

Optimal grazing of wapiti (*Cervus elaphus*) on grassland: patch and feeding station departure rules

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Summary

We studied factors which may shape giving-up decisions of wapiti grazing grassland patches (area where a wapiti initiates and terminates a feeding sequence) and feeding stations (area within a patch that a wapiti can reach without moving its forelegs). In grassland patches, cropping rate decreased after a critical period, whereas at feeding stations cropping rate increased with cumulative bites consumed. The number of feeding stations grazed, number of bites taken and grazing time did not dictate the termination of grazing in a patch. Wapiti gave up a patch only after the cropping rate at a feeding station dropped below the seasonal expectation during trials on lush pasture in May, but gave up after the cropping rate dropped below the seasonal expectation at two consecutive feeding stations in March/April and August when foraging conditions were less favourable. This confirmed a prediction of the marginal value theorem. Wapiti did not give up a feeding station according to bites taken, grazing time or cropping rate, but they left feeding stations when their lateral neck angle reached a critical point suggesting a biokinetic explanation. Leaving feeding stations when ungrazed forage can no longer be reached and patches when intake rate drops both appeared to be rules used by wapiti grazing grasslands of the boreal mixed wood forest.

Keywords: elk; optimal foraging; patch; feeding station; marginal value theorem; foraging ecology

Introduction

Charnov (1976) introduced the marginal value theorem to address the question of when a forager should leave a patch. McNair (1982) predicted longer giving-up times for better quality patches. Iwasa *et al.* (1981), testing departure strategies for a patchy environment with a stochastic model, concluded that the choice of foraging strategies depended on prey distribution. Leaving patches at fixed giving-up times was best when the variance of prey distribution among patches was high, whereas leaving patches after consuming a fixed number of prey tended to be best when variance of prey distribution was low. We were interested in how these strategies applied to the foraging of a large ruminant herbivore, the wapiti (*Cervus elaphus*).

The departure decision a forager makes is a problem of optimal allocation of foraging time, which has stimulated experiments in both laboratory and field. Cowie (1977) reported that the great tit adjusted foraging time in artificial patches according to travelling time. Hodges (1981) discovered that the bumble-bee maximized energy intake by departing from individual *Delphinium* plants when nectar intake rate fell. By computer simulation, Pleasants (1989) tested the fixed and stochastic giving-up thresholds of nectarivores with field data of Hodges (1981). He found that the threshold predicted by the marginal value theorem was optimal. Kadmon and Shmida (1992) carried out a field test of whether departure decisions of nectar-collecting bees

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were based on simple threshold or probabilistic rules. In their study, bees exhibited two distinctive departure decisions: using the probabilistic rule at the individual plant level and adjusting interflower flight distance according to the reward received at the current flower. However, these ideas have seldom been applied to grazing ruminant herbivores.

Whereas predators seek scattered prey of high nutritional quality, large herbivores confront widely dispersed, low quality food (Senft *et al.*, 1987). Foraging of large herbivores is characterized by relatively short searching time and prolonged grazing time. Also, ruminants reprocess ingested food, dividing nutritional activities between grazing and ruminating. However, like predators, herbivores face a patchy environment even on a grassland where heterogeneity is created by microenvironmental factors such as soil, moisture, slope and neighbouring plant species. Wapiti face two hierarchical levels of patchiness on grassland, namely, patches and feeding stations. We defined a patch as an area on which wapiti initiate and terminate a foraging sequence before reorienting to another location. A series of such sequences make up a foraging bout which is terminated by resting/ruminating (Gates and Hudson, 1983). A feeding station, defined as the area an ungulate can feed without moving its forelegs (Novellie, 1978), is considered a cluster of potential bites. Thus, a patch is a cluster of feeding stations. According to the marginal value theorem, wapiti should give up a patch when the rates of net gain drop to the expected net gain rate.

