Scale of Patchiness Affects the Relation Between Forage Quality and Patch Choice by Cattle

Wallis DeVries
University of California, Davis

M F. Laca
University of California, Davis

E A. Laca
University of California, Davis

SCALE OF PATCHINESS AFFECTS THE RELATION BETWEEN FORAGE QUALITY AND PATCH CHOICE BY CATTLE

Wallis DeVries, M.F. and E.A. Laca
Department of Agronomy and Range Science, University of California, Davis, CA 95616, USA

ABSTRACT

We predicted and tested the effects of scale of heterogeneity on movements and selectivity of a large grazer in a controlled field experiment. We created random mosaics of short/high quality and tall/low quality grass patches in equal proportion at grid sizes of 2x2 m and 5x5 m. Subsequently, we monitored the foraging behavior of four steers in 16 20x40 m plots over 30-minute periods. As predicted, the animals selected the short patches both by walking in a non-random manner and by concentrating their grazing time. Selectivity was more pronounced in large patches than in small ones. In contrast, the number of bites per feeding station was not affected by patch size, suggesting that selection between and within feeding stations are essentially different processes. We conclude that selectivity is facilitated by large scale heterogeneity, particularly by enhancing discrimination between feeding stations and larger selection units.

KEYWORDS

Foraging behavior, grazing, selectivity, spatial heterogeneity, cattle

INTRODUCTION

Grazing ungulates are known to graze selectively when confronted with a patchy forage distribution. Recent studies have shown that patch selection in ruminants is better explained by a maximization of daily nutrient intake rather than instantaneous nutrient intake (Wallis, DeVries & Daleboudt, 1994; Wilmshurst et al., 1995). Instantaneous intake rates on tall, mature swards may be high but daily intake may still be low due to gut fill constraints. Selecting forage from shorter swards with lower cell wall content leads to a higher daily nutrient intake. However, this does not explain the partial preferences that are often observed in grazing animals. A potential explanation for partial preferences may lie in the spatial arrangement of different forage patches. Distel et al. (1995) have shown that patch residence time in cattle confronted with two patch types of different profitability can be adequately described by a marginal value rule consisting of a trade-off of intake and travel. Yet, it remains unknown to what extent patch selection is affected by the grain size of the environment.

The following experiment was designed to test the hypothesis that grazing selectivity for low-biomass, high-quality patches is hampered when patches are small. Small patches should impair the ability of grazers to avoid poor areas and return or stay within preferred areas. On this basis we predicted that: (1) grazers should select for the patch allowing highest daily nutrient intake; (2) search should be non-random, with a greater proportion of the foraging path in the most profitable patch; (3) selectivity for preferred patches should be stronger as more behavioral steps are involved in the index of selectivity; (4) selectivity should increase with increasing patch size; (5) the efficiency of search, as measured by the total number of feeding stations and bites found per unit distanced walked, should increase with increasing patch size; (6) in large patches the foraging path should be less tortuous than in small patches; (7) in large patches the residence time and number of bites per feeding station should be less than in the small patches, because the overall environment experienced by the animal would be better.

METHODS

The experiment was conducted in an irrigated Setaria lutescens-grassland. We created 16 20x40 m plots with random mosaics of short/high quality and tall/low quality patches in equal proportion and at grid sizes of 2x2 m and 5x5 m. The pasture was cut entirely in mid-June and fertilized with ammonium nitrate 2 weeks later (90 kg N/ha). Short patches were cut again in early august, fertilized anew (180 kg N/ha) and cut for the last time 2 weeks later so that all plots had the same regrowth period before the experiment, which started 2 weeks later.

Four 30-month old Hereford crossbred steers (604-710 kg) were brought to the pasture 4 days before the start of the observations. They were allowed access to a pasture with similar patch mosaics for 520 min/day on average (including time in experimental plots). During the experiment, 2 consecutive observation periods of 30 minutes per plot were recorded, starting at sunrise. The steers were grazed together and in each plot one focal animal was observed, giving duplicate observations per animal for each of the two patch size treatments. Sounds and images were recorded with a video camera from a 3.5 m high platform. The day prior to the observations, vegetation height was measured and standing crop was sampled in each patch type in 5 randomly chosen 0.1 m^2 quadrats and analyzed for fiber. Dry matter digestibility was estimated by the summative equation (Goering & Van Soest, 1970). Bite frequencies were converted to intake data by calibration with depletion curves determined afterwards in stall trials with sods cut from the same pasture. Maximum daily intake was estimated using a fill constraint of 1.1 g NDF/kg body weight (Mertens, 1987). Path tortuosity was determined by fractal analysis (Nams, 1996).

