The effects of human disturbance on the activity of wild reindeer in different physical condition.

Effekter av menneskelige forstyrrelser på aktiviteten til villrein i forskjellig fysisk kondisjon

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Abstract. We compared two Norwegian wild reindeer herds, Knutshø in excellent physical condition and Hardangervidda in poor physical condition, before and during disturbance by human hunters in order to test whether physical condition effected foraging strategy under stress. Both herds were being regularly hunted (man had been a natural predator on reindeer since prehistoric time). The well-fed Knutshø animals were ca. 30% larger at the start of the hunting season in late August. Before exposure they foraged less and walked more, i.e. were more selective than the Hardangervidda animals which were in energetically lower condition and foraged significantly more and spent less time moving between habitat patches and less time standing.

After exposure to hunters disturbed Knutshø animals aggregated into significantly larger groups than before hunting and stood alert more, while Hardangervidda animals spent the same minimum amount of time foraging but moved significantly more and spent almost no time standing.

The frequency of disturbance was not significantly different between the two herds and their speeds of movement after disturbances were similar. The hunter kill success rate was also similar in the two areas.

The energetic costs, measured as relative body weight loss during the hunting season, was higher for the initially less well-fed Hardangervidda animals, and higher for both herds compared to that from a less disturbed herd (Forelhogna).

We hypothezise that while standing still and alert in aggregated groups is risky, it is still more risky to move, but potentially more rewarding if a better habitat could be found. More well-fed Knutshø animals, which aggregated and stood still, conserved allready stored energy, compatible with a time minimizer risk aversive strategy. The Hardangervidda animals which were in poorer condition increased travelling time to an extent that suggested a risky nutrient miximizer strategy in the phase of stress.

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Sammendrag: For å teste om fysisk kondisjon innvirket på beitestrategien, sammenlignet vi to norske villreinflokker, Knutshø i utmerket fysisk kondisjon og Hardangervidda i dårlig fysisk kondisjon før og etter forstyrrelser av jegere. Begge flokker er regelmessig jaktet på (menneske har vært naturlig predator på rein siden førhistorisk tid). De velnærte rein på Knutshø var 30% tyngre enn sine artsfeller på Hardangervidda ved starten av jaktsesongen sent i august. Før jakten beitet de mindre og gikk mer, d.v.s. var mer selektive enn Hardangervidda-reinen. Disse var energetisk sett i en dårligere forfatning, beitet mer og brukte mindre tid både til å gå mellom beiteområdene og til å stå.

Etter å ha blitt utsatt for forstyrrelser av jegere, samlet Knutshø-reinen seg til større grupper enn før jakten og sto mer vaktsomme. Hardangervidda-reinen derimot, brukte den samme minimumstid til beiting, men gikk signifikant mer enn før jakten. Den brukte heller nesten ingen tid til å stå i ro.

Hyppigheten av forstyrrelser var ikke signifikant forskjellig mellom de to grupper og deres bevegelseshastighet etter forstyrrelse var den samme. Jegernes jaktsuksess i form av fellinger var også den samme i de to områder.

Energiutgiftene, målt som relativt tap av kroppsvekt gjennom jaktsesongen, var høyere for Hardangervidda-reinen med dårligere ernæringsstatus i startfasen. For begge flokker var energiutgiftene høyere sammenlignet med en mindre forstyrret reinflokk (Forelhogna).

Vi tror at, selv om det å stå stille og vaktsomt i samlet flokk er risikofylt, så er det enda mer risikofylt å bevege seg, noe som dog kan være mer lønnsomt, om de finner et bedre beiteområde. Mer velfødd Knutshø-rein, som samlet seg og sto i ro, bevarte mer av sin allerede opplagrede næringsenergi, noe som minimaliserer tidsforbruk til næringssøk og som er en risikoavvergende strategi. Hardangervidda-rein, som var i dårligere hold, økte tiden for beitesøk i en grad som antyder en mer risikofylt strategi under stresspåvirkning for å maksimalisere beiteopptak.

