

SEASONAL ACTIVITY PATTERNS OF MOOSE ON THE KENAI PENINSULA, ALASKA

John S. Bevins¹, Charles C. Schwartz² and Albert W. Franzmann²

¹Deceased, John was lost at sea north of Barrow, Alaska on a polar bear survey flight on October 11, 1990. This paper was prepared by him prior to his death. John was associated with the Alaska Coop. Wildl. Res. Unit, University of Alaska, Fairbanks; Alaska 99775 during this study. ²Alaska Dept. of Fish and Game, Moose Research Center, Soldotna, AK 99669.

ABSTRACT: We obtained monthly estimates of 24-hour activity patterns of moose (*Alces alces*) on the Kenai Peninsula, Alaska, during winter and summer. Activity levels of moose during winter overlapped between areas of high and low deciduous browse availability. Shorter resting periods occurred during summer months ($x = 105$ min), than during winter months ($x = 171$ min), resulting in increased activity levels from winter ($x = 486$ min) to summer ($x = 622$ min). No consistent pattern was found in the difference in active period length between summer ($x = 80$ min) and winter ($x = 81$ min). Estimates are useful for predicting total energy expenditure of moose. Large variations in activity levels among individual moose point out the importance of obtaining unbiased samples from populations.

ALCES VOL. 26 (1990) pp.14-23

Recently, efforts have been made to construct models for estimating nutritional carrying capacity of moose range (Hubbert 1987). These models attempt to balance energy requirements of animals with energy supplied by the range. Energy expenditure by moose varies seasonally and among individuals (Regelin *et al.* 1981, Renecker and Hudson 1983) and accurate energy budgets are therefore necessary to estimate an animal's daily and seasonal energy needs. Activity is a major component of this energy budget. Observations of moose and other ruminants indicate that almost all of their time is spent either resting/ruminating or searching for and ingesting food (Bubenik 1960, Collins *et al.* 1978, Moen 1978, Cederlund 1981).

Food intake rates of northern ruminants are reduced in habitats where forage availability is low (Collins *et al.* 1978, Trudell and White 1981, Wickstrom *et al.* 1984, Renecker and Hudson 1986a), suggesting that activity level may therefore be a useful indicator of food availability. However, Cederlund *et al.* (1989) were unable to demonstrate significant differences in activity levels of moose on 2 winter ranges of different forage quality.

North-temperate and northern ruminants undergo seasonal fluctuations in activity lev-

els (Craighead *et al.* 1973, Cederlund 1981, Georgii 1981), which may result from endogenous changes influenced by environmental cues (Aschoff 1963) as an adaptation to food scarcity and snow conditions during winter (Craighead *et al.* 1973, Roby 1980, Cederlund 1981, Georgii 1981, Jingfors 1982).

This study was conducted to obtain estimates of activity components of moose in southcentral Alaska during winter and summer months. We also wanted to 1) test whether winter activity levels of moose differed between areas of low and high deciduous browse availability and 2) determine if a seasonal difference in activity level was due to differences in forage processing time (resting bout length), ingestion time (active bout length), or a combination of both.

STUDY AREA

This study was conducted within four 2.6 km² enclosures (pens 1-4) at the Moose Research Center (MRC), a research facility of the Alaska Department of Fish and Game located on the north-central Kenai Peninsula, Alaska. The pens were within a 1250 km² area that was burned by wildfire in 1947 (Oldemeyer and Regelin 1987) and consisted

of a mosaic of mature white (*Picea glauca*) and black (*Picea mariana*) spruce/deciduous forest, spruce-paper birch (*Betula papyrifera*) regrowth and spruce regrowth. Sedge meadows, ponds and small lakes also occur in all pens. Additional tree species include aspen (*Populus tremuloides*), willow (*Salix* sp.) and cottonwood (*Populus trichocarpa*). Lowbush cranberry (*Vaccinium vitis-idaea*) was the most prevalent understory species.

