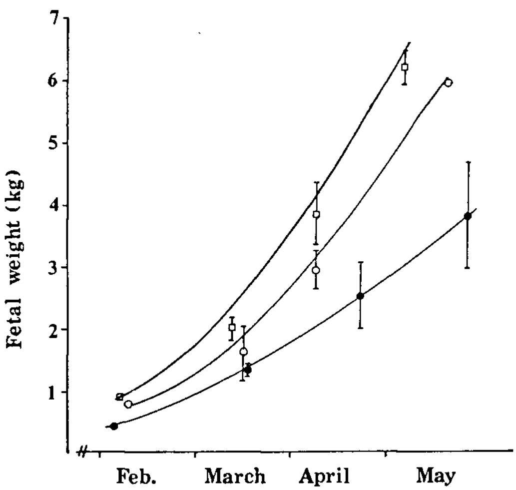

Fig. 1. Time-specific exponential growth curves from three of the study herds. The curves were fitted on the mean weights (given with SD, shown as vertical bars).
Legends: ● Hardangervidda, ○ Knutshø, □ Forelhogna.

Fig. 1. Tidsbestemte eksponentielle fostervekst-kurver i tre av stammene. Kurvene er tilpasset de midlere månedsvektene. Varians på middelvektene er vist som standard avvik i vertikale streker.
Symboler: ● Hardangervidda, ○ Knutshø, □ Forelhogna.

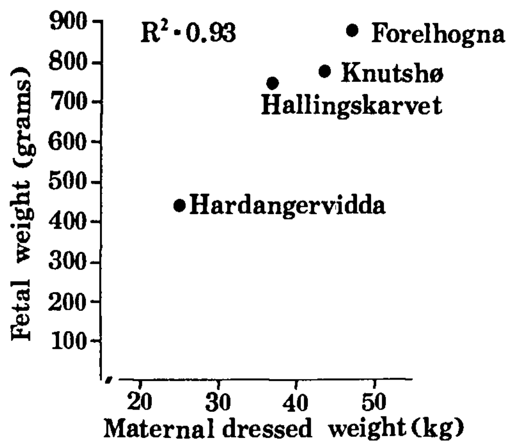

Fig. 2. Mean fetal weights in February in relation to mean maternal dressed weights.

Fig. 2. Gjennomsnittlige fostervekter i februar i forhold til gjennomsnittlige slaktevekter hos simlene.

and the Knutshø calves or fetuses ($p>0.05$). The Hardangervidda fetuses, corrected for differences in calving dates, were significantly smaller during the course of gestation ($p<0.001$). Live birth weights in the Hardangervidda herd were 40% lower than in the two other herds. In addition, the Hardangervidda calves were, on the average, born on May 27, on May 18 in Knutshø and on May 7 in Forelhogna.

The effects of maternal size

Fig. 2 shows the mean fetal size from the four herds in mid-February in relation to mean maternal size. There was a significant increase in the time-specific fetal size in relation to maternal weight ($R^2 = 0.93$, $p<0.001$). Fig 3 shows the fetal sizes of individual does from three of the herds, Hardangervidda, Knutshø and Forelhogna in April. Fetal size increases as a power function of maternal size by a factor of 0.63 which is in general agreement with data for ungulates (Robbins and Robbins 1979), and indicates that reproductive effort is relatively greater for the smallest, and in this case, most resource-limited does. The relationship is highly significant ($R^2 = 0.63, p<0.001$). Maternal weights are shown in Tab. 1. Between February and April the weights decreased 6 - 12% in Forelhogna, Knutshø and Hardangervidda. Weight decrements against time of gestation were not significantly different between the herds (ANOVA F=9.86, $p>0.05$).

The difference in weights between Forelhogna and Knutshø was not significant in any of the three periods ($p>0.05$), but the Hardangervidda does were significantly smaller at all times ($p<0.001$), on the average only 54-61% the size of those from the other two herds.

This indicates that the initial weight difference at birth is never compensated for, and in fact increased post-natally until after maturity.

The effects of maternal age

As stated in the introduction there is an intimate relationship between age and body condition, due to reproductive effort, as shown for red deer.