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Skogland, T. & Grøvan, B. 1988 Ihmisen aiheuttaman häirinnän vaikutus eri kuntoisten villipeurojen aktiivisuuteen.

Yhteenveto: Vertasimme kahta norjalaista villipeuralaumaa, Knutshöen erittäin hyväkuntoista ja Hardangerviddan huonokuntoista laumaa. Ennen ja jälkeen metsästäjien häirinnän testasimme vaikuttaako kunto peurojen ravinnon käyttöön stressin aikana. Molempia laumoja on metsästetty säännöllisesti (ihminen on olut peurojen luontainen vihollin je esihistoriaaalisista ajoista alkaen). Hyväkuntoisessa Knutshöen laumassa peurat olivat noin 30% suurempia metsästyskauden alkaessa elokuun lopulla. Ennen härinitää ne laidunsivat vähän, vaelsivat enemmän ja olivat valikoivampi kuin Hardangerviddan peurat, jotka olivat energeettisesti heikommassa kunnossa ja laidunsivat merkitsevästi enemmän ja kuluttivat vähemmän aikaa liikkumiseen eri laidunalueiden välillä ja myös seisomiseen.

Metsästyksen alettua Knutshöen peurat kokoontiuvat suurempiin ryhmiin kuin aikaisemmin ja sesoskelivat pelokkaina enemän. Hardangerviddan peurat käyttivät puolestaan vähän aikaa ruokailuun mutta liikkuivat merkitsevästi enemmän eivätkä käyttäneet juuri aikaa seisomiseen.

Häiriötilanteiden määrissä eri laumojen välillä ei ollut tilastollista merkitsevyyttä ja niiden liikkumisnopeudet häiröiden jälkeen olivat samanlaiset. Metsästäjien saaliit oliva samanlaiset näillä kahdella alueella. Energian kulutus mitattuna suhteellisena painon menetysenä metsästysaikana oli suurempi jo lähtövaiheessa heikompikuntoisimmilla Hardangerviddan peuroilla, ja se oli myös suurempi molemmilla laumoilla kuin vähemmän häiritytllä laumalla (Forelhogna).

Me oletamme, että sesominen ja häirintä isoissa laumoissa on riskitekijä. Vielä suurempi riski on liikkua, mutta potentiaalisesti se on parempi, jos hyviä laidunalueita lövtyy. Hyväkuntoiset Knutshöen peurat, jotka kokoontuivat ja sesoivat hiljaa, säästivät jo koottuja energiavarastoja. Hardangerviddan peurat, jotka olivat huonommassa kunnossa, lisäsivät suuresti vaellusta. Stressin aikana on hyvin mahdollista, että peurat eivät voi maksimoida ravinnon käytön strategiaa.

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Introduction

Optimal foraging theory suggests that nutrient maximization entails preferential plant and habitat choice within the constraints of foraging time and digestive capacity, while time minimization entails obtaining minimum nutrient requirements with the least foraging time (Schoener 1971, Belovsky 1978, 1984, Stephens and Krebs 1986).

But energy maximization alone may not account for all foraging decisisons when a foraging animal is vulnerable to predators (or hunters). Among central place foraging small mammals like hoary marmots (*Marmota caligata*) and squirrels (*Sciurus carolinensis*) where the distance travelled from safe terrain is a measure of risk, it has been found that hoary marmot habitat use correlated positively with food abundance and negatively with predation risk (Holmes 1984) while grey squirrels rejected more energetically profitable food as a function of distance from cover and the size of less profitable food items (Lima and Valone 1986). A similar result was found for Atlantic salmon *Salmo salar* juveniles feeding under experimental predation risk (Metcalfe *et al.* 1987).

Thus an increase in the risk of predation can cause a shift from a strategy which maximizes foraging efficiency to one less efficient but safer (e. g. Schoener 1971).

