NOTE TO USERS

Page(s) missing in number only; text follows. Page(s) were scanned as received.

86

This reproduction is the best copy available.

UMI®

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

DISSERTATION

RESPONSES OF HERBIVORES TO HETEROGENEITY IN FORAGE RESOURCES EXPRESSED AT MULTIPLE SPATIAL SCALES

Submitted by

Kate R. Searle

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2004

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

UMI Number: 3160055

INFORMATION TO USERS

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleed-through, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

UMI®

UMI Microform 3160055

Copyright 2005 by ProQuest Information and Learning Company.

All rights reserved. This microform edition is protected against unauthorized copying under Title 17, United States Code.

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

COLORADO STATE UNIVERSITY

August 17th, 2004

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY KATE R. SEARLE ENTITLED RESPONSES OF HERBIVORES TO HETEROGENEITY IN FORAGE RESOURCES EXPRESSED AT MULTIPLE SPATIAL SCALES BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Committee on Graduate Work

Bruce A. Wunder

N Thompson Hobbs

Advisor

Department Head

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ABSTRACT OF DISSERTATION

RESPONSES OF HERBIVORES TO HETEROGENEITY IN FORAGE RESOURCES EXPRESSED AT MULTIPLE SPATIAL SCALES

Understanding responses of organisms to spatial heterogeneity in resources has emerged as an important challenge in contemporary ecology. I examined responses of foraging herbivores to multi-scale heterogeneity in plants, implementing several empirical experiments to seek answers to key questions that have arisen from theoretical foraging theory.

First, I sought to understand how fine scale heterogeneity controls intake rate for large herbivores. The gain function describes the amount of food consumed in a patch as a function of patch residence time. I evaluated the strength of evidence in data for alternative gain function forms of mule deer (*Odocoileus hemionus*) and blue duikers (*Cephalophus monticola*) feeding in patches composed of different plant species and plant sizes. I found that gain functions decelerated continuously with patch residence time, but the nature of the deceleration depended on patch characteristics, notably plant size. I elucidated the mechanisms causing deceleration. I demonstrated that unwarranted assumptions about the shape of gain functions can have fundamental effects on predictions of patch models.

Second, I asked the question, “Is the behavior observed at coarse scales in a patch hierarchy the collective outcome of fine scale behaviors or, alternatively, does the spatial context at coarse scales entrain fine scale behavior?” I created a 2 level patch hierarchy,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

and examined effects of the geometry of the hierarchy on residence time of foraging grizzly bears, mule deer, and collared lemmings. I developed a set of competing models predicting residence time as a function of patch size and distance among patches, and examined the strength of evidence in data for each model. Models that included patch mass and inter-patch distance as independent variables successfully predicted observed residence times. Grizzly bears and mule deer responded to differences in patch geometry at multiple scales. In contrast, the residence times of collared lemmings were simply predicted by the mass of food in patches and were uninfluenced by differences in the surrounding spatial context.

Third, I sought to understand if herbivores choose patches to maximize food intake rate or to reduce risk of starvation in variable environments. Moreover, I examined the possibility that intake rate maximization was dependent on the spatial scale of patchiness. Two currencies have been used to assess the patch preferences of herbivores—intake rate maximization and risk sensitivity. I found that collared lemmings did not consistently select patches that maximized their intake rate at either scale studied. Instead, lemmings consistently chose patches offering the least variation in food reward over the course of the experiment. I interpret these results as evidence for risk-averse foraging strategies, which are predicted for continuous foragers aiming to minimize risk of starvation.

Finally, I discuss the question of how much time a foraging herbivore should spend in a patch of food. This question poses a central challenge in classical foraging theory. However, there remains uncertainty about the relevance of the patch paradigm to foraging decisions by large herbivores. I examined evidence for successfully predicting

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

and quantifying patch departure decisions for large mammalian herbivores foraging across several spatial and temporal scales. I found strong evidence that departure decisions at fine scales are influenced by trade-offs between maximizing intake rate and food quality. In addition, classical models for departure decisions at larger spatial scales, particularly the marginal value theorem, appear inadequate. I advocate exploring alternative models for predictions of residence time at the patch scale.

Kate R. Searle
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Fall 2004

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CONTENTS

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Introduction

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The activities of large herbivores are an important influence on ecological communities and ecosystems. Ungulates modify nutrient cycles (Ruess and McNaughton 1987), soil properties (Pastor and Naiman 1992), net primary production (Frank and McNaughton 1993), and fire regimes (Madany and West. 1983). As a consequence, ungulates are important agents of change in ecosystems, responding to and creating spatial heterogeneity (Hobbs 1996). This interaction is notable in its spatial extent---large herbivores are highly mobile, and may cross plant-community boundaries as many as 50 times/day (Senft et al. 1987). Hence, the impacts of large herbivores are experienced across multiple scales.

Ecologists describe spatial aggregations of resources as patches. The patch concept has played a central role in ecology as a description of spatial patterns. Environments can be patchy in many different ways, and these differences are often used as measures of spatial heterogeneity in resources. Defining patches is principally an exercise in abstraction (Kotliar and Wiens 1990), however the concept of patches remains central to contemporary thinking about heterogeneity (Hobbs 1999). For herbivores, a patch can be defined as an area of forage, delimited spatially, contrasting in biomass, plant species, or plant age. These differences create opportunities for acquiring energy and nutrients during foraging. Patches occur across a hierarchy of spatial scales, such that a patch at a given scale has an internal structure that reflects patchiness at finer scales. The responses of herbivores are generally not limited to a single scale, and thus this hierarchical structure of patchiness is expected to be important in understanding herbivore responses (Senft et al. 1987, Kotliar and Wiens 1990). Differential responses of herbivores to patchiness in resources at multiple scales means that herbivores are

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

selective in terms of their choice of landscape characteristics. It is this selection process that we wish to understand, in relation to choice of foraging sites, and movements of herbivores across landscapes.

To address the issue of resource heterogeneity I developed experiments to augment understanding of how mammalian herbivores respond to heterogeneity expressed at multiple scales. Specifically:

Chapter 1: I identified mechanisms that control small-scale intake (gain functions) of herbivores foraging in small patches.

Chapter 2: I developed and compared alternative models for patch departure decisions of large herbivores at several spatial scales. I asked "Is the behavior observed at coarse scales in a patch hierarchy the collective outcome of fine scale behaviors or, alternatively, does the spatial context at coarse scales entrain fine scale behavior?"

Chapter 3: I identified spatial scales of variation exerting a predominant influence on herbivore foraging. I sought to understand if herbivores choose patches to maximize food intake rate or to reduce risk of starvation in variable environments. Moreover, I examined the possibility that intake rate maximization was dependent on the spatial scale of patchiness.

Chapter 4: I reviewed the 'patch' concept in applications to large mammalian herbivore foraging. What have we learnt about how herbivores from patch departure decisions across multiple spatial and temporal scales?

Literature cited

Frank, D. A., and S. J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oeocologia **96**:157-161.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management **60**:695-713.

Hobbs, N. T. 1999. Responses of large herbivores to spatial heterogeneity in ecosystems. Pages 97-129 *in* H. G. Jung and G. C. Fahey, editors. Nutritional Ecology of Herbivores: Proceedings of the Vth International Symposium on the Nutrition of Herbivores. American Society of Animal Science, Savory IL.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure - a hierarchical framework for the study of heterogeneity. Oikos **59**:253-260.

Madany, M. H., and N. E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology **64**:661-667.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist **139**:690-705.

Ruess, R. W., and S. J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. Oikos **49**:101-110.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience **37**:789-799.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Chapter One

Gain functions for large herbivores: tests of alternative models

(accepted for publication in Journal of Animal Ecology)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

1. The gain function describes the amount of food consumed in a patch as a function of patch residence time. Gain functions play a central role in foraging theory but alternative functional forms portraying dynamics of gain have not been evaluated. I evaluated the strength of evidence in data for alternative gain functions of mule deer (*Odocoileus hemionus*, Rafinesque 1817) and blue duikers (*Cephalophus monticola*, Blythe 1848) feeding in patches composed of different plant species and plant sizes.
2. Gain functions decelerated with patch residence time, but there was considerable variation amongst individual animals and patch types in the nature of this response. Asymptotic and piecewise-linear models received the greatest support in the data.
3. Deceleration in gain was caused by a composite of effects that retarded instantaneous intake rate including reductions in bite mass and increases in bite interval (time between successive bites). Bite interval increased as a result of increases in processing time of accumulated forage in the mouth, rather than increases in time allocated to cropping.
4. I demonstrated that unwarranted assumptions about the shape of gain functions can have profound effects on predictions of patch models. Predictions of the classical patch model using purely asymptotic gain functions contrasted sharply with predictions of model averaged gain functions that were supported by data.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Introduction

A central problem in foraging ecology focuses on a simple question: given several patch types to choose from, how do foragers allocate their time among those patches? Answering this question requires describing the interplay between the time animals commit to residing in patches and the time they spend traveling from patch to patch. One of the classical abstractions in foraging theory, the patch model ([Charnov, 1976 #1824], predicts that animals should reside in patches as long as their instantaneous rate of energy gain exceeds the rate of gain averaged across all patches available. Applying the patch model depends on identifying the relationship between cumulative gain of energy and patch residence time, hereafter referred to as the gain function. The gain function has direct consequences for the predictions of the patch model--even small changes in gain function shape cause marked differences in predictions of patch residence time (Astrom, Lundberg, & Danell 1990; Olsson, Brown, & Smith 2001).

Early efforts to test the patch model focused on nectarivores and seed-predators (Pyke 1978; Giraldeau & Kramer 1982; Pleasants 1989), but recently, effort has been invested in applying the model to large herbivores (Jiang & Hudson 1993; Kotler, Gross, & Mitchell 1994; Laca *et al.* 1993; Shipley & Spalinger 1995). Many studies have offered qualitative support for the patch model; for example, residence time has been widely observed to increase with travel time (e.g. Astrom *et al.* 1990; Cassini *et al.* 1990; Cassini *et al.* 1993; Kotler *et al.* 1994; Shipley & Spalinger 1995). However, quantitative agreement between predicted and observed residence time had been rare (Jiang & Hudson 1993; Laca *et al.* 1993).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The failure of patch models to quantitatively predict residence time may result from using inappropriate gain functions. A variety of functions have been used to portray dynamics of gain including linear (Illius *et al.* 2002), piecewise-linear (Astrom *et al.* 1990; Shipley & Spalinger 1995), sigmoid (Ginnett *et al.* 1999), and asymptotic forms (Laca *et al.* 1994). However, there has been no attempt to evaluate the strength of evidence in data for these competing alternatives. The absence of tests of competing models is particularly problematic because some of these forms fail to meet the assumption of the patch model that cumulative gain is a continuous, decelerating function of patch residence time. Moreover, there is little understanding of how variation in patch characteristics, such as plant size and patch composition, might influence the shape of gain functions (but see Ginnett & Demment 1995; Laca *et al.* 1994). Understanding of this influence requires describing the mechanisms that drive variation in the dynamics of gain by foraging herbivores (Astrom *et al.* 1990; Olsson *et al.* 2001; Shipley & Spalinger 1995).

I investigated gain functions of mammalian herbivores feeding in patches. Our objectives were to: 1) evaluate the strength of evidence in data for alternative gain functions; 2) determine effects of patch characteristics on the gain function shape; and 3) describe mechanisms causing deceleration in gain with increasing patch residence time.

Materials and methods

Patch definition

The patch metaphor plays a central role in many ecological models, particularly foraging models. The seminal paper of Senft *et al.* (1987) offered a functional basis for defining patches for foraging herbivores. Foraging processes occurring at different

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

frequencies define different levels in a patch hierarchy. A bite forms the base of this hierarchy, and a local collection of bites, the feeding station, forms the next hierarchal level. The feeding station is defined as an area sufficiently small that it can be depleted without requiring travel. Given that dynamics at higher levels in the foraging hierarchy will be explained, at least in part, by the dynamics of intake at feeding stations, I focused our work on the feeding station scale. In the following text, I strive for simple prose by using the term "patch" synonymously with feeding station.

Candidate models of gain functions

By definition, the first derivative of the gain function is the instantaneous intake rate, which is determined by the animal's functional response to patch characteristics. The shape of the gain function is controlled by the way that instantaneous intake rate changes over time. Foragers will experience diminishing returns and gain functions will decelerate if instantaneous intake rate declines as patches are depleted. Instantaneous intake rate of herbivores feeding in patches can be estimated using the model of (Spalinger & Hobbs 1992),

$$I = \frac{SR_{\max}}{hR_{\max} + S} \tag{1}$$

where I is the intake rate (g/min), S is the mass of a bite consumed by the animal (g), R_{max} is the maximum rate of processing of plant tissue in the mouth (g/min), and h is the time required to crop plant tissues from the plant (min). I formed candidate models of gain functions by making assumptions about how S, h, and R_{max} change with patch residence time (Table1.1).

Mechanisms causing deceleration

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Non-linearity in gain functions occurs when parameters (P) regulating instantaneous intake rate change with residence time (t). I evaluated support in data for models representing intake parameters (P) as a constant ($P = c$), and as linear ($P = a + bt$) and exponential ($P = ae^{bt}$) functions of patch residence time. Evaluated parameters included bite mass ($P = S$, g DM), cropping time ($P = h$, min), bite interval ($P = h + S/R_{max}$, equation 1, min), processing time ($P = 1/R_{max}$, equation 1, min/g DM), and chewing rate (P = chews/min). To evaluate these models, I defined the total residence time as t_{final} and divided this time interval into 5 equal intervals, hereafter fifths. Each fifth included 20% of the total elapsed time between the first and last bite cropped. The use of fifths was a subjective decision to attempt to capture the temporal dynamics of intake parameters. This interval strikes a reasonable compromise between intervals that were too long (thus losing some of the important dynamics) and those that were too short (producing excessive noise). I averaged parameter values across individual animals to examine how they changed with residence time.

Gain function experiments

Characteristics of plants may affect how instantaneous intake rate changes as patches are depleted, and hence, may control the shape of the gain function. I observed gain functions of herbivores in three patch types. In the first patch type, 'alfalfa-only', I varied the size of plants and held the composition of patches constant. I hypothesized that asymptotic gain functions would receive more support in the data when plant size was large because large plants offered a greater opportunity for bite size (S) to decline as plants were consumed. In the second patch type, 'obstruction', I varied plant size and mixed fresh alfalfa with an inedible plant. I hypothesized that obstructing material would

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

reduce bite size (*S*), and increase processing time (R_{max}) and cropping time (*h*) because of the increased manipulation involved in forming and processing bites. In the third patch type, 'mixed', I varied plant size and offered different plant species. In these patches, I hypothesized that the asymptotic and sigmoid gain function models would receive more support in the data as the animals encounter different plant species within the same patch, resulting in mixed bite sizes (*S*), and processing times (R_{max}).

I conducted experiments with five female mule deer fawns ($\bar{x} = 23kg$) at the Colorado Division of Wildlife Foothills Research Facility in Fort Collins, CO, and three male blue duikers ($\bar{x} = 4kg$) at Washington State University's Small Mammal Research Facility in Pullman, WA, during August – December 2000. I used two herbivore species to attempt to capture responses across a range of herbivore body sizes. I observed cumulative consumption of dry matter by animals foraging in patches constructed by anchoring plants in plywood boards 0.5 x 0.5 m for mule deer and 0.3 x 0.6 m for blue duikers (Gross et al.1993b). The size of each feeding station was subjectively determined as the largest area each animal species could reach without moving its forefeet. A "plant" was considered a collection of shoots anchored at a single point within a patch. To form individual plants of different size, I held shoot length constant and varied the number of shoots, thereby eliminating variation in plant nutritional quality that might result from differences in plant height.

To observe effects of patch characteristics on the gain function, I held the total mass of plant tissue in a patch constant and varied plant size. In alfalfa-only patches, I offered fresh alfalfa (*Medicago sativa*) in 2, 4, 8, 20, or 40 plants (Table 1.2). In obstruction patches, I offered the same number of plants, but intermingled the alfalfa with

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

unpalatable plant tissue, dead diffuse knapweed (*Centaurea diffusa* for mule deer), and dead Russian knapweed (*Acroptilon repens*) for blue duikers. Unpalatable plants were anchored in the same hole as the alfalfa to make it difficult for the animal to crop alfalfa alone. In mixed patches, alfalfa was mixed with equal mass of willow (*Salix* spp.), Kentucky bluegrass (*Poa pratensis*), and smooth brome grass (*Bromus inermis*), which were anchored in different holes in the patch.

Total mass offered at a patch was scaled to body mass based on the functional response of each herbivore species. I estimated the smallest plant size offered as the mass that would provide an intake rate equal to 25% of R_{max} if the plant were consumed in a single bite. I created patches for the gain function trials containing multiples of this minimum plant size.

A time series of observations of mass removed from plants was obtained by videotaping foraging animals. I visually estimated the proportion of each plant cropped in each bite and noted the time when bites were cropped to the nearest 1/30 of a second. (Pilot experiments established that visual estimates of proportion removed were unbiased and accounted for 56% of the variation in measured proportions. Because our estimates were unbiased, the remaining error in visual estimates simply adds to our experimental error.) I then normalized these proportions to sum to one and multiplied them by the mass removed from each plant, measured as the difference between the plant dry mass at the start and end of the trial to estimate the mass of each bite consumed. The sum of bite masses was used to estimate cumulative gain as a function of patch residence time. Pauses in feeding caused by distractions were removed from the time-series to prevent spurious deceleration in gain (Illius and Fryxell 2002).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Parameters regulating instantaneous intake rate were estimated for animals feeding in alfalfa-only patches. Bite mass was estimated as above. Cropping time was estimated as the time between the instant an animals muzzle touched a plant until the time a bite was severed. Bite interval was estimated as the time between successive touches of the muzzle to plant before cropping. Processing time was the time devoted to chewing divided by the mass consumed over a defined interval. Chewing rate was estimated as the total number of jaw cycles per minute of feeding.

Mule deer were maintained on *ad libitum* grain pellets (Baker & Hobbs 1985), alfalfa hay, trace mineral block; blue duikers were fed *ad libitum* complete-balanced grain-alfalfa pellets, fresh willow leaves, trace mineral block. Food was removed 4 hours before each trial conducted with mule deer and 8-10 hours before each trial conducted with blue duikers.

Statistical analysis

I used likelihood based methods and information theoretics (Akaike's Information Criterion adjusted for small samples, AIC_c), to quantify strength of evidence for alternative models (Burnham & Anderson 2002). Because model parameters were estimated based on data, there is some uncertainty that the "best" model would emerge as superior if different data were used to compare alternatives. I quantified this uncertainty with Akaike weights, w_r (Burnham & Anderson 2002). Illius and Fryxell (2002) demonstrated that averaging across individuals may produce spurious evidence for patch depression. I incorporated variation among individual animals in estimates of Akaike weights for each patch type by bootstrapping from the data. I randomly sampled records (N = 1000) for individuals with replacement to calculate an average Akaike weight for

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

each patch type; 95% confidence intervals on our estimates of w_r were estimated from the upper and lower 2.5 percentiles of bootstrapped estimates.

Results

Support in the data for each of the gain function models varied across patch types. I found virtually no support in the data for linear (alfalfa-only patches, mule deer average w_r<0.0057; alfalfa-only patches, blue duikers average w_r<0.055) and only weak support for sigmoid gain functions (alfalfa-only patches, mule deer average w_r<0.034; alfalfa-only patches, blue duikers average w_r<0.18) for either species of herbivore feeding in any patch type. However, in a few cases, I observed some support for the sigmoid model (e.g. blue duiker in alfalfa-only patch with 2 plants). The majority of the support in the data was for the asymptotic and piecewise-linear models in most patch types. Hence, I will limit further presentation of results to the asymptotic and piecewise-linear models.

Support for the asymptotic and piecewise-linear models was mixed in all patch types (Table 1.3). Overall, blue duikers showed more support for the piecewise-linear model than the mule deer did, though the asymptotic model also received support in most patch types (Table 1.3). Support for these two models was split in the mule deer trials across all patch types (Table 1.3). The different patch types did not cause any consistent differences in support for the gain function models (Table 1.3).

Mechanisms causing deceleration

I observed that parameters controlling instantaneous intake rates changed dynamically with increasing patch residence time. Mean bite mass (*S,* equation 1) declined exponentially or linearly with increasing patch residence time for all plant sizes in both species (Figs 1.1a and 1.1b). However, these effects were greater for mule deer

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

than for blue duikers. This difference is expressed in the sharper decline in intake rate for mule deer feeding on large plants. In addition, the time between successive bites (bite interval, $h + S/R_{max,}$ equation 1) tended to increase linearly with patch residence time for mule deer, especially for smaller plant sizes (Fig. 1.1a). Blue duikers showed linear or exponential increases in bite interval across all plant sizes (Fig. 1.1b).

I observed mixed support for models of processing time, especially for large plant sizes. Mule deer showed an exponential increase in processing time (time spent chewing/mass consumed) with residence time in patches with large plants, in contrast to blue duikers, where processing time remained much more constant. Support for the constant model was greatest when patches consisted of smaller plants, indicating that processing time did not change with residence time for mule deer when plant size was small (Fig. 1.1a). Support for alternative models of processing time was also mixed for blue duikers when plant size was large, and similar to the mule deer, processing time remained constant with residence time in patches with smaller plant sizes (Fig. 1.1b).

Chewing rate (chews / min) increased exponentially with residence time for mule deer, although support for the linear model approached that for the exponential model as plant size decreased (Fig. 1.1a). There was mixed support for alternative models of changes to chewing rate for blue duikers feeding in patches containing large plants. However, for small plant sizes, chewing rate remained constant with residence time (Fig. 1.1b). All models of cropping time (*h*, equation 1) received support in the data for mule deer, although the constant model had the most support (Figs 1.1a and 1.1b). In contrast, blue duikers showed a linear or exponential increase in cropping time across all plant

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

sizes (Fig. 1.1b). There were no real differences in these mechanism trends over the different patch types.

Discussion

Evidence for competing gain functions

I found strong evidence that rate of gain of dry matter decelerates with increasing patch residence time for two species of herbivores foraging in patches where travel was not required to deplete the patch. Composition of patches did not affect this deceleration. Because our data offered no support for linear gain functions, and because parameters regulating intake rate were not constant with time, I can unequivocally reject the hypothesis that dry matter gain is directly proportionate to patch residence time in patches resembling those I studied.

There was marked variation in support for the asymptotic and piecewise-linear gain functions amongst individual animals and plant size. Blue duikers tended to exhibit piecewise-linear gain curves most often, though the asymptotic model also received support. Mule deer showed more or less equal support for both asymptotic and piecewise-linear gain curves over all patch types and plant sizes.

Mechanisms causing deceleration

Deceleration in gain was caused by a composite of effects retarding intake rate including reductions in bite mass and increases in time between successive bites. When plant sizes were large, bite mass declined continuously with increasing residence time. Decreasing bite mass has the effect of reducing intake rate if the time allocated to cropping and processing bites does not change (Laca *et al.* 1994). Large plants offered plant masses larger than animals are able to take in a single bite, thus allowing bite size to

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

decline as patches were depleted. Animals removed larger bites initially and consumed progressively smaller ones as plant sized was reduced. In contrast, when plants were smaller than the average bite size, animals consumed most of each plant with one large bite, subsequently removing orts after all plants were cropped. This created two linear phases to the gain function, each arising from a different bite size.