The density of moose within the burn area peaked in 1970, when Alaska Department of Fish and Game surveys estimated 3.6 moose/km². Maturity of forest regrowth and heavy utilization of deciduous browse by moose resulted in a continuous decline in the moose population and estimates fell to 0.3 moose/km² in 1986. Availability of deciduous browse was very low in all the pens, ranging from 4.4 to 14.7 kg/ha, and consisted of >95% paper birch. The importance of birch to Kenai Peninsula moose has been well documented (LeResche and Davis 1973, Sigman 1977, Oldemeyer 1981, Regelin *et al.* 1987). Lowbush cranberry was abundant in all pens and was an important supplementary food source (LeResche and Davis 1973, Oldemeyer and Seemel 1976).

METHODS

Six hand-reared and 2 wild adult cow moose were used in this study. All were instrumented with leg-mounted, tip-switch transmitters (Bevins *et al.* 1988) and 2 were randomly assigned to and placed in each of the 4 pens in late November 1985. Moose were designated numerically as to pen assigned (Moose 1-1 = moose 1 in pen 1). Data collection began in mid-December, to allow time for the moose to adjust to their new surroundings.

Pens 1 and 3 were stocked with moose so utilization of current annual growth (CAG) of deciduous browse was about 54-67% of that available to animals during winter (Bevins 1989:43-45). Pens 2 and 4 were stocked so

that deciduous browse CAG was all utilized during winter.

Two receiving stations with omnidirectional antennas were positioned for maximum reception from transmitters in all pens. A data acquisition system (DAS) (Telonics Inc., Mesa AZ) was used to monitor transmitters and store incoming data (Bevins *et al.* 1988). Sampling was conducted during 12 4-day periods from 15 December through 7 April. Four transmitters were monitored alternately during each 24-hour period. Each transmitter was monitored continuously for 3 minutes at 15 minute intervals. Two times per week 24 hour activity data was obtained from each moose.

Transmitters were removed for refurbishing during April and May. Moose were reinstrumented and placed in the 2 pens with the most browse in late May for summer monitoring. Monitoring periods of 24 hours ran from June through late August. Each animal was monitored twice weekly during 9 sampling weeks, using the winter sampling design.

Signal patterns were interpreted to determine if moose were active or resting (lying down) during each sample period and those classified as active were further divided into segments of standing and walking (Bevins *et al.* 1988). Methods used to obtain means and standard errors around estimates of active time, walking time, and individual bout lengths from the activity data were discussed in Bevins *et al.* (1988). Standard errors include within-day and among-day error. Days with at least 1400 minutes of usable data were analyzed to determine activity levels. Seasonal comparisons in daily activity level, duration of active and resting bouts, and number of bouts per day were made using a 2-way analysis of variance (ANOVA) (Sokal and Rohlf 1969) on ranked estimates and using moose and season as the independent variables.

RESULTS

Activity data were obtained for 153 24-hour periods (>1400 min) during winter and for 98 periods during summer (Table 1). Moose 3-2 died in late February, 2 days following immobilization to replace her torn transmitter harness. Malfunctions of 2 transmitters during summer resulted in only 8-10 summer estimates for each moose. Data were categorized by month; few usable samples were collected in late December so these were pooled with January data.

Mean time spent active during a 24-hour period for an individual during a winter month ranged from 349 to 587 minutes (24-41% of a 24-hour day) (Table 1). Although large differences occurred among individuals and among months for individuals, there was no consistent trend to suggest differences among months or among pens with different levels of deciduous browse CAG availability. The greatest differences in activity levels occurred among animals within the same treatments during each month. Activity levels were highly variable among days for individual moose during each month. Mean time spent active during a 24-hour period by an individual during summer months ranged from 427 to 838 minutes (Table 2). When all values for each moose were pooled by season, rela-

tive activity levels of individuals were similar during both seasons. Mean 24-hour activity levels of individuals were from 83 to 178 minutes higher in summer than winter. Moose were significantly more active in summer than winter ($p < 0.0001$).

Bout Lengths

The average number of bouts per day (active and resting) was significantly higher in summer than winter ($p < 0.0001$). Monthly mean active bout lengths of individuals ranged from 62 to 113 minutes during winter and from 54 to 113 minutes during summer months (Table 2) resulting in no significant difference ($p > 0.91$). Monthly mean resting bout lengths ranged from 144 to 215 minutes during winter and from 81 to 139 minutes during summer months (Table 2) resulting in significantly higher bout lengths in winter ($p < 0.0001$).

