Effect of Forage Depletion on the Feeding Rate of Wapiti

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Abstract

We evaluated forage intake rates of wapiti *(Cervus elaphus nelsoni)* during the depletion of a grass sward over a 7-day period. Bite sizes increased linearly with forage biomass and plant height within the range of our data. Maximum foraging rates of 45 cropping bites per minute declined exponentially at bite sizes greater than 0.2 g. Consumption rates increased asymptotically with forage biomass to a predicted asymptote of 17.6 g/min although the highest value observed was 12.6 g/min at a biomass of 2367 kg/ha. Average daily forage removals through grazing and trampling (not distinguished) were 9.5 kg per animal and did not decline as biomass was reduced from approximately 2,400 kg/ha to 800 kg/ha.

Wapiti forage extensively on grass openings which are interspersed throughout the aspen boreal forest (Gates and Hudson 1981). These grasslands usually develop following disturbance by fire, or mechanical removal of the aspen-dominated forest cover.

The modest productivity of these grasslands belies their high grazing value. Forage growth begins soon after spring snowmelt and forage quality in winter is protected from weathering by a protective snow cover (Nietfeld 1983). Wapiti prefer grass uplands even whey they have been grazed to short uniform lawns and forage availability would be expected to limit intake. This study documents the effects of declining forage biomass on forage intake and foraging behavior of wapiti.

Methods

Study Area and Animals

We conducted the experiment in a grassland enclosure at the Ministik Field Station, 30 km southeast of Edmonton, Alberta. A 0.15-ha enclosure protected by a 4-strand electric deer fence was established on a representative grassland. The main vegetation components of the grassland were bluegrass *(Poa pratensis)*, smooth brome *(Bromus inermis)*, white clover (*Trifolium* spp.) and dandelion *(Taraxacum officinale)*. The enclosure was left ungrazed until it had matured in late August.

Two tame adult non-lactating females and 2 yearling (1 male, 1 female) wapiti were placed in the enclosure to defoliate vegetation over a 7-day period (Aug. 3-9, 1983). Heavy stocking and a short trial period on mature pasture was used to minimize the complicating effects of pasture growth. The animals grazed the area surrounding the enclosure prior to the trial thus an adjustment period was not considered necessary.

Vegetation Measurements

Vegetation was sampled each day of the experiment using 10 randomly distributed 0.5 × 0.25-m plots. Within each plot, 10 measures of plant height were taken. Plant density was measured in a 100-cm² subplot every second day. Plots were then clipped to ground level for an estimate of biomass. Samples were oven-dried at 60°C to constant weight and expressed as kg dry matter/ha.

Foraging Behavior

The wapiti were confined to the enclosure throughout a 7-day trial. We recorded the foraging sequences of each animal on a tape cassette during a regular foraging bout each morning. The number of cropping bites was recorded, as were the number of steps and feeding stations (location an animal grazed without moving either forefoot). Data analyses were based on a sample 3-10 minute session for each animal each day, using the determined rates: bites/min, steps/min, and stations/min.

Diet samples were collected by following each animal and hand picking 50 "bites" to duplicate as closely as possible the amount and species composition ingested. Samples were dried at 60°C to constant weight, and bite size was estimated on a dry weight basis as an average for all animals. Consumption rates (g/min) were estimated by multiplying bite rate by bite size. Diet samples for each animal each day were analyzed for crude protein by the macro-Kjeldahl method.

Relationships were tested by linear regression except for the asymptotic regression of consumption rate against forage biomass which was fit by nonlinear asymptotic regression (Dixon 1981).