Deceleration in gain functions was also promoted by increases in the time interval between bites, which resulted primarily from increases in processing time in patches with larger plants as patches were depleted. In addition, increases in time allocated to chewing in the latter stages of patch depletion contributed to deceleration in gain for mule deer, as the animals switched from ingestion of plant material to processing of material accumulating in the mouth. Processing time increased with patch depletion in our study because animals increased their investment in chewing of accumulated material in the mouth, as demonstrated by our measurements of chewing rate. This result can be interpreted as a decline in bite rate because 1/bite interval is equivalent to bite rate. The bite interval increased as a result of increases in time devoted to investment in chewing, and processing of accumulated plant material in the mouth.

Others have observed that gain decelerates because increases in bite rate fail to compensate for declines in bite mass with increasing residence time (Laca *et al.* 1994, Ginnett *et al.* 1999, but see Illius *et al.* 2002). In our study, bite rate *declined* as residence time increased, thereby amplifying the effect of declining bite mass, particularly in patches with smaller plants. Increases in processing time did not fully explain this trend when plants were small. Instead, cropping time increased with patch depletion for both species in patches with smaller plants because animals found it more difficult to crop tiny

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

remaining pieces of plant tissue. This increase in cropping time experienced in the final stages of depletion of patches with small plants, combined with changes to bite mass may provide a mechanism for the observed piecewise-linear gain functions.

Our findings resemble those of Ginnett *et al.* (1999) and Laca *et al.* (1994) in providing evidence for deceleration of gain as a result of declining bite mass as patches are depleted. Our work also supports earlier findings (Ginnett *et al.* 1999; Laca *et al.* 1994) that patch characteristics modify the effect of residence time on changes in bite mass, and consequently, on deceleration in gain. In particular, Ginnett *et al.* (1999) also found that patches composed of small plants were less likely to produce continuously decelerating gain functions because bite mass was relatively insensitive to patch depletion when plants were small.

However, earlier work failed to examine strength of evidence for alternative functional forms describing cumulative gain in relation to patch residence time. Visual inspection of plots in Laca *et al.* (1994: Figs 1 and 2) indicates that comparison of the asymptotic gain functions with piecewise-linear was probably warranted in their analysis. Moreover, Laca *et al.* (1994:713) pointed out that their failure to observe a "...pronounced reduction in slope..." of gain functions probably resulted because animals were not allowed to graze long enough at feeding stations. This adds credence to our finding that the assumption of continuously decelerating gain functions at feeding station scales may not be warranted for all patch types.

Illius et al. (2002) observed linear gain functions by roe deer feeding in browse patches. They demonstrated that decelerating gain functions were not observed in browse patches because increased bite rate compensated for declines in bite mass as patches were

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

depleted. Consistent with Illius et al (2002), I found bite size declined as patches were depleted, although the magnitude of the change in bite mass in our study was greater and thus, caused a greater deceleration in the gain function. However, contrary to Illius et al. (2002), our results showed cropping time and processing time *increased* with patch residence time. Thus, our work contrasts with Illius et al. (2002) in demonstrating that changes in cropping and processing time of accumulated food in the mouth amplify rather than oppose, the decelerating effect of declines in bite mass as patches are depleted. Illius et al. (2002) showed on theoretical grounds that patch depression in browsers is unlikely to occur if foraging is described by Spalinger-Hobbs (1992) process 2 (dispersed apparent plants) or process 3 (concentrated apparent plants), if declines in bite size are small, which I would expect when herbivores forage on browses where bite size is controlled by leaf size. Under these circumstances the Spalinger-Hobbs (1992) functional response model predicts approximately linear gain functions. However, in grazers, bite size may decline dramatically during patch depletion because bite size is controlled by sward height and bulk density, as demonstrated in this study, and therefore the gain curves for process 2 or 3 foraging can be markedly non-linear. These findings illustrate that browses and herbaceous plants exert fundamentally different control on gain function shape.

Consequences of findings for predicting optimum patch residence time

Unwarranted assumptions on the shape of gain functions can have profound effects on predictions of models predicting patch residence time. To illustrate, I used data from the mule deer trials to compare the predictions of the patch model (marginal value theorem, MVT) using purely asymptotic gain functions (which were not justified by the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

data in all but the largest plant sizes) with model-averaged (Burnham & Anderson 1988) gain functions (which were justified by the data). I based MVT predictions on 4 single-species patch types (containing 2, 4, 8, and 20 plants with total mass = 2.73 g DM mule deer) and 5 inter-patch distances (1, 2, 5, 10, 20 m). These distances were used to estimate encounter rates with patches, using foraging velocity data from Shipley et al. (1996). I can be confident that I met the assumption of continuously decelerating gain because all gain functions, model averaged and asymptotic, included derivatives defined at all points.

The model averaged result predicted residence times that were several fold longer than were predicted by the asymptotic model in the patch type offering small plants (Fig. 2.1). This was because of the influence of piecewise-linear gain functions, which represent cumulative gain in represented by two linear phases. With purely asymptotic gain functions, optimal residence time increased monotonically towards a plateau with increasing inter-patch distance (Fig. 2.1). However, for model averaged gain functions, particularly for patches with smaller plants (8 plants and 20 plants), the relationship took on an approximately piecewise-linear form (Fig. 2.1). Because there are two predominantly linear phases to the model averaged gain functions in these patch types, there are two corresponding approximately linear phases in the relationship between inter-patch distance and optimal residence time predictions. These two phases represent optimal residence times that fall on either side of the inflexion point (parameter τ) in the model averaged gain functions. Consequently, residence time predictions for model averaged linear gain functions tended to fall further to the right of the gain function curve than for asymptotic gain functions when plants were small.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Conclusions

I conclude that rate of gain of dry matter by large herbivores feeding in herbaceous patches is likely to decelerate as patches are depleted. Deceleration in gain is promoted by declines in bite size, and increases in time between successive bites. However, there is considerable variation in gain curve shape amongst individual animals and across plant sizes.

I have shown that the assumption of constant parameters (R_{max}, h) and driving variables (S) in the model of Spalinger and Hobbs (1992) will hold only if patches are not depleted, as might occur for example, when animals move continuously through a sward. When patch depletion occurs, reductions in bite size and increases in cropping and processing time cause gain functions to decelerate. These results have implications for understanding animal movement in heterogeneous environments. For example, reduction in intake rate in a patch may stimulate movement to undepleted patches. Our studies show that such reductions occur.

Acknowledgements

This work was funded by National Science Foundation grants to Hobbs and Wunder (DEB 9981368) and to Shipley (DEB 9981242). I am grateful to the staff of the Colorado Division of Wildlife Foothills Research Facility at Fort Collins, CO. We thank C. Bishop, W. Mulherin, M. Rice, and E. Wheeler for assistance in animal care and field trials in Fort Collins. We are grateful to B. Davitt for the use of his nutrition lab, and M. Fisher and S. Plank for assisting in the blue duiker trials. This work could not have been completed without Tom Hobbs, Thea Vanvervelde, and Lisa Shipley.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Literature Cited

Astrom, M., Lundberg, P., & Danell, K. (1990) Partial Prey Consumption by Browsers - Trees as Patches. *Journal of Animal Ecology*, **59**, 287-300.

Baker, D.L. & Hobbs, N.T. (1985) Emergency feeding of mule deer during winter: tests of a supplemental ration. *Journal Wildlife Management*, **49**, 934-942.

Burnham, K.P. & Anderson, D.R. (1998) Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Charnov, E.L. (1976) Optimal foraging, the Marginal Value Theorem. *Theoretical Population Biology*, **9**, 129-136.

Ginnett, T.F., Dankosky, J.A., Deo, G., & Demment, M.W. (1999) Patch depression in grazers: the roles of biomass distribution and residual stems. *Functional Ecology*, **13**, 37-44.

Ginnett, T.F. & Demment, M.W. (1995) The functional-response of herbivores - analysis and test of a simple mechanistic model. *Functional Ecology*, **9**, 376-384.

Giraldeau, L.A., and D. L. Kramer (1982) The Marginal Value Theorem: A quantitative test using load size variation in a central place forager, the eastern chipmunk. *Animal Behaviour*, **30**, 1036-1042.

Gross, J.E., Shipley, L.A., Hobbs, N.T., Spalinger, D.E., & Wunder, B.A. (1993) Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology*, **74**, 778-791.

Illius, A. W., Duncan P., Richard C., and Mesochina P. (2002) Mechanisms of functional response and resource exploitation in browsing roe deer. *Journal of Animal Ecology*, **71**, 723-734.

Illius, A.W. & Fryxell, J.M. (2002) Methodological problems with estimating patch depression during resource depletion. Oikos, 98, 558-559.

Jiang, Z. & Hudson, R.J. (1993) Optimal grazing of wapiti *Cervus elaphus* on grassland patch and feeding station departure rules. *Evolutionary Ecology*, **7**, 488-498.

Kotler, B.P., Gross, J.E., & Mitchell, W.A. (1994) Applying patch use to assess aspects of foraging behavior in Nubian ibex. *Journal of Wildlife Management*, **58**, 299-307.

Laca, E.A., Distel, A., Griggs, T.C., & Demment, M.W. (1994) Effects of canopy structure on patch depression by grazers. *Ecology*, **75**, 706-716.

Laca, E.A., Distel, R.A., Griggs, T.C., Deo, G.P., & Demment, M.W. (1993). Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilisation. In Proceedings of XVII International Grassland Congress, pp. 709-701, New Zealand and Queensland, February 1993.

Olsson, O., Brown, J.S., & Smith, H.G. (2001) Gain curves in depletable food patches: A test of five models with European starlings. *Evolutionary Ecology Research*, **3**, 285-310.

Pleasants, J.M. (1989) Optimal foraging by nectarivores: a test of the Marginal Value Theorem. *American Naturalist*, **134**, 51-71.

Pyke, G.H. (1978) Optimal foraging in hummingbirds: testing the Marginal Value Theorem. *American Zoologist*, **18**, 739-752.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Sala, O.E., & Swift, D.M. (1987) Large herbivore foraging and ecological hierarchies. *Bioscience*, **37**, 789-799.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Shipley, L.A. & Spalinger, D.E. (1992) Mechanics of browsing in dense food patches effects of plant and animal morphology on intake rate. *Canadian Journal of Zoology*, **70**, 1743-1752.

Shipley, L.A. & Spalinger, D.E. (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.

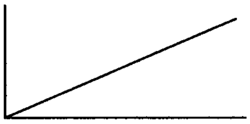
Shipley, L.A., Spalinger, D.E., Gross, J.E., Hobbs, N.T., & Wunder, B.A. (1996) The dynamics and scaling of foraging velocity and encounter rate in mammalian herbivores. Functional Ecology, 10, 234-244.

Spalinger, D.E. & Hobbs, N.T. (1992) Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist*, **140**, 325-348.

Ungar, E.D., Seligman, N.G., & Demment, M.W. (1992) Graphical analysis of sward depletion by grazing. *Journal of Applied Ecology*, **29**, 427-435.

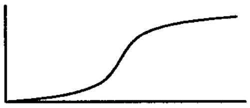
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 1.1. Candidate gain function models for mule deer and blue duikers feeding in fresh alfalfa patches.

Gain function Model	Shape	Equation
Linear		$G(t)=I\cdot t$
	If *S, R_{max},* and *h* remain constant as the patch is depleted then *I* does not change and the gain function will be a linear function with slope = *I* and intercept = 0.	
Piecewise-Linear		$G(t)=\begin{cases}\alpha+\beta_1 t & \text{if } t\le\tau\\ \alpha\tau+\beta_2(t-\tau) & \text{if } t>\tau\end{cases}$
	If the animal uses a "horizon" grazing style (Ungar *et al.* 1992) where it depletes the patch in layers, then it's foraging can be portioned into phases defined by each layer. Within each phase, I assume that bite mass remains relatively constant, as does processing rate and cropping time. In this case, the gain function, therefore, will consist of at least two linear phases, with a change in slope (i.e., intake rate) when the upper layer is depleted (Olsson *et al.* 2001). The parameter β_1 is instantaneous intake rate in the initial phase of patch depletion (g/min); β_2 is intake rate in the second phase of patch depletion (g/min); and τ is the residence time when intake rate decelerates (min).	
Asymptotic		$G(t)=\dfrac{\alpha\cdot t\cdot mass}{\alpha\cdot t+mass}$
	If cropping time (*h,* eq. 1*)* increases, or processing rate (R_{max}, eq. 1) or bite mass (*S*, eq. 1) decline continuously with residence time, then the gain function will be best represented as continuously decelerating asymptotic curve, where the asymptote is the total mass or energy in the patch attainable only at infinite time. The parameter α is the initial instantaneous intake rate (g/min) at time = 0 and *M* is the initial mass of forage in the patch (g dry matter).	

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Sigmoid



$$G(t) = \frac{\alpha \cdot t^2 \cdot mass}{\alpha \cdot t^2 + mass}$$

If a foraging animal does not reach its maximum intake rate immediately upon entering a patch, for example because it is making decisions on which plants to consume, then intake rate will accelerate before declining. The parameter α is the initial instantaneous intake rate (g/min) at time = 0 and M is the initial mass of forage in the patch (g dry matter).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 1.2. Patch types offered to 5 mule deer (*Odocoileus heminonus*) at Colorado State University and 3 blue duikers (*Cephalophus monticola*) at Washington State University during the summer of 2000. R_{max} is the maximum rate of intake as measured in preliminary functional response trials with these animals.

		Individual plant mass (g dry matter)		Number of trials					
				Patch type: alfalfa-only		Patch type: obstructed		Patch type: mixed	
%R_{max}	Number of plants per patch	Mule deer	Blue duikers	Mule deer	Blue duikers	Mule deer	Blue duikers	Mule deer	Blue duikers
25	40	0.068	0.012	5	4	4	3	3	3
50	20	0.137	0.024	5	5	5	3	3	3
125	8	0.341	0.047	4	5	5	3	3	3
250	4	0.683	0.059	3	5	5	3	3	3
500	2	1.366	0.095	5	0	0	3	0	0

Table 1.3. Number of instances for support for each gain function model for mule deer and blue duikers feeding in alfalfa patches (-- trials not completed). Instances of support are all those cases where the model received the greatest support in the data (w_r).

Patch type	Number of plants	Asymptotic		Piecewise-Linear		Linear		Sigmoid	
		Mule deer	Blue duikers	Mule deer	Blue duiker	Mule deer	Blue duiker	Mule deer	Blue duiker
1	2	2	0	2	0	0	1	1	2
	4	2	1	2	2	0	0	0	0
	8	1	1	3	1	0	0	0	1
	20	1	1	4	2	0	0	0	0
	40	3	0	2	3	0	0	0	0
2	2	--	0	--	1	--	1	--	1
	4	3	1	2	2	0	0	1	0
	8	2	1	3	1	0	1	0	0
	20	3	1	2	2	0	0	0	0
	40	3	0	1	3	0	0	0	0
3	4	5	1	0	1	0	0	0	1
	8	1	0	4	2	0	0	0	1
	20	0	1	3	2	1	0	0	0
	40	1	1	1	1	2	1	0	0

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 1.4. Parameter values for the best-fitting gain function model in each patch type and corresponding plant size. Models were fit to data for individual mule deer and blue duikers foraging in each patch type and plant size, and the model with the highest Akaike weight was selected.

Species	Patch type	Number of plants	Model	Parameters		
Mule Deer	Alfalfa-only	2	Asymptotic	α 0.234	M 3.384	
		4	Piecewise-linear	τ 12.548	B_1 0.15	B_2 0.017
		8	Piecewise-linear	τ 5.056	B_1 0.09	B_2 0.046
		20	Piecewise-linear	τ 30.31	B_1 0.081	B_2 0.004
		40	Piecewise-linear	τ 35.421	B_1 0.054	B_2 0.012
	Obstructed	2	--	--	--	--
		4	Piecewise-linear	τ 3.177	B_1 0.118	B_2 0.036
		8	Asymptotic	α 0.066	M 6.746	
		20	Asymptotic	α 0.051	M 5.004	
		40	Asymptotic	α 0.023	M 5.732	
	Mixed	4	Asymptotic	α 0.192	M 2.845	
		8	Piecewise-linear	τ 7.56	B_1 0.146	B_2 0.023
		20	Piecewise-linear	τ 18.619	B_1 0.08	B_2 0.038
		40	Asymptotic	α 0.048	M 7.443	
Blue Duikers	Alfalfa-only	2	Sigmoid	α 0.002	M 0.382	
		4	Piecewise-linear	τ 32.826	B_1 0.009	B_2 0.003
		8	Asymptotic	α 0.014	M 0.667	
		20	Asymptotic	α 0.008	M 1.424	
		40	Piecewise-linear	τ 10.386	B_1 0.007	B_2 0.003
	Obstructed	2	Sigmoid	α 0.0005	M 0.4	

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

	4	Piecewise-linear	τ 47.281	B_1 0.006	B_2 0.004
	8	Piecewise-linear	τ 0.265	B_1 0.092	B_2 0.003
	20	Asymptotic	α 0.005	M 0.695	
	40	Piecewise-linear	τ 85.277	B_1 0.003	B_2 0.001
Mixed	4	Piecewise-linear	τ 32.04	B_1 0.006	B_2 0.001
	8	Piecewise-linear	τ 6.235	B_1 0.017	B_2 0.007
	20	Piecewise-linear	τ 42.2	B_1 0.002	B_2 0.001
	40	Piecewise-linear	τ 4.729	B_1 0.008	B_2 0.003

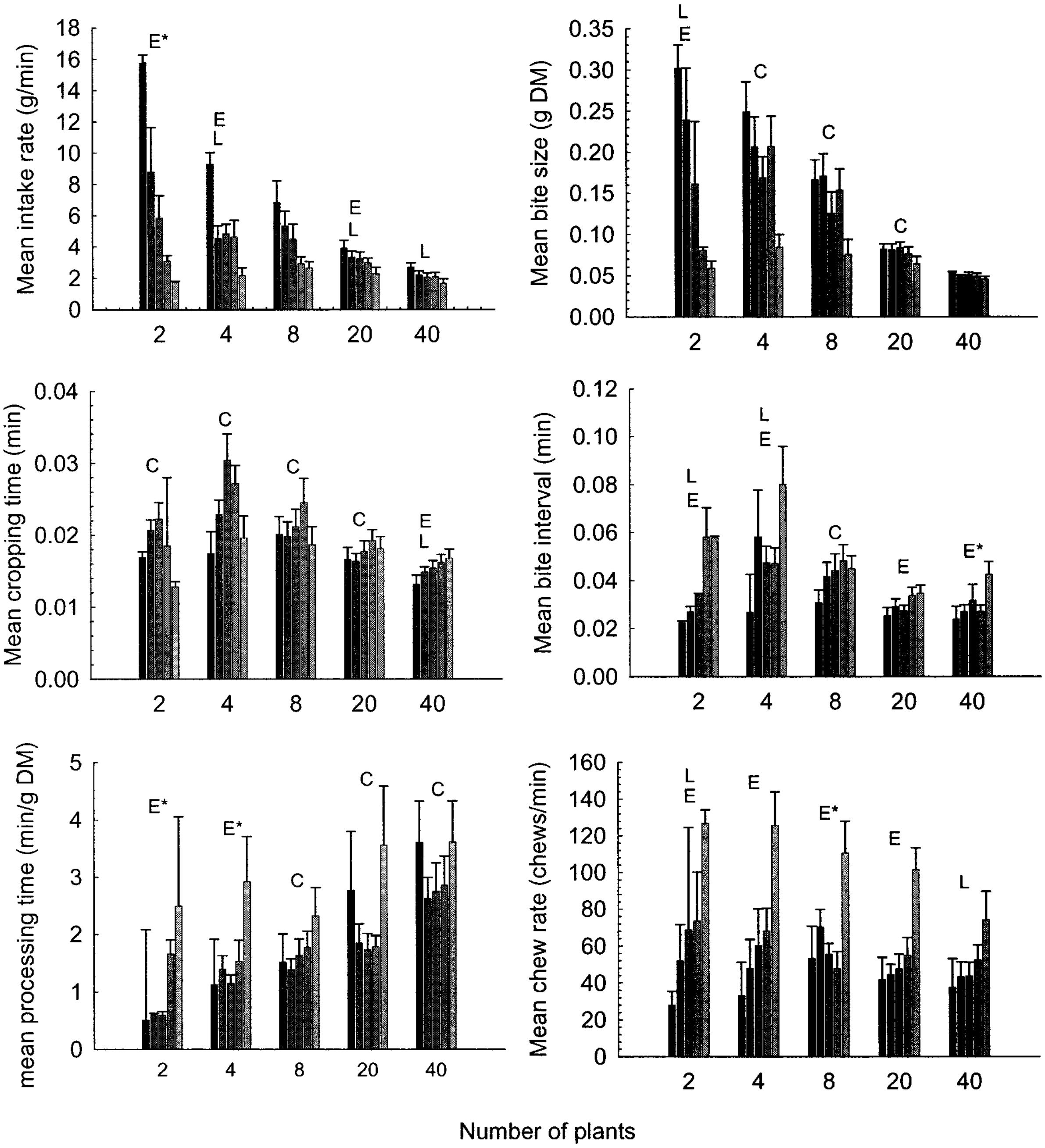


Figure 1.1a. Analysis of changes in parameters of functional response during patch depletion for mule deer. Total residence time is divided into 5 equal intervals (fifths). Bars show mean value for each parameter by fifth, with error bars representing one standard error. Grouped bars show changes to parameter value for each patch type (i.e., number of plants) in successive fifths. Model selection results are displayed for each patch type above grouped bars (C: constant model, L: linear model, E: exponential model). Letter indicates that the model received an Akaike weight equal to or greater than 0.40. Asterix (*) indicates that the model received an Akaike weight of equal to or greater than 0.75. Letters are arranged in order of descending support in the data.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

