PATCH-LEVEL FORAGING BEHAVIOR OF BISON AND CATTLE ON TALLGRASS PRAIRIE

By

JAY DANIEL KERBY

Bachelor of Science

Oregon State University

Corvallis, Oregon

2000

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the degree of
MASTER OF SCIENCE
December, 2002

PATCH-LEVEL FORAGING BEHAVIOR OF BISON AND CATTLE ON TALLGRASS PRAIRIE

Thesis Approved:

David M Engle
Thesis Advisor

Timothy J. Pettibone
Dean of the Graduate College

ACKNOWLEDGEMENTS

I would like to thank the USDA National Research Initiative Competitive Grants Program and the Oklahoma Agricultural Experiment Station for their support in funding this project. When exploring opportunities for graduate school, the chance to join several large, nationally-noted rangeland programs arose. Thankfully, Chad Boyd and Amy Smith persistently suggested Oklahoma State University. Five minutes after meeting with my advisor Dr. Engle I was convinced that the opportunity at OSU was clearly brightest. My judgment was accurate. Dr. Engle is an excellent scientist and first-class gentleman. He has guided me through this process and been endlessly patient throughout. It has been my privilege to learn from and work with him.

Throughout the course of this project, my committee members, Drs. Fuhlendorf and Bidwell were invaluable for discussion, support, and advice. For statistical advice I relied on Drs. Goad and Payton. I must thank the OSU Rangeland Fire Crew, particularly Chris Stansberry and John Weir for sharing knowledge, advice, and experience and for "not letting classes get in the way of my education." I would also like to thank my fellow graduate students; Ph.D. candidates Amy Ganguli, Wade Harrell, and Darrell Townsend for scholarly and worldly advice; M.S. candidates Chris O'Meilia and Aaron Roper for struggling through the same obstacles with me.

The Tallgrass Prairie Preserve is a special place, a glimpse into the past. The ability to conduct research on the Preserve was a rare opportunity and lends me great perspective. I would like to thank The Nature Conservancy and Director of Science and Stewardship Bob Hamilton for access, support, and living facilities during data collection on the Preserve.

Finally I would like to thank my family, my brother Jeff, parents Bob and Carol. My brother has provided me with motivation throughout my life, sometimes competitively, but with only the best results. His own success is a source of pride and encouragement for myself. I dedicate this work to my parents, who convinced me that any goal is achievable and that education puts those goals within reach. They never expected that I would take that notion so literally and make a career of academia.

TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

Table Page

CHAPTER II

LIST OF FIGURES

Figure Page

CHAPTER II

CHAPTER III

CHAPTER I

INTRODUCTION

This thesis is composed of 2 manuscripts that are formatted for submission to scientific journals. Chapter 2 is formatted for submission to Oecologia, a publication of the International Association for Ecology. Chapter 3 is formatted for submission to Applied Animal Behaviour Science, a publication of the International Society for Applied Ethology.

CHAPTER II

FORAGING BEHAVIOR OF BISON GRAZING A MOSAIC LANDSCAPE CREATED BY A FIRE-GRAZING INTERACTION

Abstract

Many species of large ungulates are known to exhibit sexual segregation at multiple levels. North American Bison (*Bos bison*) exhibit sexual segregation via their diet and habitat level foraging behavior. Mature male bison select a higher proportion of warm-season grasses than do mature female bison. Mature male bison also form independent groups, but mature female bison form mixed groups that include calves and juveniles. Little is known about the patch-level foraging behavior of bison, thus the objective of our study was to investigate the patch-level foraging behavior of bison on a heterogeneous landscape maintained by fire. We describe the patch-level foraging paths of bison in multiple vegetation patches with contrasting structure and composition through 3 seasons. Mature female bison respond to differences in vegetation structure and composition among patch types and seasons by adjusting the velocity and tortuosity of foraging paths. Mature male bison are generally unresponsive to changes in vegetation structure and composition among patches and seasons. These results show that bison do exhibit patch-level segregation. This segregation may result from contrasting nutritional requirements of mature female and mature male bison and differences in the dynamics of mature male bison groups and mixed groups that include mature female bison.

Keywords: Patch-level foraging paths; Sexual segregation; Tallgrass prairie; Landscape heterogeneity

Introduction

Grazing ungulates often live in heterogeneous landscapes where forage resources are unevenly distributed in desirable and undesirable patches. On pre-European North American prairies the variable timing, pattern, and intensity of wildland fires created a heterogeneous distribution of vegetation patches (Kay 1998). Selective grazing of these patches by bison (*Bos bison*) shaped vegetation structure and composition, promoting species diversity and stability (Vinton et al. 1993, Hartnett et al. 1996, Knapp et al. 1999). This interaction of fire and grazing created a shifting mosaic of patches that varied in time since and season of disturbance (Fuhlendorf and Engle 2001).

Large ungulates grazing in mosaic environments make hierarchical foraging decisions (Senft et al. 1987; Bailey et al. 1996). At the smallest level, diet is chosen by bite selection. Feeding site and patch selection occurs at intermediate levels and at the largest levels plant communities, habitat and home range are chosen. These foraging decisions are also made at different temporal scales, seconds for bite selection, minutes-hours for patch selection, days-weeks for habitat scale decisions (Bailey et al. 1996). The mechanisms that drive foraging decisions at different levels may occur independently or be the aggregate result of decisions made at other levels. Decisions may be driven by the forage resource (Bradbury et al. 1996, Wilmhurst et al. 1999, Bergman et al 2000) or based on non-forage factors. Non-forage factors that can influence ungulate grazing pattern are topography (Gillen et al. 1984), thermal environment

(Rittenhouse and Senft 1982, Prescott et al 1994), predation (McNaughton 1984), and social organization (Jarman 1974, Belovsky 1986).

A prominent social structure of many large ungulate herds is sexual segregation. Ungulates often exhibit sexual segregation via their habitat (Jakimchuk et al. 1987, Ginnett and Demment 1997, Coppedge and Shaw 1998) and diet selection (Kie and Bowyer 1999, Post et al 2001). Functional differences in foraging behavior may also create patch-level sexual segregation among ungulates. Sexual segregation by bighorn sheep has been attributed to differences in time budgets and movement patterns of males and females (Ruckstahl 1998). Female bighorn graze longer and travel further during foraging bouts, while males ruminated longer and spent less time grazing and traveling. Sexual segregation in bighorns would be inevitable unless males and females synchronize their grazing and ruminating behaviors. Synchronization and aggregation would lead to lower nutritional status and fitness, outweighing the benefits of group cohesion.

Bison exhibit sexual segregation at the diet and landscape levels. Overall bison show strong diet selectivity for graminoids (Coppedge et al. 1998), however mature males select diets with higher proportions of C4 grasses than do mature females, juveniles, and calves (Post et al. 2001). Groups of mature males spatially segregate from mixed bison groups (mature cows, juveniles, calves) within landscapes by their preference/avoidance of burned patches within and between seasons (Coppedge and Shaw 1998). Less is known about the patch-level foraging behavior of bison, but it is plausible that bison also exhibit patch-level segregation. Understanding multi-scale foraging behavior is necessary to complete our picture of the ecological foraging hierarchy of bison (Shaw 1997) and may provide further insight into the underlying mechanisms that drive sexual segregation in bison. Therefore, the objective of our experiment was to evaluate patch-level foraging behavior of bison. Specifically we describe attributes of the patch-level foraging paths of bison grazing in a heterogeneous environment created by a shifting mosaic of burning. We test the influence of sex-age class, patch type, and season on four attributes of bison foraging paths.

Methods

Study Area and Sampling Period

Field observations of bison foraging behavior were conducted on the Nature Conservancy's Tallgrass Prairie Preserve. The Tallgrass Prairie Preserve is located in northeastern Oklahoma on the southern extension of the Flint Hills region. The Flint Hills are native tallgrass prairie, having escaped cultivation due to shallow soils. Vegetation composition is dominated by *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*, and *Schizachyrium scoparium*. The bison herd on the Tallgrass Prairie Preserve consists of 1535 individuals; 536 mature females, 93 mature males, 345 juvenile females, 192 juvenile males, and 369 calves (pers. comm. R.G. Hamilton, The Nature Conservancy). Due to the absence of large native carnivores, anthropogenic culling is used to simulate predation. The herd resides year-round in a 5800 hectare pasture. Management in the bison pasture attempts to mimic historic conditions, to create a shifting mosaic of disturbance. Multiple patches are burned in the spring and late summer or fall using prescribed fire. The patches created are variable in timing, distribution, and size (Figure 1).

We grouped patches into 5 types based on burn season and time (Table 1). The vegetation structure and composition of these patches is diverse and strongly influenced by grazing, season of fire and interval length since burning (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001). Recently burned patches (0-6 months) are maintained in short structure by frequent grazing, creating grazing lawns (Table 1). Patches burned in fall are maintained as grazing lawns initially, but become dominated by forbs following disturbance. With the removal of grazing pressure these patches begin to transition back to a tallgrass dominated community in several years. Likewise, patches burned in spring favor begin to accumulate litter as grazing pressure shifts to more recently burned patches, releasing the patches to recover towards pre-burn conditions. Undisturbed patches are dominated by warm-season tallgrass species and have the tallest structure and greatest amounts of litter biomass. These contrasting vegetation characteristics present a variable forage source in terms of quality and quantity to bison. Forage in grazing lawn patches is high quality because of nutritious regrowth, but quantity is limited by frequent grazing. In undisturbed patches forage quantity is high, but abundant standing litter limits quality. Forage quality in post-disturbance patches is intermediate, depending on the season of burning and the degree of recovery.

Three sampling periods represent periods of contrast between bison nutritional demand and forage quality and quantity. Data collection was conducted during fall (12-29 October 2001), spring (16 April - 4 May 2002),and summer (16 June-5 July 2002). In fall nutritional demand on mature females is low and high on mature males recovering from stress during rut. In spring nutritional demand on mature females is high due to gestation and lactation (Shaw and Carter 1989). In fall and spring seasons, forage quality is high in grazing lawn patches, but limited by slow growth and frequent grazing. In summer forage quality is high in grazing lawn patches and quantity is not limiting due to peak growth rates by warm season tallgrasses.