We addressed departure rules for both hierarchical levels of resource heterogeneity. For grassland patches, we asked whether wapiti depart after grazing a fixed number of feeding stations, after consuming a fixed number of bites, after a fixed time or after the cropping rate dropped below the seasonal expectation. For feeding stations within patches we asked whether wapiti leave feeding stations after consuming a fixed number of bites, after a fixed time or after the cropping rate dropped below the seasonal expectation or other threshold. We provide evidence that wapiti terminated foraging after the cropping rate dropped below the seasonal expectation in the patch. Neither foraging time, bites consumed nor cropping rate seemed to serve as departure rules at feeding stations. However, the neck angle of grazing wapiti seemed constant when leaving feeding stations suggesting that biokinetic factors played an important role.

Methods

Study area

The study was conducted at the Ministik Wildlife Research Station, Alberta, Canada, an area characterized by low hills with scattered lakes and ponds. The growing season begins in late April and ends in October. Permanent snow cover is established in November. The major vegetation types are *Populus* forest, *Bromus-Poa* grassland and *Carex* wetland. Grasslands, comprising most of the area of the pasture used in this study, were dominated by brome grass (*Bromus pumpehianus*) and Kentucky bluegrass (*Poa pratensis*). Dicots included dandelion (*Taraxacum officinale*), clovers (*Trifolium* spp.), *Achillea millefolium*, *Aster* spp., *Cirsium arvense* and *Fragaria virginianus*.

Animals and trials

We carried out the study with six tame female wapiti at three points in the snow-free season of 1991: 23 March – 3 April (spring, snow melt and grass emergence), 22–30 May (summer and grass leafed) and 15–22 August (early autumn, grass seeds ripened). We recorded foraging behaviour

with a pocket computer (TRS-80 PC, Tandy, Tx, USA) programmed to record each animal's identity, behaviour and occurrence of the behaviour (Jiang and Hudson, 1993). The duration of a behaviour state was determined by the built-in timer and its frequency was calculated instantaneously. We used the computer to record bites, number of feeding stations, steps and cropping rates. We began the observation by selecting a group member at random and continued sequentially until all animals were observed. During the March/April trial, we recorded 39 foraging sequences and 711 feeding stations, 23 foraging sequences and 782 feeding stations in May and 73 foraging sequences and 1025 feeding stations in August. Cropping rate was calculated as the bites taken from a feeding station divided by the time elapsed between steps. The seasonal expectation of cropping rate was calculated as the mean of the cropping rates at all feeding stations in the season.

Herbage biomass and qualities

We measured the above-ground grassland biomass by clipping ten random 0.5×0.5 m samples and by determining plant height at 22 random points during each seasonal trial. We sorted the samples into green and dead material and dried them at 60° C. Subsamples were dried at 110° C to determine dry matter (DM). Gross energy content of grass samples was determined with a bomb calorimeter (PARR Instrument Company, IL, USA). Crude protein content was calculated with total nitrogen determined by the macro-Kjeldahl method (Association of Official Analytical Chemists, 1984). Neutral detergent fibre (NDF) was determined according to Goering and Van Soest (1970).

Geometry of grazing wapiti

To define feeding station dimensions, we measured angles of the trunk (trunk angle) and lateral neck (neck angle) in relation to a hypothetical horizontal plane above the animal (Jiang and Hudson, 1993). Trunk angle is fixed in most situations because wapiti normally move their hind legs at same time as the forelegs. Neck angle is dynamic because wapiti orient to potential bites by moving their necks. We recorded 20 trunk and neck angles of each wapiti with protractors in May and August.

Statistics

The cropping rate at feeding stations within a patch is a time series. In each season, we pooled the cropping rates at the last five feeding stations before departing patches and calculated the autocorrelation of cropping rates. We tested the hypotheses that the number of feeding stations, number of bites or foraging time were the same in patches of March–April, May and August with ANOVA. We also tested the hypotheses that cropping rates at the last one to five feeding stations before leaving a patch were the same as the seasonal expectation. We studied bites per feeding station with foraging time at feeding stations as a covariate and tested the hypotheses that wapiti consumed the same number of bites or grazed the same duration at each feeding station. The data were transformed to their square roots to achieve normality (Sokal and Rohlf, 1989). We also tested the hypothesis that the neck angles of wapiti leaving feeding stations were the same for individual wapiti and were independent of the number of bites consumed at the feeding stations. We analysed forage characteristics (biomass, height, gross energy, protein and NDF) with MANOVA (multivariate analysis of variance) and conducted multiple comparison among means with the Tukey–Kramer method (Sokal and Rohlf, 1989). Data were summarized as mean \pm 1 SE (number of observations), except where specified otherwise and differences were considered significant where the probability of a type 1 error did not exceed 0.05.