Fig. 4 shows that maternal weights are significantly correlated with age in all the study populations. In the most well-fed herds body size increases with age during most of the adult life-span, while with increasing food-limitation body condition begins to deteriorate after about 5 years of age, as shown for the Hardangervidda does.

Since fetal size was strongly correlated with maternal size, it is to be expected that fetal size also correlates with maternal age. Fig. 5 shows that fetal size only correlates with maternal age in those herds where body condition of does do not deteriorate with age (Forelhogna and Knutsho). This suggests, that under food-limitation, the ability to grow a large fetus will depend on body condition among middle to old-age does. The data furthermore suggest that for a given age, reproductive costs are greater under food-limitation, since neither fecundity nor survival differed significantly for the ages 3-10 years of age in any of the herds (Skogland 1984b, in press.).

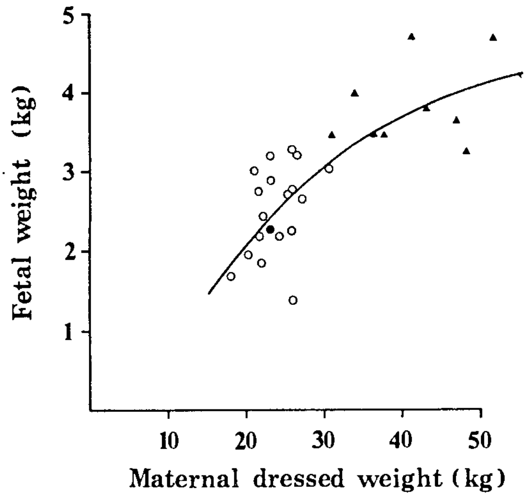

Fig. 3. The relationship between fetal weight and maternal dressed weights in April.
Legends: ○ Hardangervidda, ▲ Knutshø, ▲ Forelhogna. Closed sircle indicates more than one plot.

Fig. 3. Forholdet mellom fostervekt og simlenes slaktevekter i april.
Symboler: ○ Hardangervidda, ▲ Knutshø, ▲ Forelhogna. Lukket sirkel indikerer mer enn én prøve.

Fetal and calf mortality

Out of a culled sample of 70 does ≥1 yrs. of age from the Hardangervidda herd, 86% ± 0.03 SE were pregnant. By the time of calving a field sampling count of does with live calves showed that 50% ± 2.22 SE of the does had a calf (sample size=1911). This indicated a loss of 42% during the last part of gestation and neonatally. By mid-summer the proportion of does with a live calf had dropped to 39% ± 0.77 SE (sample

Table 1. Maternal dressed weights (kg).

Tabell 1. Gjennomsnittlige slaktevekter hos simlene (kg).

Herd	February			March			April		
Flokk	H.v.	Kn.hø	F.hogna	H.v.	Kn.hø	F.hogna	H.v.	Kn.hø	F.hogna
n	(14)	(7)	(7)	(26)	(7)	(8)	(20)	(9)	(9)
x̄	25.3	43.28	46.79	24.73	40.87	43.87	23.8	39.89	41.89
±SD	3.43	8.82	4.95	2.79	2.56	5.51	2.86	3.21	6.15

H.v.: Hardangervidda
Kn.hø: Knutshø
F.hogna: Forelhogna

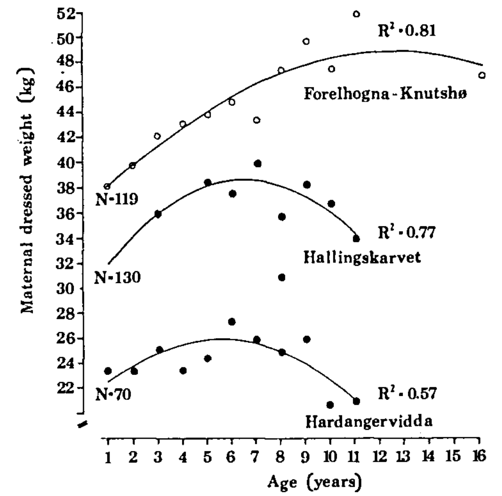

Fig. 4. The realtionship between mean maternal dressed weights and age in the four study herds. The Forelhogna and Knutshø data have been pooled since they did not differ in size. Data from the autumn hunting season have also been added for these herds (Skogland 1983, 1984b).