Furthermore, fitness is the result of lifetime performance, so that foraging decisisons at one time cannot easily be isolated from other events. There are times when an animal needs to lay down energy reserves for anticipated future costs, or food stress may occur due to changing environmental conditions so that optimal foraging must be considered as a dynamic concept, with a continual shifting of the relative costs and benefits of the different behavioral options. Metcalf and Furness (1984) found that allocation of time to antipredatory behaviour decreased prior to migration in order to build the necessary fat deposits to endure the migratory flight and egg-laying period among ruddy turnstones (*Arenaria interpres*). In a winter food-limited and predator-free environment in the high arctic Svalbard reindeer (*Rangifer platyrhynchus*) spent more time foraging and put on more fat deposits during the summer season than mainland reindeer exposed to predators and human hunters. The faster growth rate in summer, despite lower plant biomass was considered a consequence of more grazing time and less energy spent on avoidance activities among Svalbard reindeer (Reimers 1980).

In predator exposed environments Belovsky (1978, 1984) found that diet selection among moose (*Alces alces*) on Isle Royale in the USA and kudu (*Tragelaphus strepsiceros*) in Africa was a nutrient maximization process, while Skogland (1980, 1984a, and Trudell and White 1981) showed that reindeer in different environments choose habitats of highest quality and quantity in winter and summer, while the acceptance range of plants increased. Vivås and Sæther (1987) showed that moose spent longer time in habitats of higher food sapling density, while Baharav and Rosenzweig (1985) found that dorcas gazelles (*Gazella dorcas*) adandoned habitat patches because they had been partly depleted. These studies support the diet nutrient maximizer hypothesis. The nutrient maximizer attempts to ingest the greatest intake of some nutrient in the available foraging time. If nutrients incrementally determines survival and reproductive success, the nutrient maximizer will have the greater fitness the more it ingests. On the other hand, the time minimizer which achieves its minimum nutrient requirements in the least foraging time, presumably will limit its exposure to deleterious factors like predation. These two dichotomous strategies are endpoints along a continuum and it is conceivable that individuals and populations faced with food limitation or predation compromise between these dichotomies in relation to age, sex, or in order to maximize their fitness.

The object of this paper is to explore such a possible foraging dichotomy with wild reindeer in relation to food limitation and risk aversion.

Two populations of wild reindeer, one in excellent physical condition on abundant winter food (Knutshø) and one winter foodlimited (Hardangervidda), both subjected to a regular annual hunting by man during autumn, were selected for comparison.

A summary of differences in life history parameters between the two populations is given by Skogland (1983, 1984b, 1985, 1988a, b). Density-dependent food limitation in winter led to smaller body size by a delay in calving time and depressed fetal growth and increased neonatal mortality as well as a longer lactation period into the summer season among the Hardangervidda females. These effects were further enhanced by increased tooth wear with age from foraging on less preferred plants on overgrazed winter range. A consequential effect on digestive capaeity of the more abundant high quality summer range and thus a lowered net life-time energy gain during half their mature life.

Thus optimal foraging had a fitness component and foraging could not be separated from its temporal components at other seasons of the year.

When foraging in open habitats of a similar physiognomic character, reindeer in different populations has to anticipate the risk of detection by man as a predator in a like manner. Vulnerability in general is related to physical condition. Reindeer have mainly three options in risk aversion; use of refuge habitats, aggregation, or increased alertness by changes in their daily time budgets. We studied which option or options were selected during disturbance.

Materials and methods

Daily activity was studied by following wild reindeer groups on the ground as long as possible during daylight hours with the aid of binoculars and tripod-mounted 16-36X spotting scopes. Group activity was divided into five categories, grazing, lying, walking/running and «other» (Gaare *et al.* 1975). The last category which consists of grooming, nursing, social conflicts etc comprised less than 1% of all observations and were discarded from further analyses for the purposes of this report. The number of animals engaged in each activity was counted every 15 minutes. Movement speed was obtained by noting the distance that observation groups moved during their observation time.