Foraging paths

To achieve our objective of determining the effects of season, patch-type, and sex-age class on bison foraging behavior we chose to quantify the patch-level foraging paths of bison. Foraging paths are evidence of decisions that organisms make (With 1994, Nams 1996, Westcott and Graham 2000). Foraging paths may provide insight into the spatial scales at which a grazing herbivore perceives its environment (Ward and Saltz 1994, Etzenhouser et al. 1998, Wallis de Vries et al. 1999). The four foraging path attributes that we use to describe bison foraging behavior are foraging velocity, turning angle, feeding station selection, and tortuosity. We define foraging velocity (m min^{-1}) as the rate of movement by a focal individual while actively grazing (Shipley et al 1996). Feeding station selection (FS min^{-1}) is the rate of feeding stations selected by the focal individual. We define a feeding station as a specific location where grazing occurs without movement of the front feet (Jiang and Hudson 1993). Turning angle is an angle (θ) between -180 and 180, and is the extent of direction change while grazing. The tortuosity of foraging paths is described by fractal dimension (D), which is a mathematical description of complexity (Mandelbrot 1983). Straight lines (or paths) have lower values of D, as lines become more tortuous and complex the value of D increases. D has been used to describe the movement paths of acridid grasshoppers (With 1994), avian frugivores (Westcott and Graham 2000), and small ungulates (Etzenhouser et al. 1998). Movement may be scale dependant or scale independent, changing with habitat structure or complexity (Wiens et al. 1995, Wiens and Milne 1989).

We observed foraging paths during periods of active grazing, morning (0600-1000) and late afternoon or evening (1600-2000). We chose focal individuals at random for observation. The patch type and sex-age class of the focal individual was identified. Observation was conducted during a grazing bout, defined as a string of feeding stations selected uninterrupted by other activities. Observation continued until cessation or interruption of grazing bout. Criteria for interruption included resting, rumination, transition to a new patch, and interaction with other bison (play, fighting, nursing, etc.)

Foraging velocity, turning angle, and tortuosity are derived from XY coordinates of foraging paths. The bearing and range from observer to focal individual was recorded every 2 minutes using a forester's compass and laser rangefinder. Using bearing and range, we reconstructed each foraging path in a spreadsheet program to generate XY coordinates for each 2-minute interval. Feeding station selection was recorded from randomly selected individuals within active grazing bouts, simultaneous with collection of XY coordinates. Tortuosity for each movement path was calculated over multiple spatial scales (1.3-77.2 m) to test the scale-dependence of path tortuosity. All calculations of tortuosity were performed using the program Fractal 3.0 (Nams 1996).

Data Analysis

To test the effect of season, vegetation patch-type, and sex-age class on bison foraging behavior we analyzed foraging path attributes using the PROC MIXED procedure (SAS Institute 1989). Foraging paths less than 8 minutes in duration were excluded for foraging velocity and turning angles, paths less than 20 minutes were excluded for calculation of tortuosity. Because the distribution of turning angles was equal between $+\theta$ and $-\theta$ (right and left turns), we used absolute values of turning angles for analysis. All patches were observed in 3 seasons except for Spring 2002 burn patches, which were only included in spring and summer observations. Tests of effect slices for foraging velocity, feeding station selection, and turning angle were executed for interactions of sex-age class, patch-type, season, and all combinations thereof.

Tests for tortuosity were similarly executed for interactions of sex-age class, patch-type, season, and spatial scale. Spatial scales of tortuosity were reclassified into 3 groups for analysis (small scale < 5 m, intermediate scale = 5-10 m, large scale > 10 m). The small scale is less than mean step sizes (~5 m), thus foraging paths appear linear and values of tortuosity should be low and unaffected by any variable. At the intermediate scale, large ungulates grazing in heterogeneous environments are known to exhibit non-random foraging patterns (Vinton et al. 1993, Wallis De Vries et al. 1999). Because D is calculated on a logarithmic scale, the large scale represents the final 1/3 of data points for D. Sample size was sufficient to analyze all variables for mature females and mature males, data for juvenile females and juvenile males are not included.

Results

Foraging Velocity

Foraging velocity of mature females differed among patch types and seasons, but forage velocity of mature males differed less. Foraging velocity of mature females differed among patch types in 3 seasons of observation (Figure 2). In fall foraging velocity of mature females was more rapid in grazing lawn patches and grass transition patches than in forb transition patches. Foraging velocity in spring was rapid in grass transition patches, slow in forb transition patches. In summer, foraging velocity of mature females was more rapid in recently burned forb transition patches (burned < 6 months ago) than in grazing lawn patches and less recently burned forb transition patches (burned >1 year ago).

Within patches, foraging velocity of mature females changed through seasons, but foraging velocity of mature males remained similar among seasons. Foraging velocity of mature females in grazing lawn patches, grass transition patches, and forb transition patches changed through seasons, but foraging velocities in undisturbed patches were similar among seasons. Foraging velocity in grazing lawn patches declined from fall to summer and increased from fall to summer in forb transition patches.

Turning Angle

Like foraging velocity, turning angle of cows differed among patch types and seasons, but turning angle of bulls differed little. Turning angles of cows differed among spring and summer seasons, but not fall season (Figure 3). In spring turning angles were widest in grazing lawn patches and undisturbed patches, and narrowest in grass transition patches. In summer turning angles of mature females were wider in undisturbed patches than all other patches.

Within patches, turning angles of mature females changed through seasons, turning angles of mature males did not. Turning angles of mature females in undisturbed patches and grass transition patches were similar in fall and spring, increasing in summer. Turning angles of mature females in grazing lawn patches and forb transition patches changed little between seasons.

Feeding station selection rate

Rate of feeding station selection by mature females varied among patches within fall and spring seasons, feeding station selection by mature males varied among patches in all seasons (Figure 4). Feeding station selection by mature females in fall and spring was most rapid in low biomass grazing lawn patches and least rapid in undisturbed patches. Feeding station selection by mature males followed the same pattern as females in the fall, rapid in grazing lawns and slow in undisturbed patches. Contrary to mature females, feeding station selection by mature males in spring was faster in recently burned (< 6 months) forb transition patches than all other patches. Feeding station selection by mature males in summer was most rapid in recently burned forb transition patches, least rapid in grass transition patches and undisturbed patches.

Within grass transition patches and undisturbed patches, feeding station selection rate by both mature females and mature males remained similar in fall and spring, but declined into summer. Within forb transition patches and grazing lawn patches, feeding station selection by mature females was more rapid in spring than in fall or summer, but mature males differed little among seasons.

Path Tortuosity

Results showed that at small (< 5 m) and intermediate (5-10 m) scales tortuosity of mature female and mature male bison foraging paths in all seasons and patches did not differ. Differences of path tortuosity did occur at large scales amongst seasons and patches. Tortuosity of mature bison female foraging paths varied among patches in spring and summer seasons (Figure 5). In spring tortuosity of mature females was greater in grazing lawn patches than other patches. Mature female tortuosity in summer was greater in grazing lawn patches and grass transition patches than other patches. Tortuosity of mature male foraging paths varied among patches in summer, being greatest in grazing lawn patches, intermediate in forb transition patches, and least in grass transition patches and undisturbed patches.

Among seasons, tortuosity of mature female bison foraging paths changed little in grazing lawn patches and undisturbed patches, but did change in forb transition patches and grass transition patches. Unlike mature females, tortuosity of mature male foraging paths was steady among seasons in forb transition patches and differed among seasons in grazing lawn patches and undisturbed patches.

Discussion

Our results confirm that mature bison females and mature bison males exhibit patch-level segregation via their foraging behavior. Females and males responded to vegetation patch types differently within seasons and among seasons. Differences in forage quality and quantity may explain sexual segregation by mature male and mature female bison. Females in all seasons responded to patch type by adjusting foraging velocity and/or path tortuosity (Figure 6). Females reduced foraging velocity in forb transition patches in fall season, possibly searching for highly preferred cool-season graminoids (Coppedge et al. 1998) that are more available in recently disturbed patches (i.e. grazing lawns and forb transition patches). During spring, the period of highest nutritional demand (Shaw and Carter 1989), mature females increased path tortuosity in high quality grazing lawn patches. Summer is the period of maximum forage growth and quality and mature females responded to increased forage biomass by reducing foraging velocity in all patch types except forb transition patches. In contrast to mature females, mature males exhibited similar foraging velocity regardless of season or patch type, and similar path tortuosity in all patches in both fall and spring (Figure 7). Because of their large body size, mature males are able to more efficiently utilize low quality forage (Post et al. 2001), thus nutritional demand may be such that it is not necessary for them to continuously adapt foraging behavior to changing forage characteristics.

Another explanation for the patch-level foraging behavior differences between mature male and mature female bison are the social interactions (or lack thereof) within distinct male groups and mixed female groups. Mature male bison graze in small, loosely associated groups, whereas mixed groups of mature females and juveniles tend to graze close together in large cohesive herds (Schuler 2002). Foraging paths of males were in general more tortuous than females across all patches and seasons. Because dominant mature females compete for high quality forage (Lott and Galland 1987) and aggressive behavior among individuals increases with group size and proximity (Rind and Phillips 1999), mature females may adjust foraging paths to avoid conflict with adjacent group members. In contrast, mature males in small, loose groups infrequently interact and are free to forage within a patch without conspecific interference.

Mature female bison in mixed groups also possibly are employing a time-minimizing foraging strategy. Yearling bison grazing variable patches of sedges in northern Canada graze to minimize time spent foraging rather than maximize energy intake during a foraging bout (Bergman et al. 2001). Although this strategy conflicts with the classical assumption of maximization of energy intake (Stephens and Krebs 1986), mature female bison grazing on the southern Great Plains may take a similar approach. In large mixed groups a few dominant individuals determine herd movements (McHugh 1972), so most individuals may graze to minimize foraging time because patch residence and inter-patch movement is unpredictable.

Differences in the patch-level foraging behavior of mature male and mature female bison lend support to the functional differences hypothesis for sexual segregation. As we have demonstrated, foraging paths of mature female and male bison differ within distinct vegetation patches within a landscape. For example, while foraging in a grazing lawn patch in the summer, mature females grazing slowly in a linear pattern would be unlikely to remain in a cohesive group with mature males grazing the same patch rapidly in a tortuous pattern (Figures 6 and 7, top right path). Synchronization would require one or both sexes to adjust their patch-level foraging behavior, possibly reducing fitness (Ruckstahl and Neuhaus 2002).

Sexual segregation by bison at multiple spatial scales may have important ecological implications for tallgrass prairie managed with bison and fire. Given bison are a keystone species (Knapp et al. 1999), then differences between mature males and females in diet selection, patch-level foraging behavior, and habitat selection may influence the distribution of vegetation biomass (Coppedge et al 1998), plant species composition (Day and Detling 1990), and diversity

(Steinauer and Collins 1995, Knapp et al. 1999). Furthermore, given sexual segregation, additional bison-mitigated disturbances such as wallowing, rubbing, and urine/fecal deposition are likely distributed differently by mature male and mature female bison.

Acknowledgements

We thank the USDA National Research Initiative Competitive Grants Program for their support in funding this project and The Nature Conservancy for access and support during data collection on the Tallgrass Prairie Preserve. This article is published with the approval of the director, Oklahoma Agricultural Experiment Station.

