

寒带针阔混交林中美洲马鹿的昼夜 采食节律与食物、气温的关系

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野生反刍动物一天中大部分时间用于摄食与反刍。为了适应采食生态环境与食物类型,野生反刍动物的行为表现出高度可塑性。反刍动物的采食活动节律受到食物摄入速率和消化能力的影响。摄入速率又受食物丰度、分布和动物的采食经验的影响。动物的消化能力则与食物质量、消化性能、排空速率以及消化道的充盈程度有关。一年四季中,美洲马鹿(*Cervus elaphus nelsoni*)的采食频次和持续时间变化很大。在加拿大阿尔伯达中部的针阔混交林中,我们研究了食物质量和丰度、气温对美洲马鹿的昼夜采食节律的影响。食物丰度影响了摄食速率。食物质量决定了消化道内容物的排空速率和消化速率。春天,当气温适中,可消化性高的青草茂盛时,美洲马鹿具有多相采食活动节律(较均匀分布的多个采食周期)。此时,瘤胃的排空可能引发采食。夏天,午间高温抑制了采食活动。此时,美洲马鹿的采食活动呈双峰型。冬天,尽管美洲马鹿的采食量下降,由于食物的纤维索含量高,美洲马鹿仍花费较多的时间反刍咀嚼,但这些活动多集中于气温较高的午间。极度低温会抑制美洲马鹿的摄食。而当气温回升后,美洲马鹿会补偿性地延长采食时间。美洲马鹿的昼夜采食节律季节性变化是其适应北方寒带气候和觅食环境的生态行为机制。

关键词 美洲马鹿; 活动节律; 寒带针阔混交林

更 正

因作者疏忽,本刊第16卷第3期发表的“马边大风顶自然保护区大熊猫对竹类的选择利用”一文的研究方法中选择系数公式 $W_i = r_i p_i / \sum r_i p_i$ 有误,正确的公式为 $W_i = (r_i / p_i) / \sum (r_i / p_i)$,特此更正。

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AMBIENT TEMPERATURE, FOOD AND FORAGING ACTIVITIES OF WAPITI, *CERVUS ELAPHUS* *NELSONI*, IN ASPEN BOREAL FOREST

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Abstract

Activity rhythms of wapiti in aspen-boreal forests are polyphasic with fewest feeding bouts in mid-winter and summer (5.6/d) and most frequent feeding bouts in spring (9.2/d). Digestive kinetics, forage quality and availability as well as ambient temperature emerged as key factors regulating seasonal feeding rhythms. Forage availability influenced intake rate hence feeding bout length whereas food quality determined passage and digestion rates. Rumen repletion and depletion set the base line for hunger and the desire to eat. When high quality forage was available in late spring, wapiti had a polyphasic foraging pattern (evenly distributed multiple foraging bouts). However, high ambient temperature suppressed feeding during mid-day in summer, inducing a crepuscular foraging pattern. Wapiti were able to compensate in subsequent foraging bouts for foraging time lost due to extreme ambient temperatures.

Key words Wapiti (*Cervus elaphus nelsoni*); Activity rhythm; Aspen boreal forest

Deciding when and where to forage is an important aspect of trophic adaptation among wild ruminants (Senft et al., 1987). Foraging orientation may take place at different spatial and temporal scales. For example, some cervids move between widely separated summer and winter ranges (Morgantini et al., 1988; Brown, 1992). Others show more local seasonal movements (Bowyer, 1981; Mann et al., 1989; Gillingham et al., 1992). Beside spatial or vectorial movements, cervids often express well-developed seasonal diel activity rhythms (Gates et al., 1983; Renecker et al., 1990).

The diel pattern of wapiti, a large cervid occupying mountains, forests and parkland in central and western North America, varies from polyphasic (evenly distributed multiple foraging bouts) in winter and spring to biphasic (two main foraging bouts in early morning and late evening) in summer and autumn (Gates et al., 1981). Foraging bouts are both more frequent and evenly spaced throughout the day in spring than in winter.