Dressed body weights of adult females ($\geqq 3$ years of age as determined by tooth eruption patterns) were obtained from carcasses shot by hunters at Knutshø during 1979-1985, and from Hardangervidda from 1979-1984, as well as from the Forelhogna herd in 1985, living adjacent to the Knutshø area, and of comparable physical condition to Knutshø animals (Skogland 1983), but less disturbed during hunting (T. Skogland unpubl. observations).

Relative weight loss from the early to late part of the hunting season was measured as W_1-W_2/W_1 where W_1 and W_2 represents dressed body weight during the early and late season.

Back fat thickness on collected carcasses were measured following standard procedures (Langvatn 1977).

The activity data were collected from Hardangervidda during the summer/autumn of 1984 by Kolle (1985) and the Knutshø activity data in 1985 by Grøvan (1986).

Weather conditions in the form of high temperatures, low winds and high moisture favours the harassing activity by biting mosquitoes and other insects in late summer (Gaare *et al.* 1975, Skogland 1984a, Boertje 1985) and strongly effects activity of reindeer. For comparison only days without visual harassment by insects were used for analysis. Activity budgets before and during disturbance by hunters were analyzed with a chi-square test for k independent observations. All activities were treated as following multinomial distributions. Differences in movement speed were tested with the Mann-Witney U-test.

Herd size at Hardangervidda in the summer of 1984 was 20 000 animals and in the summer of 1985 it was 1700 animals at Knutshø, based on aerial census data (T. Skogland unpublished data). The size of the Hardangervidda range is 8000 sq.km and the Knutshø range is 1600 sq.km. Both areas are of comparable undulating alpine barren tundra with altitudes between 1000 - 1600 m. The Hardangervidda winter range was overgrazed with about 1/5 the available lichen biomass as that at Knutshø (Skogland 1983), while summer ranges in the Western parts of the Hardangervidda and Knutshø areas were largely composed of comparable calciphilous vascular vegetation types, although the Knutshø range is slightly less favourable in terms of summer rainfall or snowmelt.

During 1984 a hunting quota of 13 600 animals was issued at the Hardangervidda, on the assumption that usually 50% was shot. The large quota was given in order to reduce the population size to a level more compatible with range conditions. The Knutshø quota in 1985 was 500 animals, again issued on the assumption of 50% being shot.

Results

Before opening of the annual hunting season in late August (25 August) 27% of the observed groups of reindeer at Knutshø and 29% at Hardangervidda were disturbed in their activity by humans (hikers and sports fishermen) at an average rate of one per 10 hours of observation in both areas. During the hunting season, 92% of the groups of reindeer observed at Knutshø and 81% at Hardangervidda were disturbed in their activity by hunters (by gunshots, sight or smell of humans), at an average rate of 6 incidences per 10 hours at Knutshø and 8 at Hardangervidda.

Grazing and walking dominated over all other activities before exposure to hunters (Table 1). Prior to exposure to hunters, the differences in the distribution of activities between Knutshø and Hardangervidda animals were statistically significant ($p < 0.05$, $X^2=9.25$, 3 d.f.). The herd differences in the distribution of daily activities increased during the hunting season (< 0.001, $X^2=29.33$, 3 d.f.). Activity differences before and during exposure to hunters were significantly different for standing which increased and walking/running which decreased among the Knutshø animals. The Hardangervidda animals increased significantly walking/running activity (more than doubled) with a corresponding lower incidence of lying activity. Thus the two dominant activity patterns as-

Table 1. Percentage daily activity time for wild reindeer in the two study areas before, during and after a 1 month «predator disturbance» period. Activity is given as mean ± SE.

Tabell 1. Daglig aktivitetstid (i %) for villrein i de to studieområder før og etter en måneds «predator-forstyrrelse». Aktivitet er gitt som middel ± SE.

