SEASONAL ACTIVITY OF THE DENALI CARIBOU HERD, ALASKA

Sesongmessige svingninger av aktiviteten i Denali karibu-flokk, Alaska

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Summary: Activity of female and young caribou in the Denali herd was studied from June 1978 through April 1980 to help assess the food availability/nutritional status of this reduced population. No nutritional stress was evident as inferred by the greater activity of Denali caribou in late winter compared with starving caribou in West Greenland and by the low proportion of time spent grazing in spring compared with reindeer on overgrazed ranges in Norway. Also, low proportions of time were spent running from insects due to relatively few insects and a high availability of insect-relief sites. A low proportion of time was spent cratering due to windswept conditions. Activity budgets calculated from complete active-rest cycles and accompanied by the duration of active and rest periods may be useful indicators of relative food availability/nutritional status, particularly in late winter/early spring. Duration of active periods is presumably most strongly related to rumen fill, and, thus, food availability. Duration of rest periods was not significantly different among seasons ($P<0.05$), except when insects, rutting bulls, and, presumably, mushroom-searching altered active-rest cycles.

Key words: Activity, Alaska, behaviour, caribou, *Rangifer tarandus granti.*

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Sammendrag: Aktiviteten hos simler og ungdyr i Denali karibou-flokk ble studert fra juni 1978 til utgangen av april 1980 som hjelpemiddel for å bestemme næringstilbud/ernæringsstatus i denne reduserte karibu-stamme. Ingen ernæringsmessig stress var åpenbar, noe som kan utledes av den større aktivitet hos Denali karibu på senvinteren sammenlignet med sultende karibu i Vest-Grønland samt den lave andel av beiting sammenlignet med rein på overbelastede beiter i Norge. Videre ble en lav andel av tiden brukt til å rømme fra insekter, fordi insektplagen var relativt liten og at det var lett adgang til områder der dyrene kunne befri seg fra insektene. Graving krevde også liten andel av tid takket være vindblåste snøforhold. Aktivitetsbudsjetter beregnet ut fra totale aktivitets-/hvilesykluser kan være nyttige indikatorer på relativ næringstilbud/ernæringsstatus, særlig på senvinter og tidlig vår. Varigheten av aktive perioder er sannsynligvis mest knyttet til vomfylde og, derfor, til næringstilbud eller næringstilgjengelighet. Varigheten av hvileperioder var ikke signifikant forskjellig mellom sesonger ($P<0.05$), unntatt når insekter, brunstige bukker og, sannsynligvis også, soppsøking forandret aktivitet-/hvilesykluser.

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INTRODUCTION

Several authors have emphasized the usefulness of activity studies in judging the relative nutritional status of *Rangifer* and/or range condition of a herd (Segal 1962, Gaare et al. 1975, Reimers 1980, Roby 1980).

From June 1978 through April 1980, the Denali caribou herd was studied to assess the role of energetics/nutrition in the decline of the herd from approximately 20.000 — 30.000 animals during 1942 (Murie 1944) to the low of 1.000 — 1.500 animals during this study. A nutritional model was developed (Boertje 1981) from estimates of diet composition (Boertje 1984), forage quality, and seasonal energy requirements (Boertje 1985).

Relationships between activity budgets and the duration of active and rest periods have not previously been described in *Rangifer* studies. Calculations of caribou/reindeer activity budgets have seldom been accompanied by the duration of active and rest periods (Segal 1962, Gaare et al. 1975) and never before with data on statistical variability.

Purposes of this paper are to: (1) document and explain seasonal activity budgets and patterns of female and young caribou in the Denali herd, (2) compare the results with those from other herds to help assess the Denali herd's relative food availability/nutritional status, and (3) recommend methods for standardizing collection and analysis of *Rangifer* activity data.

STUDY AREA

The present range of the Denali caribou herd is centered within Denali National Park (Figure 1). The herd currently numbers 2500 — 3000 animals and occupies approximately 5220 km^2. Vegetation was described previously (Boertje 1984).