We hypothesized that this diel rhythm results from both internal physiological and

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external environmental factors. The internal physiological rhythm arises from the rumen repletion-depletion cycle which determines satiety and the desire to eat. Availability, distribution and structure of forages influence intake rate and consequently the duration of feeding bouts. Forage quality dictates the speed of rumen emptying by the linked processes of digestion and passage and thus determines the length of resting/rumination bouts. Ambient temperature and other pre-emptive environmental or social factors can momentarily override hunger. When ambient temperature is within the thermal neutral zone of wapiti, the polyphasic foraging pattern may largely reflect the underlying rumen cycle.

This study was conducted to document seasonal activity cycles of wapiti in aspen boreal habitats and to probe the interplay of intrinsic and extrinsic determinants. Time and space orientations of birds and small mammals can be studied in the laboratory (Falk et al. 1992), but it is more difficult to manipulate the environment of large ungulates and we had to rely on observational methods involving comparisons of activities among seasons and among days with contrasting weather conditions.

RESEARCH AREA AND METHODS

The study was conducted at the Ministik Wildlife Research Station, Alberta, Canada (53°18'N, 114°35'W). The region is a mosaic of aspen forests, open grasslands, sedge wetlands and sloughs, and is considered to be on the southern fringe of the boreal mixed-wood forest (Rowe, 1972). Gates et al. (1981) classified the vegetation of the research station into 5 types: poplar forest (*Populus* spp.), upland and lowland grasslands, sedge wetland and willow margin. The winters are cold with January temperatures which range from -49°C to 10°C. Generally, snow cover persists from late November till mid-March. By late March, most of the grasslands are snow free. Summers are warm with temperature occasionally reaching 30°C. Annual precipitation is about 500 mm of which about a quarter is snow. Rain falls mainly in May, June and July.

We observed six two-year-old non pregnant female wapiti. During winter (January, February and March), they were offered alfalfa hay but they depended solely on native forage for the rest of the year. A vibracorder (Kienzle Apparate G. M. b. H., Villingen, Schwarzwald, Germany), an accepted device for recording activity of grazing animals (Mosley et al. 1987), was suspended from a loosely fitted neck collar during January 24~30 (winter), May 8~25 (spring) and July 20~24 (summer). To calibrate the vibracorders and determine the proportion of active time spent feeding and resting time spent ruminating, we conducted dawn to dusk scans in each season (specifically on January 6, April 4, May 16 and August 18). Active/resting time series were summarized for 30 min intervals from vibracorder data.

To determine the proportion of active time spent feeding and proportion of bedding time spent ruminating, we conducted dawn to dusk behavior scans using a scan interval

of 10 min. Grazing time was calculated as the recorded active time (vibracorder) multiplied by the proportion of the observed active time spent feeding (scan). Rumination time was calculated similarly from the recorded resting time and the proportion of observed resting time spent ruminating. Behavioral synchronization was expressed with the following index (SI):

$$SI(t) = \frac{\max_{i=1,n}(Bi(t)) - \min_{i=1,n}(Bi(t))}{m} \quad (1)$$

where, Bi is behavior i occurring at time t , n is the number of behavior occurrences at time t , m is the number of animals observed. SI equals 1 when all animals are engaged in the same activity, whereas when SI equals 0 when each animal is engaged in a different activity.

We also recorded habitat selection and behavior of focal animals with a pocket computer (TRS-80 PC, Tandy, TX, USA) programmed for field ethological studies. Rumination was recorded as chews or seconds per bolus. After recording about 20 boli from an individual, we moved to another until all ruminating wapiti were studied. Using results for dry matter (DM) intake from Jiang et al. (1992) and Jiang (1993), we calculated mean intake rates (g/min). Following grazing wapiti, we clipped pasture forages to simulate the diet of wapiti and determined the neutral detergent fiber (NDF, A. O. A. C. 1984) of the clipped forage samples. Rumination times were expressed as min/kg DM or min/kg NDF (considered cell wall, CW).

To test the periodicity of seasonal foraging bouts, we calculated autocorrelations of the foraging time series. We also calculated cross-correlations between the time series of ambient temperature and foraging, as well as that of rumination and foraging (Wilkinson, 1992). ANOVA of the number and duration of foraging or rumination bouts, and of chews or seconds per bolus were conducted with SuperANOVA (Abacus Concepts, 1989). The Tukey-Kramer method (Sokal et al., 1981) compared differences among seasonal means.