Results

Departure from grassland patches

The behaviour of wapiti was most distinctive in May and was characterized by a large number of feeding stations per patch, bites per patch and longer grazing time per patch (Fig. 1). In March/April and August, wapiti grazed fewer feeding stations, took fewer bites per patch and had a shorter grazing time.

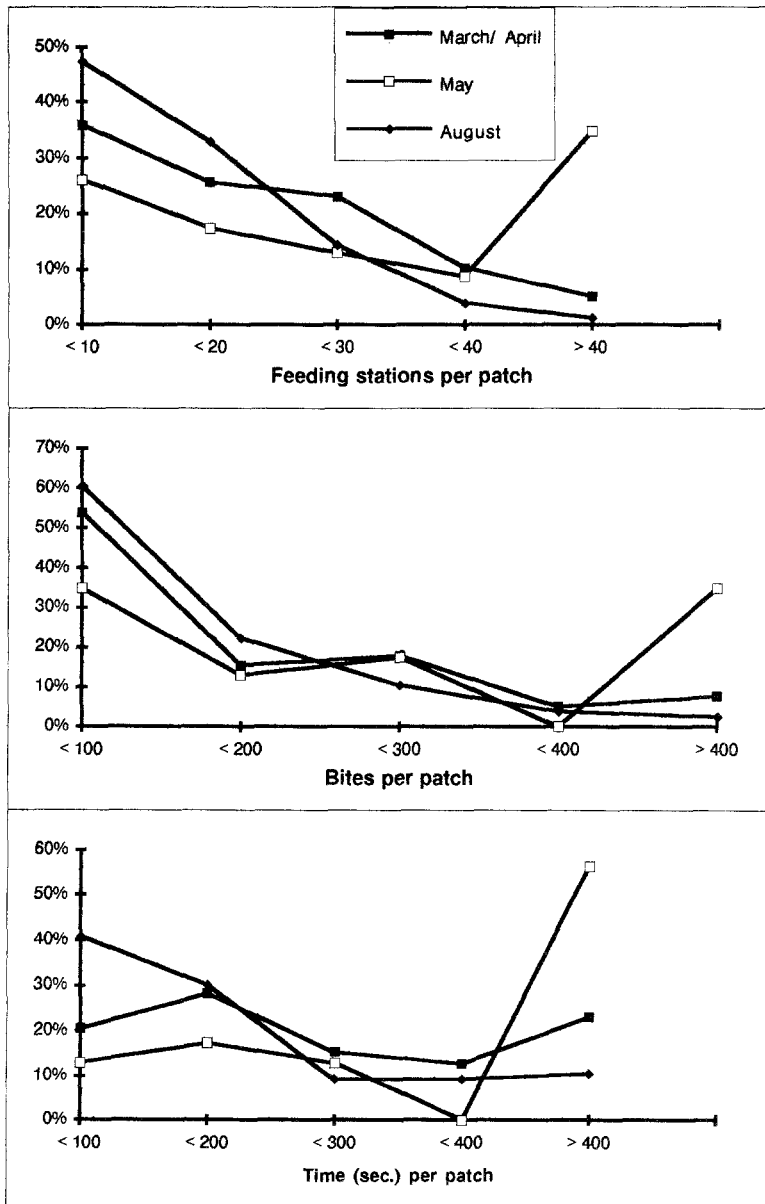


Figure 1. Frequency distributions of feeding stations, bites and foraging time per patch.