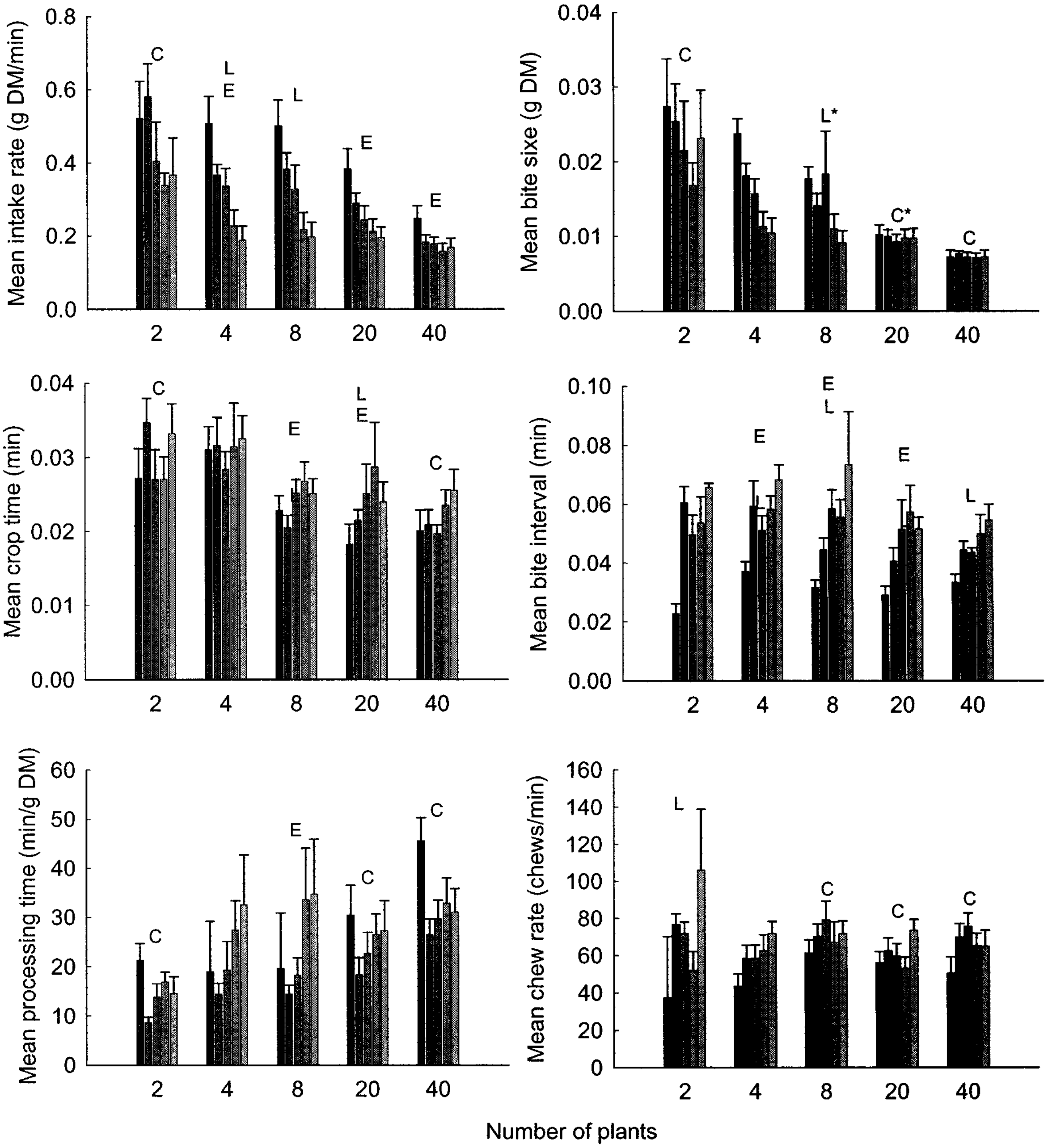


Figure 1.1b. Analysis of changes in parameters of functional response during patch depletion for blue duikers. Total residence time is divided into 5 equal intervals (fifths). Bars show mean value for each parameter by fifth, with error bars representing one standard error. Grouped bars show changes to parameter value for each patch type (i.e., number of plants) in successive fifths. Model selection results are displayed for each patch type above grouped bars (C: constant model, L: linear model, E: exponential model). Letter indicates that the model received an Akaike weight equal to or greater than 0.40. Asterix (*) indicates that the model received an Akaike weight of equal to or greater than 0.75. Letters are arranged in order of descending support in the data.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

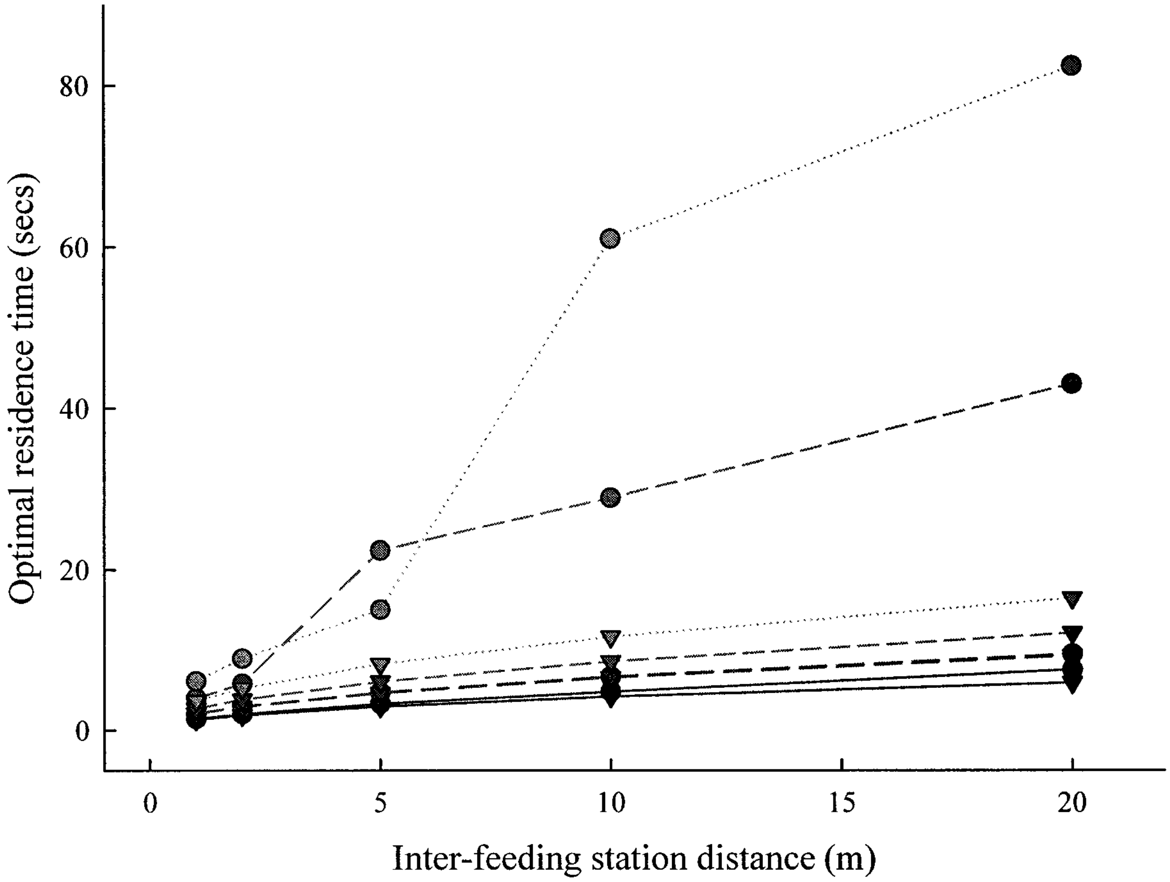


Figure 1.2. Model predictions for patch residence times for mule deer feeding in alfalfa-only patches. Lines with circles represent model-averaged predictions, lines with triangles represent predictions generated using asymptotic gain function models only. Residence time predictions are shown for 4 patch types (patches with 2 plants: solid line; patches with 4 plants: long dashed line; patches with 8 plants: short dashed lined; patches with 20 plants: dotted line).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Chapter Two

Bottom Up And Top Down Controls On Patch Residence Time In Foraging Hierarchies.

(*Ecology, in review*)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Abstract

Understanding responses of organisms to spatial heterogeneity in resources has emerged as a fundamentally important challenge in contemporary ecology. I examined responses of foraging herbivores to multi-scale heterogeneity in plants. I asked the question, "Is the behavior observed at coarse scales in a patch hierarchy the collective outcome of fine scale behaviors or, alternatively, does the spatial context at coarse scales entrain fine scale behavior?" To address this question I created a nested, 2 level patch hierarchy, and examined effects of the geometry of the hierarchy on residence time of foraging grizzly bears, mule deer, and collared lemmings. I developed a set of competing models predicting residence time as a function of patch size and distance among patches, and examined the strength of evidence in data for each model. Models that included patch mass and inter-patch distance as independent variables successfully predicted observed residence times. In contrast, models based on the marginal value theorem produced biased and erroneous predictions for both mule deer and collared lemmings. Grizzly bears and mule deer responded to differences in patch geometry at multiple scales. In contrast, the residence times of collared lemmings were simply predicted by the mass of food in patches and were uninfluenced by differences in the surrounding spatial context. This is likely due to differences in the natural history of the three study species.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Introduction

Ecologists describe spatial aggregations of resources as patches. Environments can exhibit resource patchiness in many different ways. Describing the functional significance of patches remains a central challenge for understanding how spatial heterogeneity in environments shapes the operation of ecological processes (Kotliar and Wiens 1990, Kolasa and Pickett 1991, Ritchie 1998, Zollner and Lima 1999, Johnson et al. 2001).

The seminal paper of Senft et al. (1987) provided a conceptual framework for understanding how patchiness at multiple scales influences foraging decisions by large herbivores. Foraging herbivores react to variation in the distribution of forage resources at several, nested spatial scales. Large patches can be seen as spatial aggregations of small patches; small patches can be viewed as spatial aggregations of plants, and plants can be seen as aggregations of bites. Behavioral processes that respond to variation in resources at the patch level include residence time and turning frequency, while behavioral processes that operate at the level of the plant include choosing bites and cropping them. Although the hierarchical structure of plant communities provides a useful metaphor for understanding the effects of heterogeneity on foraging behavior, we do not yet have a full empirical understanding of how herbivores recognize and incorporate these hierarchical spatial patterns into their foraging decisions.

It follows from these ideas that all foraging decisions made by large herbivores are embedded in a specific spatial context. An important question in the study of large herbivore foraging focuses on understanding decisions on residence time in patches (e.g. (Charnov 1976, Cassini et al. 1993, Laca et al. 1993; but see Jiang and Hudson 1993,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ward and Saltz 1994, WallisDeVries et al. 1998, Wilmshurst et al. 1999). Attempts to answer this question have emphasized testing the marginal value theorem (MVT, Charnov 1976), which predicts that animals foraging in a two level hierarchy of resources should spend more time in patches as the distance among patches increases, or as the energy return within patches increases. I contend that the emphasis on the MVT is excessively narrow, and that the question of residence time should be recast to provide more general insight into the effects of spatial heterogeneity on foraging behavior. Thus, I asked the question, how does spatial variation at a higher level in a patch hierarchy affect behavior at a lower level? Or, more precisely, is the behavior observed at coarse scales in a patch hierarchy simply the summation of fine scale behaviors or, alternatively, does the spatial context at coarse scales entrain fine scale behavior? If animals simply respond to heterogeneity at lower levels in the foraging hierarchy, then foraging process are controlled from the bottom up. If animals also respond to higher levels, then top down forces also exert control.

Posing these questions as hypotheses requires us to define some terms. I define a bite as a mass of plant tissue that can be consumed in single cropping motion. I define a feeding station as an aggregation of bites that is sufficiently concentrated in space that all bites can be consumed by a herbivore without travel. I define a small patch as an aggregation of feeding stations such that the distance between feeding stations is smaller than the distance between patches. I define a large patch as an aggregation of small patches. My specific hypotheses depict two alternate interpretations of the influence of patch geometry on residence time decisions at two of these spatial scales – the feeding station and the small patch. First, at the feeding station scale:

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Hypothesis 1a: Residence time in a feeding station is the sum of the time required to consume bites contained within it and does not depend on the larger spatial context formed by the geometry of the patch.

Hypothesis 1b: Residence time in a feeding station responds to characteristics of the feeding station and to patch geometry. Residence time at feeding stations cannot be predicted based on bite characteristics alone.

Second, at the small patch scale:

Hypothesis 2a: Residence time in small patches is the sum of the time required to consume feeding stations and the time required to travel among them. Small patch residence time does not depend on the larger spatial context formed by the geometry of the large patch.

Hypothesis 2ba: Residence time in small patches is entrained by pattern at large patch scales such that variation in the large patch influences small patch residence time. Small patch residence time cannot be predicted based on the characteristics of feeding stations alone.

Methods

Design and procedures

I observed responses of foraging herbivores to variation in the geometry of a 2 level hierarchy consisting of feeding stations of plants nested within small patches (Fig. 2.1). To vary the geometry of this hierarchy, I manipulated the mass of plants within a feeding station and the distance between feeding stations and the distance between small patches (Fig. 2.1, Table 2.1).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Experiments were conducted with, four grizzly bears (*Ursus arctos* $\bar{x}$ = *520kg*), 2 males and 2 females, 7 yearling female mule deer (*Odocoileus hemionus* $\bar{x}$ = *23kg*), and 7 male collared lemmings (*Dicrostonyx groenlandicus* $\bar{x}$ = *0.065kg*). I manipulated spatial arrangements of plant tissue by varying the amount of food in a patch and the distances between feeding stations and patches In the grizzly bear trials, feeding stations consisted of a 1.22 x 2.44 m piece of plywood on which fresh apples of two sizes were placed. In trials with mule deer, feeding stations were constructed with 0.6x0.6m plywood boards anchored to the ground. Boards were drilled in a systematic pattern to offer up to forty individual plants (fresh willow *Salix* spp). Stems of the plants were anchored in holes drilled in the boards by the camming action of inverted rubber stoppers. Feeding stations in the lemming trials consisted of loose bites of fresh alfalfa of two sizes, offered within a cardboard structure. Collections of three boards/cardboard structures (feeding stations) formed as patches. The quantity *d1* was the distance among feeding stations and the quantity *d2* was the distance among patches (Fig. 2.1)

By varying the inter-feeding station and inter-small patch distances I was able to create 10 (grizzly bear and lemming trials) or 11 (mule deer trials) different geometries for the 9 feeding stations (Table 2.1).

Grizzly bear feeding stations had 1-10 large bites on a feeding station. For each large bite offered, five small bites (0.5 g dry matter each) were offered to create a patch in which a decelerating gain function was possible. Because male bears weighed about twice what females did (males: 695kg, females: 350kg), I used larger bites for males. For males, large bites were defined as one half an apple or 15 g dry matter. For females, large bites were defined as one quarter of an apple or about 7.5 g dry matter. For the mule deer

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

I offered 1-5 alfalfa plants (4.0g wet) per feeding station. In the lemming trials I offered 1-10 large bites (0.03g wet) mixed with an equal total mass of small bites (0.006g wet). The number of bites per feeding station was assigned systematically in each trial to assure that each animal experienced a range of forage masses in each trial (Table 2.1). I used plants of similar size and maturity to assure that nutritional quality of plants was relatively constant.

A trial consisted of observing foraging behavior of a single animal foraging in a patch hierarchy. As the animal foraged, I recorded the time spent at each feeding station and the time spent traveling among feeding stations. Animals were observed until they had visited all patches or until they lost interest in feeding. Residence times were calculated as the difference between arrival and departure times. Time that animals arrived at and departed from patches were obtained from video replays of all trials for mule deer. In grizzly bear trials I recorded events as they occurred used an audiorecorder. Periods of inactivity were removed from calculations of residence and travel times. If animals were inactive for more than one minute, trials were discarded.

Animals were fasted before each trial to promote active foraging (grizzly bears and mule deer ≈ 4 hr, collared lemmings: ≈ 6 hr), and to attempt to maintain animals at a standard energy state before all trials. Individual animals were released into a fenced pasture or arena containing the patch hierarchy. For mule deer and collared lemmings the area was denuded of all other vegetation so animals were only able to feed from the created patches. The grizzly bear's enclosure had naturally growing grass and clover present during the trials, but the animals only fed on the food provided by us during the trial.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Fitting marginal value models (see below, Analyses) to the data required estimating gain functions for each herbivore species and each feeding station type. These estimates were obtained from separate trials following procedures described in (Searle et al. *Journal of Animal Ecology, in press*).

Analysis

I tested our hypotheses by examining the strength of evidence in data for a hierarchical family of models predicting residence time based on patch geometry. The basic model structure predicted residence time was proportionate to the mass in the feeding station or small patch, with an additional amount of time spent in each patch that was insensitive to patch characteristics and the spatial arrangement of patches (Eq. 2).

$$R = k_1 + (k_2 \cdot mass) \qquad (1)$$

where k_1 is the time spent in the patch independent of its mass, and k_2 is the rate of processing of plant mass. I also explored the use of asymptotic functions of mass as well as linear functions with no intercept. These were not supported by the data and hence, I limit my discussion to inferences built from equation 1.

I built upon this basic structure of equation 1 by incorporating the spatial context at higher levels in the hierarchy allowing me to express my hypotheses mathematically in the following models:

At the feeding station scale:

Hypothesis 1a: $R = k_1 + (k_2 \cdot mass)$

Hypothesis 1b: $R = k_1 + (k_2 \cdot mass) + (a \cdot \mathrm{d1})$

or $R = k_1 + (k_2 \cdot mass) + (a \cdot \mathrm{d1}) + (b \cdot \mathrm{d2})$

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Under Hypothesis 1b I also incorporated interaction terms in additional models to represent an effect of *mass* on distances *d1* and/or *d2*:

$$R = k_1 + (k_2 \cdot mass) + (a \cdot \mathrm{d1}) + (c \cdot mass \cdot \mathrm{d1})$$

$$R = k_1 + (k_2 \cdot mass) + (a \cdot \mathrm{d1}) + (b \cdot \mathrm{d2}) + (c \cdot mass \cdot \mathrm{d1} \cdot \mathrm{d2})$$

At the small patch scale:

Hypothesis 2a: $R = k_1 + (k_2 \cdot mass) + (a \cdot \mathrm{d1})$

Hypothesis 2b: $R = k_1 + (k_2 \cdot mass) + (a \cdot \mathrm{d1}) + (b \cdot \mathrm{d2})$

With models representing an interaction between *mass* and/or *d1* and *d2*:

Hypothesis 2a: $R = k_1 + (k_2 \cdot mass) + (a \cdot \mathrm{d1}) + (c \cdot mass \cdot \mathrm{d1})$

Hypothesis 2b: $R = k_1 + (k_2 \cdot mass) + (a \cdot \mathrm{d1}) + (b \cdot \mathrm{d2}) + (c \cdot mass \cdot \mathrm{d1} \cdot \mathrm{d2})$

where *a* and *b* are additional time spent in, or time subtracted from feeding stations or patches per unit distance *d1* or *d2*.

Much work has attempted to validate Charnov's (1976) marginal value theorem, which predicts patch residence time as a function of patch depression and inter-patch distance. In addition to the five models formed above, I included a family of models motivated by the marginal value theorem. The marginal value theorem seeks to maximize the average rate of energy intake (*E*) is defined as:

$$E = \frac{\sum_{i=1}^{n} \lambda_i g_i(t_i) - s}{1 + \sum_{i=1}^{n} \lambda_i t_i} \qquad (2)$$

Here, λ_i is the encounter rate with patches of type *i*; $g_i(t_i)$ is the gain function for patch type *i*; *s* is the cost of search per unit time. For herbivores foraging at small scales, I

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

assume search costs are close to zero and constant across all patch types (Stephens and Krebs 1986). Thus I maximized the average intake rate for the entire foraging arena by choosing an optimal vector of t_i's, hence finding the optimal residence time for each patch type. I used non-linear numerical search (Newton's method) to find the optimal residence times for mule deer and collared lemmings foraging at feeding stations. I did not use the marginal value theorem to predict patch residence times, because I was unable to get good measurements of gain functions at this scale. Gain functions for the different feeding station types were measured a priori and were found to decelerate continuously with increasing time spent in the feeding station, meeting the assumptions of the model. This analysis was not conducted for the grizzly bears because gain functions did not continuously decelerate with increasing residence time.

I used likelihood-based methods and information theoretics (Akaike's Information Criterion adjusted for small samples, AIC_c), to quantify strength of evidence for alternative models and to estimate their parameters (Burnham and Anderson 2002). Because model parameters were estimated based on one data set, there is some uncertainty that the "best" model would in fact emerge as superior if different data were used to compare alternatives. I quantified this uncertainty with Akaike weights, w_r (Burnham and Anderson 2002). I wished to assess how the relative weight of evidence for each model changed when I included the larger spatial context of the patch hierarchy. I was unable to quantify the evidence for the importance of each variable (*mass*, *d1* and *d2*) in our set of candidate models using relative variable importance (Burnham and Anderson 2002) because the variables were distributed over unequal numbers of models . Therefore, at the feeding station scale, I recalculated Akaike weights for only those

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

models predicting residence time as a function of *mass*, *mass* and *d1*, and *mass* and *d2*, and used these Akaike weights to calculate evidence ratios (Burnham and Anderson 2002). At the patch scale, I calculated evidence ratios for the two competing models identified in the methods.

Results

Linear models successfully predicted residence times for all three animal species at the two spatial scales (Figs 2.3, 2.4, 2.5). At the feeding station scale, data from the grizzly bear and mule deer trials showed clear support for Hypothesis 1b, that residence time at feeding station scales responded to the mass of food at the feeding station and the larger spatial context (Table 2.2). The grizzly bears demonstrated clear support for the model that included both distances *d1* and *d2*. There was poor support for any models that included an interaction between *mass* and distance in the grizzly bear data. Therefore both mass and distance influence residence time of grizzly bears at feeding stations, however the effect of mass did not depend on the effect of distance.

At the feeding station scale, the mass-only model had very little support in the data for mule deer. For models that contained mass and distance, support was approximately evenly split over all models that included the main effects of mass and distance alone and models that also included a *mass* x distance interaction. When models included an interaction term, mule deer tended to spend less time in patches as distance increased. (Tables 2 and 3).

In contrast, the collared lemmings showed some support for Hypothesis 1a--the mass-only model received some support at the feeding station scale, though the best model included an interaction between feeding station mass and inter-small patch

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

distance (Table 2.2). This suggests that at the feeding station scale, residence time for collared lemmings was the sum of the time required to consume bites within feeding stations, with a weak interaction between mass in feeding stations and inter-small patch distances.

At the small patch scale, the grizzly bear and mule deer data exhibited clear support for Hypotheses 2b. The best approximating model in both cases represented residence time based on behaviors within the small patch and the embedding context. Thus, successful models included effects of mass, distance between feeding stations, and distance between small patches. These models also included an interaction between the mass of small patches, and both measures of distance (Table 2.2).

In contrast Hypothesis 2a received the most support for collared lemmings, suggesting that for this species, residence time in small patches is the sum of the time required to consume feeding stations and the time required to travel among feeding stations (Table 2.2) and is insensitive to the surrounding spatial context.

Parameters controlling response to inter-feeding station and inter-patch distance were negative for the mule deer. Therefore, contrary to the predictions of the Marginal value theorem, mule deer spent *less* time in feeding stations and patches as distances between them increased (Table 2.3). This trend was also found for the grizzly bears at both feeding station and patch scales, in relation to the parameter relating residence time to inter-feeding station distance (Table 2.3). In this respect, only the collared lemmings increased residence time as inter-feeding station and inter-patch distances increased, as predicted by the marginal value theorem.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The parameter *k1* in our models can be interpreted as a constant amount of time an animal spends in a patch irrespective of patch characteristics or spatial context. This parameter did not change greatly between species, despite the wide range in body mass. In the grizzly bear trials parameter *k1* ranged from 1-3 seconds in feeding stations, and 1-6 seconds in patches. For the mule deer parameter *k1* ranged from 0-7 seconds in feeding stations, and 9-34 seconds in patches. In feeding stations parameter *k1* ranged from 4-8 seconds for collared lemmings, and from 22-30 seconds in patches.