RESULTS

Seasonal activity patterns

Activity patterns changed among seasons. Activity patterns were polyphasic in winter but the frequency and duration varied among days. Wapiti were more active during daylight when it was relatively warm; night feeding bouts were shorter in winter than spring. Wapiti had regular and frequent foraging bouts in spring (April and May) when temperatures remained between -4 and 19°C . Diel activity patterns in summer were biphasic; feeding bouts were commonly absent at midday when ambient temperature were above 23°C . Short bouts at noon were diversions and involved little grazing.

Autocorrelation analyses indicated weak 24 h periodicity in January and March. March had two and six h periodicity within 24 h. April had one h periodicity within a 24 h cycle. In May, 24 h periodicity was weak but there were significant two h cycles.

In July, besides the significant 24 h periodicity, there also were 12 h and two h cycles. Synchronization of activity was highest in summer and second highest in early spring in free-ranging wapiti (Table 1). When wapiti had supplementary food in winter, they bedded next to the hay source and synchronized activities least compared with other seasons.

Table 1. Rumination and feeding parameters of wapiti in relation to season and forage

	January	April	May	July/August
Synchroniz- ation index	0.75±0.04 (56) ^{a*}	0.95±0.02(82) ^b	0.79±0.03 (87) ^b	0.96±0.01 (95) ^b
Forage				
DM(%)	88±1(2) ^a	29±1(2) ^b	23±1(2) ^a	32±1(2) ^b
NDF(%)	68±1(2) ^a	70±2(2) ^b	36±1(2) ^a	48±1(2) ^a
Rumination				
Min/bout	153±5(39) ^a	85±8(49) ^{ab}	82±5(55) ^b	129±9(28) ^a
Bouts/d	5.6±0.4(7) ^a	7.0±0.5(7) ^a	9.2±0.4(6) ^b	5.6±0.4(5) ^a
Min/kg DM	219±1(7) ^a	220±1(7) ^a	66±1(6) ^b	96±1(5) ^a
Min/kg NDF	322±1(7) ^a	314±1(7) ^a	183±1(6) ^b	199±1(5) ^a
Chews/bolus	59±2(40) ^a	51±2(40) ^{ab}	35±3(40) ^{ab}	48±2(40) ^b
Feeding				
Mean intake rate (g/min)	5.5±0.2(7) ^a	2.9±0.3(7) ^b	12.4±0.4(6) ^a	9.8±0.4(5) ^a
Cell wall intake (kg/d)	2.1±0.1(7) ^a	1.7±0.1(7) ^a	2.6±0.1(6) ^b	3.6±0.1(5) ^a
Min/bout	115±10(39) ^a	118±9(49) ^a	70±2(55) ^b	149±10(24) ^a
Bouts/d	5.6±0.3(7) ^a	7.3±0.6(7) ^b	9.2±0.5(6) ^a	4.8±0.2(5) ^a

* Data presented as mean±standard error (sample size)

No significant differences between the data that have the same superscripts in the same row ($P < 0.05$)

WINTER

Wapiti adjusted their lying posture, huddled, exposed their body surfaces to sunshine and reduced activities during cold winter nights. Although food was abundant, mean intakes remained low (Table 1). Rumination expressed per kg dry matter intake were longest among all seasons. On average, rumination bouts were longer than feeding bouts.

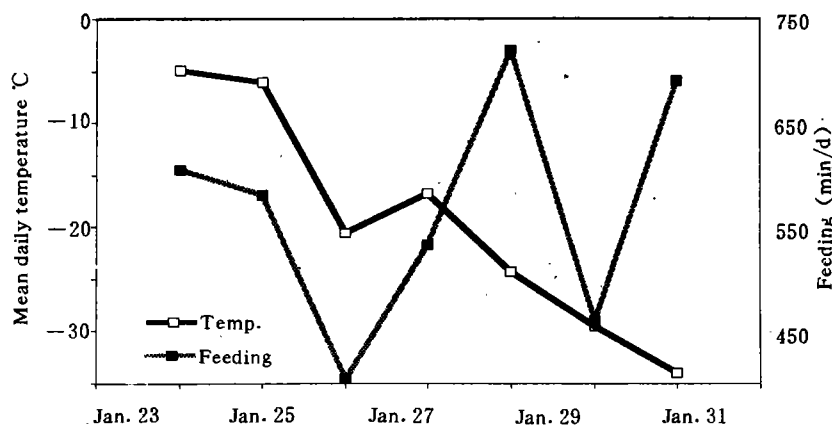


Fig. 1 During a chronic cold period in January, wapiti No. 8806 compensated for decreased feeding on certain days with longer feeding on subsequent days

