

Progress Report

Collaborative Research: Responses of Herbivores to Spatial Heterogeneity Expressed at Multiple Scales DEB-9981368

N. T. Hobbs, L. A. Shipley, B. A. Wunder, and J. W. Thomas

Overview

Spatial heterogeneity in plant communities arises from variation in the way that plant tissue is arrayed in space. For any given scale, the same biomass of plants can be displayed by large plants rooted sparsely or by small plants rooted close together. Leaves grow in a variety of shapes and sizes, appearing in canopies with diverse architectures. The consequences of these different geometries for foraging by herbivores remain poorly understood. We are examining the ability of competing models to predict foraging behavior of large herbivore in environments where spatial heterogeneity in plants is expressed at several scales. Our objectives include:

- 1) Identifying spatial and temporal scales of variation in plant tissue exerting a predominant influence on herbivore foraging, particularly decisions on when to enter and when to leave plant patches.
- 2) Developing simple models predicting movement paths of herbivores in relation to spatial variation in foods.
- 3) Scaling the parameters in these models to animal body mass.
- 4) Determining influence of spatial heterogeneity on foraging efficiency.

Outcomes of our first nine months of work are

- 1) Hand-rearing 15 mule deer fawns for use as experimental subjects.
- 2) Submission of 2 manuscripts and 2 abstracts reporting previous and current work:

Hobbs, N. T., J. E. Gross, L. A. Shipley, D. E. Spalinger, and B. A. Wunder. Submitted. Functional response of herbivores in heterogeneous environments: A contest among models. In review, *American Naturalist*.

Searle, K. R., N. T. Hobbs, T. Vandervelde, L. A. Shipley, and B. A. Wunder. Submitted. Gain functions in small patches for a large herbivore: Evaluating evidence for competing models. In review, *Ecological Society of America*

Vandervelde, T. L. A. Shipley, K. R. Searle, N. T. Hobbs, and B. A. Wunder. Submitted. Gain functions for blue duikers in small patches: Does plant geometry matter? In review, *Ecological Society of America*.

Zynel, C. A. and B. A. Wunder. Submitted. Limits to food intake by the Prairie Vole: Effects of time for digestion. In review, *Functional Ecology*.

- 3) Completion of a key experiment identifying sources of heterogeneity in plants controlling the shape of the gain function of herbivores at small patch scales.

In this report, we focus on accomplishment (3).

Motivation

A pivotal experiment in our future research requires manipulating the geometry of plant tissue at three, nested scales. These manipulations will allow us to examine which scale exerts the greatest influence on animal responses to spatial pattern. Scales of interest include the small patch, the large patch, and the cluster. We define a small patch as plant tissue that is sufficiently concentrated in space that a herbivore can consume the patch without moving its feet. A large patch is defined as a collection of small patches where small patches are sufficiently far apart that encounter rate with small patches influences patch depletion rate. Clusters are spatial concentrations of large patches which, again, are sufficiently dispersed to allow interpatch distance to influence depletion rate. We are working towards an experiment to examine the strength of evidence for competing models predicting residence time of foraging herbivores in patches at these three, hierarchical scales. Models will include combinations of functional forms predicting 1) constant residence time 2) residence time proportionate to patch biomass and 3) residence time determined by marginal value considerations of energy gain. Because each model can be applied at a separate scale, we will examine a minimum of 27 alternatives.

The success of this experiment will turn on our ability to control the shape of the gain function at all three scales. Although it is relatively clear that manipulating interpatch distance can affect the gain function at the scale of the large patch and the cluster, it was uncertain whether we could successfully manipulate the shape of the gain function at small patch scales. Moreover, understanding the characteristics of plants that control the gain function at small patch scales has emerged as an important question in its own right (Astrom et al. 1990, Laca et al. 1994a, Laca et al. 1994c, Laca and Ortega 1995, Shipley and Spalinger 1995, Ginnett et al. 1999).