Time Spent Walking

Monthly averages of time spent walking by individuals ranged from 8 to 89 minutes per day during winter and 13 to 201 minutes per day during summer (Table 2). These estimates include only those walking bouts involving at least 3 steps, due to the similar signal patterns produced by shorter walking bouts and comfort movements. There was a fourfold difference in time spent walking dur-

Table 1. Time spent active (min) during a 24-hour period for moose in four 2.6 km² pens at the Moose Research Center, Kenai Peninsula, Alaska, during winter 1985-86.

| Treat | Moose | Jan | | | Feb | | | Mar | | |
|-------------------|------------------|----------|----------|------|----------|----------|------|----------|----------|------|
| | | <i>n</i> | <i>x</i> | SE | <i>n</i> | <i>x</i> | SE | <i>n</i> | <i>x</i> | SE |
| High ^a | 1-1 ^b | 8 | 426.5 | 25.1 | 6 | 348.8 | 29.3 | 6 | 499.0 | 40.3 |
| | 1-2 | 8 | 547.0 | 39.7 | 6 | 474.5 | 17.6 | 6 | 497.8 | 40.0 |
| | 3-1 | 8 | 507.8 | 27.9 | 6 | 516.7 | 19.1 | 7 | 473.9 | 23.3 |
| | 3-2 | 8 | 472.5 | 30.6 | 6 | 535.2 | 40.7 | | | |
| Low | 2-1 | 8 | 495.8 | 33.5 | 6 | 401.5 | 23.0 | 7 | 407.6 | 26.6 |
| | 2-2 | 8 | 566.3 | 27.6 | 6 | 503.0 | 19.9 | 5 | 521.4 | 21.2 |
| | 4-1 | 6 | 502.2 | 46.9 | 6 | 445.0 | 27.3 | 7 | 408.7 | 24.2 |
| | 4-2 | 7 | 579.3 | 16.4 | 6 | 465.7 | 22.7 | 6 | 481.2 | 33.0 |

a High and low browse current annual growth availability.

b The first digit refers to the pen, the second the animal.

Table 2. Activity budget data for 8 moose at the Moose Research Center, Kenai Peninsula, Alaska, during winter and summer 1985-86.

| Month | n | Minutes active | | | Minutes walking | | |
|--------|---|------------------------|------|--------------------|-----------------|------|------------|
| | | \bar{x} ^a | SE | range ^b | \bar{x} | SE | range |
| Jan | 8 | 517.2 | 19.9 | 426.5-587.0 | 36.3 | 6.9 | 7.9-62.1 |
| Feb | 8 | 461.3 | 21.9 | 348.8-535.2 | 34.8 | 10.2 | 8.3-89.0 |
| Mar | 7 | 469.3 | 16.9 | 407.6-521.4 | 31.7 | 4.6 | 12.7-42.6 |
| Winter | x | 485.7 | 14.8 | 424.9-534.5 | 34.4 | 4.7 | 12.3-52.5 |
| Jun | 7 | 676.7 | 51.6 | 427.2-837.5 | 108.1 | 24.2 | 16.6-201.0 |
| Jul | 7 | 582.4 | 24.2 | 467.8-648.3 | 59.4 | 14.6 | 21.8-126.3 |
| Aug | 7 | 604.3 | 21.2 | 503.6-687.3 | 68.0 | 19.1 | 13.2-136.3 |
| Summer | x | 622.1 | 24.6 | 540.3-712.4 | 78.4 | 16.6 | 17.5-130.2 |

| Month | n | Active bout length | | | Resting bout length | | |
|--------|---|--------------------|------|--------------------|---------------------|-----|-------------|
| | | \bar{x} | SE | range ^b | \bar{x} | SE | range |
| Feb | 8 | 81.9 | 3.8 | 64.7-97.1 | 76.0 | 4.9 | 153.8-196.2 |
| Mar | 7 | 79.6 | 6.2 | 61.6-112.8 | 166.2 | 8.9 | 143.9-215.2 |
| Winter | x | 79.8 | 3.9 | 69.0-99.8 | 171.1 | 5.1 | 158.1-193.1 |
| Jun | 7 | 91.1 | 10.6 | 54.5-136.2 | 98.0 | 5.0 | 85.5-122.0 |
| Jul | 7 | 74.5 | 8.3 | 54.3-111.0 | 106.7 | 7.7 | 81.3-133.8 |
| Aug | 7 | 78.1 | 4.7 | 57.3-93.6 | 115.2 | 6.3 | 96.2-139.8 |
| Summer | x | 80.6 | 7.0 | 59.3-109.9 | 105.4 | 6.0 | 87.5-131.9 |