Literature Cited

Bailey DW et al. (1996) Mechanisms that result in large herbivore grazing distribution patterns. Journal of Rangeland Management 49:386-400

Bergman CM, Fryxell JM, Gates CC, Fortin D (2001) Ungulate foraging strategies: energy maximizing or time minimizing? Journal of Animal Ecology 70:289-300

Bradbury JW, Vehrencamp SL, Clifton KE, Clifton LM (1996) The relationship between bite rate and local forage abundance in wild Thomson's gazelles. Ecology 77:2237-2255

Coppedge BR, Engle DM, Toepfer CS, Shaw JH (1998a) Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. Plant Ecology 139:235-246

Coppedge BR, Leslie DM, Shaw JH (1998b) Botanical composition of bison diets on tallgrass prairie in Oklahoma. Journal of Range Management 51:379-382

Coppedge BR, Shaw JH (1998) Bison grazing patterns on seasonally burned tallgrass prairie. Journal of Range Management 51:258-264

Day TA, Detling JK (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180-188

Etzenhouser MJ, Owens MK, Spalinger DE, Murden SB (1998) Foraging behavior of browsing ruminants in a heterogeneous landscape. Landscape Ecology 13:55-64

Gillen RL, Krueger WC, Miller RF (1984) Cattle Distribution on Mountain Rangeland in Northeastern Oregon. Journal of Range Management 37:549-553

Ginnett TF, Demment MW (1997) Sex differences in giraffe foraging behavior at two spatial scales. Oecologia 110:291-300

Hartnett DC, Hickman KR, Walter LEF (1996) Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management 49:413-420

Jakimchuk RD, Ferguson SH, Sopuck LG (1987) Differential Habitat Use and Sexual Segregation in the Central Arctic Caribou Herd. Canadian Journal of Zoology-Revue Canadienne De Zoologie 65:534-541

Jarman P (1974) The social organisation of antilope in relation to their ecology. Behaviour 58:215-267

Jiang Z, Hudson RJ (1993) Optimal grazing of wapiti on grassland: patch and feeding station departure rules. Evolutionary Ecology 7:488-498

Kay CE (1998) Are ecosystems structured from the top-down or bottom-up: a new look at an old debate. Wildlife Society Bulletin 26:484-498

Kie JG, Bowyer RT (1999) Sexual segregation in white-tailed deer: Density-dependent changes in use of space, habitat selection, and dietary niche. Journal of Mammalogy 80:1004-1020

Knapp AK et al. (1999) The keystone role of bison in North American Tallgrass Prairie. Bioscience 49:39-50

Lott DF (1991) American Bison Socioecology. Applied Animal Behaviour Science 29:135-145

Lott DF, Galland JC (1987) Body mass as a factor influencing dominance status in American bison cows. Journal of Mammalogy 68:683-685

Mandelbrot BB (1983) The fractal geometry of nature. W.H. Freeman, New York

McHugh T (1972) The time of the buffalo. Alfred A. Knopf, New York

McNaughton SJ (1984) Grazing Lawns - Animals in Herds, Plant Form, and Coevolution. American Naturalist 124:863-886

Nams VO (1996) The VFractal: a new estimator for fractal dimension of animal movement. Landscape Ecology 11:287-297

Post DM, Armbrust TS, Horne EA, Goheen JR (2001) Sexual segregation results in differences in content and quality of bison (Bos bison) diets. Journal of Mammalogy 82:407-413

Prescott ML, Havstad KM, Olsonrutz KM, Ayers EL, Petersen MK (1994) Grazing Behavior of Free-Ranging Beef-Cows to Initial and Prolonged Exposure to Fluctuating Thermal Environments. Applied Animal Behaviour Science 39:103-113

Rind MI, Phillips CJC (1999) The effects of group size on the ingestive and social behaviour of grazing dairy cows. Animal Science 68:589-596

Rittenhouse LR, Senft RL (1982) Effects of daily weather flucuations on the grazing behavior of cattle. In: Western Section, American Society of Animal Science, vol. 33

Ruckstuhl KE (1998) Foraging behaviour and sexual segregation in bighorn sheep. Animal Behaviour 56:99-106

Ruckstuhl KE, Neuhaus P (2002) Sexual segregation in ungulates: a comparative test of three hypotheses. Biological Reviews 77:77-96

SAS Institute Inc. 1989. SAS/STAT® user's guide, version 6, fourth edition, volume2. SAS Institute, Inc., Cary, North Carolina.

Schuler KL (2002) Seasonal variation in bison distribution and group behavior on Oklahoma Tallgrass Prairie. In. Oklahoma State University

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. Bioscience 37:789-799

Shaw JH (1997) Bison ecology-what we do and do not know. In: Irby LR, Knight JE (eds) International Symposium on Bison Ecology and Management in North America. Montana State University, Bozeman, Montana, pp 113-120

Shaw JH, Carter TS (1989) Calving patterns among American Bison. Journal of Wildlife Management 53:896-898

Shipley LA, Spalinger DE, Gross JE, Hobbs NT, Wunder BA (1996) The dynamics and scaling of foraging velocity and encounter rate in mammalian herbivores. Functional Ecology 10:234-244

Steinauer EM, Collins SL (1995) Effects of Urine Deposition on Small-Scale Patch Structure in Prairie Vegetation. Ecology 76:1195-1205

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, New Jersey

Towne EG (1999) Bison performance and productivity on tallgrass prairie. Southwestern Naturalist 44:361-366

Vinton MA, Hartnett DC, Finck EJ, Briggs JM (1993) Interactive effects of fire, bison grazing, and plant comunity composition in tallgrass prairie. American Midland Naturalist 129:10-18

WallisDeVries MF, Laca EA, Demment MW (1999) The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121:355-363

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

Westcott DA, Graham DL (2000) Patterns of movement and seed dispersal of a tropical frugivore. Oecologia 122:249-257

Wiens JA, Crist TO, With KA, Milne BT (1995) Fractal patterns of insect movement in microlandscape mosaics. Ecology 76:663-666

Wiens JA, Milne BT (1989) Scaling of 'landscape' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology 3:87-96

Wilmshurst JF, Fryxell JM, Farm BP, Sinclair ARE, Henschel CP (1999) Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1223-1232

With KA (1994) Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns. Functional Ecology 8:477-485

Table 1. General vegetation characteristics of five patch types on a fire managed tallgrass prairie grazed by free-ranging bison.

	Sampling Period		
Patch burn type	Fall 2001	Spring 2002	Summer 2002
Unburned	Undisturbed	Undisturbed	Undisturbed
Fall 2000	Forb transition	Forb transition	Forb transition
Spring 2001	Grass transition	Grass transition	Grass transition
Fall 2001	Grazing lawn	Forb transition	Forb transition
Spring 2002	n/a	Grazing lawn	Grazing lawn

Fig.1 Distribution of five vegetation patch types in Tallgrass Prairie Preserve bison pasture, Osage Co., Oklahoma. Patches are defined by time since burning and season of fire.

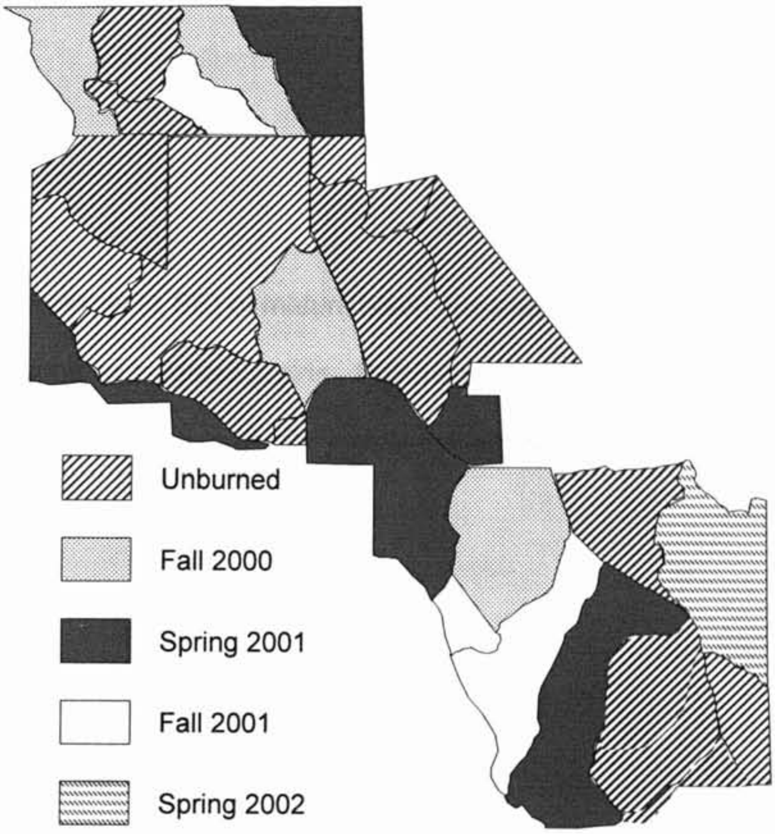

Unburned
Fall 2000
Spring 2001
Fall 2001
Spring 2002

Fig.2 Foraging velocity (± SE) of mature bison females and males grazing five distinct patch types on tallgrass prairie. Patch level foraging velocity differs within season at $p<0.05$ (**), $p<0.10$ (*), or is not significant (ns).

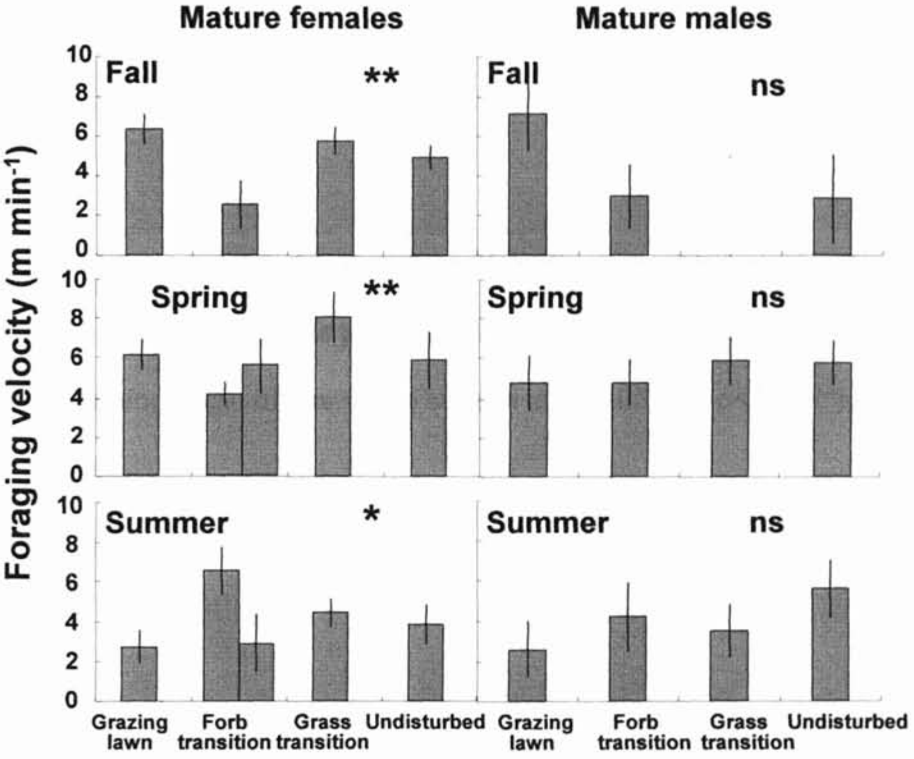

Mature females
Mature males
Foraging velocity (m min-1)
Fall
**
Fall
ns
Spring
**
Spring
ns
Summer
*
Summer
ns
0
2
4
6
8
10
Grazing lawn
Forb transition
Grass transition
Undisturbed
Grazing lawn
Forb transition
Grass transition
Undisturbed

Fig.3 Turning angle (± SE) of mature bison females and males grazing five distinct patch types on tallgrass prairie during fall, spring, and summer seasons. Patch level turning angle differs within season at $p<0.05$ (**), $p<0.10$ (*), or is not significant (ns).