I used evidence ratios (Burnham and Anderson, 2002, pp. 77-79) to assess the change in the weight of evidence when the larger spatial context was added to models predicting residence time. At the feeding station scale, the weight of evidence was greater for models including the larger spatial context for both grizzly bears and mule deer. The model including parameters *d1* and *d2* had 34 times the support in the data than the *mass*-only model for grizzly bears, and 17 times the support for the model that included parameter *d1*. This suggests that grizzly bears do use inter-feeding station distances, but that more important are small patch distances in the formation of residence time decisions. Mule deer showed no support for the *mass*-only model, though there was uncertainty as to whether inter-feeding station or inter-small patch distance was more important to their residence time decisions. The best model included parameters *mass*, *d1* and *d2*, but it only received between 1.5-2.0 times the support of models that included only one of the distance parameters. There was also uncertainty as to how collared lemmings use forage mass and spatial context to form feeding station residence time decisions. The *mass*-only model received 1.5-2.0 times the support of models that included either inter-feeding station or small patch distance, suggesting that residence

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

time decisions were not influenced by the larger spatial context. However, the model that received the most support was the interaction model that included *mass* and inter-small patch distance, though this model had only 3.25 times the weight of evidence of the *mass*-only model.

At the patch scale, weights of evidence for grizzly bears and mule deer demonstrated that these species incorporated information from the patch hierarchy into their residence time decisions. The weight of evidence for the model that included an interaction between *mass* and both distance parameters had more than 5 times the support of any other model in the grizzly bear data, and over 48 times the support for any of the alternative models in the mule deer data. In contrast, collared lemmings showed clear support for the model that did not include the larger spatial context, or an interaction between parameters in small patches. This model received more than 3.5 times the support of any of the alternative models.

When the classic view of encounter rates was used ($1/\lambda_i$ = the number of patches of type *i* divided by the time required to travel the total distance traversed, i.e. the sum of the *d1*'s and *d2*'s) predicted residence times consistently underestimated the observed residence times for mule deer (Fig. 2.2a). Similarly, observed residence times in the lemming trials were not successfully predicted by the marginal value theorem (Fig. 2.2b), with considerable spread around the 1:1 line. All Akaike weights for the classic Marginal value theorem were less than 0.01.

Mule deer tended to revisit feeding stations less as inter-feeding station distance increased ($F_{1,37}$: 7.90, $P<0.01$, $r^2=0.18$). Mule deer also revisited patches less as the distance between patches increased ($F_{1,37}$: 9.63, $P<0.01$, $r^2=0.21$). For the collared

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

lemmings there was no detectable relationship between inter-feeding station distance and the tendency for animals to revisit ($F_{1,38}$: 0.04, P=0.85, r^2=0.00). Grizzly bears tended to revisit feeding stations more frequently when inter-feeding station distances were low ($F_{1,38}$: 15.6, P<0.01, r^2=0.29), and revisited patches less as inter-patch distance increased ($F_{1,38:}$ 7.92, P<0.01, r^2=0.17).

Discussion

Our empirical models based on mass and distance characteristics of the patch hierarchy successfully predicted observed residence times in food patches at two spatial scales (feeding stations nested within small patches) for grizzly bears, mule deer and collared lemmings. In contrast, the marginal value model, which predicted residence time based on maximization of average intake rates, produced biased and erroneous residence time predictions for both mule deer and collared lemmings at the feeding station scale.

The marginal value theorem predicts that maximizing food intake rate requires animals to spend more time foraging within patches as distances between patches increase. Our observations for collared lemmings qualitatively supported this prediction in both feeding stations and patches. In contrast, grizzly bears and mule deer showed the opposite response to distance between patches. Grizzly bears spent less time in feeding stations and patches as distance between feeding stations increased, and mule deer spent less time in feeding stations and patches as inter-feeding station and inter-small patch distances increased. These observations contrast to published results for several herbivore species (e.g., Shipley and Spalinger 1995, Laca et al. 1993).

There are several potential explanations for these unconventional results. Because distances in the trials were fairly small in relation to distances normally traveled by these

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

animals (Parker et al. 1996) travel may not have been costly enough to provoke the anticipated response predicted by optimization of energy. It is also possible that the animals did not recognize feeding stations as separate patches. For instance, grizzly bears did not increase residence time at either scale until inter-small patch distances were approximately 3 times greater than inter-feeding station distances. In addition, grizzly bears revisited feeding stations more when inter-feeding station distances were small. If the animals did not recognize distinct feeding stations or small patches with small distances, the predictions of the marginal value model would not apply until distances became sufficiently large to provoke a response. Our trials were also fairly short, and so it is possible animals were not able to forage for long enough to gain sufficient information about patch characteristics to form optimal decisions. Furthermore, the MVT assumes that all patches are not entirely depleted over the observational period, an assumption that this experiment clearly violated. Thus, although there are several possible explanations for the failure of the MVT to predict the behaviors I observed, the central conclusion remains that simpler models, like those I used, may be more predictive. Previous workers (e.g. Cassini et al. 1993, Laca et al. 1993) have failed to compare the MVT with competing alternatives, so it is difficult to assess the generality of this conclusion.

The mass of food available at the feeding station or small patch was important in all successful models. However, for mule deer and grizzly bears the larger spatial context of feeding stations, and small patches in particular, was also important when forming residence time decisions. These results lend support for Hypotheses 1b and 2b, suggesting that for these two herbivore species the embedding spatial context influences

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

animal decisions on residence time in patches. Thus, decisions in a forging hierarchy respond to top down and bottom up controls. Moreover, there appears to be an interaction between forage mass and inter-small patch distance within the hierarchy, particularly at higher levels. Thus, the magnitude of the influence of lower level characteristics of the hierarchy depends on the influence of higher level characteristics.

In contrast to mule deer and grizzly bears, the residence times of collared lemmings appeared to be simply the sum of behaviors at lower scales in the hierarchy. Residence time in small patches was best predicted by models that included the mass of the small patch and the inter-feeding station distance, suggesting that collared lemmings seem to be more influenced by internal characteristics of patches than the larger spatial context. Although, in feeding stations, there was some uncertainty as to which model best predicted residence times of this species. Hence, at larger spatial scales, the behavior of collared lemmings at one level of the patch hierarchy was indeed the summation of behaviors at lower levels. Because collared lemmings naturally feed in linear runways (Banfield 1974, Godin 1977), the ability to detect patchiness and spatial context may be irrelevant. That is, collared lemmings would derive no benefit from incorporating this information into their foraging strategy.

Despite differences in body size, taxonomy, life history characteristics, and foods offered, the parameter in the empirical models representing additional constant periods of time spent in patches (k_1) was approximately the same for these three mammalian herbivores. Time spent in a patch may include a mechanical and volitional component. Mass of food offered per bite, feeding station and small patch were scaled to body mass in these experiments, thus I would expect approximately equal cropping and processing

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

time across animals. In addition, it seems that the volitional component, where animals spend time assessing information about the current patch upon arrival, is also relatively constant across these three herbivore species.

Others have found that foraging herbivores respond selectively to resources at different spatial scales (Ward and Saltz 1994, Moen et al. 1997, Wilmshurst et al. 1999, Dumont et al. 2002, Edenius et al. 2002). For instance, foraging elk have been found to employ different departure rules at the feeding station and patch scales (Jiang and Hudson 1993). Fortin et al. (2002) proposed that diet choice becomes scale sensitive when digestive constraints limit the daily forage intake of an animal. They found that the food intake of free-ranging bison was likely limited by ingestion time over short time periods (foraging bouts), but limited by digestive constraints over long periods of time (days). The results of their study were suggestive of patterns of diet selection by bison more consistent with short-term maximization of energy intake. Our study indicates that grizzly bears and mule deer are capable of recognizing and responding to spatial variation in resources expressed at small spatial scales. This is consistent with previous findings showing that large herbivores maximize intake rates at small spatial scales (Distel et al. 1995, Fortin et al. 2002).

Foragers that are able to detect 'patchiness' at fine scales benefit from greater opportunity to allocate time efficiently in response to spatial heterogeneity in resource abundance (Schmidt and Brown 1996, Fierer and Kotler 2000). Previous research has demonstrated that herbivores are capable of discriminating between food patches at small spatial scales. Fox squirrels have been found to distinguish between patches at scales of $0.04m^2$ (Schmidt and Brown 1996), and two desert rodent species were able to recognize

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

distinct patches on scales of $0.14m^2$ (Fierer and Kotler 2000). Sheep have been shown to effectively discriminate between food items at fine spatial scales (pellets of 5mm) (Edwards et al. 1994), and Laca et al. (1994) demonstrated that cattle could discriminate and respond to heterogeneity in forage density on a scale of $0.45m^2$. Moose responded more to characteristics of individual trees than to the composition of stands (Danell et al. 1991). Clearly, herbivores are capable of discriminating variation in resources at small spatial scales, and hence able to exploit this variation to maximize some currency.

I have demonstrated that the response of mule deer and grizzly bears to heterogeneity at fine spatial scales is shaped by heterogeneity at larger scales. This implies that these animals respond to patchiness on several spatial scales. Behaviors at the feeding station and small patch scales were directly influenced by spatial characteristics at the two levels in the patch hierarchy: inter-feeding station and inter-patch distance. Thus, behavior at each level in the hierarchy is not simply the sum of behaviors at lower levels for these two species. In contrast, residence time decisions made by the smaller herbivore species did not utilize information from upper levels of a foraging hierarchy.

Acknowledgements

This work was funded by National Science Foundation grants to Hobbs and Wunder (DEB 9981368) and to Shipley (DEB 9981242). I am grateful to the staff of the Colorado Division of Wildlife Foothills Research Facility at Fort Collins, CO, for help with the mule deer trials. We thank S. Albers, K. Bikowski, C. Bishop, S. Hobbs, W. Mulherin, L. Reynolds, and M. Rice for their invaluable assistance in animal care and field trials in Fort Collins. We appreciate the generosity of C. T. Robbins for allowing us

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

to use the grizzly bears and facilities at the Bear Conservation and Research Center at Washington State University in Pullman, Wash. We thank T. Tollefson and M. Fisher for help in conducting experiments with the bears. We also thank M. McClure for reviewing preliminary versions of this manuscript. This work could not have been completed without Tom Hobbs, Lisa Shipley, Thea Vandervelde, and Bruce Wunder.

Literature Cited

Banfield, A. W. F. 1974. The mammals of Canada, Reprinted 1981 edition. University of Toronto Press, Toronto.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition. Springer-Verlag, New York.

Cassini, M. H., G. Lichtenstein, J. P. Ongay, and A. Kacelnik. 1993. Foraging Behavior in Guinea-Pigs - Further Tests of the Marginal Value Theorem. Behavioural Processes **29**:99-112.

Charnov, E. L. 1976. Optimal foraging, the Marginal Value Theorem. Theoretical Population Biology **9**:129-136.

Danell, K., L. Edenius, and P. Lundberg. 1991. Herbivory and Tree Stand Composition - Moose Patch Use in Winter. Ecology **72**:1350-1357.

Distel, R. A., E. A. Laca, T. C. Griggs, and M. W. Demment. 1995. Patch selection by cattle: Maximization of intake rate in horizontally heterogeneous pastures. Applied Animal Behaviour Science **45**:11-21.

Dumont, B., P. Carrere, and P. D'Hour. 2002. Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. Animal Research **51**:367-381.

Edenius, L., G. Ericsson, and P. Naslund. 2002. Selectivity by moose vs the spatial distribution of aspen: a natural experiment. Ecography **25**:289-294.

Edwards, G. R., J. A. Newman, A. J. Parsons, and J. R. Krebs. 1994. Effects of the scale and spatial distribution of the food resource and animal state on diet selection: an example with sheep. Journal of Animal Ecology **63**:816-826.

Fierer, N., and B. P. Kotler. 2000. Evidence for micropatch partitioning and effects of boundaries on patch use in two species of gerbils. Functional Ecology **14**:176-182.

Fortin, D., J. M. Fryxell, and R. Pilote. 2002. The temporal scale of foraging decisions in bison. Ecology **83**:970-982.

Godin, A. J. 1977. Wild mammals of New England. Johns Hopkins University Press, Baltimore.

Jiang, Z., and R. J. Hudson. 1993. Optimal grazing of wapiti cervus-elaphus on grassland patch and feeding station departure rules. Evolutionary Ecology **7**:488-498.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia **127**:590-602.

Kolasa, J., and S. T. A. Pickett. 1991. Ecological Heterogeneity. Springer-Verlag.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure - a hierarchical framework for the study of heterogeneity. Oikos **59**:253-260.

Laca, E. A., A. Distel, T. C. Griggs, and M. W. Demment. 1994. Effects of canopy structure on patch depression by grazers. Ecology **75**:706-716.

Laca, E. A., R. A. Distel, T. C. Griggs, G. P. Deo, and M. W. Demment. 1993. Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilisation. Pages pp 709-701 *in* Proceedings of XVII International Grassland Congress, New Zealand and Queensland February 1993.

Moen, R., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. Ecology **78**:505-521.

Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1996. Foraging efficiency: Energy expenditure versus energy gain in free-ranging black-tailed deer. Canadian Journal of Zoology-Revue Canadienne De Zoologie **74**:442-450.

Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology **12**:309-330.

Schmidt, K. A., and J. R. Brown. 1996. Patch assessment in fox squirrels: the role of resource density, patch size, and patch boundaries. American Naturalist **147**:360-380.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience **37**:789-799.

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.

Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press.

WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1998. From feeding station to patch: scaling up food intake measurements in grazing cattle. Applied Animal Behaviour Science **60**:301-315.

Ward, D., and D. Saltz. 1994. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. Ecology **75**:48-58.

Wilmshurst, J. F., J. M. Fryxell, B. P. Farm, A. R. E. Sinclair, and C. P. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology-Revue Canadienne De Zoologie **77**:1223-1232.

Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology **80**:1019-1030.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 2.1. Inter-feeding station (*d1*) and inter-small patch (*d2*) distances offered to grizzly bears, mule deer, and collared lemmings in the two-level patch hierarchy.

	d2 (m)		
d1 (m)	Grizzly bears	Mule deer	Collared lemmings
0.5	--	--	0.3,0.9,1.8,2.7
1	--	--	0.9,1.8,2.4
2	4,8,12,16	4,8,12,16	1.2,1.8
3	--	--	1.2
4	8,12,16	8,12,16	--
6	12,16	12,16	--
8	16	16	--

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 2.2. Akaike weights (w_r) calculated for all models predicting residence time at feeding stations and small patches for grizzly bears, mule deer, and collared lemmings foraging in the two-level patch hierarchy.

		w_r		
Spatial scale	Model	Grizzly bears	Mule deer	Collared lemmings
Feeding station	(*mass*)	0.02	0.00	0.16
	(*mass, d1*)	0.04	0.16	0.11
	(*mass, d2*)	0.15	0.19	0.08
	(*mass, d1, d2*)	0.68	0.29	0.04
	(*mass*d1*)	0.03	0.10	0.05
	(*mass*d2*)	0.08	0.14	0.52
	(*mass*d1*d2*)	0.00	0.12	0.02
Small patch	(*mass, d1*)	0.04	0.01	0.64
	(*mass, d1, d2*)	0.02	0.01	0.18
	(*mass*d1*)	0.15	0.02	0.04
	(*mass*d1*d2*)	0.80	0.97	0.13

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 2.3. Parameter values for models used to predict residence time for grizzly bears, mule deer, and collared lemmings at both spatial scales (feeding station and small patch).

		Parameter value		
	Model	Grizzly bears	Mule deer	Collared lemmings
Feeding station	(*mass*)	*k1* 1.01	*k1* 0.00000001	*k1* 7.70
		k2a 1.76	*k2* 2.52	*k2a* 64.4
		k2b 0.12		*k2b* 147.9
	(*mass, d1*)	*k1* 2.85	*k1* 4.00	*k1* 5.89
		k2a 1.76	*k2* 2.54	*k2a* 58.0
		k2b 0.12	*a* –1.07	*k2b* 154.9
		a –0.47		*a* 1.62
	(*mass, d2*)	*k1* 0.92	*k1* 6.28	*k1* 5.88
		k2a 1.76	*k2* 2.53	*k2a* 36.1
		k2b 0.12	*a* –0.54	*k2b* 192.1
		a 0.01		*a* 0.32
	(*mass, d1, d2*)	*k1* 1.45	*k1* 7.00	*k1* 4.54
		k2a 1.76	*k2* 2.53	*k2a* 63.9
		k2b 0.12	*a* –0.70	*k2b* 145.6
		a –0.64	*b* –0.37	*a* 1.69
		b 0.18		*b* 0.26
	(*mass***d1*)	*c* 0.00029	*c* –0.06	*c* 121.2
	(*mass***d2*)	*c* 0.000089	*c* –0.038	*c* –92.4
	(*mass***d1***d2*)	*c* 0.00003	*c* 0.0019	*c* –18.3
Patch	(*mass, d1*)	*k1* 6.31	*k1* 23.64	*k1* 25.5
		k2a 1.79	*k2* 2.23	*k2a* 24.0
		k2b 0.12	*a* –3.27	*k2b* 158.4
		a –1.43		*a* 5.30
	(*mass, d1, d2*)	*k1* 1.95	*k1* 34.30	*k1* 22.7
		k2a 1.79	*k2* 2.19	*k2a* 61.6
		k2b 0.13	*a* –2.07	*k2b* 98.3
		a –1.96	*b* –1.18	*a* 5.43
		b 0.53		*b* 0.70
	(*mass***d1*)	*c* 0.00033	*c* 0.33	*c* 174.2
	(*mass***d1***d2*)	*c* 0.000024	*c* 0.023	*c* –17.5

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

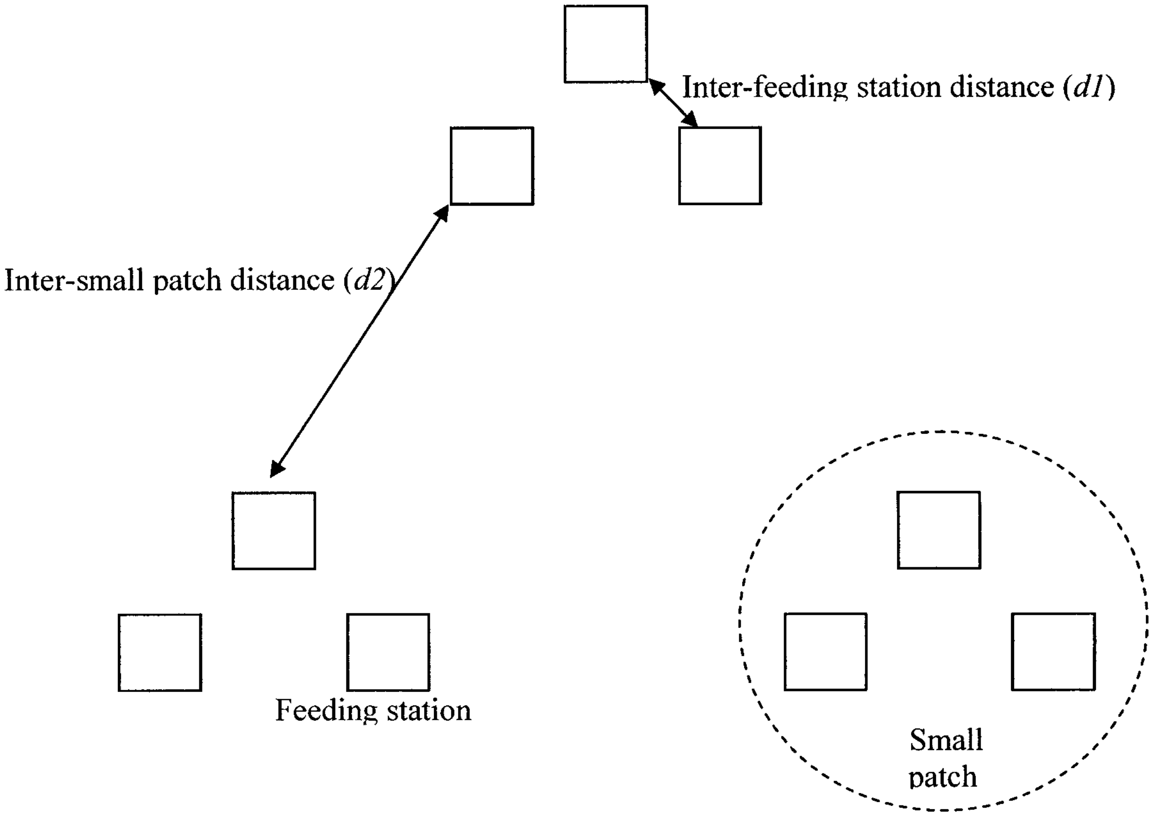


Figure 2.1. Hierarchical patch design for trials with grizzly bears, mule deer, and collared lemmings.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

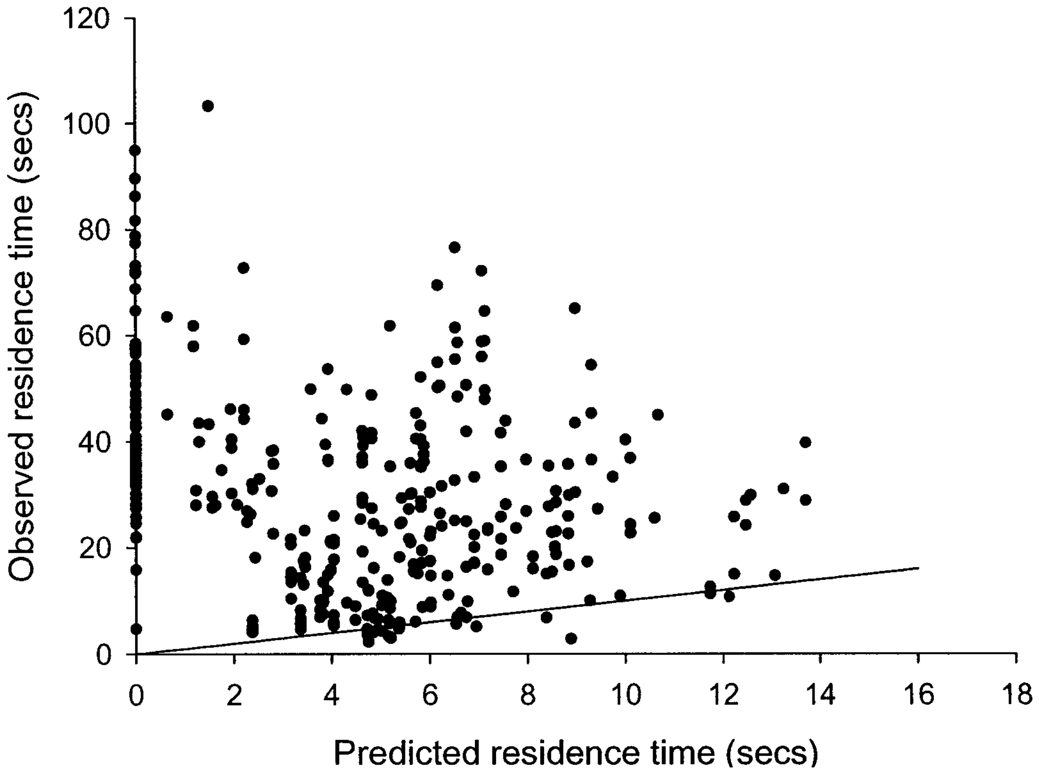


Figure 2.2a. Observed versus predicted residence times for the Marginal Value Theorem for mule deer foraging at feeding stations, where $1/\lambda_i$ = the number of patches of type *i* divided by the time required to travel the total distance traversed, i.e. the sum of the *d1*'s and *d2*'s.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

