Abstract The notion that spatial scale is an important determinant of foraging selectivity and habitat utilization has only recently been recognized. We predicted and tested the effects of scale of patchiness 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 2×2 m and 5×5 m. Subsequently, we monitored the foraging behaviour of four steers in 16 20×40 m plots over 30-min periods. As predicted on the basis of nutrient intake maximization, the animals selected the short patches, both by walking in a non-random manner and by additional selectivity for feeding stations. The tortuosity of foraging paths was similar at both scales of patchiness but 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. Mean residence time at individual feeding stations could not be successfully predicted on the basis of the marginal-value theorem: the animals stayed longer than expected, especially in the less profitable patch type. The distribution of the number of bites per feeding station suggests a constant probability to stay to feed or to move on to the next feeding station. This implies that the animals do not treat larger patches as discrete feeding stations but rather as a continuous resource. Our results have important implications for the application of optimal foraging theory in patchy environments. We conclude that selectivity in grazers is facilitated by large-scale heterogeneity, particularly by enhancing discrimination between feeding stations and larger selection units.

Key words Foraging behaviour · Grazing · Spatial heterogeneity · Patch selection · Cattle

Introduction

Grazing ungulates are known to graze selectively when confronted with a patchy forage distribution. They concentrate on short, leafy swards that contain relatively high concentrations of nutrients (Jarman 1974; McNaughton 1984) but do not necessarily yield the highest intake rate (Illius et al. 1987; Langvatn and Hanley 1993; WallisDeVries and Daleboudt 1994; Wilmshurst et al. 1995). In ruminants, the daily intake of abundant low-quality forage will be constrained by the passage rate through the digestive tract. It has therefore been proposed that ruminant grazers trade off forage quality and quantity to maximize daily instead of instantaneous nutrient intake (Fryxell 1991). Results of several grazing studies have confirmed this hypothesis (WallisDeVries and Daleboudt 1994; Wilmshurst and Fryxell 1995; Wilmshurst et al. 1995). However, in neither of these studies was selection directed exclusively at the most profitable patches. 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 *Bos taurus*, confronted with two patch types of different profitability, can be adequately described by a marginal-value rule (Charnov 1976), consisting of a trade-off between intake at the current depleting patch and travel to feed at the next, as yet undepleted patch. Partial preferences can also arise because the ability to discriminate between alternative forages becomes limited. On the one hand, selectivity may be expected to grow stronger as the differences between alternatives increase (WallisDeVries and Daleboudt 1994), because the reward of selecting becomes greater. On the other hand, selectivity should also increase with improving opportunity to select, which depends largely on the spatial arrangement of the forage types. At the extremes, it appears that selection is little affected by small-scale
heterogeneity at the level of the feeding station (Griggs et al. 1991; J.A. Dankosky, unpublished data) but is profoundly affected by large-scale heterogeneity at the landscape level (WallisDeVries and Schippers 1994). Thus, we surmise that besides the spatial arrangement of patches, the scale of patchiness is another major determinant of selectivity during grazing.

The role of scale in foraging ecology is often ignored. Thus, daily intake is often viewed as the product of instantaneous intake rate and grazing time (Hodgson 1982). Yet, this is only true in perfectly homogeneous environments. In the face of environmental heterogeneity, extrapolation from one scale level to another requires the integration of processes at various scales (Turner et al. 1989; Demment et al. 1995; Laca and Ortega 1995). For grazing herbivores the notion of scale has been incorporated in conceptual hierarchical foraging models (Senft et al. 1987; Stuth 1991; Bailey et al. 1996). Several spatial levels are recognized, each with its own corresponding behaviour and time scale. At the smallest scale, bite formation takes place. Local depletion and selection are the main motivations for short-term movements within a feeding bout between bite locations (head movements), between feeding stations (a single step) and between patches (series of steps). At larger scales of time and space, decisions are made on the selection of plant communities, landscape types and seasonal ranges. Selection can occur at each scale level and may accumulate across scale levels.