a Monthly estimates were obtained for each of 7-8 individuals from several daily estimates (2-8/ mo). Monthly means and standard errors were calculated from the 7-8 estimates

b Low and high estimates of individual moose

ing active periods between the most sedentary and most mobile animals in winter. Those moose found to be most sedentary in winter were also less mobile in summer. A greater discrepancy between individuals occurred in summer.

DISCUSSION

Variability in Activity Level

High variability in activity levels among MRC moose and between days for individuals concurs with data reported for northern ruminants (Georgii 1981, Phillips *et al.* 1973). Mean activity levels for individual MRC

moose during winter differed by a maximum of 110 minutes, or by 7.6% of a 24-hour period. An 8% difference occurred in average time spent walking while active between the most mobile and most sedentary moose. Differences in energy cost between individuals may have been as high as 5% based on an estimated 33% increase in energy costs for feeding versus ruminating moose and an estimated 30% increase in energy cost of walking over feeding (Reneker and Hudson 1983). Differences between individuals may reflect different energy balance strategies. The most active individuals may be more discriminat-

ing in diet selection, thereby offsetting increased energy use with increased energy intake.

Differences Between Treatments During Winter

High individual variability contributed to overlapping activity levels between pens with low and high browse availability. Moose with adequate browse may have been more discriminate in their feeding tactics. They were observed using a much higher proportion of their active periods to feeding, but intake rates were not measured so it was unclear whether or not they consumed more forage within the same amount of time (Bevins 1989). We concur with Cederlund *et al.* (1989) that the amount of time spent active per day by moose during winter is a poor indicator of habitat quality.

Comparisons with Other Winter Studies

Average activity levels for individual MRC moose during winter ranged from 425 to 535 minutes per day ($x=486$ min/day). This range was between estimates reported by Risenhoover (1987) for moose in Denali National Park (DNP) (390 min/day) and Isle Royale National Park (IRNP) (534 min/day), where forage abundance and diversity was greater. Monthly mean values for moose in 2 study areas in Sweden ranged between 420 and 480 minutes per day for January through March, but rose significantly in April and May (Cederlund *et al.* 1989).

Confinement of MRC moose to 2.6 km² pens probably had little influence on activity levels, since free-ranging moose in DNP and IRNP moved only an average of 1095 m/day and 1282 m/day, respectively, during winter (Risenhoover 1987). Averages of from 11 to 13 bout changes per 24 hours for MRC moose were similar to numbers previously reported (DesMueles 1968, Franzmann *et al.* 1976, Reneker and Hudson 1983, Risenhoover 1987, Cederlund *et al.* 1989).

Average resting period lengths for moose

during February and March (176 and 166 min, respectively) were slightly shorter than for DNP moose (means from 178-192 min for four 2-week periods) and IRNP moose (means from 183-204 min for four 2-week periods) during the same months (Risenhoover 1987). Reneker and Hudson (1983) reported mean bedded periods of 135 minutes for 2 cow moose in Alberta during December. In Sweden, mean values ranged from 140 to 175 minutes for moose between January and March (Cederlund *et al.* 1989).

Average active period estimates for MRC moose during February (82 min) and March (80 min) were somewhat longer than for moose in DNP (51-73 min for four 2-week periods), but averages were much longer for moose at IRNP (91-106 min for four 2-week periods) (Risenhoover 1987) where forage biomass was higher than at the MRC. Moose at IRNP were selective and 88% utilization occurred on 5 of 16 food species consuming an estimated 18% of CAG. In contrast, MRC moose used only 1 or 2 deciduous browse species and a very high percentage of CAG was consumed. MRC moose also made high use of lowbush cranberry. A difference in snow depths between study areas may have been an important factor. MRC moose movements were not inhibited by snow and they had free access to ground vegetation throughout winter. Snow restricted movements and buried ground vegetation at IRNP (Risenhoover 1987). Study animals in Sweden were active during 63-68 minute periods from January to March (Cederlund *et al.* 1989).