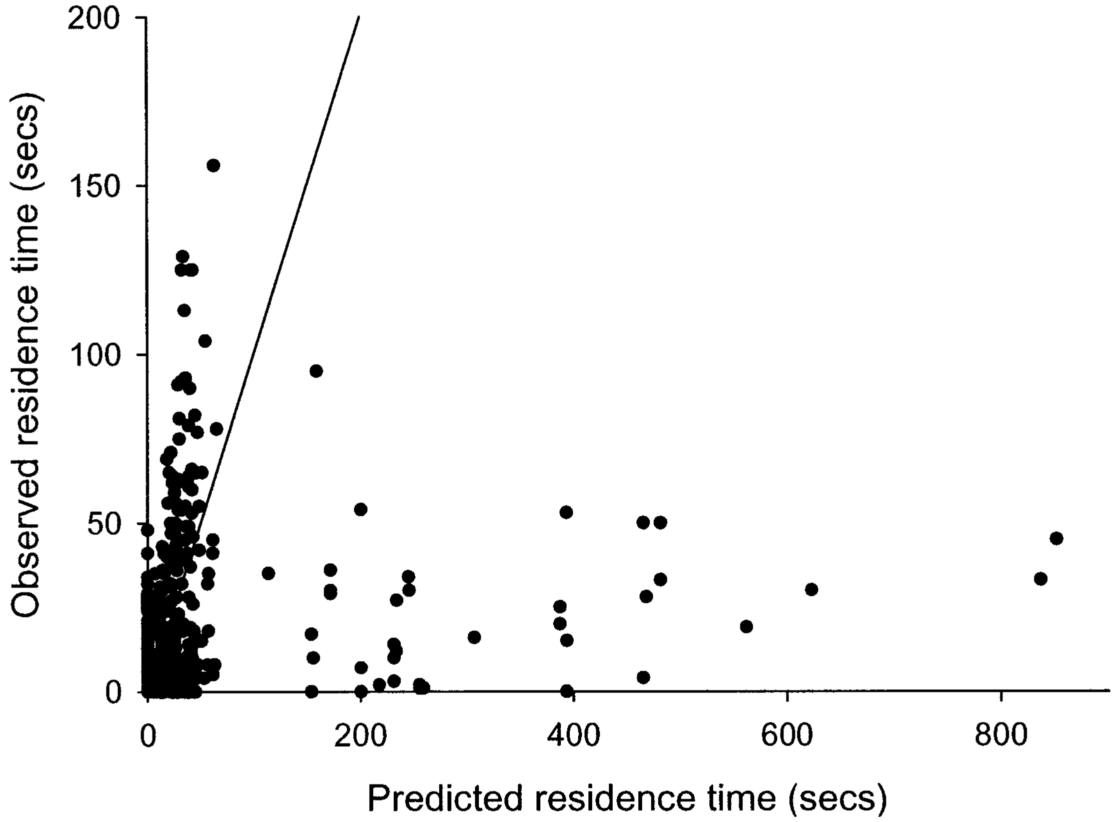


Figure 2.2b. Observed versus predicted residence times for the Marginal Value Theorem for collared lemmings foraging at feeding stations, where $1/\lambda_i$ = the number of patches of type *i* divided by the time required to travel the total distance traversed, i.e. the sum of the *d1*'s and *d2*'s.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

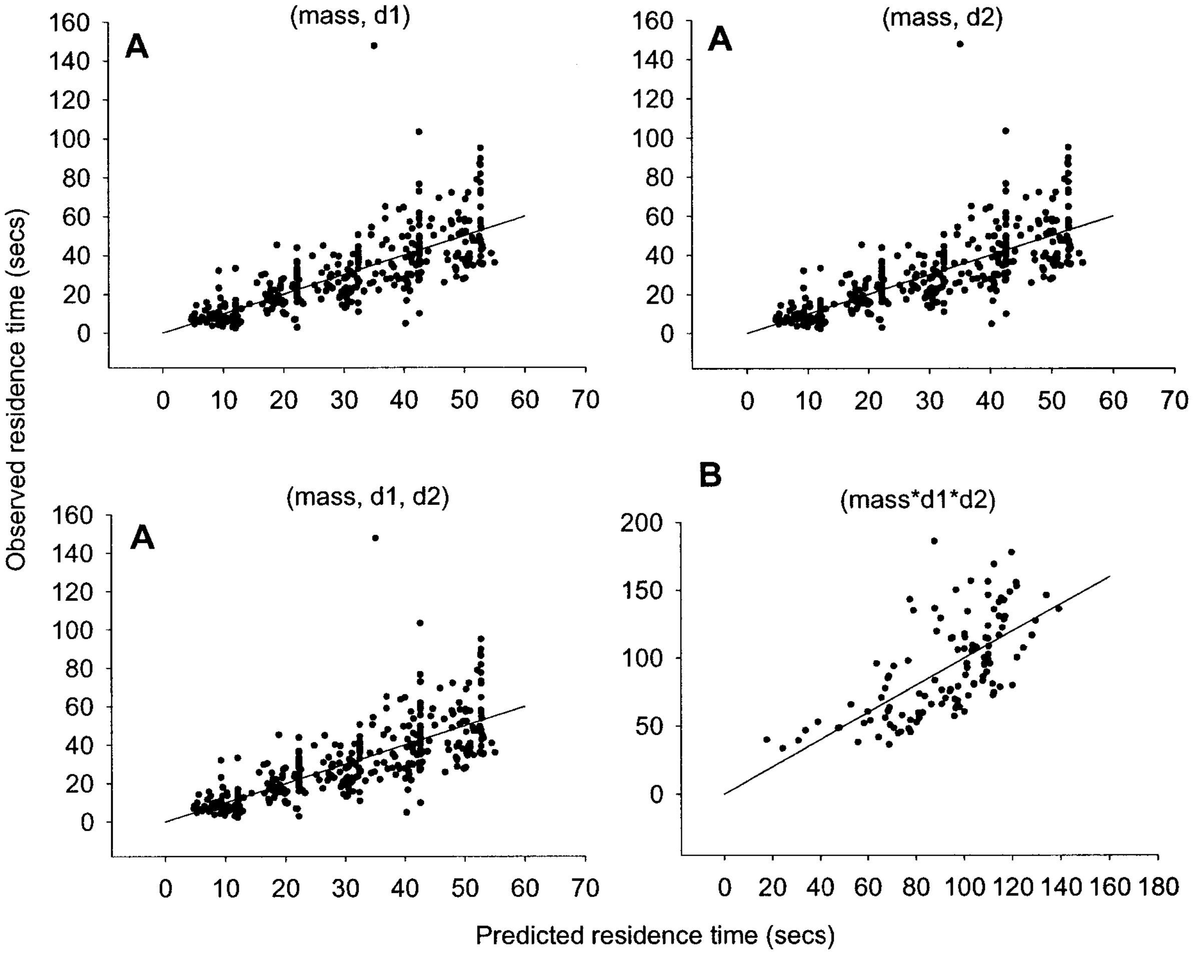


Figure 2.3. Observed versus predicted residence times for the three best approximating models (given $w_r > 0.10$) for mule deer foraging at the feeding station scale (A), and at the small patch scale (B).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

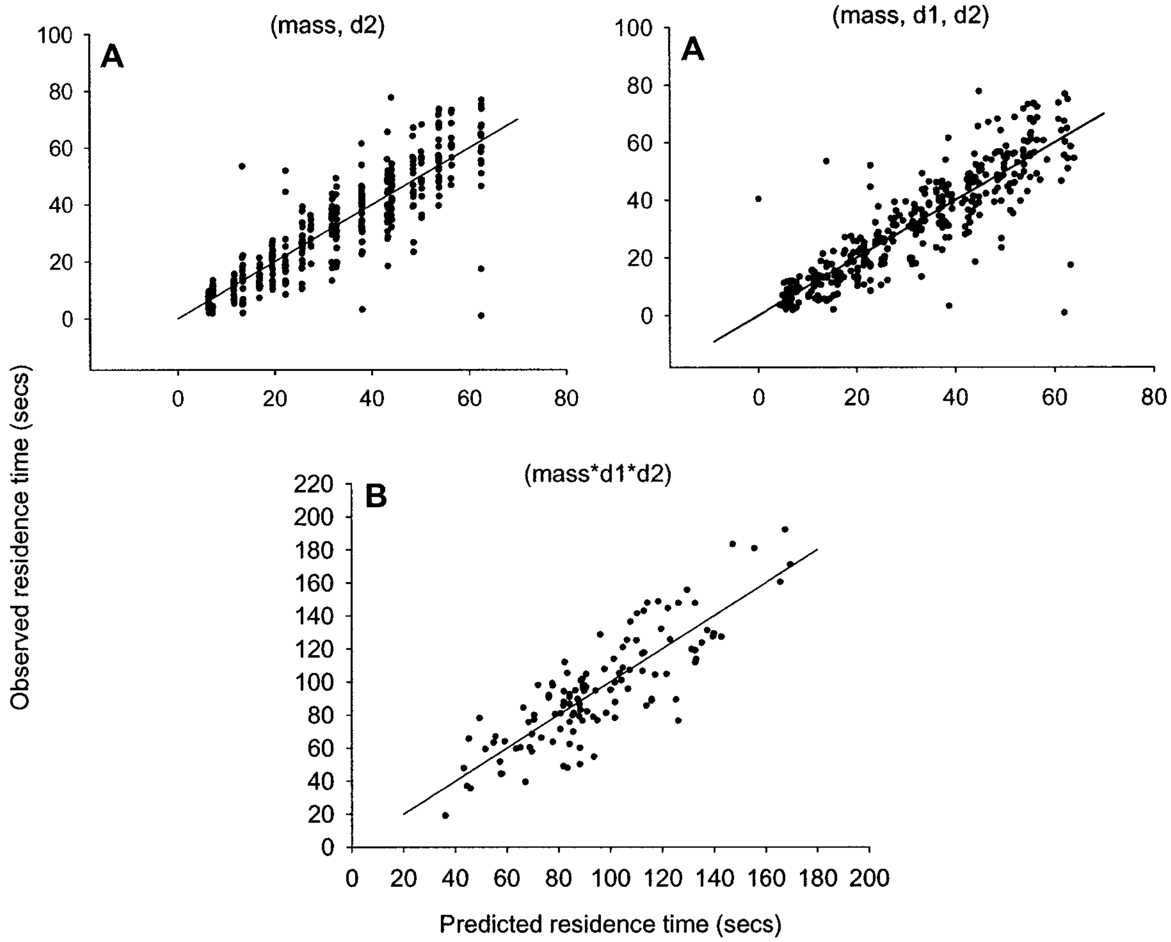


Figure 2.4. Observed versus predicted residence times for the three best approximating models (given w_r>0.10) for grizzly bears foraging at the feeding station scale (A), and at the small patch scale (B).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

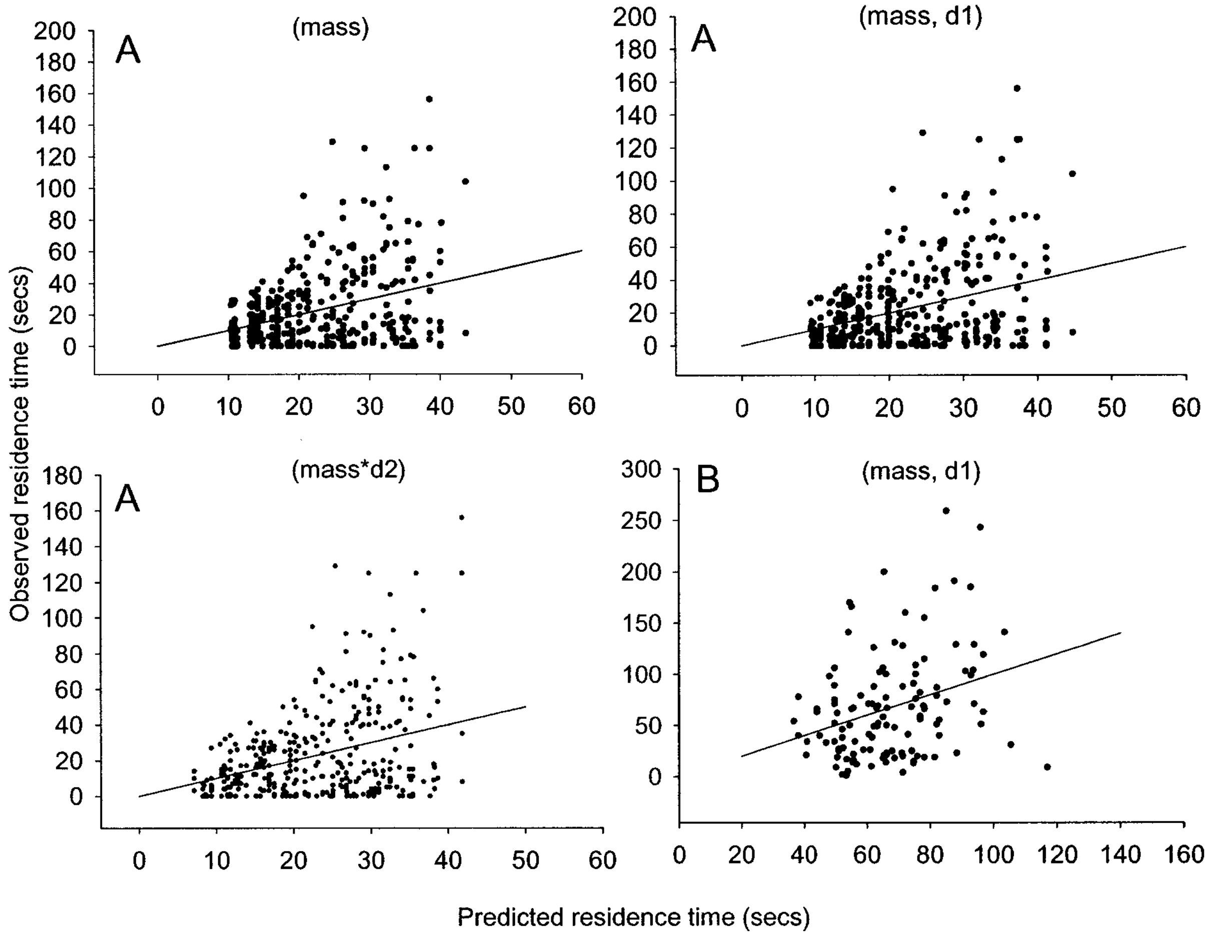


Figure 2.5. Observed versus predicted residence times for the three best approximating models (given w_r>0.10) for collared lemmings in feeding stations (A), and at the small patch scale (B).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Chapter Three

Preference in patchy landscapes: The influence of scale-specific intake rates and variance in reward

(*Behavioral Ecology, in review*)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Abstract

Understanding the responses of foragers to patchy distributions of resources has formed a fundamental challenge in behavioral ecology. Two currencies have been used to assess the patch preferences of herbivores—intake rate maximization and risk sensitivity. I wished to understand if small mammalian foragers, Collared lemmings (*Dichrostonyx groenlandicus*), choose patches to maximize food intake rate or to reduce risk of starvation in variable environments. Moreover, I examined the possibility that intake rate maximization was dependent on the spatial scale of patchiness. I designed an experiment offering two alternative patches of food, varying the predictability of food rewards and the potential intake rate at different spatial scales. Collared lemmings did not consistently select patches that maximized their intake rate at either scale studied. Instead, lemmings consistently chose patches offering the least variation in food reward over the course of the experiment. Collared lemmings used prior knowledge gained from previous foraging bouts to assess food variability. I interpret these results as evidence for risk-averse foraging strategies, which are predicted for continuous foragers aiming to minimize risk of starvation.

Keywords: patch selection, maximization of intake rate, Collared lemmings, risk-sensitive foraging.

Introduction

Foraging decisions ultimately determine the energy balance of animals, and in so doing influence body mass, reproductive success, and survival. Most food resources are aggregated in patches and it follows that a key component of successful foraging is deciding how to respond to these aggregations (Senft et al. 1987, Laca and Ortega 1995,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bailey et al. 1996, Ritchie 1998, Hobbs 1999, WallisDeVries et al. 1999, Bergman et al. 2001, Johnson et al. 2001, Dumont et al. 2002). Foraging herbivores encounter food resources that are arranged in hierarchies where patches of plant tissue at fine scales are often nested within larger, coarse scales patches (Senft et al. 1987, Bailey et al. 1996, Hobbs 1999). This patchiness creates two dimensions of variability that potentially shape foraging choices. The first dimension is scale dependent rates of energy gain (Fortin et al. 2002). Patchily distributed resources can offer high intake rates averaged over fine scales of time and space and low intake rates at coarse scales or vice versa (Figure 1). Thus, it is possible that herbivores respond to particular scales in the patch hierarchy. Revealing such responses will allow us to identify scales of heterogeneity that are *functionally* important to the foraging herbivores (Senft et al. 1987, Kotliar and Wiens 1990, Bailey et al. 1996, Hobbs 1999).

The second dimension influencing foraging choices in patch hierarchies is predictability of resources. Patchy distributions of resources force variance in encounter rates with resources relative to uniform or random distributions (Adler et al. 2001). This variance means that foragers must consider the uncertainty of obtaining food along with the average rate of intake. Foraging animals may choose strategies that minimize the risk associated with different feeding options rather than those that maximize intake rate. Risk-sensitive foraging applies when animals are affected by the variance in the pay-off obtained from alternative foraging options to a greater extent than by the average pay-off (Kacelnik and Bateson 1996).

Thus, it is plausible that herbivores foraging in patch hierarchies may be influenced by features of plants that control the average rate of intake, or, alternatively,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

may be more strongly influenced by the predictability of intake than by its average. If the responses of animals are shaped by average rates of food intake, then it follows that herbivores may be sensitive to variability in intake rate expressed at different spatial scales.

To better illustrate the hypotheses that follow, consider an example. We have a hypothetical patch containing plants that are not easily detected by herbivores. Within this patch search time is a significant component of the total foraging time. When plants are encountered, however, handling time is low and hence intake rate is high. Thus, intake rate is rapid at fine scales because of low handling time, but slow at coarse scales because of high search time. Alternatively, consider a patch where foods are easily detected so that search time is low. However, these foods have high handling times which means that discovered foods must be consumed relatively slowly. In this case, intake rate is slow at fine scales because of high handling time but is rapid at coarse scales because of low search time. Presume that the two patches offer exactly the same rate-averaged intake rate. That is, the rate averaged over a foraging bout of a given length, the potential intake rate, is exactly the same in the two patches. Which patch would herbivores prefer? Are they more sensitive to fine or coarse scale controls on intake rate? Does the average intake rate matter in their patch choices more than the variance in intake rate?

To address these questions, I tested three competing hypotheses about the way that herbivores evaluate and select food patches:

1. Herbivores prefer patches where average intake rate is greatest at fine spatial scales as a result of brief handling time.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

2. Herbivores prefer patches where intake rate is greatest at coarse scales as a result of brief search time.
3. Herbivores are not influenced by average intake rate, but prefer patches where encounter with foods is most predictable.

Methods:

Experimental design

I investigated patch choices of collared lemmings (*Dichrostonyx groenlandicus*) given three alternatives: maximization of food intake at fine scales, maximization at coarse scales, and minimization of variance in food intake. Explaining these alternatives requires defining some terms. I define a *bite* as a dry mass of forage that could be consumed with a single cropping motion. A *feeding station* consists of a collection of bites that can be consumed without requiring the animal to move its feet. A patch is a spatially aggregated collection of feeding stations. *Potential intake rate* is the approximate maximum dry mass of forage that could be obtained per unit time spent foraging.

I offered a range of patch geometries to experimental animals to assure that our hypotheses made distinct, competing predictions about the animals' behavior. Pairs of patches of forage containing fresh alfalfa were offered in a foraging arena, a 3.6*3.6m square of plywood with borders, 30cm high (Fig. 3.2). Each patch contained twenty feeding stations, and each patch contained the same total forage mass. The total mass provided in each patch was approximately a single "meal" for a collared lemming, the amount of food required to fill the gut. I estimated the gut capacity of collared lemmings

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

to be similar to that of prairie voles (1g dry matter, Zynel and Wunder (2002), and thus provided lemmings with 1.65g dry matter of food in each patch.

Five combinations of two patch types, ‘variable’ and ‘constant’, were offered to experimental animals (Table 3.1). In the constant patch, plant geometry was not varied so that potential intake rate remained constant across all patch combinations. However, in the variable patch, I manipulated bite size to force an increasing large advantage in potential intake rate at the feeding station scale as bite size increased (Fig 3A). At the same time, I manipulated the encounter rate with feeding stations in the variable patch to force an advantage in intake rate at the patch scale when bite sizes were small and a disadvantage at the patch scale when bite sizes were large (Fig. 3.3B). Under the hypothesis of intake maximization at the feeding station scale, I should observe a gradual increase in preference for the variable patch as bite sized increased (Fig. 3.3C). Under the hypothesis of intake rate maximization at the patch scale, I should observe switching in preference between patches at intermediate bite sizes (Fig. 3.3D). Under the hypothesis of maximizing predictability, I should observe a consistent preference for the constant patch relative to variable one (Fig. 3.3E).

Feeding stations were contained within 14 x 14 cm tetrahedral houses with two entrance holes on opposite sides (Fig. 3.1). Houses reduced visibility of food and provided a secure place for animals to feed. It was important for food to be hidden because risk can only be a factor in foraging decisions if foragers are not able to precisely determine the pay-offs from alternative options at the time of forming a patch choice (Bateson 2002). In both patch types there were 20 14cm by 14cm tetrahedral houses, all of which contained food. In the variable patch type, houses containing food were

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

interspersed with 30-60 houses without food. In the constant patch, houses were interspersed with 30-60 14 x 14cm canopies that provided cover from above but were open on all sides, allowing animals to see that they did not contain food (Fig. 3.1).