A continental montane climate predominates in Denali National Park. However, average snowfall immediately south of the Alaska Range (307 cm ± 100 (SD)), which includes the Cantwell calving ground, is much higher than the average (178 cm ± 72) just north of the Alaska Range (U.S. Weather Bureau).

MATERIALS AND METHODS

Caribou were observed with a spotting scope (15X-60X) or binoculars (10x50) and activity was recorded for caribou groups containing adult females and young. Activity of males older than 3 yr was excluded. Caribou were observed during all daylight hours and observations were continued until dark, until the caribou sensed me, or until caribou movements precluded viewing. Caribou movements and weather were monitored at 15-min. intervals. Distances between individuals in a «group» did not exceed 300 m, and were usually within 100 m.

Caribou activity patterns and activity budgets were documented. «Activity pattern» refers to the cycling and duration of active-rest periods. An «active-rest» period or cycle is the total time spent in a non-lying (active) period and adjacent lying (rest) period. A rest period was considered terminated and an active period initiated when most caribou in a group ceased lying, and vice versa. Duration of active and rest periods were

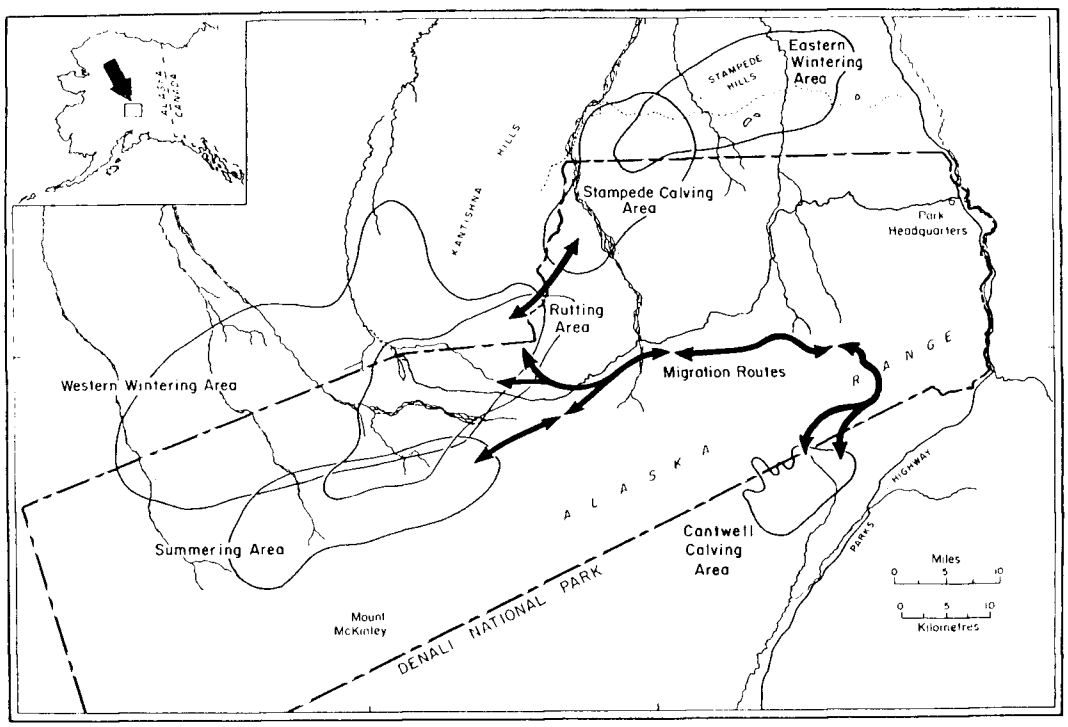

Figure 1. Seasonal ranges of the Denali caribou herd, Alaska, 1978 — 80.
Sesongbeiter for Denali karibu-flokk, Alaska, 1978 — 80.