Seasonal Differences in Activity

Increase in activity levels by MRC moose from winter to summer was consistent with what has been found for cervids (Knorre 1959, Craighead *et al.* 1973, Simpson 1976, Ellenberg 1978, Gates 1980, Cederlund 1981, Georgii 1981, Reneker and Hudson 1983). This increase coincided with higher forage quality (Oldemeyer *et al.* 1977), forage intake (Schwartz *et al.* 1984, Reneker and Hudson

1985) and metabolic rate (Reneker and Hudson 1983, Regelin *et al.* 1985). Our data suggest that seasonal differences in activity levels were reflections of food processing time, as influenced by these factors.

Seasonal Differences in Resting Bout Length

Shorter resting bouts observed for all MRC moose during summer reflected a higher quality diet, increased metabolic rates and higher nutritional requirements. Summer forage was lower in fiber and more digestible than the winter diet (Regelin *et al.* 1987, Reneker 1987). Shorter rumination periods are required to reduce particle size (Van Soest 1982), Robbins 1983) resulting in faster passage rates (Pearce and Moir 1964, Reid *et al.* 1979, White *et al.* 1984). Intake is a function of passage rate. When food is cleared from the rumen, space is available for more ingestion to occur (Moen 1973). Therefore, moose on a high plane of nutrition in summer would require shorter periods to process foods and have shorter resting bouts than moose on high fiber diets in winter.

Shorter resting bouts for MRC moose in summer concur with those reported for other species. Several authors have reported an increase in the number of active bouts from winter to summer for northern ruminants, suggesting that individual resting bouts were shorter (in Cederlund 1981). Miquelle and Jordan (1979) reported 7 to 8 feeding periods per day for moose during summer in IRNP, which was similar to MRC moose. Cederlund (1981) found that roe deer (*Capreolus capreolus*) had shorter resting periods in summer than in winter.

Seasonal Differences in Active Bout Length

There was no consistent pattern to indicate differences in active bout lengths of MRC moose during winter and summer. Since moose are eating to rumen fill or satiation (Ammann *et al.* 1973), they apparently do so in approximately the same time during both seasons.

The length of an active bout is dependent on the space in the rumen at the beginning of the bout and habitat characteristics such as forage availability, quality and distribution. Dry matter intakes of moose in Alberta were lower in winter than summer, due to lower bite rates, smaller bite sizes and higher search effort. It may be that during summer when resting bouts are terminated there is relatively more space in the rumen available for ingestion of additional food. Forage is processed more quickly during summer, but resting bouts are of shorter duration. A small portion of the rumen is emptied during an individual resting bout, since rumen turnover time varies from 16 to 32 hours for moose (Schwartz *et al.* 1988).

Other factors influenced length of active bouts differently between seasons. Some moose spent a much larger portion of their active time travelling during summer than winter. Day length may also be a consideration, although our data indicate moose were equally active during day and night. There is good evidence that moose and other northern ruminants are most active near sunrise and sunset (Best *et al.* 1978, Georgii 1981, Russell and Martell 1986, Cederlund *et al.* 1989).

Active bout lengths were highly variable during both seasons. Periods of activity may be reduced to avoid heat stress during periods of warm ambient temperatures in both seasons (Knorre 1959, Edgerson and McConnell 1976, Reneker and Hudson 1986b). Ambient temperatures were above upper critical temperature of -5 C in winter and 14 to 20 C in summer (Reneker and Hudson 1986b) during periods of both seasons for MRC moose. Moose were observed to seek shade and ponds during hot days in summer. Shorter feeding periods on hot days may have been compensated for by longer feeding bouts during cooler portions of the day. Although the thermoneutral zone for moose appears to extend below -30 C (Reneker and Hudson 1986b) during winter and low temperatures do not necessarily affect their

activity level (Risenhoover 1986), moose may seek thermal cover where food availability is lower during colder weather (Yazan and Glushkof 1969).

Georgii (1981) found that active periods were shorter during winter than summer for red deer (*Cervus elaphus*) and during winter numerous short bursts of activity were common. However, his animals were fed at feeding stations that concentrated individuals and probably minimized search time. No difference in active bout length between summer and winter were detected for roe deer, but bouts were longer in spring and fall (Cederlund 1981).