It is well established that bite size controls intake rate within feeding stations, while encounter rate can control intake rate when feeding stations are sufficiently far apart or difficult to locate (Spalinger and Hobbs 1992, Gross et al. 1993a, Gross et al. 1993b). Therefore, I manipulated bite size to control potential intake rates at the feeding scale and presence or absence of food in houses to control potential intake rate at the patch scale. I created different bite sizes of alfalfa using hole punches to make discs of alfalfa leaves of varying size and mass. Bite size in the constant patch was 0.0025g dry matter (DM). I used five different bite sizes in the variable patch that were each paired with a constant patch in the trials. The dry mass of the variable patch bite sizes were 0.0025g, 0.004g, 0.006g, 0.008g and 0.025g, and will henceforth be used to refer to the five patch combinations that were presented to collared lemmings in the course of the experiment (Table 3.1, Figure 3a-b). Pilot experiments using methods described by Gross et al. (1993b) allowed us to estimate the effect of these different bite sizes on potential intake rate at feeding station scales (Table 3.1). Potential intake rate at patch scales was manipulated by altering the proportion of houses that contained food in the variable patch, thereby increasing the variance in encounter rate with feeding stations and permitting control over the average intake rate. A higher percentages of empty houses in the variable patch forced lower potential intake rate because animals had to spend more time searching for feeding stations within houses. Pilot experiments allowed us to calibrate the density of feeding stations to potential intake rate at patch scales (Table 3.1).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Observations

All trials were conducted at Colorado State University, using seven male collared lemmings. Trials were conducted in the arena, with the two food patches occupying opposite sides of the arena (Fig. 3.1). A trial consisted of observations of a single collared lemming for 10 minutes. I recorded the amount of time an animal spent in each of the two patches during these foraging bouts, and weighed all remaining food at the beginning and end of each trial to establish how much mass was eaten from each patch during the trial. Any brief periods of inactivity were removed from the total time recorded. If animals were inactive for more than three minutes, trials were discarded. I accounted for changes in dry matter of plants that occurred due to desiccation during the trial using reference samples. Animals were acclimated to feeding in houses and utilizing the arena before commencement of trials.

The five patch combinations were run in random order (0.008g, 0.025g, 0.0025g, 0.004g, 0.006g), over the summer and fall of 2003 (Table 3.1). For each of the five patch combinations I repeated trials four times with each of the seven collared lemmings to evaluate if animals used past experience to better match their preference to the most profitable patch. Because of this, I always kept the patch combinations in the same location within the arena throughout the experiment.

Between trials, animals were housed individually, and fed *ad libitum* on rabbit food pellets, with free access to tap water. Animals were fasted for 4-8 hours before trials, and so were maintained in negative energy balance during all trials. The animals lost weight during the days when trials were run (up to approx. 10% body mass), but

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

recovered lost weight overnight once trials were completed and animals had *ad libitum* access to food.

Analysis

Observed patch intake rates for each patch offered were calculated as the mass removed from the patch divided by the time spent in a patch over the course of one trial. I wished to quantify how patch selection varied over the course of the experiment. I used two measures of patch selection: the mass removed from each patch, and the amount of time spent foraging in each patch. To explain variation in these responses I used log ratios of the response variables (Illius et al. 1999). For the mass removed from each patch, I calculated the natural logarithm of the ratio of the mass removed from the constant patch over the mass removed from the variable patch under the four patch combinations. Because I applied a stopping rule, only allowing the animals to feed for 10 minutes, I could not treat the time spent in each patch as independent. Instead, I treated pairs of the time spent in each patch as scaled compositional data and analyzed the natural logarithm of the ratio of the time spent in each patch (Illius et al. 1999). I converted the absolute time spent in each patch to a proportion. If animals spent no time in a patch the corresponding log ratio could not be formed, hence when animals spent no time in a patch I adjusted the time spent in that patch to one second. Analyses of variance were conducted using the corresponding log ratios (SAS Institute V8, 2002). Because the analyses produced very similar results when using the mass consumed or the proportion of time spent per patch, I have limited the results and discussion to the analysis of the proportion of time spent per patch.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Results

Observed intake rates at patch scales did not vary in the constant patch (Fig. 3.4; $F_{4,125}=1.93$, $P=0.11$), and increased or declined with increasing bite size in the variable patch (Fig.4). This means that our treatments exerted the desired effect on intake rates.

In our experiments collared lemmings did not select patches that maximized potential intake rate at either the feeding station or patch scale. Instead, collared lemmings spent more time in the constant patch in trials where bite size offered in the variable patch increased from 0.0025g, to 0.025g. At the low end of this gradient intake rate was greater at the patch scale in the variable than in the constant patch. At the upper end of this gradient, intake rate was greater at the feeding station scale in the variable patch than in the constant patch. Thus, our observations argue that collared lemmings did not seek to maximize intake rate at either scale (Figs 3.5-3.6, Table 3.2).

Averaged across trials, the mean proportion of time collared lemmings spent foraging in the constant patch was three fold greater than time spent in the variable patch (Table 3.2). I observed trends in preference that appeared to be related to the sequence of trials. In the first patch combination (0.008g) collared lemmings spent more time in the variable patch than the constant patch (Figs 3.5, 3.6). In subsequent trials, collared lemmings spent a higher proportion of the total foraging time in the constant patch compared to the variable patch (Figs 3.5, 3.6). The strength of the preference for the constant patch increased over the course of the experiment ($F_{4,125}=17.31$; $P<0.0001$). Collared lemmings increased the proportion of time spent in the constant patch between the first and fifth patch combinations ($F_1=31.2$; $P<0.0001$) and the first and second versus the fourth and fifth patch combinations ($F_1=48.22$; $P<0.0001$).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion

Collared lemmings did not consistently choose patches that maximized potential intake rate at either the feeding station or patch scale. Rather, they showed a strong preference for the patch where resources were predictable. This behavior suggests that collared lemmings are risk-averse foragers, preferring to minimize the variance in intake rate rather than maximizing the expected intake rate at any particular spatial scale.

Foraging animals experience variance in food encounter rate when food is distributed in patches. In our experiment one patch remained constant in terms of food intake rate at both spatial scales, whereas the alternative patch varied in intake rate at two spatial scales over the five patch combinations that were offered. Throughout the experiment collared lemmings were exposed to two sources of variation in food reward in the variable patch. First, the presence of empty feeding stations in two of the variable patch types (bite size = 0.008g, 0.025g, Table 3.1) meant that collared lemmings experienced variability in food reward within trials. Second, as potential intake rates were manipulated in the variable patch over the course of the experiment, the animals experienced variability among trials. The strongest preference for the constant patch occurred in later trials, where there was no variation in food reward within the patches at the feeding station scale because all houses contained feeding stations in each patch. This preference therefore demonstrates clear risk-averse behavior at the patch scale. Because the source of the variation at the patch scale lay in differences *between* alternative patch combinations, the collared lemmings apparently used information from past patch combinations to assess variance in food reward in present patches, otherwise the need to sample the two patches would have weakened the preference for the constant patch. This

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

suggests that collared lemmings based their patch preferences on a longer time scale than previously demonstrated for other small mammal species (e.g. common shrews *Sorex araneus*, (Barnard et al. 1985). It seems that collared lemmings are capable of remembering variation in food reward over several days, and applying this knowledge to immediate patch choice decisions.

Foraging animals are often faced with uncertainty, caused by the inherent stochasticity of resource supply over time and space (Lawes and Perrin 1995). Small herbivores, such as collared lemmings, have a limited capacity to store energy as fat (Barnard and Brown 1985, Lawes and Perrin 1995) and this limitation creates a threshold in the value of energy consumption; once that threshold is met, additional gains of energy have little value. When an animal must meet some critical requirement, natural selection may well operate strongly on the animal's ability to assure this requirement is met (Caraco 1980, Stephens 1981, Stephens and Krebs 1986, Lawes and Perrin 1995). Risk-sensitive foraging theory predicts that such animals should respond not only to overall prey abundance, but also the *variance* in prey abundance, because variance more directly correlates with the chance that a forager will fail to meet threshold level of intake, which, in turn increases the risk of starvation. Variation may attach a risk to utilization of the resource, introducing some probability that the forager will do poorly because of the stochastic nature of the reward (Caraco 1980). In these circumstances, I can expect foraging animals to make choices that minimize the probability of failing to meet the critical energy requirement, rather than acting to maximize the net rate of energy gain.

Collared lemmings experience winter conditions for at least 8 months of the year (Reid and Krebs 1996). Higher metabolic costs induced by cold temperatures may

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

diminish energy for body growth after maintenance requirements are met (Reid and Krebs 1996). This implies the existence of a critical level of resources that must be reached, because growth to a larger body mass and more rounded shape are adaptive for energy conservation (Malcolm and Brooks 1993) and reproduction in cold environments (Collier et al. 1975). Collared lemmings are therefore likely adapted to foraging in such a way as to minimize the probability of falling below this critical level of resources to ensure survival, and enhance reproductive success.

Houston and McNamara (1985) demonstrated that the optimal diet policy for continuous foragers that are able to forage during both day and night is to take all prey items that result in a net energy gain. Adaptations to this model have further demonstrated that the optimal prey choice for continuous foragers does not depend on energy reserves as it does for foragers that have a limited time available for foraging activities (Barnard et al. 1985). When two food options are presented with the same mean reward rate, but different variances, then the option with the smaller variance should always be chosen (Barnard et al. 1985). In essence, continuous foragers should always exhibit risk-averse behavior when choosing between alternative food options. Barnard and Brown (1985) subsequently developed and tested a more realistic model, which assumes that the forager is randomly interrupted during foraging for variable periods. These interruptions could be a consequence of a lack of food, escape behaviors, resting/sleeping, or territorial disputes between conspecifics, approximating the likely foraging activity budget for species such as collared lemmings (Brooks 1993, Predavec and Krebs 2000). This model predicts that foragers should be risk-prone when the interruption probability is high in order to maintain sufficient reserves to get through an

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

interruption should it occur. Alternatively, when the interruption probability is small, or when reserves are either very low or very high, it is optimal to be risk-averse (Barnard et al. 1985).

The results of our study can be examined in light of the predictions from this model. I found that collared lemmings preferred patches that offered predictable resources over those that offered greater average returns. Furthermore, the strength of the preference for the constant patch consistently increased as the experiment progressed. Collared lemmings are known to forage continuously throughout the day and night, with males exhibiting two peaks in movement (0800hrs and 2000hrs) and females showing a single peak at 1400hrs in the Canadian Arctic (Brooks 1993, Predavec and Krebs 2000). Activity distributions of collared lemmings from these two studies do show marked declines at certain times of day, suggesting that collared lemmings experience interruptions to the foraging process, probably linked to paternal care of young, mating activities, territorial disputes (Blackburn et al. 1998, Predavec and Krebs 2000), and predator avoidance (Brooks 1993). Following the model of Barnard et al. (1985) collared lemmings fit the scenario developed for a continuous forager that faces interruptions. This model predicts that collared lemmings should exhibit risk-prone behavior when interruption probability is high, and be risk-averse when interruption probability is low (Barnard et al. 1985). In our experiment the animals experienced interruptions to the foraging process when they were fasted before trials. At all other times, animals had *ad libitum* access to food. Although the lemmings were almost certainly in negative energy balance during the trials, their access to food was not interrupted frequently, only for a single, predictable period immediately before trials. Because collared lemmings are

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

continuous foragers in their natural environment, risk-averse behavior is likely adaptive under natural conditions. This adaptation, in conjunction with *ad libitum* access to food at all other times, likely promoted the risk-averse behavior that I observed. In addition, because collared lemmings utilize a diet of mostly vegetation their food supply is relatively abundant, even in winter, and as such, individuals may not expect to be in energy deficit at the end of the day (Lawes and Perrin 1995). In this case, animals may not be able to reliably perceive or predict circumstances under which risk-prone behavior may be optimal. The cost of being risk-prone under the wrong conditions is large compared to the benefit under the right conditions (Houston and McNamara 1985), and hence animals should be expected to show risk-averse behavior.

Field studies have indicated that the brown lemming (*Lemmus sibiricus*) is a time-minimizer when foraging (Peterson and Batzli 1984), consistent with predictions from optimal foraging theory for a species that suffers high predation. Schmidt et al. (2002) have suggested that collared lemmings in Greenland may be time-minimizing foragers, evidenced by larger females occupying higher quality habitat and moving less frequently than smaller females. Collared lemmings face high predation risk, both when foraging (foxes, aerial predators), and when in burrows (ermine) (Reid and Krebs 1996, Predavec and Krebs 2000). Studies have shown that predation may be as high as 50% for collared lemmings in Canada (Wilson et al. 1999), and so any mechanism that reduces the risk of predation would be advantageous. Other studies have suggested that collared lemmings respond to predation risk when foraging. These findings offer evidence that collared lemmings in natural settings are likely to forage in a risk-sensitive manner, maximizing survival probability by minimizing the time spent foraging when predation risk is high.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

This strategy would lead to selection of food patches with the greatest intake rates, such that a critical minimum threshold of food can be acquired in the least amount of time. It is possible that the animals in our experiment perceived the artificial foraging arena as a safe area, devoid of predation risk, and so relaxed a strategy of intake rate maximization in favor of selection of patches with the most predictable food reward. However, the collared lemmings in our experiment did avoid open areas within the arena, suggesting that they did perceive some level of risk associated with utilizing the arena. The appropriate strategy for these animals appears to be context dependent. When risk of starvation is paramount, it pays animals to forage in the most predictable patches where acquisition of a minimum threshold of energy is guaranteed. However, when risk of predation presents the greatest threat to survival, animals benefit from using time-minimizing strategies, using patches with the greatest rate of energy return per unit time.

Other small mammal species have been observed to forage in a risk-sensitive manner. However, variation in food amount and energy budgets has led to inconsistent results in several small mammal species (Ito et al. 2000). Common shrews were risk-prone under positive energy budgets, and risk-averse when under negative energy budgets, however the tendency towards risk-averse behavior above requirement was greater than towards risk-proneness below (Barnard and Brown 1985). Rats under positive energy budgets were also found to be risk-prone (Hastjarjo et al. 1990). However, rats under negative energy budgets have been found to be indifferent to variation in reward (Hastjarjo et al. 1990, Lawes and Perrin 1995, Ito et al. 2000). Rats have also been found to prefer constant food rewards under positive energy budgets (Ito et al. 2000). Round-eared elephant shrews (*Macroscelides proboscidius*) under negative energy budgets were found

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

to be risk-averse foragers, and showed indifference to variation in reward when under positive energy budgets (Lawes and Perrin 1995).

The distribution of food resources into patches creates opportunities for alternative foraging strategies where animals may either seek to maximize scale dependent intake rate, or minimize the variance in encounter rates with food rewards. Our previous work (Searle et al. *in review*) has demonstrated that collared lemmings do not incorporate information about the spatial context of food patches when forming residence time decisions, which implies that they are maximizing some currency other than net intake rate. Combined with the results of this study, collared lemmings appear to be risk-sensitive foragers, exhibiting risk-averse behavior when under negative energy balance. This behavior can be explained in light of their specific ecology, as small, continuous foragers, preferring a diet of vegetation, and faced with high predation risk.

Acknowledgements

This work was funded by the National Science Foundation (DEB-9981368). I am grateful to the staff of the Lab Animal Research Facilities at Colorado State University for their care of the collared lemmings, and to Dr. T. Nagy for his assistance in acquiring the animals. K. Bikowski, S. Hobbs, S. Merrill, L. Reynolds, and T. Wojtovicz provided invaluable assistance in experimental trials. This work could not have been completed without Tom Hobbs, Bruce Wunder, and Lisa Shipley.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Literature Cited

Adler, P. B., D. A. Raff, and W. K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia **128**:465-479.

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management **49**:386-400.

Barnard, C. J., and C. A. J. Brown. 1985. Risk-sensitive foraging in common shrews. Behavioral Ecolgy and Sociobiology **16**:161-164.

Barnard, C. J., C. A. J. Brown, A. I. Houston, and J. M. McNamara. 1985. Risk-sensitive foraging in common shrews: an interruption model and the effects of mean and variance in reward rate. Behavioral Ecolgy and Sociobiology **18**:139-146.

Bateson, M. 2002. Recent advances in our understanding of risk-sensitive foraging preferences. Proceedings of the Nutrition Society **61**:509-516.

Bergman, C. M., J. M. Fryxell, C. C. Gates, and D. Fortin. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? Journal of Animal Ecology **70**:289-300.

Blackburn, G. S., D. J. Wilson, and C. J. Krebs. 1998. Dispersal of juvenile collared lemmings in a high-density population. Canadian Journal of Zoology **76**:2255-2261.

Brooks, R. J. 1993. Dynamics of home range in collared lemmings. Academic Press, London.

Caraco, T. 1980. On foraging time allocation in a stochastic environment. Ecology **61**:119-128.

Collier, B. D., N. C. Stenseth, S. Barkley, and R. Osborn. 1975. A simulation model of energy aquisition and utlisation by the brown lemming at Barrow, Alaska. Oikos **26**:276-294.

Dumont, B., P. Carrere, and P. D'Hour. 2002. Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. Animal Research **51**:367-381.

Fortin, D., J. M. Fryxell, and R. Pilote. 2002. The temporal scale of foraging decisions in bison. Pages 970-982 *in* Ecology.

Gross, J. E., N. T. Hobbs, and B. A. Wunder. 1993a. Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size? Oikos **68**:75-81.

Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993b. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. Ecology **74**:778-791.

Hastjarjo, T., A. Silberberg, and S. R. Hursh. 1990. Risky choice as a function of amount and variance in food supply. Journal of the Experimental Analysis of Behavior **53**:155-161.

Hobbs, N. T. 1999. Responses of large herbivores to spatial heterogeneity in ecosystems. Pages 97-129 *in* G. C. Fahey, editor. Nutritional Ecology of Herbivores: Proceedings of the Vth International Symposium on the Nutrition of Herbivores. American Society of Animal Science, Savory IL.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Houston, A. I., and J. M. McNamara. 1985. The choice of two prey types that minimises the probability of starvation. Behavioral Ecolgy and Sociobiology **17**:135-141.

Illius, A. W., I. J. Gordon, D. A. Elston, and J. D. Milne. 1999. Diet selection in goats: A test of intake-rate maximization. Ecology **80**:1008-1018.

Ito, M., S. Takatsuru, and D. Saeki. 2000. Choice between constant and variable alternatives by rats: effects of different reinforcer amounts and energy budgets. Journal of the Experimental Analysis of Behavior **73**:79-92.

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia **127**:590-602.

Kacelnik, A., and M. Bateson. 1996. Risky theories - the effects of variance on foraging decisions. American Zoologist **36**:402-434.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure - a hierarchical framework for the study of heterogeneity. Oikos **59**:253-260.

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.

Lawes, M. J., and M. R. Perrin. 1995. Risk Sensitive Foraging Behavior of the Round-Eared Elephant Shrew (Macroscelides Proboscideus). Behavioral Ecology and Sociobiology **37**:31-37.

Malcolm, J. R., and R. J. Brooks. 1993. The adaptive value of photoperiod-induced shape changes in the collared lemming. Academic Press, London.

Peterson, R. M., and G. O. Batzli. 1984. Activity periods and energetic reserves of the brown lemming in northern Alaska. Holarctic Ecology **7**:245-248.

Predavec, M., and C. J. Krebs. 2000. Microhabitat utlisation, home ranges, and movement patterns of the collared lemming in the central Canadian Arctic. Canadian Journal of Zoology **78**:1885-1890.

Reid, D. G., and C. J. Krebs. 1996. Limitations to collared lemming population growth in winter. Canadian Journal of Zoology **74**:1284-1291.

Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology **12**:309-330.

Schmidt, N. M., T. B. Berg, and T. S. Jensen. 2002. The influence of body mass on daily movement patterns and home ranges of the collared lemming. Canadian Journal of Zoology **90**:64-69.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience **37**:789-799.

Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist **140**:325-348.

Stephens, D. W. 1981. The logic of risk-sensitive foraging preferences. Animal Behaviour **29**:628-629.

Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press.

WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia **121**:353-363.

Wilson, D. J., C. J. Krebs, and T. Sinclair. 1999. Limitation of collared lemming populations during a population cycle. Oikos **87**:382-398.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Zynel, C. A., and B. A. Wunder. 2002. Limits to food intake by the Prairie vole: effects of time for digestion. Functional Ecology **16**:58-66.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 3.1. Potential intake rates of collared lemmings in feeding stations or patches containing either constant bite sizes and densities, or variable bite sizes and densities of fresh alfalfa. Intake rates were estimated using functional response for lemmings feeding on fresh alfalfa.

Order of presentation of patch	Patch Type	Bite mass S (g DM)	Ratio of houses to feeding stations	Number of bites per feeding station	Potential feeding station intake rate (g DM/min)	Potential patch intake rate (g DM/min)
--	Constant	0.0025	20/20	33	0.27	0.05
3	Variable	0.0025	20/20	33	0.27	0.13
4	Variable	0.004	20/20	20	0.31	0.14
5	Variable	0.006	20/20	14	0.33	0.15
1	Variable	0.008	50/20	10	0.35	0.01
2	Variable	0.025	60/20	3	0.38	0.005

Table 3.2. Log ratios and 90% confidence intervals (CI) for the proportion of time collared lemmings spent in each patch type. Negative values for log ratios for the proportion of time spent per patch show that lemmings spent more time in the variable patch than the constant patch. Positive values for log ratios for this variable show that lemmings spent more time in the constant patch than the variable patch. The strength of the preference is indicated by the value, i.e. more positive log ratios show a stronger preference for the constant patch.