Chronic cold interrupted this feeding rhythm. From January 23 to 31, ambient temperature decreased from -5°C to about -35°C . In response, wapiti No. 8806 first reduced daily feeding time consecutively for three days as the temperature dropped, then increased as cold persisted in the fourth and fifth day, and reduced again in the sixth day before finally increasing on the seventh day (Fig. 1).

Early spring

Number of feeding bouts increased from winter to early spring when wapiti started to graze new growth ($P < 0.05$, Table 1). Because green forages were not available in April, mean intake rate declined to its lowest level. To satisfy energy and nutrient requirements, wapiti spent 14.6 h per day foraging. Feeding bouts were longer than rumination bouts during this period. Ambient temperature varied little and had minimal; the cross correlation between ambient temperature and activity was not significant ($P > 0.05$).

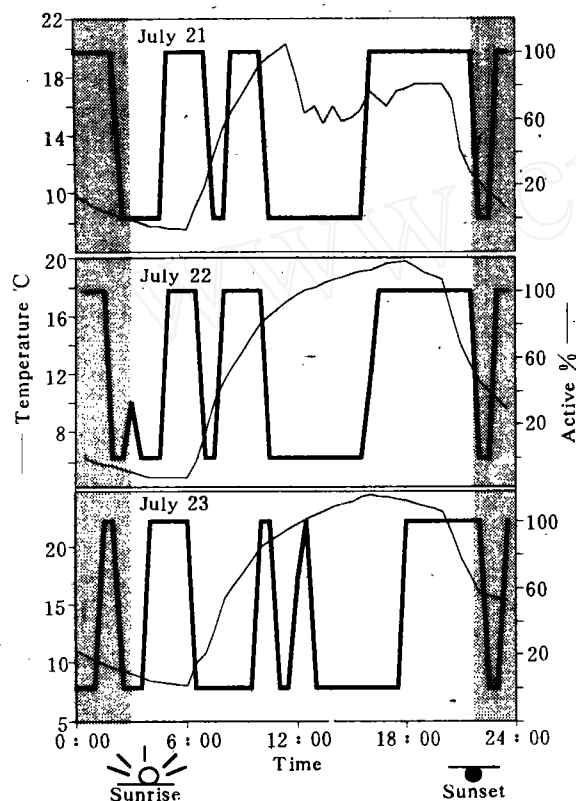


Fig. 2 In late July, wapiti No. 8811 postponed late afternoon bouts presumably to avoid heat

bouts in summer, although the rumination requirement per kg dry matter intake increased from May ($P < 0.05$). Cross correlation of resting and consecutive active bouts was significant ($P < 0.05$).

Late spring

When warm temperatures and rainfall stimulated pasture growth, mean intake rate increased sharply from April to May ($P < 0.05$, Table 1). Wapiti engaged in more foraging bouts in May than any other month ($P < 0.05$) and durations of foraging bouts decreased compared with winter ($P < 0.05$). Rumination duration was the lowest among all seasons ($P < 0.05$), amounting to only 66 min per kg dry matter intake. Because of the high intake in each feeding bout, resting bouts were longer than feeding bouts. During this period, the cross correlation of resting and active bouts was significant ($P < 0.05$).

Summer

As pasture forages matured in July and August, mean intake rate declined (Table 1). Rumination bouts were shorter than feeding

Ambient temperature profoundly influenced the timing of foraging bouts in summer. Grazing was significantly correlated with ambient temperature (cross correlation, $P < 0.05$). In late July when temperature increased above 24°C in late afternoon, wapiti No. 8811 postponed the evening foraging bout for two h (Fig. 2), thus reducing the proportional feeding time from 51% (July 22) and 58% (July 23) to 43% (July 23). The reduced foraging time was compensated in the evening so daily feeding time increased to 51% on July 24.