recorded to the nearest minute. «Activity budget» is the percentage of time that an animal spends in various activities. Activity budgets were documented by scanning a caribou group at 10-min. intervals throughout an active-rest cycle and recording the number of individuals engaged in each of the following six categories of activity:

1. Feeding — includes only the time when the caribou's lips were on or immersed in vegetation or snow while the caribou was standing or walking. I excluded searching time, time spent looking for food, to better estimate the tie spent actually ingesting food. Grazing includes both feeding and searching. Caribou standing in an insect-harassment stance with heads lowered not ingesting, but often with their lips immersed in vegetation, were distinguished from feeding caribou by the more frequent movement of feeding caribou. If a caribou moved during a 7- to 10-sec period, it was assumed feeding.
2. Lying
3. Standing — the caribou was stationary, not ingesting. Standing included activities such as urination, bush thrashing, sparring, and nursing.
4. Walking — the caribou was walking and not ingesting.
5. Running/trotting/galloping.
6. Cratering — pawing through snow.

Each scan was completed as quickly as possible, often with the use of a tally counter.

Activity budgets were calculated for each season by dividing the total number of animals in each activity by the total number of animals observed in all activities. Only data collected during complete active-rest cycles were included, except for data from the insect season. The year was divided into 5 seasons: The calving/postcalving season (22 May — 30 June), the insect season (16 July — 31 August), the pre-rut/rutting season (16 September — 31 October), the early winter season (16 November — 31 December, and the late winter season (1 March — 15 April).

Activity budgets and their variability were calculated only from data on active-rest periods and only from groups where a constant group size was observed during the active-rest period(s).

For the insect season, activity budgets and corresponding variability were calculated using data from observation periods longer than 2.5 hrs, because active-rest cycles during the insect season were never observed.

Activity budgets were not calculated for the midwinter season (1 January — 29 February) or migrations because of the low number of observations. Migrations divided the seasons, except the winter seasons.

Contingency tables were used to compare activity budgets among designated seasons (excluding midwinter) and between adult females and calves during 22 May — 30 June. The F-test and the Newman-Keuls Test (Zar 1974) were used to detect differences in the duration of active and rest periods among seasons. The T-Test was used to analyze for differences in elevations of grazing areas.

RESULTS

Activity during the calving/postcalving season

Adult caribou spent a higher proportion of time lying during the calving/postcalving season (52%) than during other seasons (19 — 42%) (Table 1) due to short active periods relative to rest periods (Table 2). The calving period was the only season in which active periods averaged shorter duration than rest periods (Table 2). Yet, duration of rest periods did not differ significantly ($P<0.05$) among the calving/postcalving and early and late winter seasons (Table 2).

Activity budgets were significantly different ($P<0.001$) between cows and calves during the calving/postcalving period (Table 3). Calves spent only 12% of their time grazing and 70% lying, while cows spent 37% grazing and 52% lying. By mid-July, calves closely imitated activity of their dams.

Caribou reacted to the emergence of oestrid flies (21 June in 1979) by moving from 830 m ± 40 (SD) to 1080 m ± 20 ($P<0.001$) during the calving/postcalving season. Lying and particularly standing animals were often observed on lingering snowbanks during warm weather following oestrid fly emergence. The postcalving migration north across the Alaska Range (Figure 1) progressed rapidly following oestrid fly emergence.

Activity during the insect season

«Insect» in the context of «insect season» refers primarily to the presence of warble flies

Table 1. Time spent by adult female caribou and young a) in various activities withing active-rest cycles, Denali herd, 1978 — 80.

Tabell 1. Tid anvendt av voksne karibusimler og ungdyr a) til forskjellige aktiviteter innen aktivitets-/hvile omløp, Denali flokken, 1978 — 80.