Bite size (g DM)	Trial number	Mean log ratio Proportion of time spent	90% CI
0.0025	1	2.14	1.33, 2.95
	2	2.07	1.26, 2.88
	3	1.51	0.64, 2.39
	4	1.02	-0.49, 2.54
0.004	1	1.39	0.52, 2.26
	2	3.09	2.22, 3.96
	3	1.39	0.51, 2.26
	4	1.18	0.31, 2.05
0.006	1	0.77	-0.11, 1.65
	2	1.56	0.68, 2.44
	3	1.84	0.96, 2.72
	4	1.08	0.12, 2.03
0.008	1	0.12	-0.97, 1.21
	2	-0.82	-1.91, 0.27
	3	-1.58	-2.67, -0.49
	4	-1.29	-2.73, 0.15
0.025	1	-0.02	-0.72, 0.69
	2	-0.24	-0.94, 0.46
	3	1.08	-0.28, 1.78
	4	-0.05	-0.76, 0.65

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

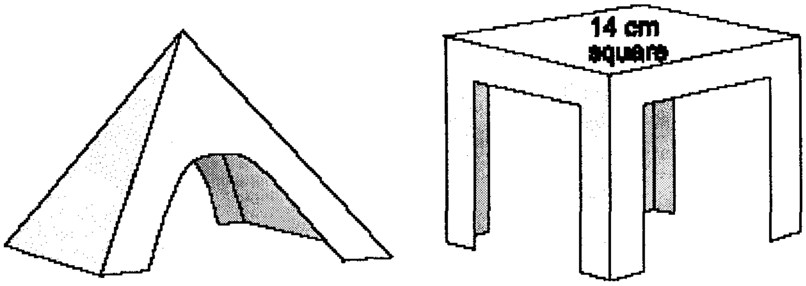


Figure 3.1. Tetrahedral house (left) and canopy (right) used to construct food patches for collared lemmings in the foraging arena. The houses were used to provide cover for feeding stations, and also reduced potential intake rate at the patch scale when left empty. Canopies were used to provide cover in patches that did not contain empty houses such that total cover remained equal in both the constant and variable patches in all trials.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

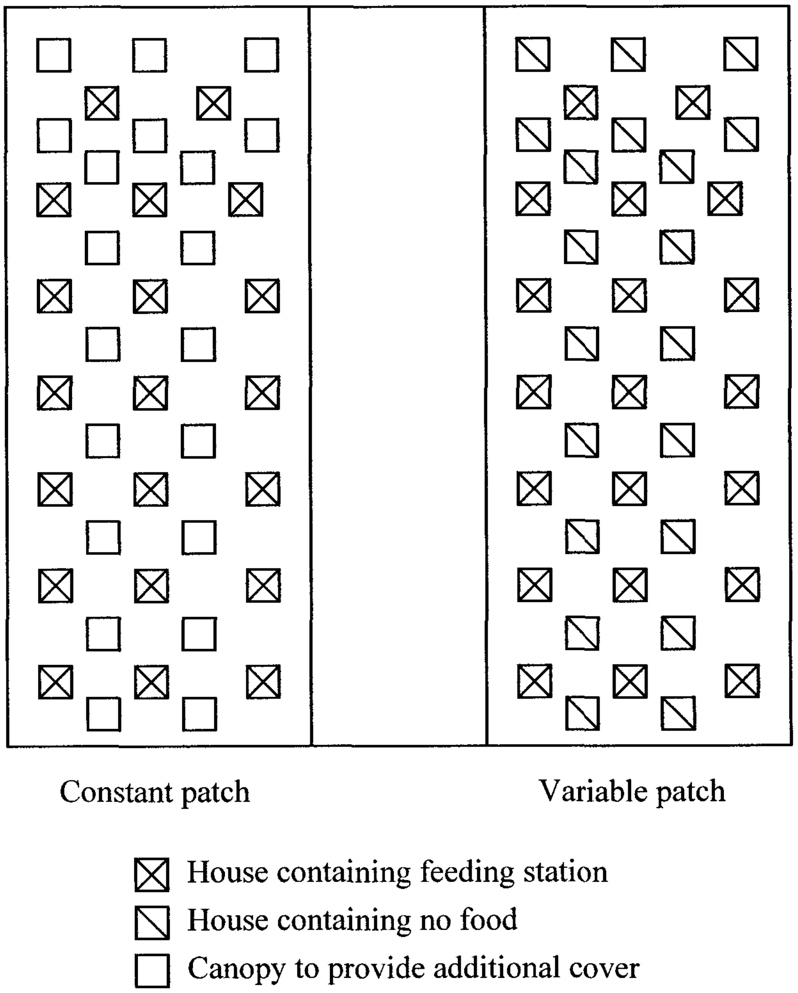


Figure 3.2. Collared lemmings were released into the foraging arena, which consisted of two distinct patches of food. The constant patch provided potential intake rates that did not vary in successive patch combinations throughout the experiment at either the feeding station or patch scale. The variable patch offered differing potential intake rates at the feeding station and patch scales in successive patch combinations. Each patch consisted of feeding stations containing food, feeding stations containing no food, or canopies used to achieve the same total cover in each patch.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 3.3. Collared lemmings were presented with 5 different patch combinations, each offering different potential intake rates at the feeding station or patch scale. Five alternative bite sizes were offered in the variable patch (solid line) to control potential intake rate at the feeding station scale (A). In addition, the encounter rate with feeding stations in the variable patch was manipulated to control potential intake rate at the patch scale (B). Bite size (0.0025g DM) and feeding station spacing did not vary in the constant patch. Competing hypotheses make distinct predictions about animal responses to this design: If foragers maximize intake at feeding station scales then the proportion of time spent feeding in the variable patch increase with increasing bite size (C). If foragers maximize intake rate at patch scales, then the proportion of time spent feeding in the variable patch should shift as bite size declines from .006 to .008 g (D). If foragers seek to minimize variance in intake rate, the proportion of time spent in the variable patch should be low throughout the experiment. (E).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

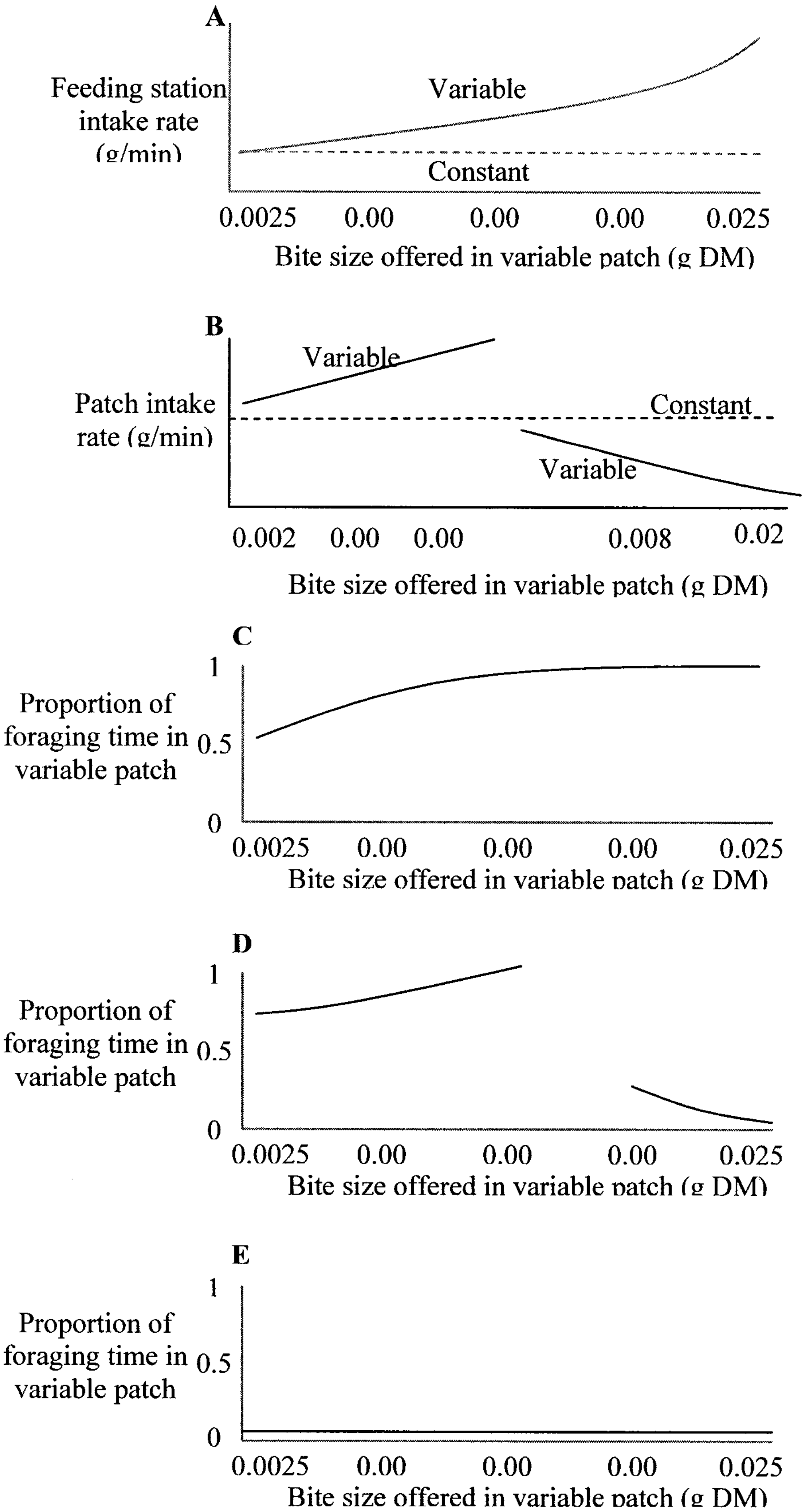


Figure 3.3.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

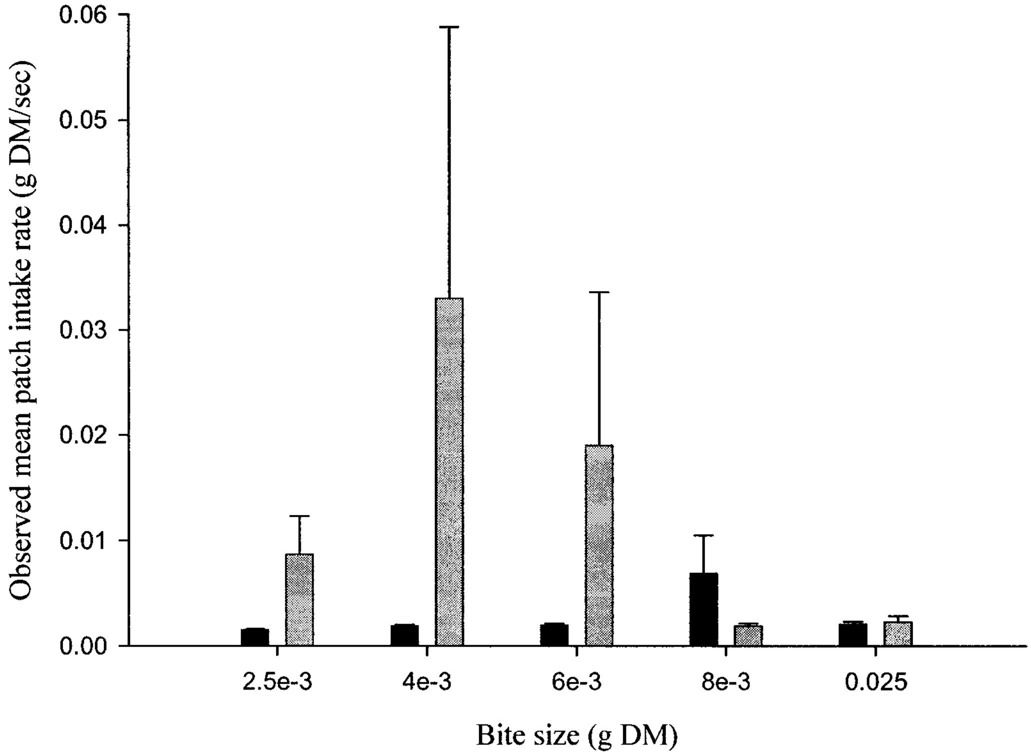


Figure 3.4. Mean patch intake rate of 7 collared lemmings in patches containing a constant bite size (black bars) and patches where bite size varied between pairings (gray bars). Observed patch intake rate is averaged over the four repetitions, and placed in chronological order of pairings. Error bars represent one standard error.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

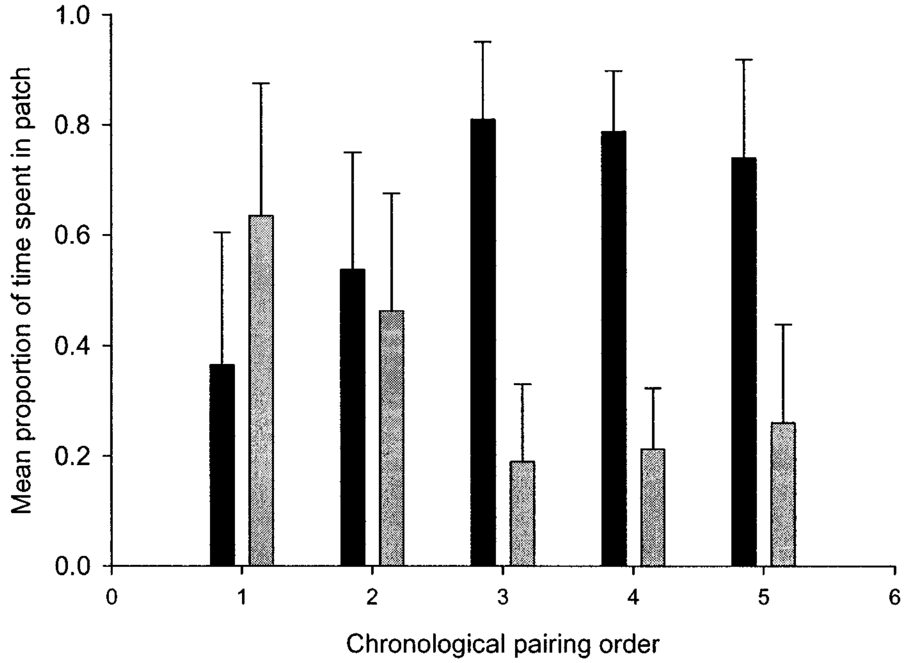


Figure 3.5. Mean proportion of time 7 collared lemmings spent in patches containing a constant bite size (black bars) and patches where bite size varied between pairings (gray bars). Proportion of time spent is averaged over the four repetitions, and placed in chronological order of pairings. Error bars represent one standard error.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

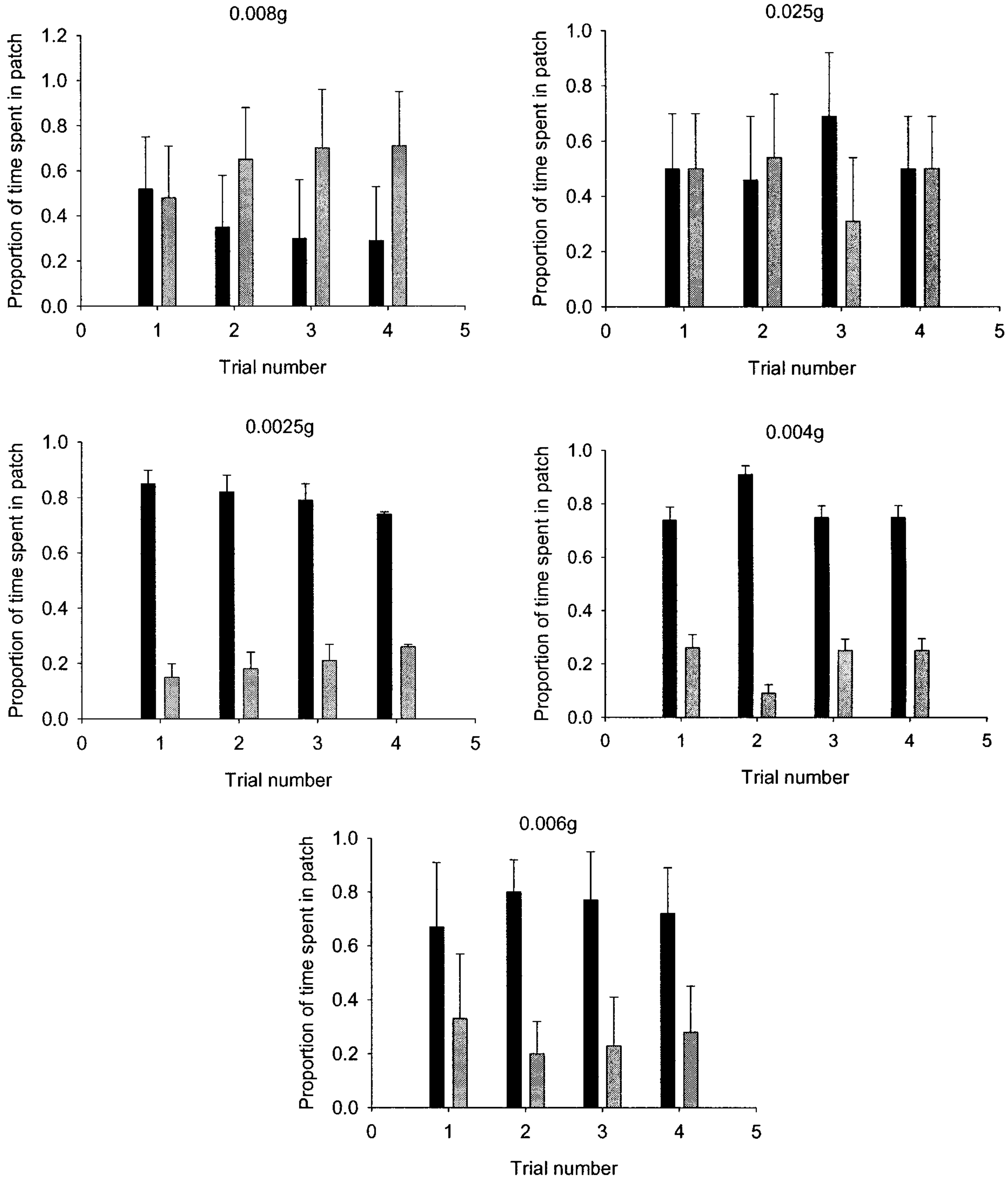


Figure 3.6. Mean proportion of time 7 collared lemmings spent in patches containing constant bite sizes (black bars) and patches where bite size varied between pairings (gray bars), by consecutive repetitions (1-4). Error bars represent one standard error.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Chapter Four

Should I stay or should I go? Patch departure decisions by herbivores at multiple scales.

(*Oikos, in review*)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Summary

The question of how much time a foraging herbivore should spend in a patch of food poses a central challenge in classical foraging theory. However, there remains uncertainty about the relevance of the patch paradigm to foraging decisions by large herbivores. This paper examines evidence for successfully predicting and quantifying patch departure decisions for large mammalian herbivores foraging across several spatial and temporal scales. Departure decisions at fine scales are influenced by trade-offs between maximizing intake rate and food quality. Classical models for departure decisions at larger spatial scales, particularly the marginal value theorem, appear inadequate. I advocate exploring alternative models for predictions of residence time at the patch scale.

Introduction

One of the central challenges in classical foraging theory attempts to explain how foragers respond to foods distributed in patches. Although early work emphasized studies of predators, more recent research has focused on herbivores. Understanding responses of herbivores to patchy distributions of plants requires conceptualizing the foraging landscape and defining a currency that can be used to assign values to foraging decisions. For large herbivores, the foraging landscape can be usefully described as a nested hierarchy of aggregated resources (Senft et al. 1987, Arditi and Dacorogna. 1988, Kotliar and Wiens 1990, Devries and Daleboudt 1994, Schaefer and Messier 1995, Bailey et al. 1996, Ritchie 1998, WallisDeVries et al. 1998, Hobbs 1999, WallisDeVries et al. 1999), and energy or nutrient intake rate is the currency used to evaluate alternative strategies (Stephens and Krebs 1986, Distel et al. 1991, Shipley and Spalinger 1992, Spalinger and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Hobbs 1992a, Gross et al. 1993a, Laca et al. 1994b, Shipley et al. 1994, Distel et al. 1995, Edwards et al. 1995). Hierarchy theory provides a conceptual framework to direct the study of foraging by large herbivores across spatial scales (O'Neill et al. 1986), Senft et al. 1987, Kotlier and Wiens 1990, Bailey et al. 1996). This framework allows research to be directed at resource aggregations of functional significance to key ecological processes. For foraging herbivores these aggregations can be defined functionally using differences in the rate of a behavior or process at different spatial or temporal scales.

Food resources that herbivores exploit are generally continuous, making it difficult to define patches (Kotliar and Wiens 1990, Schaefer and Messier 1995, Roguet et al. 1998a). However, patches can be descriptively defined as discrete spatial units differing from their surroundings in nature or appearance (Wiens 1976, Kotliar and Wiens 1990), or functionally defined by a change in the rate of a process or behavior (Sih 1980, Senft et al. 1987, Bailey et al. 1996). Aggregations of plants occur at multiple scales and foraging herbivores respond in different ways to variation at these different scales. At all scales of patchiness, however, some forage material is almost always left uneaten. This underpins the classical patch problem – how do herbivores decide how much mass to consume from a patch, or alternatively, how do herbivores decide how much time to devote to exploiting a patch before moving on? This is a decision that must be made at all levels in the foraging hierarchy, from the bite up to the large patch.

A search on Web of Science (http://isi1.isiknowledge.com Science Citation Index Expanded, accessed May 2004) using the keywords 'herbivore' and 'patches' resulted in 77 papers over the period 2000-2004. Clearly, the patch concept is widely applied in the study of herbivore foraging, but is it a useful paradigm that has guided our learning about

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the patch departure decisions of large herbivores at the bite, feeding station and patch scales? A large body of theoretical and empirical literature has been developed to quantify the patch departure decisions of large herbivores, and yet the extent to which this endeavor has been successful remains unclear. In this review, I summarize the findings of studies that have sought to understand departure decisions of large herbivores foraging over several spatial scales: the bite, feeding station and patch. I define a bite as the amount of forage removed from a plant in a single cropping motion, and as such, it forms the grain of the foraging hierarchy (Kotliar and Wiens 1990). A feeding station is a collection of bites, where all bites can be removed without movement of the animal's forelegs. Patches represent collections of feeding stations, and are functionally separated from their surroundings by changes in intake rate that are incurred as animals travel between forage patches (Senft et al. 1987, Bailey et al. 1996). At each of these three scales, foraging herbivores must make a departure decision. Hence, I explore what has been learnt about departure decisions at multiple spatial and temporal scales for large mammalian herbivores.

Bites

At the smallest spatial scale, large herbivores make decisions about departing patches during the formation of bites. A foraging herbivore must decide how much material should be removed from which parts of a plant (Palo et al. 1992). Thus, decisions on bite size can be cast as patch leaving choices because the animal must decide how much of the "patch" to consume and how much to leave (Laca and Demment 1991). Bite size has an upper constraint determined by the size of the animal's mouth parts, and by the tensile strength and sizes of the leaves and stems presented by the plant

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(Illius and Gordon 1987). However, there is a certain range of plant morphologies over which animals have considerable flexibility in bite size selection (Shipley et al. 1994).

There is a fundamental trade-off that herbivores face when selecting bites – large bites offer benefits to the animals by promoting rapid instantaneous intake rate because more dry matter is consumed per cropping motion (Spalinger and Hobbs 1992b, Gross et al. 1993b). However, there are also costs associated with consuming large bites. Large bites require greater cropping and mastication effort, which also increases with forage maturity (Demment and Greenwood 1988). Because bite rate is inversely related to mastication effort, bite rate declines with greater bite sizes (Searle et al. *In press*). Increasing bite size can reduce the digestibility and nutrient content of bites because structural material tends to increase along a gradient from the distal to the basal portions of plants (Vivås and Sæther 1987, Palo et al. 1992, Shipley et al. 1999). This is particularly true for browse species; a negative relationship between digestibility, and crude protein with twig diameter has been widely demonstrated for birch (Hjeljord et al. 1982, Vivås and Sæther 1987, Sinclair et al. 1988). Grass species show a similar trend, with an inverse relationship between digestibility of energy and cell wall (fiber) content of forage (Van Soest 1981, Mould and Robbins 1982, Osbourn 1989). The proportion of cell wall in tissues increases as grasses mature and more structural support is required (Niklas 1992). More mature grasses tend to require greater processing times for herbivores (White 1983), such that both digestibility and rate of turnover of ingesta tend to be negatively related to biomass, if biomass if positively associated with plant maturation stage. As a consequence of these trade-offs in intake rate and food quality, there should be an optimal bite size at which the benefits of rapid intake rate and low

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

levels of plant toxins are balanced against diminishing returns in concentrations of digestible energy and nutrients. (Jia et al. 1995).

Browsing herbivores have demonstrated a capability to use selection at the bite level in response to this trade-off, employing strategies to maximize energy gain. Moose (*Alces alces*) in northern Sweden were found to select bites from a limited range of potential browse species (Shipley et al. 1998), usually taking only one or two bites from each plant selected for browsing. Bites were selected in relation to plant morphology - browse species offering fewer, larger stems were selected over those with many, smaller stems (Shipley et al. 1998). Models of diet optimization for browsing herbivores at the bite scale have further quantified this interpretation. Shipley et al. (1999) developed a general model that quantitatively predicted optimal bite size for browsing herbivores, defined as the bite size that results in the greatest daily net energy intake, based on constraints in harvesting and digesting foods. Tests of this model with moose, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) provided good evidence that browsing herbivores selected bite sizes in relation to the chemistry and morphology of plants, body size, and digestive strategy (Shipley et al. 1999). A model predicting optimal bite size for moose browsing on birch in Norway based on maximization of net energetic gain, incorporating intake rate and digestibility, also resulted in accurate predictions (Vivås et al. 1991).