Feeding periods for moose at IRNP averaged 56 minutes from June through August (Miquelle and Jordan 1979). However, these only included periods of continuous feeding and total active periods were somewhat longer than this. The average for IRNP moose in winter was 102 minutes, much longer than summer (Risenhoover 1987).

Deep snows for cervids have been attributed to increased searching effort (Reneker and Hudson 1986b), increased energy expenditure during foraging (Verme 1968, Parker et al. 1984, Fancy and White 1985), reduced movements (Crete and Bedard 1975, Roby 1980, Cederlund 1981), lowered forage intake (Moen 1976, 1978, Cederlund 1981) and shorter feeding periods (Cederlund 1981). Snowfall was light during this study and is of minor importance to moose activity during most winters on the Kenai Peninsula lowlands. The influence of snow on moose in other study areas (Reneker and Hudson 1986b, Risenhoover 1987) complicates the comparisons with MRC moose.

MANAGEMENT IMPLICATIONS

This study provided information on activity during winter and summer which can be applied to a carrying capacity model based on energy requirements. Mean activity values are applicable to areas with habitat conditions

similar to the MRC (heavily-utilized paper birch stands, cranberry understory available in winter). Although the average time spent walking comprises a very small portion of a day, the added energy expenditure is important and must be considered in the model.

Winter activity estimates for moose were representative of animals in poor habitat, but unimpeded by deep snow. Winter activity varied greatly among individuals, indicating that activity level is a poor indicator of habitat quality in habitats similar to the MRC. Other studies of ruminants revealed no conclusive relationship between activity and winter forage availability either.

The large variability in activity bouts among individuals illustrates the potential danger in drawing conclusions about populations when dealing with small sample sizes or treating several non-random samples from the same individual as independent observations from the population.

ACKNOWLEDGEMENTS

We appreciate the help of D.C. Johnson, F. Ausenda, P. Martin and P. Cannava with data collection. E.F. Becker and S. Thompson provided advice for statistical analysis. K. Hundertmark reviewed the manuscript. We want to thank Julia Bevins for providing the manuscript to us so we could complete the final steps in getting this information published following John Bevins untimely death. This study is a contribution of Federal Aid in Wildlife Restoration, Project W-22.

REFERENCES

- AMMANN, A.P., R.L. COWAN, C.L. MOTHERHEAD, and B.R. BAUMGARDT. 1973. Dry matter and energy intake in relation to digestibility in white-tailed deer. *J. Wildl. Manage.* 37:195-201.
- ASCHOFF, J. 1963. Comparative physiology: diurnal rhythms. *Annu. Rev. Physiol.* 25:561-600.