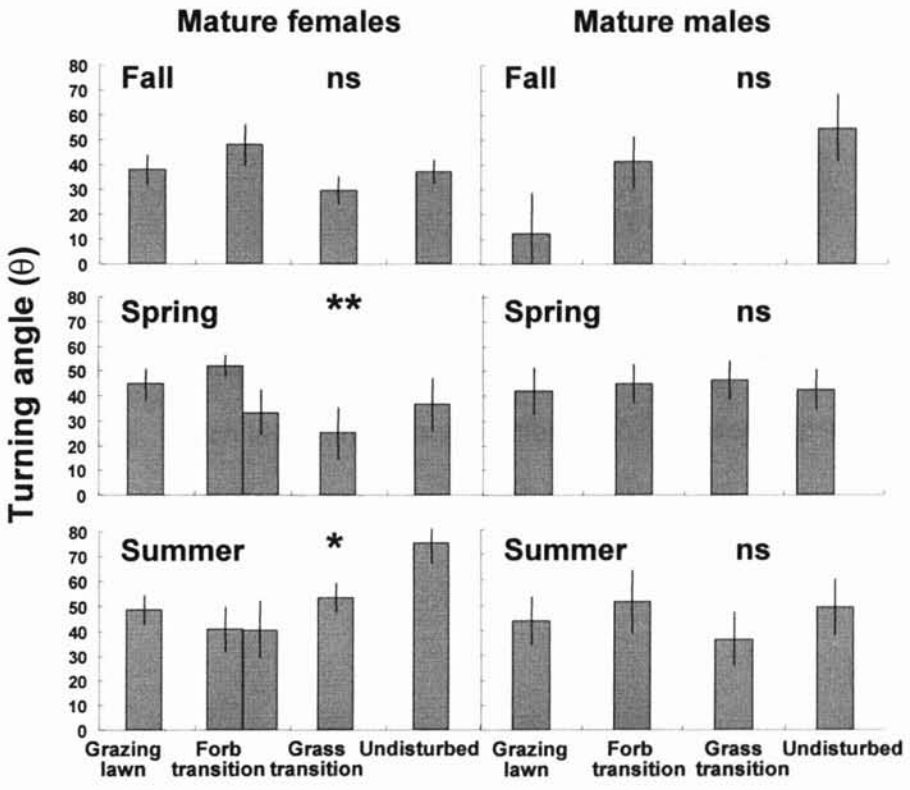

Mature females
Mature males
Turning angle (θ)
Fall
ns
Fall
ns
Spring
**
Spring
ns
Summer
*
Summer
ns
0
10
20
30
40
50
60
70
80
Grazing lawn
Forb transition
Grass transition
Undisturbed
Grazing lawn
Forb transition
Grass transition
Undisturbed

Fig.4 Rate of feeding station selection (± SE) of mature bison females and males grazing five distinct patch types on tallgrass prairie during fall, spring, and summer seasons. Patch level turning angle differs within season at $p<0.05$ (**), $p<0.10$ (*), or is not significant (ns).

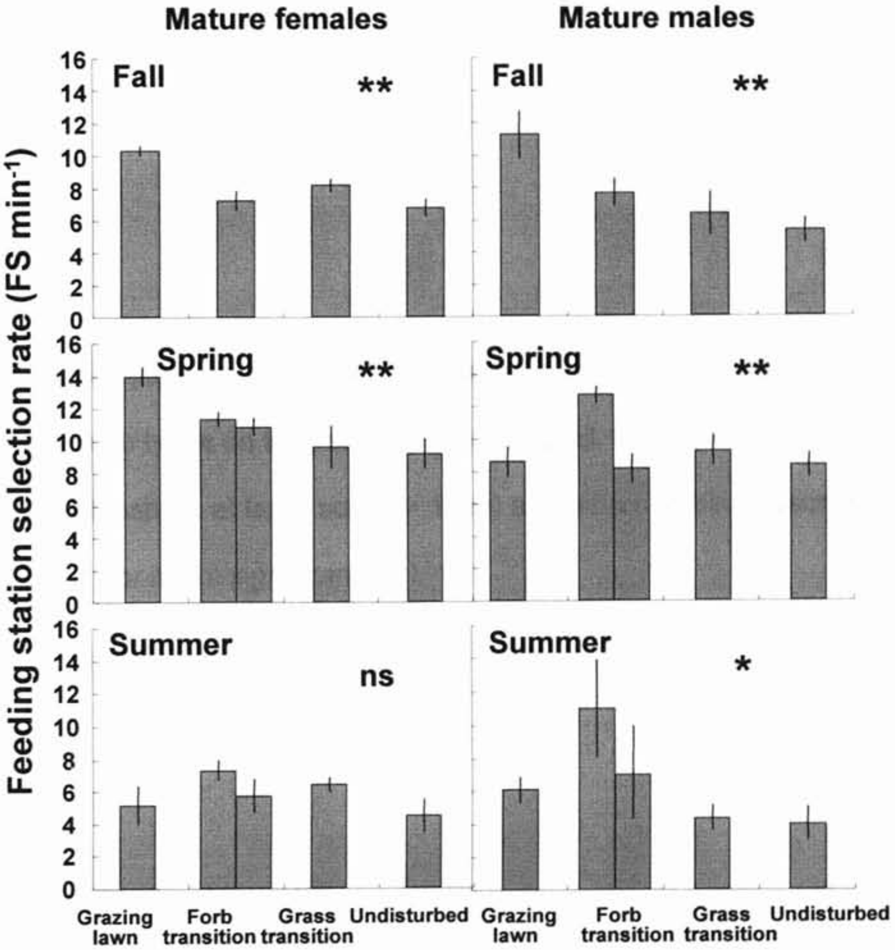

Mature females
Mature males
Feeding station selection rate (FS min^{-1})
Fall
**
Fall
**
Spring
**
Spring
**
Summer
ns
Summer
*
0
2
4
6
8
10
12
14
16
Grazing lawn
Forb transition
Grass transition
Undisturbed
Grazing lawn
Forb transition
Grass transition
Undisturbed

Fig.5 Tortuosity (D) of foraging paths of mature bison females and males grazing five distinct patch types on tallgrass prairie during fall, spring, and summer seasons. Tortuosity is at large scale (> 10 m) and differs within season at $p<0.05$ (**), $p<0.10$ (*), or is not significant (ns).

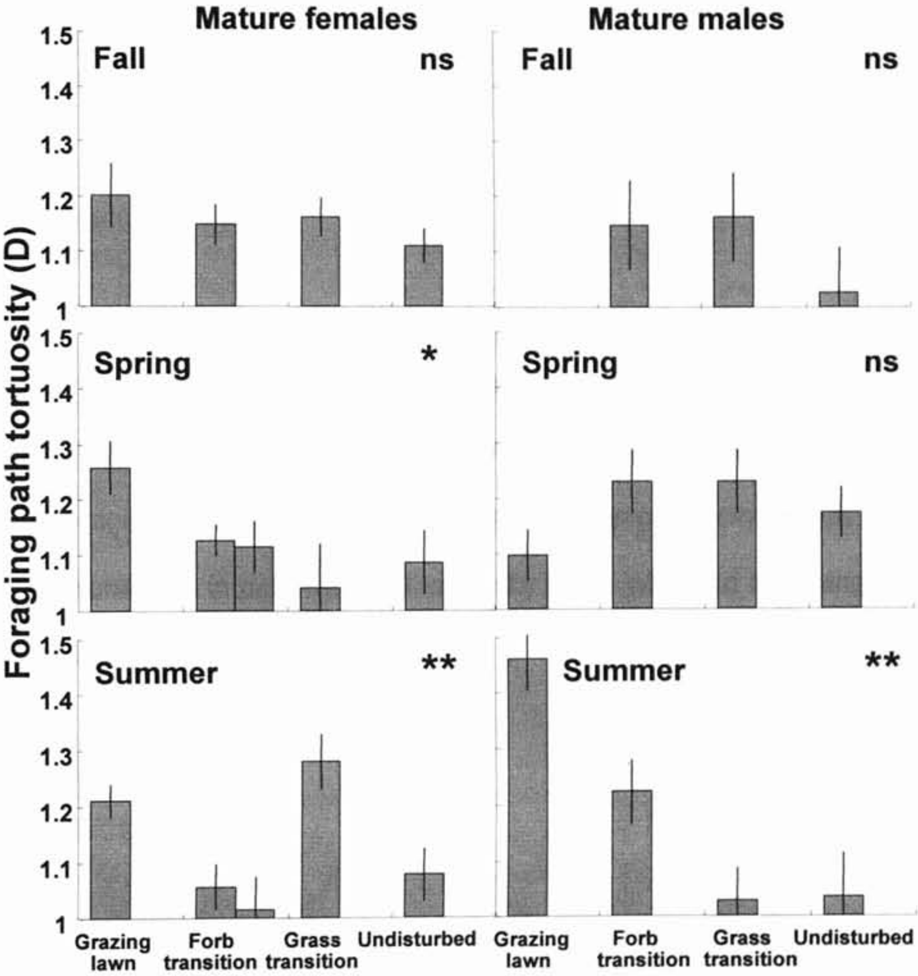

Mature females
Mature males
Fall
ns
Fall
ns
Spring
*
Spring
ns
Summer
**
Summer
**
Foraging path tortuosity (D)
1.5
1.4
1.3
1.2
1.1
1
Grazing lawn
Forb transition
Grass transition
Undisturbed
Grazing lawn
Forb transition
Grass transition
Undisturbed

Fig 6. Graphical illustration of the effect of vegetation patch type on foraging paths of mature female bison. Paths displayed are actual paths chosen to represent foraging velocity and path tortuosity. Foraging velocity (FV) is indicated by changes in path size and tortuosity (D) is indicated by changes in foraging path shape.