Browsing herbivores also have a degree of behavioral flexibility in the face of the trade off between bite size and quality when selecting bites. Moose consumed birch twigs of greater diameter as food abundance declined, with a higher proportion of the intake taken from nutritious 'top twigs' in high density plots (Vivås and Sæther 1987, Shipley

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

and Spalinger 1995). However, young white-tailed deer (*Odocoileus virginianus*) did not follow the same behavioral adjustment, likely because the smaller size of their rumen may restrict their ability to sacrifice diet quality in favor of maintaining high intake rates (Shipley and Spalinger 1995). Roe deer foraging in browse patches selected larger bites in preference to smaller ones indicating that departure decisions at the bite level are an important component of their foraging behaviors (Illius et al. 2002). Browsers have been shown to respond to both food quality and availability by eating a higher quality diet and taking less from each plant at high food densities (Vivås and Sæther 1987, Andersen and Sæther 1992, Shipley and Spalinger 1995). This accumulating evidence leads us to conclude that browsing herbivores evaluate food quality and modify their departure decisions accordingly at the bite scale.

Grazers have also been shown to make departure decisions at the scale of the bite, changing bite size in response to changes in forage characteristics. Departure decisions at the level of the bite are expressed through changes in bite size as grazers deplete forage. Declines in bite size with patch depletion have been demonstrated for grazers (Laca et al. 1994a, Ginnett et al. 1999), and large mammalian herbivores tend to graze swards systematically, removing most of the top half of the canopy before biting into the lower horizon (Laca et al. 1994a, Ungar and Ravid 1999). Laca et al. (1994c) demonstrated that cattle grazing swards of herbage selectively chose larger bites within heterogeneous top horizons. Grazing herbivores seem to select bite sizes within swards on the basis of intake rate maximization. Several studies have shown that cattle and sheep tend to bite only a fairly constant proportion of the height of herbage available (Milne et al. 1982, Barthram and Grant 1984, Laca et al. 1992). Because the top horizon of natural swards

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

usually has the highest concentration of green leaf with a high concentration of nutrients, and because leaf requires less chewing than stem and is more rapidly digested (Laca et al. 1992), animals may maximize nutrient intake rate by limiting bites to upper horizons and maintaining higher biting rates. This decline in bite size with forage depletion is a more general response for grazing herbivores than for browsers. As described above, browsers may exhibit alternative bite size responses to forage depletion, with some decreasing bite size (Illius et al. 2002), others increasing bite size (Shipley and Spalinger 1995), and others maintaining bite size (Shipley and Spalinger 1995). The more general response of grazing herbivores is likely a simple consequence of changes in sward structure as patches are depleted, with bite size largely determined by sward height, density, and presence of residual stems (Ungar et al. 1991, Laca et al. 1992, Flores et al. 1993, Laca et al. 1994d, Ginnett et al. 1999). The decline in digestibility as more proximal parts of plants are encountered is probably less important to grazing herbivores than to browsing herbivores, because grasses typically do not invest in lignin or defensive chemicals to the same degree as browse species (Foley et al. 1999).

Feeding stations

Feeding stations are defined as the area of forage an animal can reach without incurring travel. As such, they are thought to represent a useful scale of classification for the study of foraging behavior, because they represent a discrete area that can be functionally defined by movement of the grazing animal. Several studies have suggested that departure decisions for grazers in feeding stations may be related to intake rate maximization. Large herbivores tend to spend more time in feeding stations as forage biomass increases (Novellie 1978, Ruyle and Dwyer 1985, Schaefer and Messier 1995).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Muskoxen (*Ovibos moschatus*) delayed departure from feeding stations when accumulated snow amplified travel costs (Schaefer and Messier 1995). Sheep were able to maintain dry matter intake rates as forage was depleted because they spent less time in feeding stations due to an increase in biting rate within feeding stations (El Aich et al. 1989). Similar behavior was demonstrated for sheep by Roguet et al. (1998b). Green leaf mass was the principle determinant of feeding station departure for sheep grazing on cocksfoot swards, explained by the selection of grazers for green leaves (Roguet et al. 1998b).

However, other studies have shown a more mechanical mechanism for feeding station departure. WallisDeVries et al. (1998) found that grazing cattle took an average of seven bites per feeding station, and did not exhaust the top horizon before moving on. El Aich et al. (1989) found evidence that suggests free-grazing sheep spent a constant amount of time in feeding stations regardless of season. Jiang and Hudson (1993) demonstrated that departure from feeding stations in elk (*Cervus elaphus*) was stimulated by changes to the neck angle of grazing animals. They suggested a biokinetic role in departure decisions at this scale, with animals moving on when ungrazed forage can no longer be reached by movements of the head and neck alone.

Although some grazing herbivores may base decisions about when to depart feeding stations on simple intake rate maximization rules, others tend to apply a primarily mechanical process for determining when to leave feeding stations. In general, grazing herbivores tend to utilize feeding stations in such a way as to remove the more digestible forage (i.e. green leaves and top horizons) before moving on. However, whether intake rate plays a prominent role in this behavior remains unclear. At fine scales costs and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

benefits associated with alternative feeding options are small, and likely hard for herbivores to accurately assess (Roguet et al. 1998a). Under these circumstances, herbivores would be unlikely to display selective behavior at the feeding station scale because animals would have to invest considerable effort to discriminate the relative profits of alternative feeding stations. In addition, using intake rate as the currency for assessing feeding stations could be difficult for larger herbivores. This is because when feeding stations are closely aggregated the grazing rate from previous stations may affect rate estimation at subsequent stations, and because animals may fail to experience patch depression if feeding station residence time and food intake are small (Illius et al. 1992, Roguet et al. 1998a).

Patches

Patches are functionally defined as discrete spatial units differing from their surroundings by a change in the rate of a process or behavior, such as intake rate. The prevailing approach to predicting departure decisions at the patch scale invokes the marginal value theorem (Charnov 1976) which predicts that foragers will depart from a single patches when their instantaneous rate of intake drops below the average rate of intake attainable in all patches. Quantitative evidence for foraging in agreement with the MVT has been demonstrated in some large herbivores. Jiang and Hudson (1993) found that elk tended to depart from patches only after cropping rate at a feeding station dropped below the seasonal expectation on lush pasture in May, and departed patches after the cropping rate dropped below the seasonal expectation at two consecutive feeding stations in early spring, and fall, when conditions were less favorable (Jiang and Hudson

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

1993). Laca et al. (1993) found that the MVT accurately predicted patch residence times of cattle in nine different grazing environments in a mown ryegrass pasture.

However, in contrast to these two studies, the preponderance of other tests of the MVT have only been able to achieve qualitative agreement with the model's predictions. In particular, several studies have found that herbivores tend to remain longer in more profitable patches and that their residence time increases as travel time among patches increases. Vivås and Sæther (1987) and Distel et al. (1995) demonstrated that both moose and cattle increased grazing intensity (grazing time, intake) in richer patches in line with MVT predictions. Patches were depleted to a greater degree when alternative patches were poorer and distances between patches were increased (Laca et al. 1993, Distel et al. 1995). Similarly, young moose and white-tailed deer increased patch residence time as plant sizes and inter-patch distance increased. (Shipley and Spalinger 1995). Winter foraging by free-ranging moose also provided qualitative agreement for the MVT--moose increased residence time and browsed a greater number of plants in patches with high densities of saplings (Vivås and Sæther 1987). Similarly, Dorcas gazelles (*Gazella dorcas*) in the Negev desert consumed more lily bulbs in areas of highest lily density (Ward and Saltz 1994). Johnson et al. (2001) demonstrated that woodland caribou (*Rangifer tarandus*) increased foraging intensity (number of feeding sites) in areas of higher abundance of favored lichens, and greater snow depth. Giving up densities (GUDs, Brown 1988) have been used to assess if animals tend to leave all patches at the same quitting level of intake rate, as predicted by the MVT. Kotler et al. (1994) found that Nubian ibex (*Capra nubiana*) tended to equalize final food densities when foraging in patches of alfalfa or rye hay pellets in trays. More specifically, ibex were found to

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

exploit resource patches as long as the benefit of continued foraging was greater than the cost (Kotler et al. 1994).

In other studies application of the MVT has failed to match observations in a qualitative way. For instance, Schaefer and Messier (1995) failed to find support for MVT predictions at the patch scale for muskoxen feeding in the winter in the high arctic. Patch residence time showed little relationship to forage abundance or snow depth (travel costs), although muskoxen increased residence time in feeding stations, they also decreased the number of feeding stations per patch (Schaefer and Messier 1995).

A persistent problem in assessing predictions of the MVT and other models that incorporate the notion of patches arises because there is no reliable way to determine the scale at which an herbivore perceives patches. For instance, browsing herbivores may treat an individual tree or shrub as a patch, or alternatively, whole stands of trees could be considered to be a patch. Several studies have indicated that moose perceive individual trees as patches. Astrom et al. (1990) demonstrated that handling time per tree increased with increasing tree size for moose feeding on deciduous trees. Danell et al. (1991) found that moose did not consume from trees in stands in proportion to their availability, rather they disproportionately directed foraging towards more profitable tree types, indicating that selection occurs on the scale of the tree. Edenius et al. (2002) were able to show that moose did not perceive aspen stands as discrete patches, random sites and aspen stands were utilized equally by moose in terms of overall use of forage. Instead, moose appeared to use individual aspen ramets in accordance with diet theory. Spalinger and Hobbs (1992) demonstrated that there is a threshold bite density (D^*, bites/m^2) at which feeding processes change from limitation by encounter rate to limitation by chewing. This insight

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

provides a mechanistic definition for patches, suggesting that aggregations of bites need to be at least D* apart for herbivores to consider them patches. Further problems stem from use of the MVT for predicting residence times for browsing herbivores - when gain functions are linear, as has been demonstrated for several browsing herbivores (e.g. Åstrom et al. 1990, Shipley and Spalinger 1995, Illius et al. 2002) we expect animals to remain in patches until all forage is removed, because patch depression does not occur. Thus, the assumption of the MVT, that gain functions are smoothly decelerating, may not be met for browsing herbivores.

The poor quantitative agreement of MVT predictions with observed behavior may be caused by failing to properly identify the appropriate scale for applying the model, or failing to accurately quantify gain function shape. Illius et al. (2002) suggested that for browsers, short term optimization based on MVT may well be subordinated to long term optimization of diet quality. This is because there are *a priori* and empirical grounds for questioning whether optimal patch use is an appropriate model of resource use by browsing mammalian herbivores. Longer-term diet optimization, i.e. the trade-off between diet quality and daily intake rate, is a more likely explanation of their foraging behavior (Illius et al. 2002).

Alternative approaches to quantifying the patch departure decisions of large herbivores are rare, and it is only infrequently that studies have attempted to measure support for models other than the MVT. For instance, Focardi et al. (1996) found evidence for a threshold model for fallow deer, with animals abandoning patches when the forage biomass density fell below a lower dry matter threshold.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Conclusions

Quantifying decisions made by large herbivores about when to leave patches has been particularly successful at small spatial scales. It is possible to quantitatively predict optimal bite sizes for browsers based on maximization of energy gain and diet quality (Vivås et al. 1991, Shipley et al. 1999). Grazers also demonstrate a general departure strategy at the bite scale as patches are depleted, tending to systematically remove sward layers with concomitant declines in bite size. In contrast, departure decisions for herbivores at feeding station scales indicate animals may try to maximize intake, but also exhibit simple mechanical, biokinetic responses to depletion. These different responses suggest that herbivores may not be able to discriminate costs and benefits at this scale because potential gains from selectivity are too small to warrant investment in active departure decisions. At larger scales, patch departure predictions derived from the MVT suffer from a lack of quantitative support, though most empirical studies agree qualitatively with predictions. Other, more empirical, approaches to estimating patch residence times for herbivores have more recently met with success (Focardi et al. 1996), and I encourage exploring alternative avenues to the MVT.

To conclude, studying departure decisions at bite, feeding station and patch scales has clearly led to an improved understanding of the currencies and strategies employed by large herbivores foraging in complex landscapes. We now understand that scaling up ecological processes by simply changing units and implicitly expanding the spatial and temporal scales of measurement is inappropriate (WallisDeVries et al. 1998, Johnson et al. 2001). The strategies that foraging herbivores use at small spatial scales can be differentiated from those employed at upper hierarchical levels. In this way, predictions

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

that are difficult to test when observed behavior is the product of complex decisions made by animals responding to multiple variables (Johnson et al. 2001) may be broken down into their component parts. Studies of departure decision strategies at multiple spatial scales have contributed significantly to our understanding of foraging behavior. This is particularly true at small spatial scales where there are clear benefits to the use of bite size to modify trade-offs in forage quality and intake rate. However, failing to successfully quantify departure decisions at patch scales demands that alternative approaches that explore strategies outside of the MVT be employed.

Acknowledgements

This work was completed in conjunction with Tom Hobbs and Lisa Shipley.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Literature cited

Andersen, R., and B. E. Sæther. 1992. Functional response during winter of a herbivore, the moose, in relation to age and size. Ecology **73**:542-550.

Arditi, R., and B. Dacorogna. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. American Naturalist **131**:837-846.

Åstrom, M., P. Lundberg, and K. Danell. 1990. Partial Prey Consumption by Browsers - Trees as Patches. Journal of Animal Ecology **59**:287-300.

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management **49**:386-400.

Barthram, G. T., and S. A. Grant. 1984. Defoliation of ryegrass-dominated swards by sheep. Grass & Forage Science **39**:211-219.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecolgy and Sociobiology **22**:37-47.

Charnov, E. L. 1976. Optimal foraging, the Marginal Value Theorem. Theoretical Population Biology **9**:129-136.

Danell, K., L. Edenius, and P. Lundberg. 1991. Herbivory and Tree Stand Composition - Moose Patch Use in Winter. Ecology **72**:1350-1357.

Demment , M. W., and G. B. Greenwood. 1988. Forage ingestion: effects of sward characteristics and body size. Journal of Animal Science **66**:2380-2392.

Devries, M. F. W., and C. Daleboudt. 1994. Foraging Strategy of Cattle in Patchy Grassland. Oecologia **100**:98-106.

Distel, R. A., T. C. Griggs, E. A. Laca, and M. W. Demment. 1991. Cattle prefer patches that yield greater instanteous intake rate in patchy ryegrass swards. Pages 171 *in* Second Grazing Livestock Nutrition Conference. Oklahoma State University, Norman Oklahoma, Steamboat Springs Colorado.

Distel, R. A., E. A. Laca, T. C. Griggs, and M. W. Demment. 1995. Patch selection by cattle: Maximization of intake rate in horizontally heterogeneous pastures. Applied Animal Behaviour Science **45**:11-21.

Edenius, L., G. Ericsson, and P. Naslund. 2002. Selectivity by moose vs the spatial distribution of aspen: a natural experiment. Ecography **25**:289-294.

Edwards, G. R., A. J. Parsons, P. D. Penning, and J. A. Newman. 1995. Relationship between vegetation state and bite dimensions of sheep grazing contrasting plant species and its implications for intake rate and diet selection. Grass & Forage Science **50**:378-388.

El Aich, A., A. Moukadem, and L. R. Rittenhouse. 1989. Feeding station behavior of free-grazing sheep. Applied Animal Behaviour Science **24**:259-265.

Flores, E. R., E. A. Laca , T. C. Griggs, and M. W. Demment. 1993. Sward height and vertical morphological differentiation determine cattle bite dimensions. Agronomy Journal **85**:527-532.

Focardi, S., P. Marcellini, and P. Montanaro. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. Journal of Animal Ecology **65**:606-620.

Foley, W. J., G. R. Iason, and C. McArthur. 1999. Role of plant secondary metabolites in the nutritional ecology of mammalian herbivores: how far have we come in 25

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

years? Pages 130-209 *in* H. G. Jung and G. C. Fahey, editors. Nutritional ecology of herbivores: Proceedings of the Vth International Symposium on the nutrition of herbivores. American Society of Animal Science, Savoy.

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.

Gross, J. E., N. T. Hobbs, and B. A. Wunder. 1993a. Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size? Oikos **68**:75-81.

Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993b. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. Ecology **74**:778-791.

Hjeljord, O., F. Sundstol, and H. Haagenrud. 1982. The nutritional value of browse to moose. Journal of Widlife Management **46**:333-343.

Hobbs, N. T. 1999. Responses of large herbivores to spatial heterogeneity in ecosystems. Pages 97-129 *in* H. G. Jung and G. C. Fahey, editors. Nutritional Ecology of Herbivores: Proceedings of the Vth International Symposium on the Nutrition of Herbivores. American Society of Animal Science, Savory IL.

Illius, A. W., D. A. Clark, and J. Hodgson. 1992. Discrimination and patch choice by sheep grazing grass-clover swards. Journal of Animal Ecology **61**:183-194.

Illius , A. W., P. Duncan, C. Richard, and P. Mesochina. 2002. Mechanisms of functional response and resource exploitation in browsing roe deer. Journal of Animal Ecology **71**:723-734.

Illius, A. W., and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology **56**:989-1000.

Jia, J., P. Niemela, and K. Danell. 1995. Moose Alces alces bite diameter selection in relation to twig quality on four phenotypes of Scots pine Pinus sylvestris. Wildlife Biology **1**:47-55.

Jiang, Z., and R. J. Hudson. 1993. Optimal grazing of wapiti cervus-elaphus on grassland patch and feeding station departure rules. Evolutionary Ecology **7**:488-498.

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia **127**:590-602.

Kotler, B. P., J. E. Gross, and W. A. Mitchell. 1994. Applying Patch Use to Assess Aspects of Foraging Behavior in Nubian Ibex. Journal of Wildlife Management **58**:299-307.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure - a hierarchical framework for the study of heterogeneity. Oikos **59**:253-260.

Laca, E. A., U. E. D., Seligman N., and D. M. W. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass & Forage Science **47**:91-102.

Laca, E. A., and M. W. Demment. 1991. Herbivory: the dilema of foraging in a spatially heterogeneous food environment. Pages 30-44 *in* R. T. Palo and C. T. Robbins, editors. Plant Defenses Against Mammalian Herbivory. CRC Press, Boca Raton, Fla.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Laca, E. A., 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., R. A. Distel, T. C. Griggs, G. P. Deo, and M. W. Demment. 1993. Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilisation. Pages pp 709-701 *in* Proceedings of XVII International Grassland Congress, New Zealand and Queensland February 1993.

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.

Laca, E. L., R. A. Distel, T. C. Griggs, and M. W. Demment. 1994d. Effects of canopy structure on patch depletion by grazers. Ecology **75**:706-716.

Milne, J. A., H. J., R. Thompson, and W. G. Souter. 1982. The diet ingested by sheep grazing swards differing in white clover and perennial ryegrass content. Grass & Forage Science **37**:209-218.

Mould, E. D., and C. T. Robbins. 1982. Digestive capabilities in elk compared to white-tailed deer. Journal of Widlife Management **46**:22-29.

Niklas, K. J. 1992. Plant Biomechanics: An Engineering Approach to Plant Form and Function. University of Chicago Press, Chicago.

Novellie, P. A. 1978. Comparison of the foraging strategies of blesbok and springbok on the Transvaal highveld. South African Journal of Wildlife Research **8**:137-144.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A Hierachical Concept of Ecosystems. Princeton University Press.

Osbourn, D. F. 1989. The feeding value of grass and grass products. *in* W. Holmes, editor. Grass: its production and utlilzation. Blackwell, Oxford.

Palo, R. T., R. Bergstrom, and K. Danell. 1992. Digestibility distribution of phenols and fiber at different twig diameters of birch in winter: implications for browsers. Oikos **65**:450-454.

Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology **12**:309-330.

Roguet, C., B. Dumont, and S. Prache. 1998a. Selection and use of feeding sites and feeding stations by herbivores: A review. Annales De Zootechnie **47**:225-244.

Roguet, C., S. Prache, and M. Petit. 1998b. Feeding station behaviour of ewes in response to forage availability and sward phenological stage. Applied Animal Behaviour Science **56**:187-201.

Ruyle, G. B., and D. D. Dwyer. 1985. Feeding stations of sheep as an indicator of diminished food supply. Journal of Animal Science **61**:349-353.

Schaefer, J. A., and F. Messier. 1995. Winter foraging by muskoxen: a hierarchical approach to patch residence time and cratering behavior. Oecologia **104**:39-44.

Searle, K. R., T. Vandervelde, N. T. Hobbs, and L. A. Shipley. *In press*. Gain functions for large herbivores in small patches: tests of alternative models. Journal of Animal Ecology.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience **37**:789-799.

Shipley, L. A., S. Blomquist, and K. Danell. 1998. Diet choices made by free-ranging moose in northern sweden in relation to plant distribution, chemistry, and morphology. Canadian Journal of Zoology **76**:1722-1733.

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., A. W. Illius, K. Danell, N. T. Hobbs, and D. E. Spalinger. 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. Oikos **84**:55-68.

Shipley, L. A., and D. E. Spalinger. 1992. Mechanics of browsing in dense food patches effects of plant and animal morphology on intake rate. Canadian Journal of Zoology **70**:1743-1752.

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.

Sih, A. 1980. Optimal foraging: partial comsumption of prey. American Naturalist **116**:281-290.

Sinclair, A. R. E., C. J. Krebs, J. N. M. Smith, and S. Boutin. 1988. Population of snowshoe hares. III. Nutrition, plant secondary compounds and food limitation. Journal of Animal Ecology **57**:787-806.

Spalinger, D. E., and N. T. Hobbs. 1992a. Herbivore functional response: a mechanistic model of food intake rate in patchy environments. Bulleting of the Ecological Society of America **73**:209.

Spalinger, D. E., and N. T. Hobbs. 1992b. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist **140**:325-348.

Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press.

Ungar, E. D., A. Genizi, and M. W. Demment. 1991. Bite dimensions and herbage intake by cattle grazing short hand-constructed swards. Agonomy Journal **83:973-978**.

Ungar, E. D., and N. Ravid. 1999. Bite horizons and dimensions for cattle grazing herbage to high levels of depletion. Grass and Forage Science **54**:357-364.

Van Soest, P., J. 1981. Nutritional ecology of the ruminant. Cornell University Press.

Vivås, H. J., and B. E. Sæther. 1987. Interactions between a generalist herbivore, the moose *Alces alces,* and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. Journal of Animal Ecology **56**:509-520.

Vivås, H. J., B. E. Sæther, and R. Andersen. 1991. Optimal twig-size selection of a generalist herbivore, the moose *Alces alces*: implications for plant-herbivore interactions. Journal of Animal Ecology **60**:395-408.

WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1998. From feeding station to patch: scaling up food intake measurements in grazing cattle. Applied Animal Behaviour Science **60**:301-315.

WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia **121**:353-363.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ward, D., and D. Saltz. 1994. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. Ecology **75**:48-58.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos **40**:377-384.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics **7**:81-120.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.