Number of feeding stations. The mean number of feeding stations comprising a foraging sequence in a grassland patch varied significantly by season ($p < 0.05$). In March/April as snow melted and grass shoots emerged, wapiti grazed 17.4 ± 1.9 (39) feeding stations per patch. In May when pastures achieved their rapid phase of growth, this increased to 31.3 ± 0.9 (23). In August as seeds ripened and pasture quality declined, the number of feeding stations per foraging sequence declined to 12.4 ± 1.1 (76). Within seasons, feeding stations grazed per patch ranged from one to 74 feeding stations. Thus, wapiti did not leave a patch after grazing a fixed number of feeding stations.

Number of bites. Wapiti consumed significantly different bites from patches in each season ($p < 0.05$). Wapiti took 139 ± 20.0 (39) bites per patch in March/April, 247.5 ± 8.2 (23) bites in May and 108.1 ± 11.9 (79) bites in August. Within season, bites per patch ranged from one to 634 bites. Hence, wapiti did not leave a patch after a fixed number of bites.

Foraging time. Wapiti foraged in patches significantly longer during May than during March/April or August ($p < 0.05$). Wapiti stayed in March/April patches for 318.9 ± 20.0 (39)s, for 637.4 ± 49.6 (23)s in May and 108.1 ± 11.7 (79)s in August. In the same season, the foraging time in patches ranged from 2 to 1310s. Wapiti did not use foraging time as a departure rule.

Mean cropping rate at feeding stations (seasonal expectations). Cropping rates dropped before wapiti gave up patches in each season (Fig. 2). The serial autocorrelation coefficients of the means at the last five feeding stations before giving-up were 0.18 in March/April, 0.12 in May and 0.17 in August. In March/April and August, the mean cropping rate at the last feeding station was significantly lower than the second last feeding station ($p < 0.05$). However, the cropping rates at the second, third, fourth and fifth last feeding stations were not significantly different ($p > 0.05$). In May, the mean cropping rates at both the last and the second last feeding stations were significantly different from each other ($p < 0.05$) and from those at the third, fourth and fifth last feeding stations ($p < 0.05$). However, the cropping rates at the third, fourth and fifth last feeding stations were not significantly different ($p > 0.05$). In conclusion, wapiti gave up foraging when the cropping rates at one or two feeding stations dropped below the seasonal expectation.

Departure from feeding stations

Throughout the snow-free grazing season, wapiti took only slightly different numbers of bites and spent different times before advancing to the next feeding station (Fig. 3).

Number of bites. Average bites per feeding station did not change significantly ($p > 0.05$) although plant heights and biomass changed considerably from May to August ($p < 0.05$). Wapiti took 7.7 ± 0.3 (711) bites per feeding station on March/April grassland, 8.0 ± 0.2 (782) bites on May grassland and 8.6 ± 0.3 (1025) bites on August grassland. Within seasons, the bites per feeding station was not constant but a random variable. Wapiti did not depart feeding stations after consuming a certain number of bites.

Foraging time. Grazing time of wapiti at feeding stations was significantly different between seasons ($p < 0.05$). Wapiti grazed 15.4 ± 0.5 (711), 14.4 ± 0.4 (782) and 13.6 ± 0.3 (1025) s on feeding stations in March/April, May and August, respectively. Wapiti foraged less time at feeding stations in August than in March/April ($p < 0.05$) despite improved forage quality (compare protein contents, $p < 0.05$, Table 1), forage biomass ($p < 0.05$) and forage heights ($p < 0.05$). However, the difference between grazing time in March/April and May was not significant

($p > 0.05$). Grazing time per feeding station in the same season was significantly different ($p < 0.05$, Fig. 3); wapiti did not leave feeding stations after a fixed foraging time.