- BEST, D.A., G.M. LYNCH, and D.J. RONGSTAD. 1978. Seasonal activity patterns of moose in the Swan Hills, Alberta. Proc. N. Am. Moose Conf. Workshop. 14:109-126.
- BEVINS, J.S. 1989. Activity patterns of moose on the Kenai Peninsula, Alaska, as influenced by season and food availability. M.S. Thesis. Univ. Alaska, Fairbanks. 137pp.
- _____, A.W. FRANZMANN, and C.C. SCHWARTZ. 1988. Determining moose activity budgets using leg-mounted tip-switch transmitters and a computerized data acquisition system. *Alces* 24:22-33.
- BUBENIK, A. 1960. Le rythme nycthemeral et le regime journalier des angules sauvages - problemes theoriques - Rythme d'activite du chevreuil. *Mammalia* 24:1-59.
- CEDERLUND, G. 1981. Daily and seasonal activity patterns of roe deer in a boreal habitat. *Viltrevy* 11:315-353.
- _____, R. BERGSTROM, and F. SANDEGREN. 1989. Winter activity patterns of females in two moose populations. *Can. J. Zool.* 67:1516-1522.
- COLLINS, W.B., P.J. URNESS, and D.D. AUSTIN. 1978. Elk diets and activities on different lodgepole pine habitat segments. *J. Wildl. Manage.* 42:799-810.
- CRAIGHEAD, J.J., F.C. CRAIGHEAD, R.L. RUFF, and B.W. O'GARA. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison Drainage Herd as determined by biotelemetry. *Wildl. Monogr.* 33:1-50.
- CRETE, M., and J. BEDARD. 1975. Daily browse consumption by moose in the Gaspé Peninsula, Quebec. *J. Wildl. Manage.* 39:368-373.
- DESMUELES, P. 1968. Determination du nombre tas de crottins rejetes et du nombre de reposes etablies, par jour par l'original (*Alces alces*) en hiver. *Nat. Can. (Que.)* 95:1153-1157.
- EDGERSON, P.J., and B.R. MCCONNELL. 1976. Diurnal temperature regimes of logged and unlogged mixed conifer stands on elk summer range. USDA For. Ser., Pac. Northwest For. Range Exp. Stn. Res. Note PNW-277.
- ELLENBERG, H. 1978. Zur populations okologie des rehes (*Capreolus capreolus* L. Cervidae) in Mitteleuropa. *Spixiana-Zeitschrift fur Zoologie*, suppl. 2. 211 pp.
- FANCY, S.G., and R.G. WHITE. 1985. Incremental cost of activity. Pages 143-159 in R.J. Hudson and R.G. White, eds. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida. 314pp.
- FRANZMANN, A.W., P.D. ARNESON, and J.L. OLDEMEYER. 1976. Daily winter pellet groups and beds of Alaskan moose. *J. Wildl. Manage.* 40:374-375.
- GATES, C.C. 1980. patterns of behavior and performance of wapiti (*Cervus elaphus nelsoni*) in the boreal mixed wood forest. Ph.D. Thesis, Univ. Alberta, Edmonton. 240pp.
- GEORGII, B. 1981. Activity patterns of female red deer (*Cervus elaphus* L.) in the Alps. *Oecologia* 49:127-136.
- HUBBERT, M.E. 1987. The effect of diet on energy partitioning in moose. Ph.D. Thesis, Univ. Alaska, Fairbanks. 158pp.
- JINGFORS, K.T. 1982. Seasonal activity budgets and movements of reintroduced Alaska muskox herd. *J. Wildl. Manage.* 46:344-350.
- KNORRE, E.P. 1959. Ecology of the moose. Proc. Pechora-Ilyich State Nature Preserve. 7:1-167.
- LERESCHE, R.E., and J.L. DAVIS. 1973. Importance of non-browse foods to moose on the Kenai Peninsula, Alaska. *J. Wildl. Manage.* 37:279-287.
- MIQUELLE, D.G., and P.A. JORDAN. 1979. The importance of diversity in the diet of moose. Proc. N. Am. Moose Conf. Workshop 15:54-79.
- MOEN, A.N. 1973. Wildlife ecology. W.H.