Foraging behaviour over multiple scales has been investigated in a number of studies (e.g. Tinbergen 1981; Ward and Saltz 1992; Jiang and Hudson 1993; WallisDeVries and Schippers 1994; Ginnett and Demment 1997). Yet, a quantitative approach to the integration of foraging mechanisms across scale levels has only begun recently (WallisDeVries et al. 1998). Moen et al. (1997) presented a spatially explicit, quantitative foraging model for moose, but scaling issues were addressed mainly by tentative foraging rules that lack sufficient support from field data. The following experiment, using B. taurus as a model species, was designed to contribute to the quantification of foraging rules across spatial scales by examining foraging behaviour at the level of the patch and the feeding station. We specifically tested the hypothesis that grazing selectivity is hampered when the environment is fine-grained, i.e. patches are small compared to the animal’s body size. 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 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 behavioural steps are integrated in the index of selectivity; (4) selectivity should increase with increasing scale of patchiness; (5) the search efficiency, as measured by the total number of feeding stations and bites found per unit distance walked, should increase with the scale of patchiness; (6) the tortuosity of the foraging path should vary with the scale of patchiness and (7) in a coarse-grained environment, residence time and number of bites per feeding station should be less than in a fine-grained environment, because the overall environment experienced by the animal is better.

### Materials and methods

**Pasture layout and experimental protocol**

The field experiment was conducted in an irrigated *Setaria lutescens* (Weigel) Hubb. grassland. We created 16 20×40 m plots with contiguous mosaics of short/high-quality and tall/low-quality patches in equal proportion and at two grid sizes, randomly allocated to plots: fine grained of 2×2 m (200 cells per plot) and coarse grained of 5×5 m (32 cells per plot). The allocation of patch types to cells was randomized over blocks of 4×4 cells, so that an equal proportion of short and tall patches was obtained for each block of 16 cells. This small-scale randomization of the two patch types was imposed to avoid accidental clustering of patches of a certain type. 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, refertilized (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 (3–11 September).

Five 30-month-old Hereford crossbred steers (604–710 kg) were brought to the pasture 4 days before the start of observations. They were allowed access to a pasture with similar patch mosaics for 520 min/day on average (including time in experimental plots). The day prior to each observation, vegetation height was measured and standing crop was sampled in each patch type. Height measurements were made with a 0.1-m² square plate (ca 100 g) that was gently lowered onto the vegetation along a measuring rod. In fine-grained plots, one height measurement was made in the centre of each cell (100 readings per patch type) and in coarse-grained plots, one height measurement was made in every quarter of each cell (64 readings per patch type). Standing crop in each patch type was sampled in five randomly chosen 0.1-m² quadrats by clipping to a height of 2.5 cm above ground level. The regression of standing crop on sward height was used to derive a plot average following the procedures of double sampling (see Laca et al. 1989). The collected samples were dried at 60°C and analysed for fibre (Goering and Van Soest 1970) and nitrogen using the Carlo Erba technique. Dry matter digestibility (DMD, %) was estimated by the summative equation: DMD = 0.98(100–NDF)+[147.3–78.9log(100/LADF)]–13, where NDF, L and ADF denote the percentages in the dry matter of neutral-detergent fibre, lignin and acid-detergent fiber, respectively (Goering and Van Soest 1970).

On each day of the experiment, observations were collected in two plots, starting at sunrise. One observation consisted of 30 min with a 15 min break between the consecutive observations. The steers were grazed together and in each plot one focal animal was observed, giving duplicate observations for four animals for each of the two patch size treatments; the fifth animal was too shy to be handled. Sounds and images were recorded with a video camera from a 3.5-m-high platform. These records were later used to identify bites, chews, steps and grazing location. The identification of grazing location was facilitated by the placement of coordinate markers alongside the plots.

**Data analysis**

We examined grazing selectivity for different steps in the foraging process: selectivity during walking, selection of feeding stations, selection of bites and intake per bite. Selection was expressed in two ways. First, as the percentage of events per patch type, showing an integration of events over the whole foraging process from