Season *Sesong*	No. of groups *Antall grupper*	No. of graze-rest cycles (n) *Ant. beite-hvile omløp*	Mean percentage ± SD					
			Feeding *Beiter*	Lying *Ligger*	Walking *Går*	Standing *Står*	Trotting/ galloping *Trav/ gallop*	Cratering *Graver*
Calving/ postcalving *Kalving/ etterkalving*	14	17	37±5	52±8	7±4	3±4	0.9±2.0	0
Insect *Insekter*	14	16b)	33±17	19±19	21±21	25±23	1.7±2.1	0
Pre-rut/ rut *Før-brunst/ brunst*	13	16	40±4	39±5	7±3	12±7	1.2±2.0	0
Early winter *Tidlig vinter*	7	7	48±5	32±3	11±5	8±2	0.4±1.0	0.5±1.0
Late winter *Sen vinter*	7	7	53±5	42±7	4±2	2± 1	0.1±0.3	0.4±0.7

a) Data on newborn calves were excluded (see Table 3). *Data for nyfødte kalver ble utelatt (se Tabell 3)*
b) Number of observation periods longer than 2.5 hrs. *Antall observasjonsperioder lengre enn 2.5 timer.*

(Oedemagena tarandi) nasal bot flies *(Cephenomyia trompe)*, and other large flies or bees that stimulated oestrid fly defense reactions (Espmark 1968, Kelsall 1968). Mosquitoes and black flies were present in low concentrations on the calving and summer ranges (Figure 1) relative to those I have experienced on ranges of other Alaskan herds, and probably were not important factors affecting caribou activity. Insect harassment peaked from the 1st or 2nd week in July through mid- to late August, although insect avoidance behavior was observed from 21 June through 7 October in 1979.

When weather was calm and sunny, resulting in severe oestrid fly harassment (Kelsall 1968, Thomson 1977), the Denali herd moved prior to the warm portion of the day to high elevations (approximately 1700 m) 3 to 6 km from grazing areas. This movement usually occurred at a fast walk, and animals regrouped and often stood still or laid down upon reaching suitable insect-relief terrain (lingering snowbanks, glaciers, or barren ridgetops) often void of vegetation. Downward movement to grazing areas usually began by 1600 to 1700 hrs. During mild harassment, caribou often moved from grazing areas to nearby gravel bars, where some feeding occurred.

During cool, windy, and/or rainy days during the insect season (in the absence of insect attack),

Table 2. Seasonal variation in durations of active and rest periods (mean ± SD) of adult female caribou and young a), Denali herd, 1978 — 80. In comparisons among rest periods or among active periods, means with identical numerical superscripts are not siginificantly different ($P<0.05$, Newman-Keuls Test).

Tabell 2. Sesongvariasjon i varigheten av aktive og hvileperioder (gj.sn. ± SD) hos voksne karibusimler og ungdyr a) Denali flokken, 1978 — 80. I sammenligninger mellom hvileperioder og aktive perioder er gjennomsnitt med samme numeriske indikasjonstall ikke signifikant forskjellige.

Season *Sesong*	Dates *Tid*	Average rest period (min) *Gj.sn. hvileper. (minutter)*	n *n*	Average active period (min) *Gj.sn. aktiv per. (minutter)*	n *n*	Average active-rest period (min) *Gj.sn. aktiv-hvile per. (minutter)*
Calving/ postcalving	22 May — 30 Jun	105±29[1]	22	74±29[1]	17	179
Pre-rut/ rut	16 Sep — 31 Oct	78±25[2]	18	88±45[1]	16	166
Early winter	16 Nov — 31 Dec	112±12[1]	9	210±37[2]	7	322
Midwinter b)	1 Jan — 29 Feb	100±11	2	150	1	250
Late winter	1 Mar — -15 Apr	110±17[1]	7	145±21[3]	7	255

a) Data on newborn calves were excluded (see Table 3).
Data for nyfødte kalver ble utelatt (se Tabell 3).

b) Insufficient sample size during midwinter did not allow statistical comparisons with the remaining 4 seasons.
Utilstrekkelig antall observasjoner midtvinters tillot ikke statistisk sammenligning med de andre 4 sesonger.

caribou grazed (includes searching) intensively for long periods, particularly on mushrooms (Boertje 1981). These grazing periods extended to 310 min, more than 3 times longer than average active periods during adjacent seasons (Table 2). Caribou increased walking/searching activity and temporarily strayed from groups during these periods.