- Freeman and Co., San Francisco. 458pp.
- _____. 1976. Energy conservation by white-tailed deer in the winter. *Ecology* 57:192-198.
- _____. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *J. Wildl. Manage.* 42:715-718.
- OLDEMEYER, J.L. 1981. Estimation of paper birch production and utilization and an evaluation of its response to browsing. Ph.D. Thesis, Pennsylvania State Univ., University Park. 58pp.
- _____, A.W. FRANZMANN, A.L. BRUNDAGE, P.D. ARNESON, and A. FLYNN. 1977. Browse quality and the Kenai moose population. *J. Wildl. Manage.* 41:533-542.
- _____, and W.L. REGELIN. 1987. Forest succession, habitat management and moose on the Kenai National Wildlife Refuge. *Swedish Wildl. Res. Suppl.* 1:163-179.
- _____, and R.K. SEEMEL. 1976. Occurrence and nutritive quality of lowbush cranberry on the Kenai Peninsula, Alaska. *Can. J. Bot.* 54:966-970.
- PARKER, K.L., C.T. ROBBINS, and T.A. HANLEY. 1984. Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Manage.* 48:474-488.
- PEARCE, G.R., and R.J. MOIR. 1964. Rumination in sheep. I. The influence of rumination and grinding upon the passage and digestion of food. *Aust. J. Agric. Res.* 15:635-644
- PHILLIPS, R.L., W.E. BERG, and D.B. SINIFF. 1973. Moose movement patterns and range use in Northwestern Minnesota. *J. Wildl. Manage.* 37:266-277.
- REGELIN, W.L., C.C. SCHWARTZ, and A.W. FRANZMANN. 1981. Respiratory chamber for study of energy expenditure of moose. *Alces* 17:126-135.
- _____, _____, and _____.
1985. Seasonal energy metabolism of adult moose. *J. Wildl. Manage.* 49:388-393.
- _____, _____, and _____.
1987. Effect of forest succession on nutrition dynamics of moose forage. *Swedish Wildl. Res. Suppl.* 1:247-263.
- REID, C.S.W., A. JOHN, M.J. ULYATT, G.C. WAGHORN, and L.P. MILLIGAN. 1979. Chewing and the physical breakdown of feed in sheep. *Ann. Res. Vet.* 10:205-207.
- RENEKER, L.A. 1987. Bioenergetics and behavior of moose in the aspen-dominated boreal forest. Ph.D. Thesis, Univ. Alberta, Edmonton. 210pp.
- _____, and R.J. HUDSON. 1983. Winter energy budgets of free-ranging moose, using a calibrated heart rate index. *Proc. Int. Conf. Wildl. Biotelem.* 4:187-211.
- _____, and _____. 1985. Estimation of dry matter intake of free-ranging moose. *J. Wildl. Manage.* 49:785-792.
- _____, and _____. 1986a. Seasonal foraging rates of moose in aspen boreal habitats. *J. Wildl. Manage.* 50:143-147.
- _____, and _____. 1986b. Seasonal energy expenditures and thermoregulatory responses of moose. *Can. J. Zool.* 64:322-327.
- RISENHOOVER, K.L. 1986. Winter activity patterns of moose in interior Alaska. *J. Wildl. Manage.* 50:727-734.
- _____. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Ph.D. Thesis, Michigan Tech. Univ., Houghton. 108pp.
- ROBBINS, C.T. 1983. Wildlife feeding and nutrition. Academic Press, New York. 343pp.
- ROBY, D.D. 1980. Winter activity of caribou in two arctic ranges. *Proc. Int. Reindeer/Caribou Symp.* 2:527-544.

- RUSSELL, D.E., and A.M. MARTELL. 1986. Winter ecology of the Porcupine caribou herd, Yukon: Part III, Role of day length in determining activity pattern and estimating percent lying. *Rangifer* 1:253-259.
- SCHWARTZ, C.C., W.L. REGELIN, and A.W. FRANZMANN. 1984. Seasonal dynamics of food intake in moose. *Alces* 20:223-242.
- _____, _____, _____, R.G. WHITE, and D.F. HOLLEMAN. 1988. Food passage rate in moose. *Alces* 24:97-101.
- SIGMAN, A.M. 1977. The importance of the cow-calf bond to overwinter moose calf survival. M.S. Thesis, Univ. Alaska, Fairbanks. 182pp.
- SIMPSON, A.M. 1976. A study of the energy metabolism and seasonal cycles of captive red deer. Ph.D. Thesis, Univ. Aberdeen, Scotland. 241pp.
- SOKAL, R.R., and F.J. ROHLF. 1969. *Biotelemetry*. W.H. Freeman and Co., San Francisco, California. 776pp.
- TRUDELL, J., and R.G. WHITE. 1981. The effect of forage structure and availability on food intake, biting rate, bite size and daily eating time of reindeer. *J. Appl. Ecol.* 18:63-81.
- VAN SOEST, P.J. 1982. *Nutritional ecology of the ruminant*. O and B Books, Inc., Corvallis, Oregon. 374pp.
- VERME, L.J. 1968. An index to winter weather severity for northern deer. *J. Wildl. Manage.* 32:566-574.
- WHITE, R.G., D.F. HOLLEMAN, C.C. SCHWARTZ, W.L. REGELIN, and A.W. FRANZMANN. 1984. Control of rumen turnover in northern ruminants. *Can. J. Anim. Sci.* 64(Suppl.):349-350.
- WICKSTROM, M.L., C.T. ROBBINS, T.A. HANLEY, D.E. SPALINGER, and S.M. PARISH. 1984. Food intake and foraging energetics of elk and mule deer. *J. Wildl. Manage.* 48:1285-1301.
- YAZAN, T.P., and V.M. GLUSHKOV. 1969. The influence of low air temperatures on the distribution and feeding characteristics of elks. *Tr. Kirov Skh. Inst.* 21:125.