Cropping rate in relation to bites taken. Between seasons, mean cropping rates differed significantly ($p < 0.05$, Fig 4). The cropping rate was 28.8 ± 0.5 (695) bites per min in March/April, whereas 33.8 ± 0.5 (775) bites per min in May and 31.6 ± 0.5 (988) bites per min in

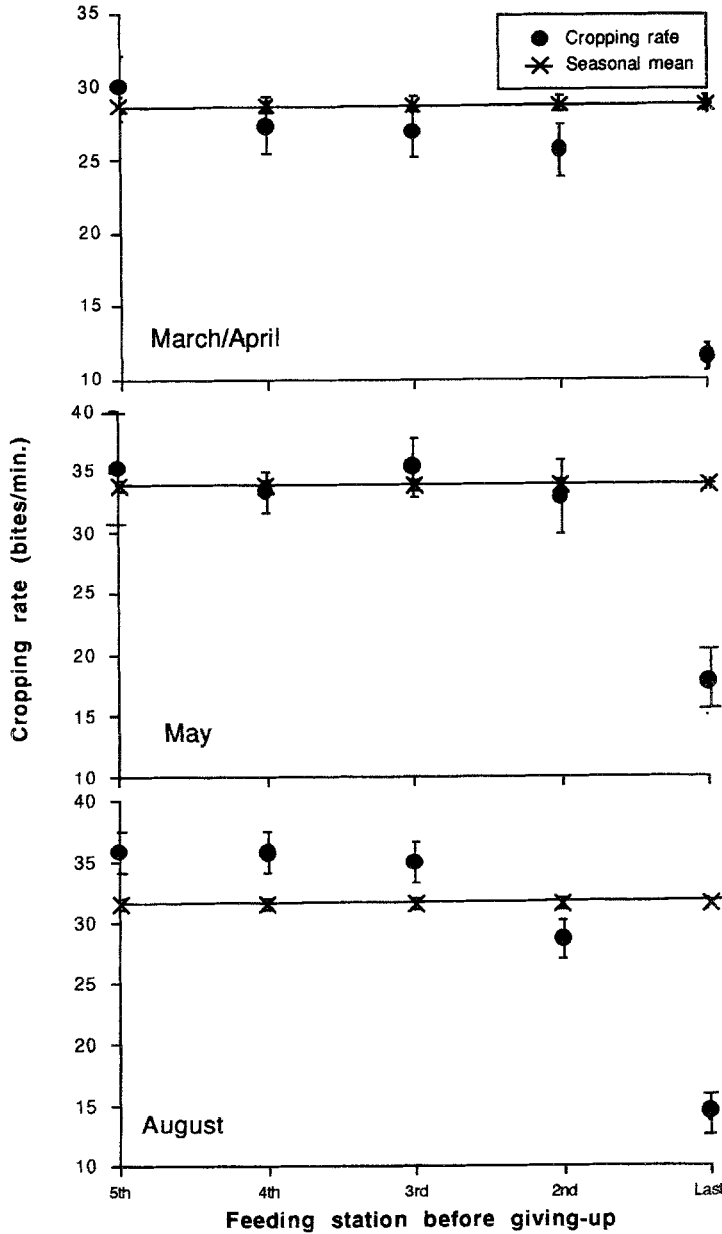


Figure 2. Cropping rates at the last five feeding stations before giving up a patch. In all seasons, wapiti terminated foraging when the cropping rate dropped below the seasonal expectation.

August. Within seasons, the cropping rate increased asymptotically with bites consumed at feeding station and was significantly different between feeding stations ($p < 0.05$, Fig. 4). As the grazing season progressed, both asymptotic cropping rates and 'saturation coefficients' increased. Wapiti did not leave feeding stations at a constant cropping rate or as cropping rate decreased.

Neck angles. Lateral neck angles of specific individuals in May and August were not influenced by seasons (Table 2, $p > 0.05$) nor the interaction between focal animals and seasons ($p > 0.05$). Wapiti did not lower their heads to regraze the same feeding station. Threshold neck angle was independent of bites consumed at the feeding stations ($p > 0.05$). Although we did not measure