DISCUSSION

Ruminants organize foraging activities into grazing and ruminating bouts (Foose, 1982). Hofmann (1989) pointed out that short but frequent foraging bouts characterize small concentrate selectors whereas fewer but longer feeding bouts characterize roughage eaters. As an intermediate mixed feeder, the wapiti modifies its diel foraging rhythm from short frequent feeding rhythm in spring to long crepuscular feeding cycle in mid summer.

Circadian activity patterns result from interactions between endogenous and environmental influences. Reticulo-rumen distention signals hunger and satiety. But this regular cycle may be interrupted by extreme thermal environment or pre-empted by other factors such as predators, disturbance or social interaction. Seasonal differences in these diel cycles can be interpreted in terms of forage biomass/quality, metabolic demands and thermal environments.

Digestive kinetics

Intake rate determines the speed of rumen repletion (Wickstrom et al. 1984) and hence the duration of foraging bouts. Mean intake rates reported here are similar to those from other studies conducted at the Ministik Wildlife Research Station (Wairimu et al., 1993, Nietfeld, 1983). In winter, intake rates appear limited mainly by low metabolic demand. In early spring before new growth emerged, low availability of pasture biomass hindered intake rate; during a 2 h grazing bout, wapiti ingested less than 350 g dry matter. In late spring, wapiti ate much faster, ingesting about 850 g dry matter during a 2h grazing bout. Late spring pasture also provided a diet with highest digestion and passage rates among all seasons (Jiang, 1993) and hence rapid rumen emptying. Forage intake rates dropped as grass swards matured (Jiang et al., 1994). However, during long early morning and evening bouts, wapiti consumed about 1500 g dry matter. High food intake in the morning and evening bouts coupled with relatively low digestion and passage rates created longer rumination/rest periods in late summer.

Scaled on a unit dry weight basis, wapiti spent more time ruminating in winter and early spring, and the least time in late spring. Wapiti ruminated green forage in spring and summer less than winter forage on unit weight fiber basis. The picture is complicated somewhat because the rumination requirement also reflects intake levels. Gates et al. (1983) found that free-ranging wapiti spent considerably more time (52%~54%) feed-

ing than wapiti offered supplemental food (39%) in winter. However, free-ranging wapiti spent 38% of their daily time ruminating whereas supplementary fed wapiti spent 47%. Longer foraging time may be due to the lower intake rate and the difference of rumination times may be due to the difference in intakes.

Rumination requirement was reflected not only by the total rumination time but also by chews per bolus. When fed alfalfa hay and weathered early spring forage, wapiti masticated each bolus almost twice as much as they did when they grazed green spring forages. Moose in the same research area masticate each bolus longer than wapiti but chews per bolus similarly increased with maturation of browse (Renecker, 1987).

Autocorrelation analyses indicated that in addition to the 24 h periodicity, there were shorter cycles which presumably represent feeding periods within a day (e. g. , two and six h periodicity in January and March and two h cycles in May). In July, the two h periodicity was nested within a 12 h crepuscular feeding cycle.

Thermal environment

In summer, heat loads depressed grazing. Parker et al. (1984) reported that wapiti in summer coat had an upper critical temperature of about 26°C. The 12 h periodicity in July implied that wapiti shifted foraging to crepuscular periods (morning/evening) especially on hot days.

The cross-correlation between ambient temperature and activity was not significant in winter. The reasons may be (1) there is no clear diurnal pattern of ambient temperature during chronic cold periods, (2) wapiti may lie down and eat when possible (Jiang et al. , 1993b), and (3) ambient temperatures in winter normally remain within the thermal neutral zone of wapiti (−20°C to 10°C, Parker et al. , 1984). However, finer grained analysis did show that feeding pattern in winter was interrupted by chronic sieges of severe cold. The lower critical temperature of wapiti in winter coat is −20°C (Parker et al. , 1983). Below this temperature, wapiti had a smaller activity range and only stood up during feeding. Reducing feeding time minimized thermoregulatory costs (Gates et al, 1979).

In summary, digestive physiology is the central stimuli of feeding and hence activity and energy budgets of wapiti. Although central, it is part of a hierarchy of priorities among control units of behavior (Alcock, 1984). Escaping from heat stress takes priorities among other possible actions in summer. In winter, extreme cold forces animals to suspend feeding until conditions improve. These suspensions of feeding are followed by compensatory feeding which under most conditions makes up any shortfall.

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