RESULTS

On the basis of forage quality data and intake curves from the sod experiments it was estimated that an 18% higher daily intake of digestible dry matter (DDM) could be achieved on the short patches than on the tall patches (Table 1; instantaneous DM intake rate was similar for both patches). Maximization for DDM-intake on a daily basis should therefore favor selection for the short patches. The animals spent more than 50% ($P=0.0002$) of their time grazing in the short patches (73.7%). Hypothesis (1) was thus accepted. The proportion of steps in short patches was higher than 50% (72.3%, $P<0.0001$) and there was a greater proportion of 'short' among feeding stations (FS, one FS being a step where one or more bites were grazed) than among non-FS steps (mean difference 34.0%, $P<0.0001$). The encounter rate with the two patch types was therefore non-random and more so for the feeding stations; hypotheses (2) and (3) were therefore supported.

The proportions of dry matter intake, time spent, number of bites and steps walked in short patches were significantly greater in the large than in the small patches (Table 2). Furthermore, there was a significantly larger proportion of FS in the large than in the small patches (Figure 1). The proportion of 'short' FS was greatest in the large patches. Conversely, the proportion of FS in 'tall' was smallest in the large patches. These results support hypotheses (4) and (5).

The fractal dimension of the foraging path increased with scale size ($P<0.0001$) and was greater than 1 ($P<0.0001$), indicating a greater path tortuosity at larger spatial scales (Figure 2). There was no difference in fractal dimension between patch sizes, however.

Hypothesis (6) was therefore not supported.

At the smallest spatial scale level of the FS, the mean residence time and mean number of bites per FS in short and tall patches were not different between patch sizes (Short: 9.6 s and 6.0 bites per FS, Tall: 25.6 s and 7.2 bites per FS), which is reflected in the ratio of intake per FS in short relative to tall patches (Table 2). Hypothesis (7) was thus rejected.

DISCUSSION

Five of the seven hypotheses on patch selection were confirmed in this experiment. Patch selection was aimed at the patch type with the highest daily DDM intake, but selection was less effective at a finer grain size of patchiness, as the animals did not adjust their movement pattern. Scale of patchiness thus offers an explanation for the occurrence of a dietary mix of different components. Selectivity was strongest when considering the proportion of bites and feeding stations. Once a FS was chosen the residence time was a function of vegetation characteristics on the site rather than spatial scale. This confirms the hypothesis that selectivity is greatest when more behavioral components (movement and selection of FS) are involved.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance by José Kok, Ganga Deo and Jo Dankosky and the financial support through BARD project IS-2331-93C.

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Table 1
Characteristics of short and tall patches with significance of difference between the patch types (NDF = neutral detergent fiber, DMD = dry matter digestibility, DMIR = dry matter intake rates, DDMI = digestible dry matter intake).

	Short	Tall	P
Standing Crop (g/m^2)	322.5	642.2	<0.0001
Height (cm)	15.9	42.8	<0.0001
%NDF	66.7	69.9	<0.0001
%DMD	51.5	45.7	0.008
DMIR (g/min)	56.2	54.0	NS
Max. Daily DDMI (kg)	5.63	4.77	not determined

Table 2
Grazing selectivity between treatments with large and small patch size and the significance of the difference between treatments (DM = dry matter, FS = feeding station). There were no significant animal effects or interactions between patch size and animals.

	Large	Small	P
%DM-intake in Short patches	88.2	65.3	0.021
%Time in Short patches	82.7	63.6	0.033
%Bites in Short patches	93.3	78.4	0.028
%FS in Short patches	94.5	82.7	0.027
%Steps in Short patches	77.2	67.0	0.019
Ratio DM-Intake/FS Short/Tall	0.49	0.49	NS

Figure 1
Feeding stations encountered and selected per step walked by steers grazing mosaics of tall, low quality and short, high quality grass patches, as affected by the scale of patchiness. All variables differed significantly between patch size treatments at the 5% level.

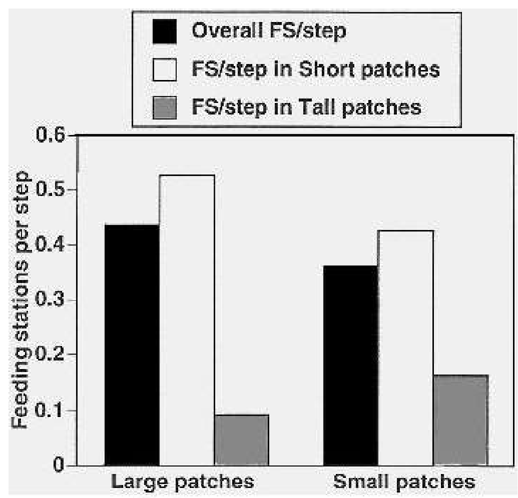

Figure 2
Relationship between the scale of measurement and the fractal dimension (D) of the grazing path of steers grazing a mosaic of tall, low quality and short, high quality grass patches. A fractal dimension of 1.0 indicates a straight path; a value of 2.0 indicates a completely random walk. Values of D between 1.0 and 2.0 reflect a patch search pattern.