Active-rest cycles were largely absent throughout the insect season due to insect-avoidance behavior and, in the absence of insect attack, infrequent rest periods. Seven of 14 groups observed over 2.5 hrs did not exhibit rest periods, except when changing weather conditions caused caribou to seek insect-relief habitat. Four groups were observed lying for 60 — 78 min ($\bar{x}$=71 min) between grazing periods, and the remainig 3 groups remained in insect-relief habitat the entire observation period.

Activity budgets were significantly different among seasons ($P<0.001$), due principally to the relatively high proportion of time spent walking and standing during the insect season (Table 1). The high proportion of time spent walking and associated high daily movement rates (22 km, Table 4) resulted both from movement to insect-relief sites and long grazing periods.

«July dispersal» (Skoog 1968) or «August dispersal» of caribou (Kelsall 1968, Curatolo 1975, Roby 1978) and the associated 3- to 8-fold increases in the proportion of time caribou allocate to running (Curatolo 1975, Roby 1978) were not observed among Denali caribou (Tables 1, 5). This difference is likely related to the relatively low numbers of insects and high availability of insect-relief terrain on the Denali Herd's range (Figure 1).

Table 3. Proportions of time that Denali cow and calf caribou allocated to various activities within active-rest cycles during the calving/postcalving season, 22 May — 30 Juni, 1978 — 79.

Tabell 3. Andel av tid anvendt av Denali karibusimler og -ungdyr til forskjellige aktiviteter innen aktivitet-hvile-omløp gjennom kalving/etterkalvingsesongen, 22. mai — 30. juni 1978 — 79.

Caribou classification *Gruppe*	No. of Graze-rest cycles (n)	Mean percentage ± SD *Gj.sn.prosent ± SD*				
		Feeding	Lying	Walking	Standing	Trotting/ galloping
Cows *Simler*	17	37±5	52±8	7±4	3±4	0.9±3.0
Calves *Kalver*	17	12±3	70±8	10±5	6±3	2.0±2.0

Tabell 4. Seasonal variation in daily movement rates (mean ± SD) of adult female caribou and young, Denali herd, 1978 — 80.

Tabell 4. Sesongvariasjoner i daglige forflytningsdistanser (Gj.sn.±SD) hos voksne karibou-simler og -ungdyr, Denali-flokken, 1978 — 80.

Season *Sesong*	Dates *Tid*	Grazing distance a) (km·day $^{-1}$) *Beite-distanse (km/dag)*	Walking distance b) (km·day^{-1}) *Gå-distanse (km/dag)*	Trotting/ galloping distance c) (km·day^{-1}) *Trav/ gallop-distanse (km/dag)*	Estimated total daily movement d) (km) *Anslått total daglig forflytning (km)*
Calving postcalving	22 May — 30 Jun	1.1±0.2	5.4±3.1	2.6±5.8	9.1
Insect	16 Jul — 31 Aug	1.0±0.5	16.2±9.2	4.9±6.0	22.1
Pre-rut/ rut	16 Sep — 31 Oct	1.2±0.1	5.4±2.3	3.5±5.8	10.1
Early winter	16 Nov — 31 Dec	1.5±0.2	8.5±3.9	1.1±2.9	11.1
Late winter	1 Mar — 15 Apr	1.7±0.2	3.1±5.4	0.3±0.9	5.1

a) Calculated as: (percentage of daily time budget spent feeding in a particular season in hrs (Table 1) x (average grazing speed). Average grazing speed was estimated from 15-min scans of grazing caribou as 0.13 km·hr^{-1}±0.08 (SD) (N=380).

b) Calculated as: (percentage of daily time budget spent walking in a particular season in hrs (Table 1) x (average walking speed=3.22 km.hr^{-1} (Thomson 1977)).

c) Calculated as: (percentage of daily time budget spent trotting/galloping in a particular season in hrs (Table 1)) x (average trotting/galloping speed = 12 km·hr^{-1} (Thomson 1977)).

d) Sum of a, b, and c above.