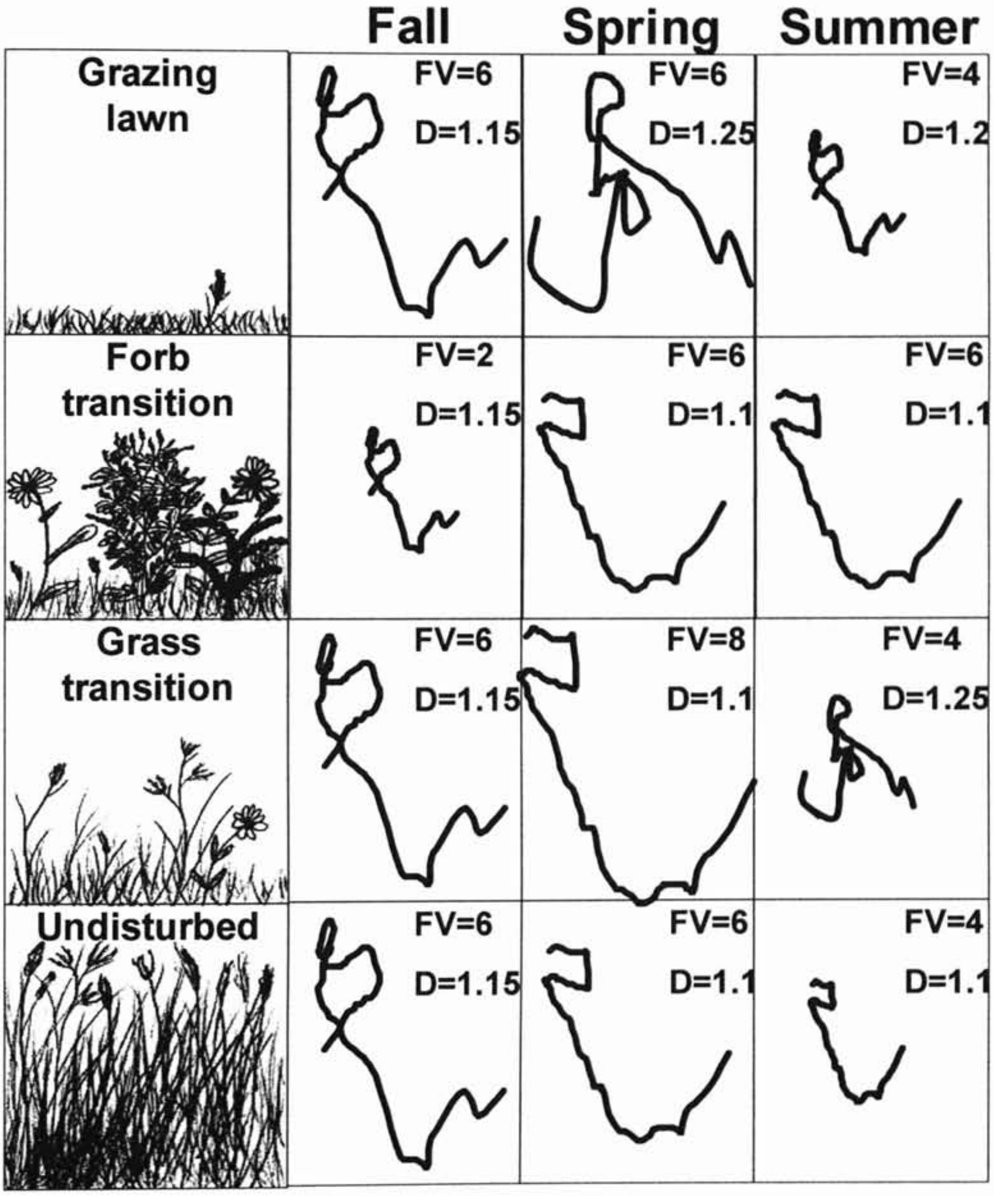
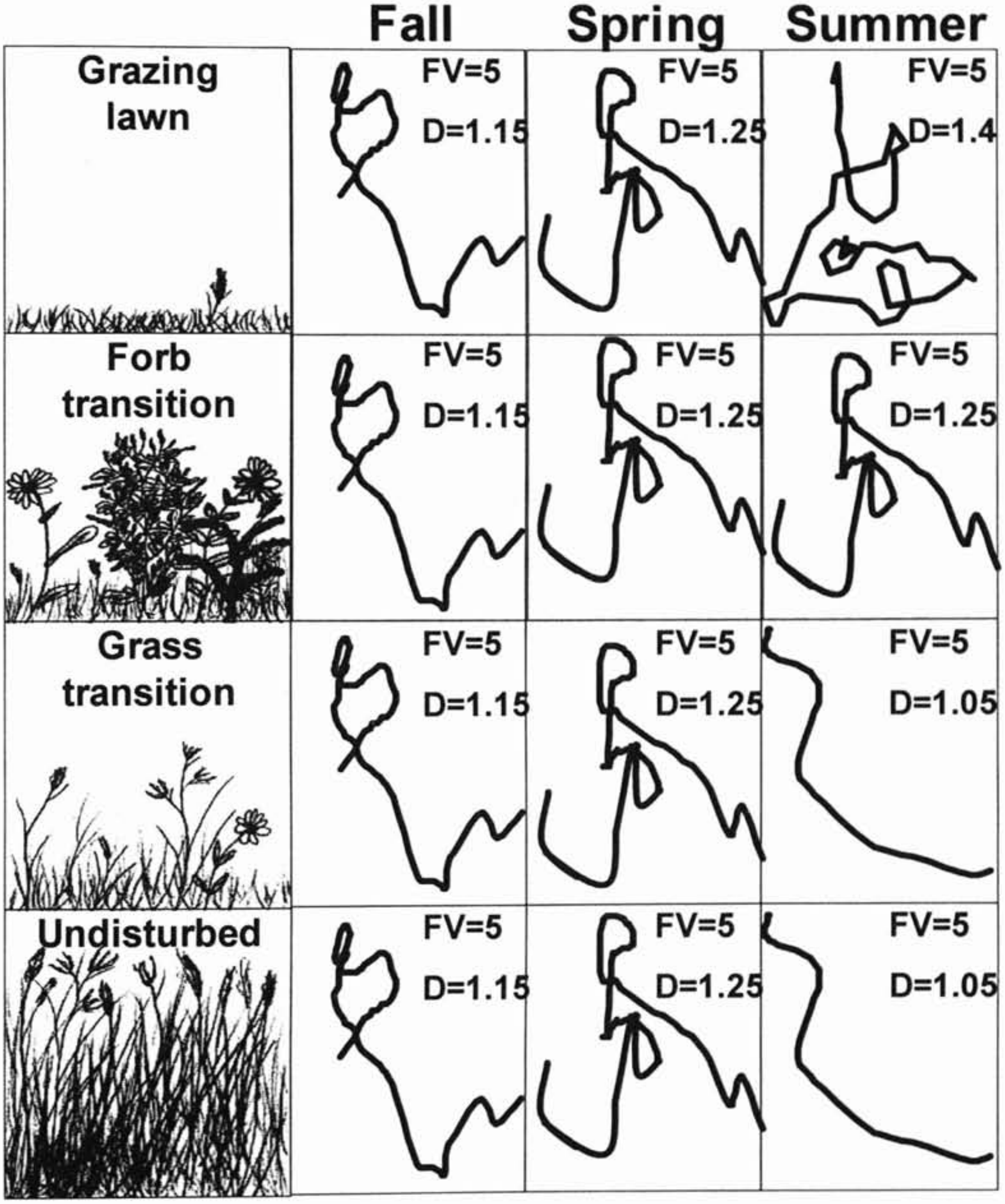

Fall
Spring
Summer
Grazing lawn
FV=6
D=1.15
FV=6
D=1.25
FV=4
D=1.2
Forb transition
FV=2
D=1.15
FV=6
D=1.1
FV=6
D=1.1
Grass transition
FV=6
D=1.15
FV=8
D=1.1
FV=4
D=1.25
Undisturbed
FV=6
D=1.15
FV=6
D=1.1
FV=4
D=1.1

Fig 7. Graphical illustration of the effect of vegetation patch type on foraging paths of mature male bison. Paths displayed are actual paths chosen to represent foraging velocity and path tortuosity. Foraging velocity is indicated by changes in path 'size' and tortuosity is indicated by path shape.


Fall
Spring
Summer
Grazing lawn
FV=5
D=1.15
FV=5
D=1.25
FV=5
D=1.4
Forb transition
FV=5
D=1.15
FV=5
D=1.25
FV=5
D=1.25
Grass transition
FV=5
D=1.15
FV=5
D=1.25
FV=5
D=1.05
Undisturbed
FV=5
D=1.15
FV=5
D=1.25
FV=5
D=1.05

CHAPTER III

INFLUENCE OF A FIRE-GRAZING INTERACTION ON THE PATCH-LEVEL FORAGING BEHAVIOUR OF YEARLING CATTLE

Abstract

Large herbivores that encounter heterogeneous forage resources are known to adapt their foraging behavior at multiple spatial and temporal scales. By implementing a patch-burning land management scheme, heterogeneous pastures were created on tallgrass prairie in Osage County, Oklahoma. We used foraging paths to describe the differences in cattle foraging behavior in heterogeneous patch-burn pastures and homogeneous complete-burn pastures. Data were collected in June 2001 and June 2002. Foraging velocity, turning angles, rate of feeding station selection, and foraging path tortuosity were the variables we used to describe foraging behavior. Foraging velocity was not influenced by year or pasture treatment. Turning angles and path tortuosity suggest that cattle in complete-burn pastures responded to small-scale heterogeneity in forage structure despite the homogeneous fire treatment applied to these pastures. Cattle in patch-burn pastures grazed almost exclusively in recent burn patches, and their turning angles and path tortuosity suggest that recent burn patches were homogeneous by comparison.

1. Introduction

Patch-burning has been proposed as a new management paradigm for management of disturbance in the tallgrass prairie to create heterogeneous landscapes (Fuhlendorf & Engle, 2001). The motivation for this proposed model is that traditional livestock management focuses on applying uniform grazing disturbance across prairie landscapes that evolved as heterogeneous environments. Research and management of grazing by domestic herbivores has focused traditionally on a goal of uniform grazing distribution. Spreading grazing disturbance evenly throughout a management unit is a management strategy that conflicts with the evolutionary history of tallgrass prairie. Prior to European settlement, fire and grazing by large herbivores interacted to create a heterogeneous prairie landscape where mosaic fires burned patches and large herbivores selectively grazed burned patches.