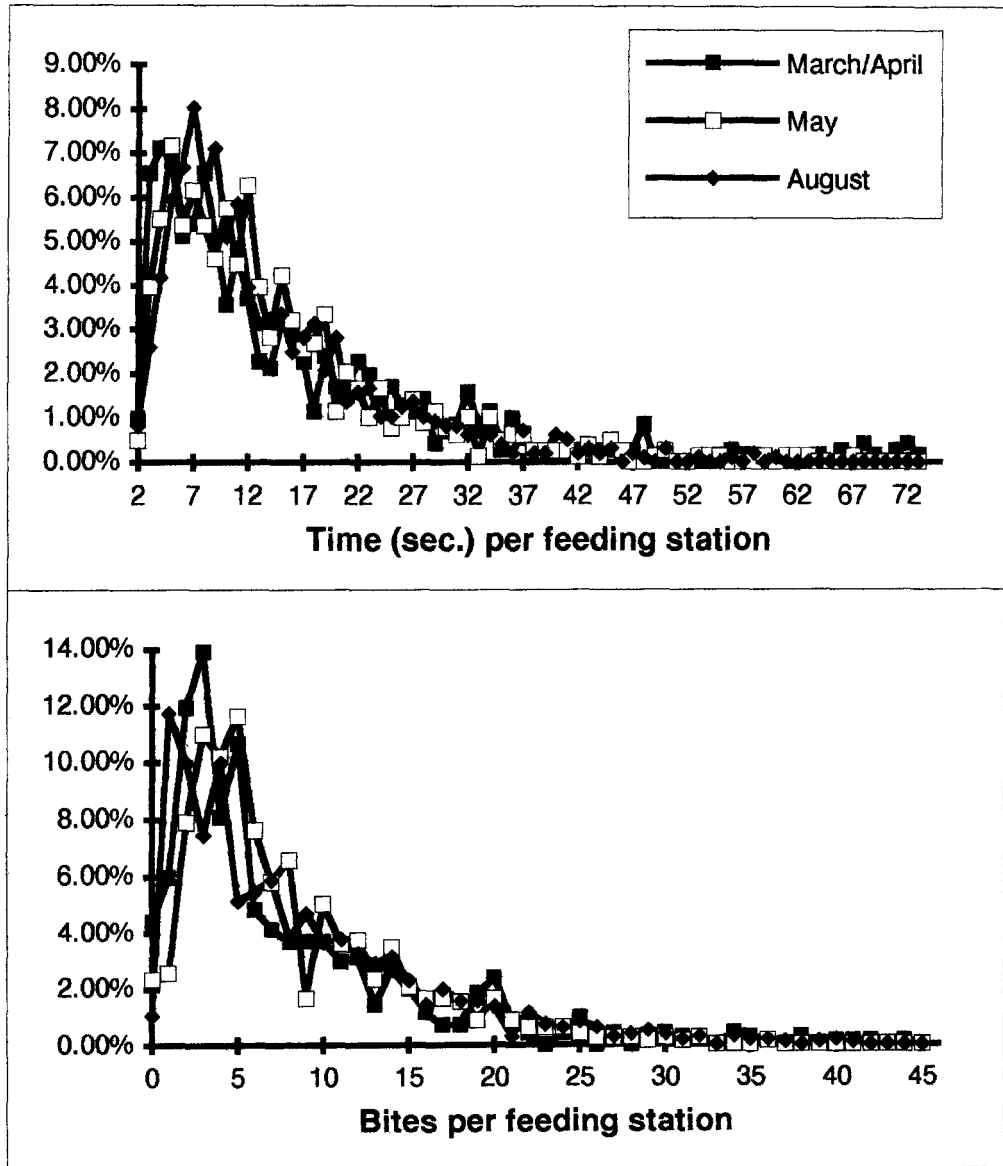


Figure 3. Frequency distribution of bites consumed and grazing time at feeding stations.

Table 1. Seasonal forage characteristics at the Ministik Wildlife Research Station

Characteristic	March–April	May	August
Biomass (g DM m ⁻²)	103 ± 43 ^{*a}	188 ± 63 ^a	371 ± 171 ^b
Sward height (cm)	3.3 ± 1.1 ^a	13.9 ± 3.8 ^b	24.0 ± 6.3 ^c
Energy (kJ g ⁻¹)	17.4 ± 0.2 ^a	18.0 ± 0.3 ^b	17.6 ± 0.3 ^b
Protein (%)	12.6 ± 0.0 ^a	16.6 ± 0.1 ^b	16.3 ± 0.2 ^b
NDF (%)	68 ± 3 ^a	64 ± 0.2 ^b	67 ± 0.5 ^a

*Data in the same row with one different superscript letter indicate a significant difference at $p < 0.05$.

neck angles in March/April, wapiti behaved similarly to those in May and August, grazing from the area near the fore-hooves to the distal end of the feeding stations. The neck angle of grazing wapiti seemed to be an indicator of feeding station departure.