Results

Daily changes in range characteristics and foraging behavior are summarized in Table 1. Declines in biomass, tiller length and plant density accompanied declines in forage moisture and dietary crude protein. The depletion of biomass was variable but daily decrements were unrelated to trial day ($P>0.05$). Each animal removed 9.5 ± 2.4 kg/day through grazing and trampling (not distinguished), a value which probably is specific to this set of experimental circumstances.
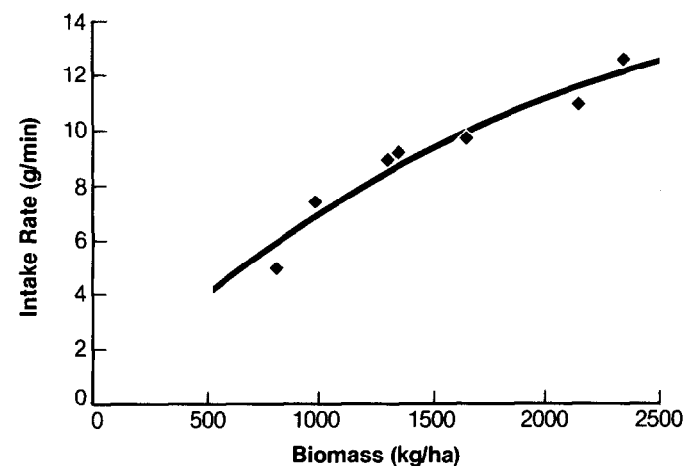

Fig. 1. *Consumption rate of wapiti in relation to forage biomass on boreal grasslands.*

As estimated bite sizes declined linearly from 0.36 g to 0.11 g with depletion of forage biomass ($P<0.005$), foraging rates (bites/-min) increased in partial compensation. Nevertheless, consump-

Table 1. Range characteristics and foraging parameters of wapiti during progressive defoliation.

Day	Biomass (kg/ha)	Tiller Length (cm)	Plant Density (No/cm²)	Dry Matter (%)	Protein Conc (%)	Intake Rate (g/min)	Cropping Rate (bites/min)	Bite Size (g)	Feeding Stations (No/min)	Steps (No/min)
1	2367 (±161)	16.0 (± .9)	57.7 (±2.1)	28.8 (±0.9)	15.9 (±0.2)	12.6 (±0.5)	35.0 (±1.2)	0.36 —	4.6 (±0.1)	7.6 (±0.6)
2	2158 (±206)	13.3 (±2.2)	— —	29.9 (±0.7)	15.0 (±0.3)	11.0 (±0.2)	36.7 (±0.7)	0.30 —	5.0 (±0.2)	7.8 (±0.5)
3	1654 (±223)	11.8 (±2.0)	51.1 (±2.4)	30.3 (±0.6)	14.1 (±0.2)	9.8 (±0.3)	39.1 (±1.2)	0.25 —	5.0 (±0.2)	6.9 (±0.4)
4	1367 (±191)	9.6 (±2.0)	— —	34.1 (±0.8)	14.1 (±0.0)	9.2 (±0.3)	43.7 (±1.3)	0.21 —	5.3 (±0.2)	7.0 (±0.5)
5	1324 (±215)	8.9 (±1.7)	24.8 (±2.0)	37.0 (±2.1)	13.7 (±0.1)	9.0 (±0.2)	44.8 (±1.1)	0.20 —	6.0 (±0.3)	7.9 (±0.6)
6	991 (±138)	7.4 (±1.4)	— —	37.7 (±1.5)	13.5 (±0.2)	7.5 (±0.2)	43.9 (±0.9)	0.17 —	5.6 (±0.2)	10.0 (±0.6)
7	823 (±69)	6.2 (±0.9)	16.9 (±1.3)	38.9 (±1.1)	13.5 (±0.1)	5.0 (±0.1)	45.3 (±1.1)	0.11 —	5.9 (±0.4)	9.5 (±1.1)

tion rate (g/min) declined from 12.6 g/min to 5.0 g/min as forage biomass declined from 2367 kg/ha to 823 kg/ha (Fig. 1). Asymptotic regression gave:

$$g/min = 17.6 * (1 - e^{-0.000505 \text{ kg/ha}}) \quad r^2 = 0.94$$

This relationship predicts a maximum consumption rate of 17.6 g/min on grasslands supporting over 2,500 kg/ha. At 1,000 kg/ha, consumption rates are reduced by one half.