Large herbivores like cattle that graze in a heterogeneous environment must make foraging decisions at multiple spatial and temporal scales (Senft et al., 1987). Cattle respond to heterogeneous environments by adjusting foraging behavior at some or all scales. Cattle adjust bite rate and step rate to compensate for changes in small scale forage availability and distribution (Chacon & Stobbs, 1976; Scarnecchia et al., 1985; Ginnett et al., 1999). Cattle faced with heterogeneous distribution of resources at larger scales alter their daily feeding patches and habitat selection (WallisDeVries & Schippers, 1994; Bailey et al., 1989; Gillen et al., 1984). Therefore, herbivores facing contrasting values of forage quality or quantity at a given scale are expected to exhibit observable foraging behavior adjustments at that scale (Hobbs, 1999). Such adaptations to vegetation heterogeneity by a herbivore can increase or decrease the pre-existing heterogeneity (Adler et al., 2001). However, our knowledge of foraging behavior and pattern is limited in heterogeneous environments (Vavra & Ganskopp, 1998), like those created by a patch-burning management scheme. Therefore, the objective of our experiment was to compare the patch-level foraging behavior of cattle grazing in traditional, homogeneous burn pastures to the foraging behavior of cattle grazing patch-burned, heterogeneous pastures. Specifically we use patch-level foraging paths to test the effects of a patch-burn management scheme on cattle foraging behavior.

2. Methods

2.1. Study Area

Field observations of cattle foraging behavior were conducted on the Nature Conservancy's Tallgrass Prairie Preserve. The Tallgrass Prairie Preserve is located in northeastern Oklahoma on the southern extension of the Flint Hills region. The Flint Hills are native tallgrass prairie having escaped cultivation due to shallow soils. Vegetation composition is dominated by *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*, and *Schizachyrium scoparium* (Coppedge et al., 1998). Data were collected in summer 2001 (12-28 June) and summer 2002 (15 June-4 July). Mean annual precipitation is 877 mm with 70%

occurring during the growing season from April to September (Bourlier et al., 1979).

The study pastures for this experiment are part of a continuing research project evaluating the effects of vegetation heterogeneity in tallgrass prairie (see Fuhlendorf and Engle 2001). Four pastures, area ranging 444-1117 ha, were included in our experiment (2 complete-burn and 2 patch-burn pastures). Complete-burn pastures were burned entirely in spring of 2001 and 2002, following traditional management practice. Patch-burn pastures were patch-burned to create a heterogeneous landscape in 2001 and 2002. Permanent markers delineate six patches in each patch-burn pasture. Each fall and spring one patch is burned, thus one-third of each pasture is burned every year. Every successive year the burning treatment shifts to patches unburned for 2 years, creating a 3-year fire-return interval. Stocking rate in 2001 in all pastures was 1.3 ha head^{-1}. Following a growing-season drought in 2001, stocking rate in 2002 was decreased to 1.6 ha head^{-1}.

The vegetation structure in patch-burn pastures is heterogeneous at the pasture scale (Fig.1) because of the contrasts among recently burned patches and unburned patches (W.C. Harrell, unpub.). Because cattle in patch-burn pastures avoid unburned patches that have abundant litter and graze almost exclusively in recently burned patches, recently burned patches have short structure that is maintained by frequent grazing (i.e. grazing lawns)(Fig.2). Repeated grazing and heavy stocking pressure maintain this vegetation structure despite rapid rates of growth by warm-season tallgrasses. This causes patch-burn pastures to be homogeneous at a small scale (Fig.1). In complete-burn pastures annual spring burning removes all litter, creating homogeneous vegetation structure at a large pasture scale (Fig. 1). Unlike cattle in patch-burn pastures, cattle in complete-burn pastures evenly distribute grazing pressure across the pasture. Even distribution and the rapid growth of warm-season tallgrasses allows vegetation growth to exceed consumption by cattle, so vegetation in complete-burn pastures has taller structure (Fig.2).

2.2. Foraging paths

To test the effects of a patch-burn management scheme on cattle foraging behavior we quantified the patch-level foraging paths of cattle. Foraging paths are evidence of decisions that organisms make (With, 1994; Westcott & Graham, 2000; Nams, 1996). Foraging paths may provide insight into the spatial scales at which a grazing herbivore perceives its environment (WallisDeVries et al., 1999; Ward & Saltz, 1994; Etzenhouser et al., 1998). The four attributes that we use to describe foraging paths are foraging velocity, turning angle, feeding station selection, and tortuosity. We define foraging velocity (m min^{-1}) as the rate of movement by a focal individual while actively grazing (Fig.3)(Shipley et al., 1996). Feeding station selection (FS min^{-1}) is the rate of feeding stations selected by the focal individual. We define a feeding station as a specific location where grazing occurs without movement of the front feet (WallisDeVries et al., 1999). Turning angle is an angle (θ) between -180 and 180, and is the extent of direction change while grazing. The tortuosity of foraging paths is described by fractal dimension (D), which is a mathematical description of complexity (Mandelbrot, 1983). Straight lines (or paths) have lower values of D (Fig. 3), as lines become more tortuous and complex the value of D increases. D has been used to describe the movement paths of acridid grasshoppers (With, 1994), avian frugivores (Westcott & Graham, 2000), and small ungulates (Etzenhouser et al., 1998). Differences in foraging path complexity may indicate changes in the spatial distribution of forage resources or habitat structure (Wiens & Milne, 1989; Wiens et al., 1995). Path complexity may be scale dependant or scale independent.

We observed foraging paths during periods of active grazing, morning and late afternoon or evening and we chose focal individuals at random for observation. Observation was conducted during a grazing bout, defined as a string of feeding stations selected uninterrupted by other activities. Observation continued until cessation or interruption of grazing bout. Criteria for interruption included resting, rumination, transition to a new patch, and interaction with other bison (play, fighting, nursing, etc.). The bearing and range from observer to focal individual was recorded every 2 minutes using a forester's compass and laser rangefinder. Using bearing and range we reconstructed each foraging path in a spreadsheet program to generate XY coordinates for each 2-minute interval. Feeding station selection was also recorded from randomly selected individuals. D for each movement path was calculated over multiple spatial scales (1.3-77.2

m) to test the scale-dependence of path tortuosity. All calculations of D were performed using the program Fractal 3.0 (Nams, 1996).

2.3. Data Analysis

We used the PROC MIXED procedure (SAS Institute 1989) to test the effect of homogeneous complete-burn pastures and heterogeneous patch-burn pastures on cattle foraging path attributes. Foraging paths less than 8 minutes in duration were excluded for foraging velocity and turning angles and paths less than 20 minutes were excluded for calculation of D. Because the distribution of turning angles was equal between $+\theta$ and $-\theta$ (right and left turns), we used the absolute values of turning angles for analysis. Spatial scales of tortuosity were reclassified into 3 groups for analysis (small scale < 5 m, intermediate scale = 5-10 m, large scale > 10 m). The small scale is less than the mean movement interval every 2 minutes (~5 m), thus foraging paths appear linear and values of tortuosity should be low and unaffected by any variables. At the intermediate scale, large ungulates grazing in heterogeneous environments are known to exhibit non-random foraging patterns (WallisDeVries et al., 1999; Vinton et al., 1993) so treatment effects should be detectable. Because D is calculated on a logarithmic scale, the large scale represents the final 1/3 of data points for D. Tests of significance for foraging velocity, feeding station selection, and turning angle were executed for interactions of all combinations of treatment, season, and year. Similar tests were executed for interactions of treatment, season, year, and spatial scale.

3. Results

Cattle adjusted foraging paths to pasture treatment and year by altering their turning angles, rate of feeding station selection, and path tortuosity. Results for cattle grazing in patch-burn pastures are from only recent burn patches within those pastures because cattle grazed almost exclusively in recent burn patches.

Foraging velocity was not affected by treatment (p=0.1481) or year (p=0.5245) (Fig.4). Turning angle of yearling cattle was influenced by the effects of year and treatment (Fig.5), but not by an interaction of year and treatment. Turning angle in patch-burn pastures was narrower than in complete-burn pastures (p=0.0123). Turning angle in 2001 was wider than in 2002 (p=0.0002).

There was an interaction between treatment and year (p<0.0001) that influenced rate of feeding station selection by yearling cattle. In 2001, feeding station selection was more rapid in complete-burn pastures than patch-burn pastures (Fig.6). In 2002 rate of feeding station selection was more rapid in patch-burn pastures than in complete-burn pastures.

At small (<5 m) and intermediate (5-10 m) spatial scales, foraging path tortuosity increased linearly with spatial scale (p<0.0001) with no relationships to treatment or year. At the large scale (>10 m), foraging path tortuosity of yearling cattle responded to an interaction between treatment and year (p=0.0506) (Fig.7). Cattle foraging paths in the complete-burn pastures in 2001 were much more tortuous than paths in patch-burn pastures in 2001 and 2002 or the complete-burn pastures in 2002.

4. Discussion

The feedback mechanism that exists between grazing behavior and the structure and spatial distribution of forage is well documented (McNaughton, 1984). Grazing at the patch-level may increase or decrease forage heterogeneity depending on stocking pressure (Fuhlendorf & Smeins, 1999). Within patches, structural heterogeneity was generally low, but greater in patch-burn pastures than in complete-burn pastures (Fig.1). Cattle did not alter foraging velocity in response to changes in forage structure. Even though vegetation height differed among years and treatments, it may not have limited intake. In heterogeneous grass swards intake is not limited until vegetation is less than 3-4 cm (Ginnett et al., 1999). Forage in our pastures was never less than 7 cm, thus cattle were able to maintain an optimum intake rate, despite altering turning angle and path tortuosity.

Foraging path tortuosity increases with increasing heterogeneity (Wiens et al., 1995; With et al., 1999; Nams, 1996) and foraging path tortuosity in our study was consistent with this prediction in patch-burn pastures in both years and in complete-burn pastures in 2002. These pastures were relatively homogeneous within patches, and cattle responded with foraging paths that had low tortuosity probably because no benefit was gained by additional searching in a homogenous resource (Ward & Saltz, 1994; Wiens & Milne, 1989). In contrast, foraging paths in complete-burn pastures in 2001 were much more tortuous suggesting a complex forage structure present at a smaller scale.

The difference between turning angles of cattle also provides evidence for the presence of small-scale forage structure in complete-burn pastures. Turning angles in patch-burn pastures were narrower than in complete-burn pastures, suggesting that cattle in complete-burn pastures were more likely to remain in small, local foraging areas.

Other studies in grasslands have shown that small-scale grazing lawns occur within structurally homogeneous pastures (Ring et al., 1985) and that large herbivores preferentially graze these small-scale lawns (Vinton et al., 1993). The size and distribution of these small-scale grazing lawns greatly depends on stocking pressure. As stocking pressure decreases, these small-scale lawns are smaller and less easily detected (Cid & Brizuela, 1998). The presence of small-scale grazing patches explains the patterns of foraging behavior that we observed. It would be beneficial for cattle to create and maintain small-scale grazing lawns in complete-burn pastures where the rapid growth by warm-season tallgrasses exceeds consumption. Thus cattle create small-scale heterogeneity and are able to select recent regrowth in grazing lawns that is highly preferred for digestibility and leaf tissue (McNaughton, 1984). In contrast, entire recent burn patches in patch-burn pastures are effectively maintained as grazing lawns because all grazing pressure is focused on one-third of the pasture and therefore these patches are relatively homogeneous.