Activity during the pre-rut/rutting season

Relatively short rest periods (Table 2) and a relatively high incidence of standing (12%, Table 1) during the pre-rut and rutting season were due in part to the disruptive behavior of bulls. Standing was also characteristic of oestrid fly harassment (Kelsall 1968) in September and early October. Rumination for short periods (5 — 10 min) while standing was common during the pre-rut and rutting season, particularly prior to and immediately following the frequent lying periods (Table 2); standing presumably replaced lying in these cases. By adding these standing periods to the rest periods, duration of rest periods in the pre-rut/rutting season would approach duration of rest periods during the calving/postcalving and winter seasons (Table 2).

Acitivity during winter seasons

Longer active periods throughout winter compared to other seasons (Table 2) were likely a result of reduced forage availability due to the senescence of non-evergreen tissue and snow cover. Snow cover, however, was incomplete on most of the eastern wintering area and a portion of the western wintering area (Figure 1) due to strong wind action. Observed caribou spent only 0.4 to 0.5% of their time cratering in winter (Table 1). However, caribou did not always crater for forage when a complete snow cover existed. Between windy periods, foraging caribou often fed through a snow cover of soft, powdery snow up to several centimeters in depth by pushing their mouths through the snow to reach vegetation. Caribou were also observed to shatter thin, hard crusts of snow with a single pawing motion, and to subsequently enlarge the feeding crater with their muzzles.

Because the lenght of rest periods throughout winter was nearly constant, variability in winter activity budgets (Table 1) can ble attributed largely to changes in the duration of active periods. The proportion of time spent walking and standing decreased as winter progressed, which shortened active periods (Table 2). Consequently, mean daily movement rates decreased approximately 50% from early to late winter (Table 4).

During the period that winter activity data were collected, cold temperatures did not measurably affect the duration of caribou active-rest cycles. Caribou exhibited normal active-rest cycles during extremely cold, calm weather (÷38 to ÷48C) in midwinter (Table 2).

DISCUSSION

Factors affecting duration of active periods

Duration of active periods appeared to be largely influenced by five factors: forage characteristics (including forage quality and availability), proportion of time spent in activities other than feeding and lying, insect avoidance, mushroom-searching activities, and activity of rutting bulls. Short active periods during the calving/postcalving season ($\bar{x}$=74 min), relative to winter values (145 — 210 min), are presumably a result in part of increased forage quality and quantity (Boertje 1981) during the calving/postcalving season. As forage quality and quantity increases in spring, the efficiency of filling the rumen increases resulting in shorter active periods (Bell 1961, Blaxter et al. 1961, Arnold 1970). Differences in duration of active periods in early (210 min) versus late winter (145 min) can ble explained by the high proportion of time spent standing (particularly sparring) and walking in early winter (19%) compared to late winter (6%). As time spent walking and standing increases, the efficiency of filling the rumen decreases resulting in longer active periods. Similarly, insect avoidance, mushroom-searching, and rutting activities resulted in longer active periods.

Factors affecting duration of rest periods

Duration of rest (lying) periods (Table 2) was presumably largely regulated by forage digestibility, rumen size and seasonal events (insect avoidance, mushroom-searching, and rutting activity) that causes caribou to stand or walk rather than lie down to ruminate/rest. Roby's (1980) observations of starving caribou in West Greenland suggested that energy conservation could also regulate duration of rest periods. Roby observed extremely long lying periods (3 — 4 hrs; Roby, pers. comm.) and an absence of active-rest cycles among starving caribou in late winter.