Fig. 4. Forholdet mellom simlenes gjennomsnittlige slaktevekter og alder i de fire villreinstammene. Materialet fra Knutshø og Forelhogna er slått sammen da det ikke var forskjellig. Det er også utvidet med noe materiale fra høst-slakting (fra jakt-tiden). Dette materialet er fra Skogland (1983, 1984b).

size=3776). The total loss in the period from late pregnancy to the end of lactation was thus 55%. Since a significant proportion of the does lost their fetus or calf, it is reasonable to suspect that it was the smallest near-term fetuses or born calves that died. A sample of 7 dead calves had mean weight of 2.98 kg ± 0.47 SE, while a sample of 11 live-caught calves had a mean weight of 3.72 kg ± 0.27 SE. The difference between the two samples is not significantly different (t = 1.47, $p > 0.10$), but the data suggest that the actual weights to be compared for growth during the last part of gestation should include the weights of the dead calves. Adjusting for this difference, the growth rate of fetuses per day (0.0087) during the last part of gestation was depressed by 42% among the Hardangervidda does.

Out of a total sample of 45 does one year and older in the Forelhogna-Knutshø herds, all were pregnant. Field sampling during calving and in summer showed that one out of 361 does had lost a calf. The calf ratios in both herds in summer indicated that no statistically significant differences in calf proportions (0.95±0.022 SE, sample size = 1058) could be found when compared to the pregnancy rate (1.0 ± 0.32 SE, sample size = 40). Thus the productivity of the Hardangervidda does was reduced by about 50%, due to food-limitation.

DISCUSSION

The nutritional requirements of the developing fetus are reflected in the energy balance of the mother. During the first part of pregnancy the energy demand is only slightly higher compared to that of barren females, but increases progressively toward the end of gestation (Maynard and Loosli 1962). In reindeer the maternal energy demand during the last 6 weeks of gestation increases, on the average, by about 15% (McEwan 1970, McEwan and Whitehead 1971, Rome 1974. Preobrazhenski (1961) estimated that an additional 30 kg of lichen was necessary for the growth of the fetus to termination. The results from this study indicate that over a 5-fold difference in food availability (see introduction) the does on overgrazed lichen ranges depressed fetal growth by about 42%. Although maternal body weights did

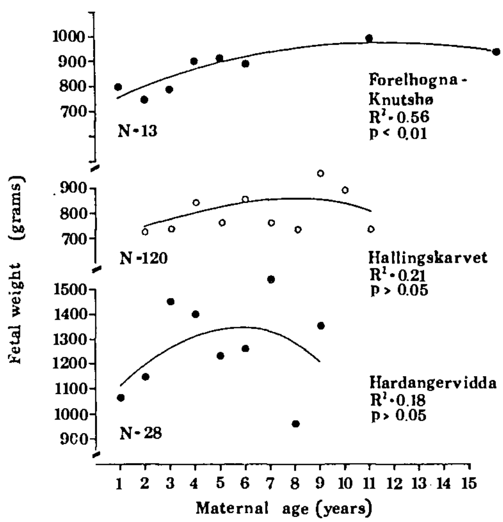

Fig. 5. Mean fetal weights in relation to maternal ages. The Forelhogna-Knutshø and the Hallingskarvet data are from February, while the Hardangervidda data are from March.

Fig. 5. Gjennomsnittlige fostervekter i forhold til simlenes alder. Materialet fra Forelhogna, Knutshø og Hallingskarvet er fra februar, mens Hardangervidda materialet er fra mars.

not decline at a different rate in the three herds during mid-pregnancy, the does from Hardangervidda lost between 21 - 27% of relative body weight between the end of Aprii until the end of calving in 1971 and 1973 respectively (Fagerhaug 1973). In both those years my field sampling indicated significant calf losses (Skogland in press). Rognmo et al. (1983) showed that reindeer does fed *ad lib* lichen during the last part of gestation maintained their body weights, which suggests that they also do so in the Forelhogna and Knutshø herds.