Number of steps/min and stations/min tended to increase with bite rates as the pasture was depleted. Over the range of conditions studied, foraging behavior (bites/step or bites/station) did not change. The animals simply foraged more quickly.

Bite sizes were linearly related to both forage biomass ($r^2 = 0.96$, $P<0.001$) and tiller lengths ($r^2 = 0.88$, $P<0.001$). For grassland forages, bite rate declined with bite sizes exceeding 0.20 g (Fig. 2). The highest rates observed were 45 cropping bites/min.
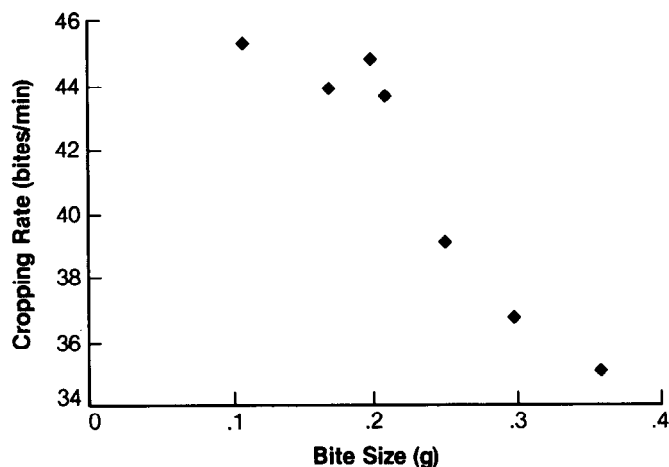

Fig. 2. *Foraging rate of wapiti in relation to bite size.*

Discussion

The maximum consumption rate of wapiti on boreal grasslands during summer was between 12.6 (observed) and 17.6 (asymptote of nonlinear regression) g/min. This is consistent with data obtained for wapiti using similar bite-weight estimate methods (Collins et al. 1978) and a less subjective technique using fistulated animals (Wickstrom et al. in press). Smaller species such as reindeer (Trudell and White 1981), mule deer (Collins and Urness

1983) and domestic sheep (Allden and Whittaker (1970) have lower maxima. Large grazers attain intake rates of approximately 18 g/min for cattle (Chacon and Stobbs 1976) and 23 g/min for bison (our unpubl. data). Clutton-Brock and Harvey (1983) reasoned that maximum foraging rates should be related to incisor row width and that this scaled allometrically to body weight ($BW^{0.33}$).

In this study, consumption rates of wapiti declined rapidly below 1,500 kg/ha. Limiting thresholds for grasslands swards probably are also related crudely to body weight. Maximum intakes of caribou occur at less than 1,000 kg/ha (White et al. 1975) whereas cattle continue to increase intake rates even when forage biomass exceeds 3,000 kg/ha (Chacon and Stobbs 1976).

Biomass is a good correlate of feeding rates only within a forage class. Widely dispersed clumps are more available at an equivalent biomass. Hence, intake relationships on mixed or shrub ranges are expected to be generally higher (White et al. 1975, Collins et al. 1983).

To compensate for smaller bite sizes on depleted or unproductive ranges, animals may increase foraging rates (cropping bites/-min) and grazing time. Assuming that a 220 kg nonlactating young female requires 4,400 g dry matter/day (2% of live weight), foraging times would have to increase from 5.8 to 14.7 hr over the 7-day trial in order to maintain the same level of intake. During summer, wapiti forage for about 9 hr daily at the field station where the study was conducted (Gates and Hudson 1981). Like other ruminants (see Trudell and White 1981), wapiti rarely extend grazing times beyond 13 hr (Gates and Hudson 1983). Therefore, to maximize productivity of wapiti, summer grassland ranges within the boreal aspen zone probably should be stocked such that forage biomass is not depleted to less than 900 kg/ha.

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