Discussion

Patch definition

Krebs *et al.* (1981) pointed out the difficulty in defining a patch when testing the marginal value theorem. We attempted to express the size of grassland patches in terms of animal behaviour as a sequence of feeding stations. The smallest unit is a feeding station which has its boundary set by the reach of wapiti. A grassland patch is a cluster of feeding stations separated from others by a break in the foraging sequence when the animal reorients to a new location. We found evidence that wapiti used different rules at each level and these changed subtly as the grazing season progressed.

Broadly similar hierarchical patch departure rules have been found in nectar-foraging bees. Kadmon and Shmida (1992) reported that bees adopted different departure strategies at different patch levels: leaving an individual plant according to a probabilistic rule and moving a distance to the next flower according to the nectar reward at the current flower.

Patches

To forage efficiently, a forager must keep track of changes that occur in its environment by learning. The state of their environment affected their subsequent foraging decision (Krebs and Inmant, 1992). Because of the positive autocorrelation of the cropping rates before leaving patches, wapiti might already have made the decision of giving-up at the second last feeding station by learning. The most striking indication that wapiti would progress to the next patch was a dramatic drop in cropping rate below the seasonal expectation. This seems to be a definitive test of the marginal value theorem. However, it is difficult to distinguish whether the animal interrupted a foraging sequence because foraging returns declined or whether feeding slowed because the animal had decided to reorient to a new patch. If we accept the former (conventional) explanation, we might wonder how cropping rates are compared. Perhaps the expected cropping rate is memorized as the frequency of head movements in grazing, a rhythm which may easily be timed with other inner physiological rhythms such as heart and respiration rate.

Seasonal changes in mean patch size may be related to both animal condition and grassland quality and heterogeneity. After a long winter, grazing and other factors such as wind and snow created considerable grassland heterogeneity. Wapiti mainly lived on weathered grass left over

from the previous year. Under such energetic stress, wapiti seemed reluctant to give up a patch. Wapiti grazed each feeding station longer and foraged for two consecutive feeding stations of low intake rates before interrupting a foraging sequence to move to another patch. Patch size in May was the greatest when fresh green grass was in surplus so wapiti could easily satisfy their growth