	Before hunting		During hunting		After hunting
Activity type	Knutshø	Hardangervidda	Knutshø	Hardangervidda	Knutshø
Grazing	35 ± 2.1	48.0 ± 2.4	31 ± 2.2	31 ± 2.2	49 ± 2.0
Standing	8 ± 1.2	1.0 ± 0.5	19 ± 1.8	2 ± 0.7	6 ± 1.0
Lying	26 ± 1.9	26.5 ± 2.1	19 ± 1.8	11 ± 1.5	35 ± 3.1
Walking/running	31 ± 2.0	24.5 ± 2.1	30 ± 2.1	56 ± 2.3	10 ± 1.4
Sample size	125	104	111	124	198

sociated with forage selection did not change among the Knutshø animals, while alertness by standing bunched together in a tight group increased. Before the hunting season the mean group size at Knutshø was 64 ± 46 SD animals, while during the last part of the hunting season about 70 % of the females and calves (with a mean group size of 800 animals) in the population were gathered in one group. At Hardangervidda the mean group size before the hunting season was 162 ± 192 SD animals, and during the hunting season it was 266 ± 243 SD animals.

Thus group size aggregation was about 7 fold higher at Knutshø than at Hardangervidda following hunter disturbances.

The Hardangervidda animals did not use the standing-alert tactic in the face of exposure to hunters almost at all, but dramatically increased their mobility at the expense of lying and foraging.

After the end of the hunting season when disturbances from humans were very low, the Knutshø animals spent most of their time on foraging and lying (no such data for 1984 from Hardangervidda were available).

The travelling speed increased significantly among both the Knutshø and Hardangervidda animals after exposure to hunters ($p=0.006$) and decreased to below the prehunting level after the end of the hunting season among the Knutshø animals (Fig. 1).

At the start of the hunting season the mean dressed body weights of adult females from Knutshø were about 30% larger than those from Hardangervidda (Table 2). From the beginning to the end of the hunting season (20-26 Aug. to 9-15 Sept.) the dressed weights from both areas decreased, but the loss in weight was not statistically significant at Knutshø ($p<0.2$, $t=0.91$, Knutshø, and $p<0.1, t=1.8$, Hardangervidda, 21 d.f.) The relative mean weight loss was twice as high from the Hardangervidda animals (10%), compared to the Knutshø animals (5%) during this period of the year when reindeer normally put on weight or fat deposits. Among the Forelhogna herd animals, from the adjacent range to Knutshø and of comparable reaction to hunters is less pronounced, body weights increased during the period of hunting (Table 2). Their relative weight gain was 5%.

Back fat thicknesses of adult females were not significantly different between the Knutshø and Forelhogna females in the early part of

Table 2. Mean ± SE dressed body weight of adult ≧ 3 years of age female reindeer culled during the first and last period of the annual hunting season.

Tabell 2. Middel ± SE slaktevekt av voksne (≧ 3 år) reinsimler samlet gjennom første og siste del av den årlige jaktsesong.

	Early season			Late season		
	N	x̄	± SE	N	x	± SE
Knutshø	(18)	41	1.25	(12)	39	1.29
Hardangervidda	(17)	29	0.97	(6)	26	0.82
Forelhogna	(21)	43	1.16	(5)	45	2.53

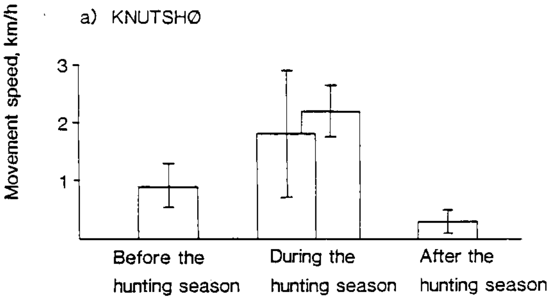
the hunting season, and did not change among Knutshø females during the hunting season, but increased among Forelhogna females. (Table 3). The Hardangervidda females had a median zero fat deposit thickness during the whole season. The back fat thicknesses were not normally distributed, suggesting that differences between lactating and barren females in fat deposits existed, but inspection of milk in the udder during the period after weaning in August is not a good indication of lactational status (Skogland 1988b). There were more barren females among the Hardangervidda reindeer than the Knutshø and Forelhogna reindeer due to higher neonatal mortality (Skogland 1984b, 1985).