Methods

We conducted three separate experiments and replicated these experiments at two research sites. At Colorado State University, experiments were performed with 5 mule deer (*Odocoileus hemionus*) fawns; at Washington State University, we worked with 5 blue duikers (*Cephalophus monticola*).

In experiment one we considered how the spatial arrangement of plant mass in small patches influences the gain function of mule deer and duikers. Five different patch types were used, each offering the same total mass of plant tissue (fresh alfalfa, *Medicago sativa*) but differing in the geometric arrangement of plants. We scaled the total plant mass contained in the patch to the intake rates of the study animals using relationships of

(Shipley et al. 1994). We created 5 patch types consisting of 2, 4, 8, 20 or 40 individual plants and we observed animals foraging in each patch type.

In experiment two, we considered how obstructing, unpalatable plant material modifies the relationships we observed in experiment 1. We offered the same patch types, but mixed each alfalfa plant with a piece of dead diffuse knapweed (*Centaurea diffusa*) to create a structurally complex mixture of palatable and unpalatable tissue.

In experiment three, we considered the influence of heterogeneity in plant species on the shape of the gain functions observed in experiment one. Again, we constructed patch types in the same manner as Experiment one by varying number of plants (4, 8, 20 and 40) while holding patch mass constant. We used four plant species-- alfalfa, smooth brome (*Bromus inermis*), sandbar willow (*Salix exigua*), and blue grass (*Poa pratensis*), which we arranged in equal proportions in the patches.

We hand-constructed patches using individual plants. We weighted plants to $\pm 10\%$ of a target mass determined by the total plant mass in the patch divided by the number of plants in the patch. Several dry matter calculations were made on each trial day and an average was taken to give the value used in the subsequent analysis. Each plant was fastened to a wooden board (50cm by 50cm) by inserting part of the plant into a hole and attaching it using a rubber stopper inserted from the underside of the board. We were careful to ensure that plant spacing remained the same in all trials. We also tried to run the trials for the different patch types on different days. All trial animals were kept off feed for at least 4 hours before the start of observations.

We videotaped all trials using a standard 8mm camcorder. The videotape was time stamped at 0.1-second intervals. We replayed videos (in slow motion when necessary) to observe the time of each bite was taken. Simultaneously, we estimated the proportion of each plant consumed. Mass removed from a plant was estimated as the normalized proportion of plant tissue removed multiplied by the initial dry mass of each plant. We estimated gain functions as the cumulative mass removed from a patch as a function of patch residence time.

Literature Cited

- Astrom, M., P. Lundberg, and K. Danell. 1990. Partial prey consumption by browsers trees as patches. *Journal of Animal Ecology* **59**:287-300.
- Burnham, K. P., and D. R. Anderson. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York. 349 pp.
- Ginnett, T. F., J. A. Dankosky, G. Deo, and M. W. Demment. 1999. Patch depression in grazers: the roles of biomass distribution and residual stems. *Functional Ecology* **13**:37-44.
- Laca, E., and I. M. Ortega. 1995. Integrating foraging mechanisms across spatial and temporal scales. Pages 129-132 in N. E. West, editor. *Rangelands in a Sustainable Biosphere*. Society for Range Management, Denver, CO.

- Laca, E. A., R. A. Distel, T. C. Griggs, and M. W. Demment. 1994a. Effects of canopy structure on patch depression by grazers. *Ecology* **75**:706-716.
- Laca, E. A., E. D. Ungar, and M. W. Demment . 1994b. Mechanisms of handling time and intake rate of a large mammalian grazer. *Applied Animal Behaviour Science* **39**:3-19.
- Laca, E. A., E. D. Ungar, and M. W. Demment. 1994c. Mechanisms of handling time and intake rate of a large mammalian grazer. *Applied Animal Behaviour Science* **39**:3-19.
- Shipley, L. A., J. E. Gross, D. E. Spalinger, N. T. Hobbs, and B. A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. *American Naturalist* **143**:1055-1082.
- Shipley, L. A., and D. E. Spalinger. 1995. Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. *Oecologia* **104**:112-121.