Seasonal fluctuations in forage digestibility and rumen size can explain the similarity in duration of rest periods among early winter, late winter, and calving/postcalving seasons (Table 2). The less digestible winter diet of the Denali herd (Boertje

Table 5. Seasonal variation in mean group size of caribou, Denali herd, 1978 — 80.
Tabell 5. Sesongvariasjoner i gjennomsnittlig gruppestørrelse i Denali karibu-flokk, 1978 — 80.

Season *Sesong*	Dates *Tidsrom*	No. of groups observed (n) *Ant. grupper observert (n)*	Group size (mean±SD) *Gruppestørr.. (Gj.sn.±SD)*
Calving/ postcalving a) *Kalving/ etterkalving*	22 May-20 Jun	28	31±24
Pre-migratory massing *Samling før vandringer*	21 Jun- 1 Jul	8	125±69
Insect *Insekter*	16 Jul-31 Aug	56	27±28
Pre-rut/rut *Før-brunst/brunst*	16 Sep-31 Oet	51	18±12
Early winter *Tidlig vinter*	16 Nov-31 Dec	45	22±15
Late winter *Sen vinter*	1 Mar-15 Apr	14	41±34

a) The last 10 days of the calving/postcalving season were included in the pre-migratory massing period.

1981), which predicts longer winter rest periods, is presumably compensated by the smaller rumen size during winter (Staaland et al. 1979). In a healthy ruminant, the rest period (including rumination) is generally considered to last until gut distension declines (Blaxter et al. 1961, Comline and Titchen 1961) and is presumably dependent largely on the digestibility of the diet and rumen size.

Use of activity data to assess relative food availability/nutritional status

A caribou herd's food availability/nutritional status is presumably affected by: (1) absolute food abundance (i.e., excluding influences of snow cover) and quality; (2) weather and climate and their effects on snow cover, snow melt, plant phenology, emergence of insects, and intensity and duration of insect harassment; and (3) availability of insect-relief sites. Boertje (1981) concluded that, in comparison to several other herds with high calf productivity and survival, the Denali herd experienced favorable weather and climatic conditions, high food quality, and high availability of insect-relief sites yet poor calf survival and/or productivity. Absolute food abundance was not measured but comparison of caribou densities among herds and experience with other caribou habitats strongly suggested that food was not limiting the Denali herd. Denali caribou studies have since documented high calf productivity and implicated predation as a major factor affecting calf survival (Singer, pers. comm.).

Comparisons of activity data from the Denali herd with data from herds experiencing poor food availability/nutritional status indicated a favorable nutritional status among Denali caribou. In Norway, a healthy population of reindeer spent

36% of their time grazing during the first 10 days following calving, compared to 54% in a nutritionally stressed population with poor winter range (Gaare et al. 1975). The Denali herd spent approximately 37% of their time feeding during a comparable time period. Also, the Denali herd's late winter activity (Table 1) and movement rates (Table 5) closely approximated Roby's (1980) description of the activity of a healthy caribou population in northern Alaska, in contrast to his description of starving caribou in West Greenland. Roby reported the following mid- and late winter conditions indicative of severe nutritional stress and poor range condition: (1) an absence of typical active -rest cycles, (2) daily movement rates of less than 1 km. day^{-1}, (3) high proportion of time lying (55%), and (4) low proportion of time (<4%) in activities other than feeding and lying.

All 4 conditions indicate reduced activity in late versus early winter. However, some reductions in activity in late versus early winter likely occur normally in the caribou's annual cycle and are not necessarily indicative of poor nutritional status (Roby 1980). For example, winter reductions in the proportion of time spent in activities other than feeding and lying in the Denali herd (20% in early winter versus 6% in late winter (Table 1)) were comparable to reductions experienced by the Central Arctic herd (17% in early winter versus 10% in late winter), where unusual winter stress and poor calf production were not noted (Roby 1980).