Discussion

The differences in foraging time between the Knutshø and Hardangervidda females before the hunting season are in support of the nutrient maximizer hypothesis as shown earlier for reindeer (see Introduction) whereby good physical condition permits a more selective foraging pattern with higher search time. The late calving season at Hardangervidda compared to Knutshø, and longer lactational period, more worn-down teeth and lack of replenished fat deposits (Skogland 1988a, b) all suggest that the Hardangervidda females were energetically in a different condition to the Knutshø females during late summer, despite lack of differences in quality of summer forage.

The two populations thus met the season of predation and hunter disturbance in substantially different physical conditions.

In facing predation one obvious possibility is to run away, but an allmost equally effective strategy is clumping (Hamilton 1971). This strategy is widely used by alpine wild reindeer herds in Norway, barren-ground caribou in North America and domestic reindeer in Finland during summer insect harassment (Thomson 1973, 1977, Skogland 1974, 1981, 1988a, Kelsall 1968, Roby 1978, Boertje 1985, Helle and Aspi 1983). However, the insect harassment clumping is usually associated with use of refuge terrain on snow fields, or in water. The use of refuge terrain to avoid predation during and after birth is common among ungulates, and has been documented for moose (Edwards 1983, Stephens and Peterson 1984), caribou (Bergerud *et al.* 1984, and Jakimchuk *et al.* 1987), and wild reindeer (Skogland 1987, 1988a). The use of refuge terrain also during disturbance by hunters has been observed in the Snøhetta herd and sometimes in the Knutshø and Hardangervidda herds (T. Skogland unpublished observations) but it apparently depends strongly on a broken terrain relief and difficult access by humans. In most hunting situations the reindeer in the two populations are therefore faced with the



b) HARDANGERVIDDA

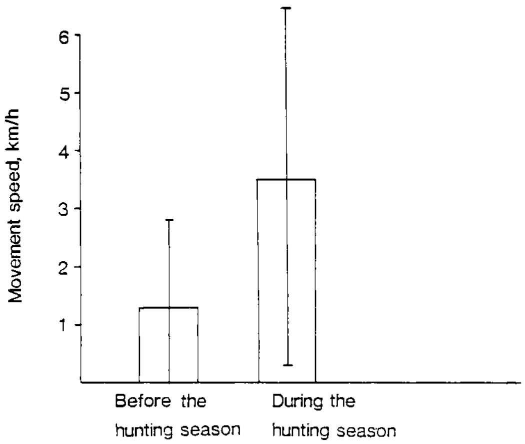


Figure 1. The mean speed of movement (Km/h ±) of reindeer at Knutshø (a) and Hardangervidda (b) before, during and after the hunting season. The larger column for movement speed during the hunting season at Knutshø excludes days without hunter disturbances.

Fig. 1. Gjennomsnitts-hastighet (km/h ±) til rein på Knutshø (a) og Hardangervidda (b) før, under og etter jaktsesongen. Den høyere søyle for bevegelseshastighet under jaktsesongen utelater dager uten jaktforstyrrelser.

decision as to run away or aggregate and be alert. It is very difficult for hunters to be able to approach cloose enough for a shot on an individual in a tightly clumped and standing group of reindeer without being detected.

The explanation for the apparent use of different escape strategies during disturbance between the two populations must probably be sought in their different physical conditions. It has been shown that age-size specific differences in risktaking exists among hoary marmots, and that these differences were related to experience and physical condition. Hungry animals were willing to take more risks by foraging longer distances away from predator-safe terrain (Holmes 1984). With more fat deposits and a generally better physical condition it would be more energy-conserving for Knutshø reindeer to aggregate and stand alert as long as there were hunters present than to move and try to find another foraging location.