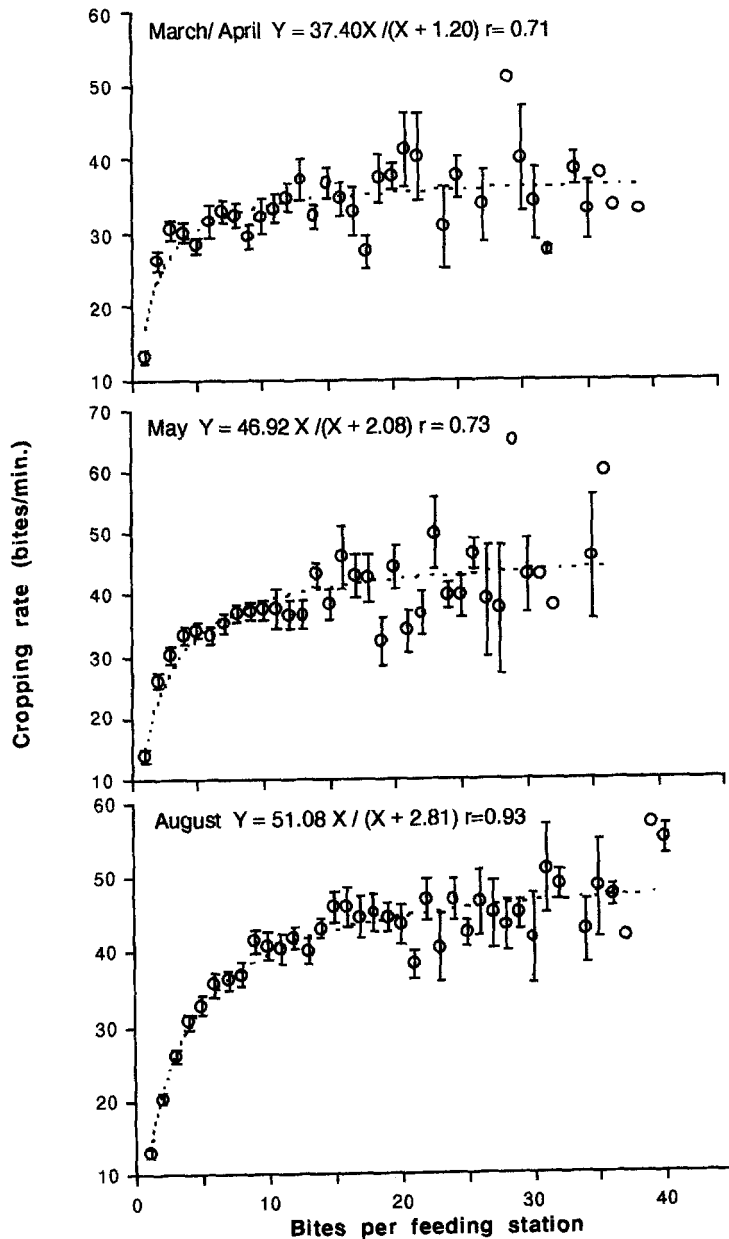


Figure 4. Cropping rates at feeding stations. The data were fitted with the Michaelis-Menton equation $Y = (m_1 \times X) / (X + m_2)$, where Y represents the cropping rate, X represents the bites consumed, m_1 is the asymptotic cropping rate and m_2 is the 'saturation coefficient'. The standard error of cropping rates increased as the bites consumed per feeding station increased due to the decreased sample size.

Table 2. Critical angles when wapiti left feeding stations

Wapiti	May		August	
	Mean (degrees)	SD (degrees)	Mean (degrees)	SD (degrees)
No. 9015	54.6°	4.5°	54.7°	3.2°
No. 9026	55.3°	3.7°	55.3°	3.6°
No. 9029	51.4°	2.9°	50.5°	3.9°
No. 9036	53.5°	3.0°	54.0°	2.6°
No. 9037	57.5°	2.6°	57.2°	2.4°
No. 9039	54.3°	4.6°	54.2°	4.1°
Mean \pm SE	54.4° \pm	2.0°	54.2° \pm	2.2°

impetus (Jiang and Hudson, 1992). Under such circumstances wapiti left a patch as soon as the cropping rate dropped below the seasonal mean. Wapiti grazed patches in May about twice as long as in spring and about six times as long as in autumn. In August, the grassland was again fragmented with small patches of matured sward, which offered foraging opportunities reminiscent of spring and departure rules appeared similar.

Feeding stations

Wapiti develop a rhythm of cropping bites and steps during grazing which determines their rate of advance. They seldom took all possible bites within reach before moving on. Presumably, foraging selectivity, reach and balance seemed to be the main factors determining behaviour at this hierarchical level. When a wapiti moves its head to search for the next bite, the gravity of the head produces a vector which acts on its shoulder. The smaller the neck angle, the greater the pulling force (Jiang and Hudson, 1993). Foraging seemed to be interrupted whenever the neck angle reaches a threshold such that the shifting centre of gravity necessitates movement of the foreleg to maintain balance.

Optimal grazing of wapiti

Wapiti terminated foraging sequences in patches as the intake rates dropped, even though they may tolerate low intake rate longer when energetically stressed. The results provided a critical test of the marginal value theorem, suggesting that wapiti foraged optimally. At feeding stations, the cropping rate accelerated as bites consumed increased. The distance between bites decreased as the number of bites consumed at a feeding station increased, a situation thoroughly explored by Holling (1959). Unless bite size declines, wapiti should graze a feeding station as long as possible. What is possible seems to have a biokinetic basis.

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