With more comparative data, activity patterns documented in the absence of insects or rutting bulls may be useful in assessing food availability/ range condition. For instance, active periods among Segal's (1962) reindeer in the Soviet Union were approximately 30 min longer than observed in the Denali herd for comparable time periods (postcalving) in the absence of insect harassment. Yet, rest periods were similar between studies. Presumably, Segal's animals had more difficulty in reaching satiety, possibly indicating a poorer range condition.

Documentation of activity budgets and patterns

Segal (1962) found that reindeer exhibit active-rest cycles of nearly constant duration during 24-hr periods within a season, unless disturbed by insects. No differences were found in the duration of active and rest periods between day and night, including overcast nights (Segal 1962). Therefore, activity budgets collected during complete active-rest cycles should accurately estimate the proportion of time spent in various activities throughout the 24-hr period or particular season.

Two methods may be used to document activity budgets during active-rest cycles. Firstly, activity of individual animals can be recorded continuously throughout the active-rest cycle. Secondly, activities of groups can be recorded by scanning the group as often as possible throughout the active-rest cycle (e.g., 5- or 10-min intervals). If scans of groups are used to calculate activity budgets, group size must either remain constant throughout each active-rest cycle or scan data must be proportionately corrected to a constant group size. If group size fluctuates throughout an active-rest cycle, proportions of active or rest time are underestimated for those scans with fewer animals.

Ideally, only data collected during complete ative-rest cycles should be used to calculate activity budgets. When conditions do not exist (e.g., insufficient daylight or vantage points) for collecting data during complete active-rest cycles, observation periods should be sufficiently long so as not to overestimate time spent lying or standing, as these activities are the easiest to observe for long periods.

Because activity patterns help explain differences in activity budgets, documentation of activity patterns should accompany activity budgets whenever possible.

CONCLUSION

Denali caribou were not experiencing low food availability or unusual nutritional stress as evident by the greater activity of Denali caribou in late winter compared to starving caribou in West Greenland and by the low proportion of time spent grazing in spring compared to reindeer on overgrazed ranges in Norway. The minor reductions in activity of Denali caribou as winter progressed compared to starving caribou in West Greenland likely did not indicate unusual nutritional stress. Reduced activity and energy expenditure in late winter acts to conserve fat and is likely a behavioral response common to *Rangifer*

resulting from the negative energy balance experienced during long arctic and subarctic winters.

Other considerations also suggest the Denali herd is not energeticaly stressed compared to other Alaskan herds. On most of the eastern wintering area and on at least a portion of the western wintering area, Denali caribou spent a minimum of time (<1%) cratering through snow to reach forage. This was due to the extreme windswept character of foraging areas, with virtually no snow remaining. Also, the influence that insects have on the energetic status of Denali caribou is likely realtively moderate due to: (1) the relative scarcity of mosquito and black fly harassment, and (2) the high availability of insect-relief sites (snowbanks and glaciers) on the summer range which reduces time spent running.

Activity data are most useful if activity budgets are calculated from complete active-rest cycles and are accompanied by the duration of active-rest periods. The dominant factor influencing seasonal differences in caribou activity budgets was the duration of active periods, except when insects, rutting bulls, and, presumably, mushroom-searching disturbed active-rest cycles. Duration of undisturbed active periods is presumably most strongly related to rumen fill and, thus, food availability. Therefore, duration of active periods may indicate relative range condition.

Late winter activity data may be useful in assessing range condition throughout winter and may give managers a key to assessing overstocked ranges. An understanding of *Rangifer* activity data in the context of population dynamics, however, will require considerable more comparative study. In North America, an absolute shortage of food has never been demonstrated to cause declines in free-ranging caribou populations. Activity data would provide managers with little useful information during declines caused by adverse snow conditions or icing.

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