The only significant difference in activity before and after hunter disturbances among the Knutshø females was the decrease in lying and increase in standing time. It is possible for them to ruminate standing instead of lying although the energy expenditure is slightly higher (Fancy 1986). The significant increase in time spent foraging and lying and lower time spent standing and moving after the hunting season suggest that the Knutshø animals were compensating for an energy loss due to disturbances during the hunting season. It has been shown previously that loss of foraging time due to strong winds and drifting snows in winter and to insect harassment in summer is compensated by significant increases in daily foraging times on subsequent days among the Hardangervidda reindeer (Skogland 1984a). Likewise, parturient and lactating females with an increased energy demand compared to the pregnancy period, increased their daily foraging time correspondingly over a period of only a few days (Thomson 1977, Skogland 1984a).

Without fat deposits and a generally poorer physical condition at the start of the hunting season the Hardangervidda reindeer would be in more need of access to food because catabolism of body proteins is only half as energy-giving as fat metabolism (Ganong 1983). Based on circumstantial evidence, Fancy (1986) suggested that a 10% increase in activity was less costly than loss of access to high quality food when body energy reserves were low. The lack of fat deposits would also mean that body weight loss would be more rapid among the Hardangervidda females under the same disturbance burden, even if they had chosen the same risk avoidance strategy as the Knutshø females by aggregating and standing. Comparison of the activity times of the Hardangervidda reindeer during hunting in 1970 and 1984, when they were in equally poor condition (Thomson 1977, Skogland 1983, 1984b), showed that they also in 1970 spent a significantly longer time walking/running and an insignificant amount of time standing compared to the Knutshø animals which suggests that the results from 1984 were not due to chance or observation bias. The relative weight loss during the hunting season in 1970 at Hardangervidda was similar to 1984, at 10% (Fagerhaug 1976).

It is therefore our suggestion that differences in physical condition dictated the choice of time minimization as a risk avoidance stra-

Table 3. Back fat thickness (mm) of adult ≧ 3 years of age femal culled during the first and the last part of the annual hunting season.

Tabell 3. Tykkelsen av ryggfettet (mm) på voksne (≧ 3 år) reinsimler samlet gjennom første og siste del av den årlige jaktsesong.

	Early season			Late season		
	N	Median	Range	N	Median	Range
Knutshø	(27)	10	0-30	(17)	10	0-30
Hardangervidda	(32)	0	0-35	(14)	0	0-10
Forelhogna	(15)	10	0-50	(4)	25	20-30

tegy among the Knutshø females and a nutrient maximization strategy with increased foraging time variance (Caraco *et al.* 1980) among the Hardangervidda females.

The presented data support the view that an increase in the risk of predation can cause a shift from a strategy which maximizes foraging efficiency to one less efficient but safer, and that foraging decisions at one time cannot be isolated from other events. The view that winter food limitation among reindeer would result in more weight loss during the late summer hunting season withoout a quantitative difference in the hunting disturbance or summer food quality would be such an event.

Reimers (1983) concluded that the maximum growth rates of reindeer at Hardangervidda were not met in summer. He suggested that «there is something limiting during summer in these herds. This something relates to range quality and harassment». Skogland (1983) however, found that morphometric growth did not vary among those herds compared to other non-food limited herds before the age of maturity. Helle and Tarvainen (1984) also found that a decreased growth and survival among reindeer calves in Finland was enforced by a preceeding harsh winter that effected maternal physical condition negatively. The results from this study on harassment effects by hunters and those from Skogland (1988b) that increased tooth wear for animals on overgrazed winter ranges had serious life history consequences including effects on digestive capacity, depressed fetal growth that was not compensated by abundant food postnatally (Skogland 1984b), and delayed time of births and a longer lactational period in summer for undernourished females (Skogland 1988a) do not support Reimers' (1983) conclusion that summer range quality differences or harassment differences caused growth differences between Hardangervidda reindeer and other reindeer in good physical condition with an abundance of seasonal forage. The presented data together with results from Skogland (1988b) support the foraging multiplier hypothesis proposed by White (1983).

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