Thus the food-limited Hardangervidda does, although they catabolized a significant proportion of body tissues, were not able to satisfy fetal energy requirements for unimpeded growth. In Rognmo *et al.*'s experiment the does on an improved diet produced calves with 18 - 23% higher birth weights. In this study I showed that food-limited does produced birth weights that were 42% lower than the average for those from the Forelhogna - Knutshø areas, and more than half the calves from Hardangervidda died before weaning.

Bergerud (1975) found a negative correlation between birth weight, survival, and winter snow depths among Newfoundland caribou. Likewise he found that smaller does produced smaller calves. Results from other ungulates indicate a nutritional influence on fetal growth and birth weights (i.e. Verme 1963 on white-tailed deer, Albon et al. 1983 on red deer, Mellor 1983 on domestic sheep). Mellors work indicated a far greater sensivity to nutritional deficiencies of the pregnant mother than had previously been suspected. In both domestic sheep and wild ungulates a significantly higher mortality have been found among the smallest neonates (Grubb 1973, Verme 1977). Rognmo et al. (1983) found in their experiments on the effects of plane of nutrition during late pregnancy on birth weights, that 28% of the calves from the smallest does without an improved diet died within 2 days post-partum.

The birth weights of the smallest does were similar to the ones found at Hardangervidda. It appears that the critical birth weight for neonatal survival is about 3.5 kg. Data on ruminants and tayassurids indicate that ungulates produce 3.5 gr of wet neonatal tissue per kilo kalory of maternal basal metabolism (Geist 1981). From the general BMW formula we can solve the equation for the body weight that produces 3.5 kg neonates. It appears that a maternal weight of 35 kg, or 19 kg dressed weight, is necessary.

If a weight loss of at least 20% occurred between late April and the first week of June at Hardangervidda, as was found in 1971 and 1973 by Fagerhaug (1973), the mean maternal weights after the end of the birth season in 1983 would be slightly less than 19 kg dressed weights. This could possibly explain the high neonatal mortality I found in 1983.

The difference in timing of births between Forelhogna and Knutshø is probably due to genetics (K. Røed pers. comm.). The Forelhogna reindeer are of a mixed semi-domestic origin from Swedish forest reindeer (J. Nordfjell pers. comm.) Most reindeer of domestic origin, now wild in Southern Norway, give birth at the same time as the Forehogna herd, e.g. the Ottadalen herd (Reimers et al. 1983).

The Knutshø and Hardangervidda herds are of wild mountain reindeer origin (Røed 1982, pers. comm.). A mid-May birth season has been commonly observed among mountain reindeer (Skogland in prep.). The difference in birth time between Knutshø and Hardangervidda is probably due to nutrition. Espmark (1980) found in experiments on penned reindeer that underfed females gave birth several days later than the control group. Nutrition has also been found to delay births in sheep (Alexander 1956).

Conversely, a late calving season could be due to a later conception caused by low-quality nutrition before the onset on estrus. Verme (1965) found that the time for onset of estrus in white-tailed deer was slightly delayed when the level of nutrition was lowered before the normal time of estrus. Smith (1964, 1965), on the other hand, found that nutritional deficiencies during the winter and spring, at the time of lambing in sheep, delayed the time for onset of estrus the following autumn.

Since there are no marked differences in the composition of the summer pastures in the three study areas included in this work (Skogland 1983), a delay in the onset of estrus due to differences in the level of nutrition before the rutting season is unlikely. I suggest that the effects of food-limitation during winter and the calving season delay the time of onset of estrus and lengthen the gestation period, with the resultant difference in timing of births shown between Knutshø and Hardangervidda. Reimers (1972, 1980, 1983) has suggested that stress, due to human disturbance, could be a contributing factor to explain delays in the time for onset of estrus, but at the moment there are no available data to show such an effect.

The results for this study thus suggest that the consequences of overgrazing and food-limitation among wild reindeer on their winter ranges have severe effects on the growth, size and survival of offspring as well as timing of births; results which have important management implications.

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