5. Conclusions

Understanding foraging behavior responses to multi-scale heterogeneity is critical to predicting the distribution of herbivory effects, particularly in ecosystems like tallgrass prairie where the fire-grazing interaction is a fundamental process. The spatial distribution of tallgrass prairie vegetation structure has important conservation and management implications (Fuhlendorf & Engle, 2001). For example, grassland-obilgate birds, which are rapidly declining, are particularly sensitive to changes in structural heterogeneity that may be influenced by herbivory (Wiens, 1974). Therefore understanding the positive and negative relationships between vegetation structures and foraging behavior of large herbivores at multiple spatial and temporal scales on tallgrass prairie is essential.

6. Literature Cited

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

Bailey, D. W., Rittenhouse, L. R., Hart, R. H., Swift, D. M. & Richards, R. W. 1989. Association of relative food availabilities and location by cattle. *Journal of Rangeland Management*, **42,** 480-482.

Bourlier, B. G., Nichols, J. D., Ringwald, W. J., Workman, P. J. & Clemmons, S. 1979. *Soil survey of Osage County, Oklahoma.*: USDA-SCS.

5. Conclusions

Understanding foraging behavior responses to multi-scale heterogeneity is critical to predicting the distribution of herbivory effects, particularly in ecosystems like tallgrass prairie where the fire-grazing interaction is a fundamental process. The spatial distribution of tallgrass prairie vegetation structure has important conservation and management implications (Fuhlendorf & Engle, 2001). For example, grassland-obilgate birds, which are rapidly declining, are particularly sensitive to changes in structural heterogeneity that may be influenced by herbivory (Wiens, 1974). Therefore understanding the positive and negative relationships between vegetation structures and foraging behavior of large herbivores at multiple spatial and temporal scales on tallgrass prairie is essential.

6. Literature Cited

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

Bailey, D. W., Rittenhouse, L. R., Hart, R. H., Swift, D. M. & Richards, R. W. 1989. Association of relative food availabilities and location by cattle. *Journal of Rangeland Management*, **42,** 480-482.

Bourlier, B. G., Nichols, J. D., Ringwald, W. J., Workman, P. J. & Clemmons, S. 1979. *Soil survey of Osage County, Oklahoma.*: USDA-SCS.

Chacon, E. & Stobbs, T. H. 1976. Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. *Australian Journal of Agricultural Research*, **27,** 709-727.

Cid, M. S. & Brizuela, M. A. 1998. Heterogeneity in tall fescue pastures created and sustained by cattle grazing. *Journal of Range Management*, **51,** 644-649.

Coppedge, B. R., Engle, D. M., Toepfer, C. S. & Shaw, J. H. 1998. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecology*, **139,** 235-246.

Etzenhouser, M. J., Owens, M. K., Spalinger, D. E. & Murden, S. B. 1998. Foraging behavior of browsing ruminants in a heterogeneous landscape. *Landscape Ecology*, **13,** 55-64.

Fuhlendorf, S. D. & Engle, D. M. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *Bioscience*, **51,** 625-632.

Fuhlendorf, S. D. & Smeins, F. E. 1999. Scaling effects of grazing in a semi-arid grassland. *Journal of Vegetation Science*, **10,** 731-738.

Gillen, R. L., Krueger, W. C. & Miller, R. F. 1984. Cattle Distribution on Mountain Rangeland in Northeastern Oregon. *Journal of Range Management*, **37,** 549-553.

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,** 27-44.

Hobbs, N. T. 1999. Responses of large herbivores to spatial heterogeneity in ecosystems. In: *Nutritional Ecology of Herbivores: Proceedings of the Vth International Symposium on the Nutrition of Herbivores* (Ed. by Jung, H.-J. G. & Fahey, G. C.), pp. 97-129. Savory, IL: American Society of Animal Science.

Mandelbrot, B. B. 1983. *The fractal geometry of nature*. New York: W.H. Freeman.

McNaughton, S. J. 1984. Grazing Lawns - Animals in Herds, Plant Form, and Coevolution. *American Naturalist*, **124,** 863-886.

Nams, V. O. 1996. The VFractal: a new estimator for fractal dimension of animal movement. *Landscape Ecology*, **11,** 287-297.

Ring, C. B., Nicholson, R. A. & Launchbaugh, J. L. 1985. Vegetational traits of patch-grazed rangeland in west-central Kansas. *Journal of Range Management*, **38,** 51-55.

SAS Institute Inc. 1989. SAS/STAT® user's guide, version 6, fourth edition, volume2. SAS Institute, Inc., Cary, North Carolina.

Scarnecchia, D. L., Nastis, A. S. & Malechek, J. C. 1985. Effects of Forage Availability on Grazing Behavior of Heifers. *Journal of Range Management*, **38,** 177-180.

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

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.

Vavra, M. & Ganskopp, D. 1998. Grazing behavior in ungulates: current concepts and future challenges. *Annals of Arid Zone*, **37,** 319-335.

Vinton, M. A., Hartnett, D. C., Finck, E. J. & Briggs, J. M. 1993. Interactive effects of fire, bison grazing, and plant comunity composition in tallgrass prairie. *American Midland Naturalist*, **129,** 10-18.

WallisDeVries, M. F., Laca, E. A. & Demment, M. W. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia*, **121,** 355-363.

WallisDeVries, M. F. & Schippers, P. 1994. Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. *Oecologia*, **100,** 107-117.

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

Westcott, D. A. & Graham, D. L. 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*, **122,** 249-257.

Wiens, J.A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. American Midland Naturalist, **91**, 195-213.

Wiens, J. A., Crist, T. O., With, K. A. & Milne, B. T. 1995. Fractal patterns of insect movement in microlandscape mosaics. *Ecology*, **76,** 663-666.

Wiens, J. A. & Milne, B. T. 1989. Scaling of 'landscape' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology*, **3,** 87-96.

With, K. A. 1994. Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns. *Functional Ecology*, **8,** 477-485.

With, K. A., Cadaret, S. J. & Davis, C. 1999. Movement responses to patch structure in experimental fractal landscapes. *Ecology*, **80,** 1340-1353.

Fig. 1 Structural heterogeneity in complete-burn pastures and patch-burn pastures in 2001 and 2002. Heterogeneity is defined by the standard deviation of vegetation height among patches and among pastures.

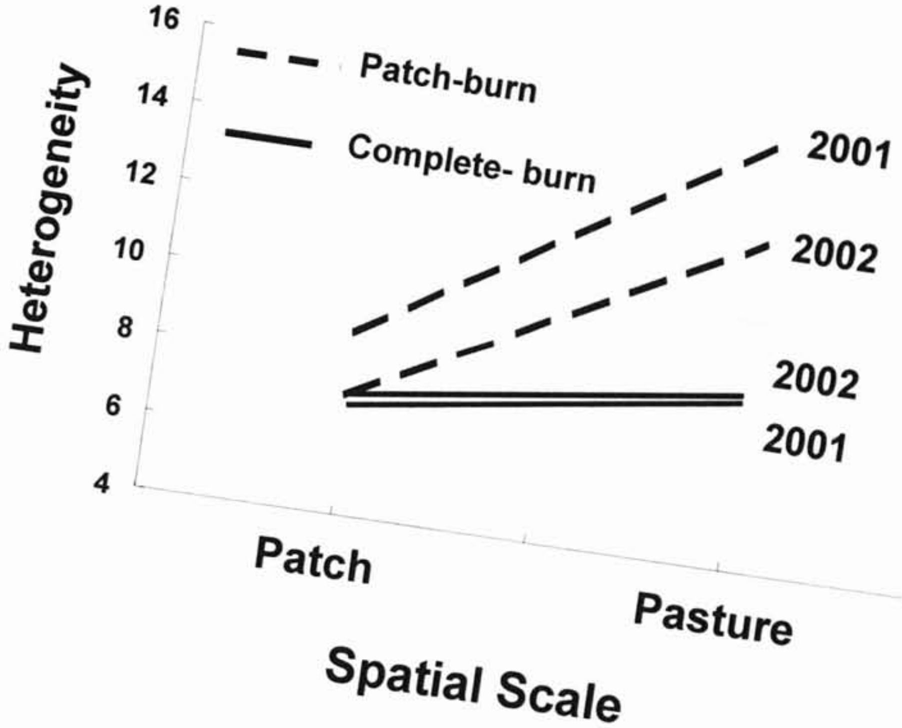

16
14
12
10
8
6
4
Heterogeneity
Patch-burn
Complete- burn
2001
2002
2002
2001
Patch
Pasture
Spatial Scale

Fig. 2 Vegetation heights in complete-burn pastures and recent burns in patch-burn pastures. Data are not included for unburned portions of patch-burn pastures because cattle grazed almost exclusively in recent burns. A growing-season drought occurred in 2001, thus vegetation height was generally less in 2001 than in 2002, a normal year.

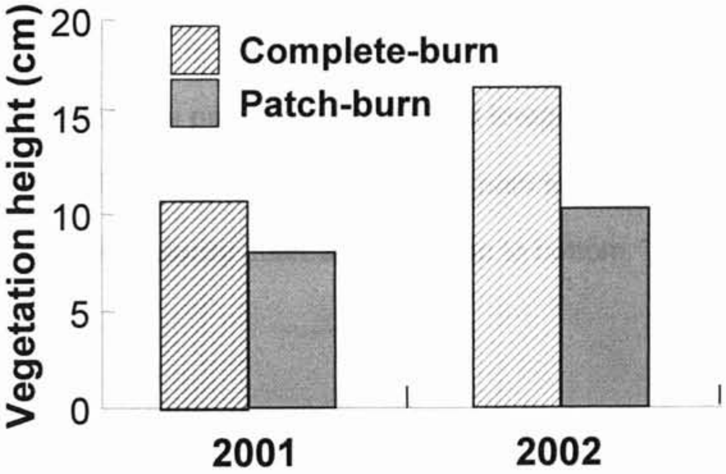

Vegetation height (cm)
20
15
10
5
0
Complete-burn
Patch-burn
2001
2002

Fig.3 Examples of how path tortuosity (D) and foraging velocity (FV) describe foraging paths of yearling cattle. In this figure path tortuosity increases from right to left and foraging velocity decreases from top to bottom.

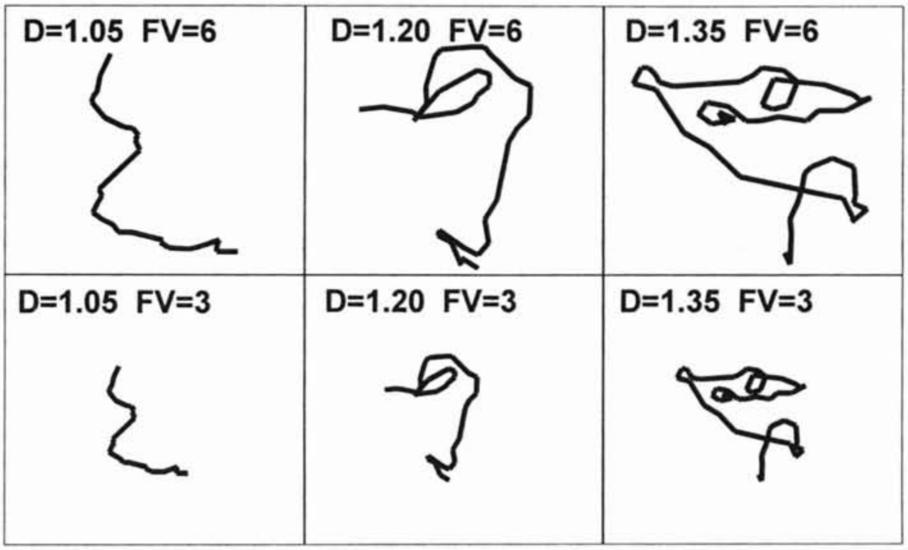
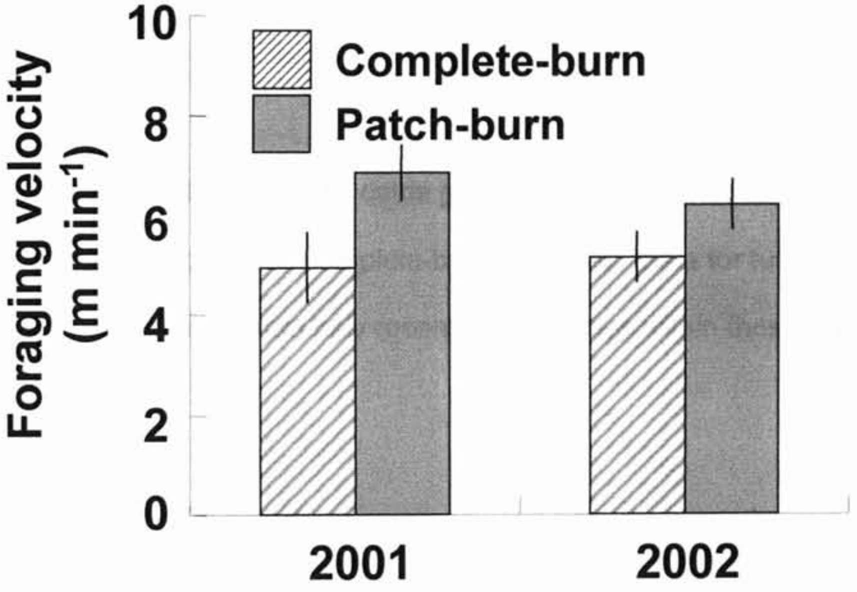

D=1.05 FV=6
D=1.20 FV=6
D=1.35 FV=6
D=1.05 FV=3
D=1.20 FV=3
D=1.35 FV=3

Fig. 4 Foraging velocity of yearling cattle grazing in heterogeneous patch-burn pastures and homogenous complete-burn pastures. Data for foraging velocity in patch-burn pastures is from only recent burn patches within those pastures.



10
8
6
4
2
0
Foraging velocity
(m min-1)
Complete-burn
Patch-burn
2001
2002

Fig. 5 Turning angle of yearling cattle grazing in heterogeneous patch-burn pastures and homogenous complete-burn pastures. Data for turning angle in patch-burn pastures is from only recent burn patches within those pastures.

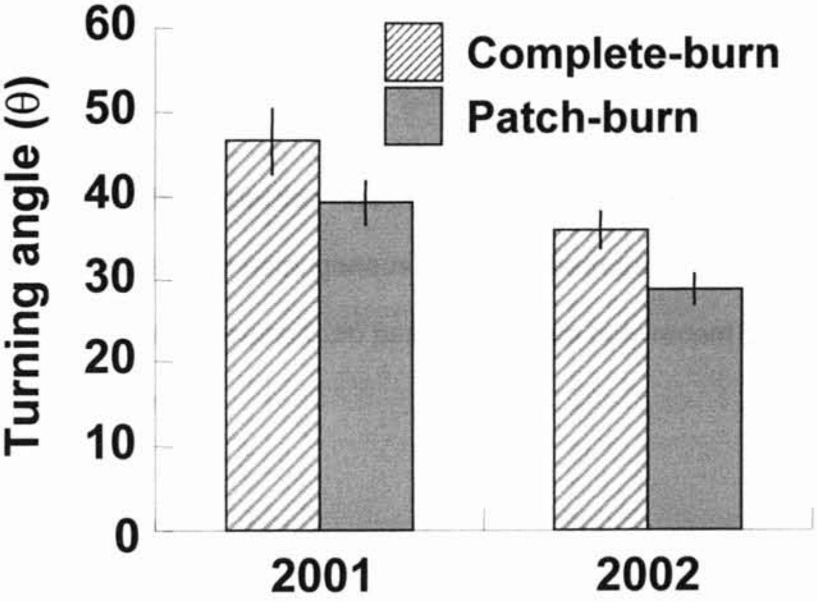

Turning angle (θ)
60
50
40
30
20
10
0
Complete-burn
Patch-burn
2001
2002

Fig. 6 Feeding station selection rate of yearling cattle grazing in heterogeneous patch-burn pastures and homogenous complete-burn pastures. Data for feeing station selection rate in patch-burn pastures is from only recent burn patches within those pastures.

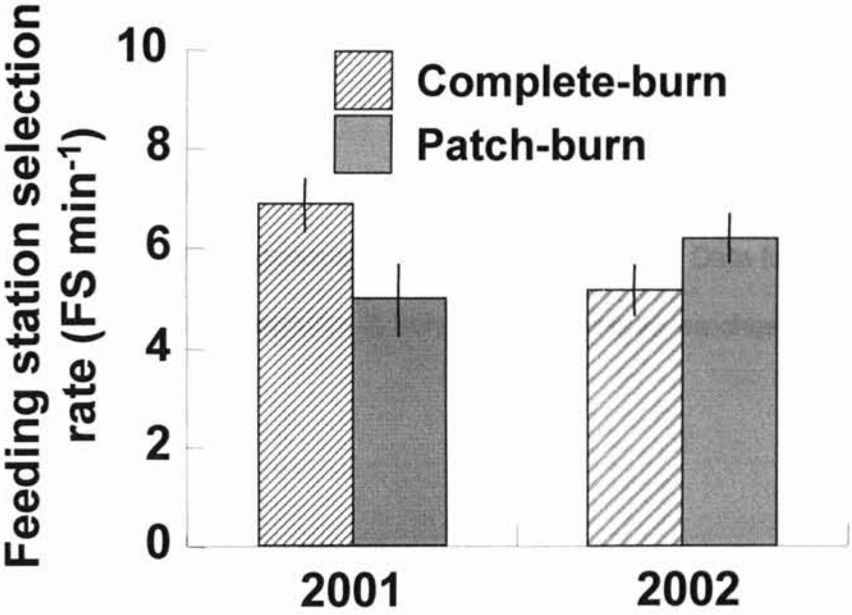
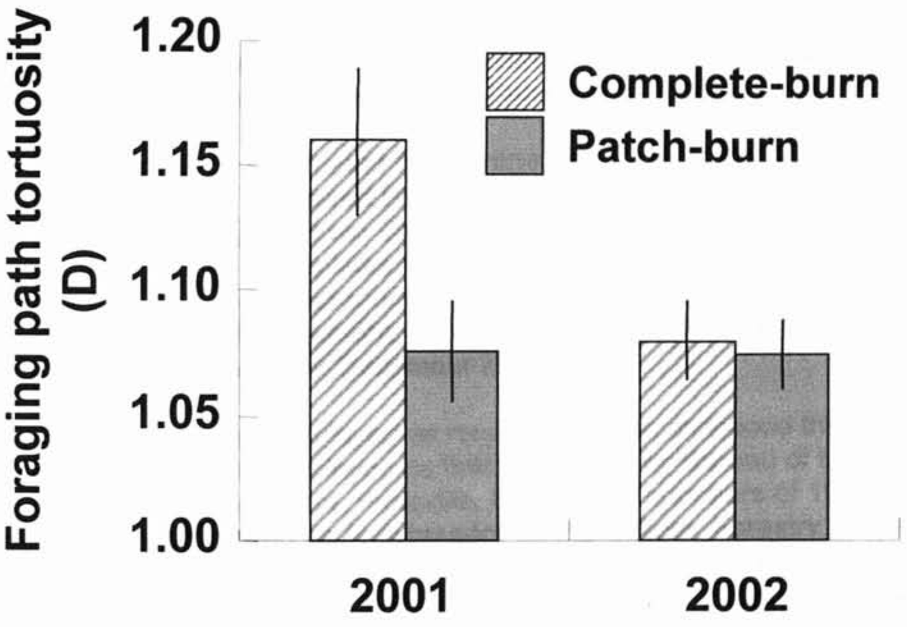

Feeding station selection rate (FS min^{-1})
10
8
6
4
2
0
Complete-burn
Patch-burn
2001
2002

Fig.7 Foraging path tortuosity of yearling cattle grazing in heterogeneous patch-burn pastures and homogenous complete-burn pastures. Data for foraging path tortuosity in patch-burn pastures is from only recent burn patches within those pastures.


Foraging path tortuosity (D)
1.20
1.15
1.10
1.05
1.00
Complete-burn
Patch-burn
2001
2002

VITA 2

Jay Daniel Kerby

Candidate for the Degree of

Master of Science

Thesis: PATCH-LEVEL FORAGING BEHAVIOR OF BISON AND CATTLE ON TALLGRASS PRAIRIE

Major Field: Plant and Soil Sciences

Biographical:

Personal Data: Born in Toppenish, Washington, on 2 November 1977, the son of Robert V. and Carol A. Kerby.

Education: Graduated from Crane Union High School, Crane, Oregon in 1996. Received Bachelor of Science degree in Rangeland Resources from Oregon State University, Corvallis, Oregon in June 2000. Completed the requirements for the Master of Science degree in Agronomy, with a specialization in Rangeland Ecology and Management, at Oklahoma State University, Stillwater, Oklahoma in December 2002.

Experience: Employed as ranch hand from childhood through high school; employed as field technician by Bureau of Land Management, Prineville, Oregon, for summers of 1998 and 1999; employed as Ambassador for Agriculture, Forestry, and Natural Resources by College of Agriculture, Oregon State University, from 1999 to 2000; employed as research technician by Agricultural Research Service, Burns, Oregon, for summer of 2000; employed as graduate research assistant by Oklahoma State University from 2000 to 2002

Professional Memberships: The Society for Range Management, Ecological Society of America