The ecology of reintroduced elk in Theodore Roosevelt National Park, North Dakota
by Jerry Allen Westfall

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
The ecology of a population of Rocky Mountain elk (Cervus elaphus nelsoni), reintroduced into the South Unit (SU) of Theodore Roosevelt National Park (TRNP) in 1985, was studied from 1987-1988. Eight elk, previously equipped with radio-collars, were relocated daily during 4 seasons. At each observation, location, activity, habitat use, and behavior were noted. The population grew at a logarithmic growth rate of 0.31 over 4 years. Elk were segregated into a bull and a cow-calf group that only associated during the rut. Home ranges were largest in winter for the cow-calf group (62.6 km^2) and in summer for the bull group (80.0 km^2). Adult and yearling males preferred more rugged habitats than females. Elk exhibited crepuscular activity during spring and summer but remained active throughout diurnal hours in winter. Elk fed primarily in upland grasslands in all seasons. Rocky Mountain juniper (Juniperus scopulorum), in breaks habitats, was used as overhead cover during midday hours in spring and summer. Elk did not use overhead cover in winter but bedded near foraging areas.

Humans on foot were more disturbing to elk than stationary vehicles or horseback riders. Elk did not respond to humans >1,000 m away, but always displaced when approached <100 m. A dominance hierarchy of bison (Bison bison) > feral horses (Equus caballus) > elk > mule deer (Odocoileus hemionus) was observed at TRNP. Elk habitat selection was most correlated to horses during the growing season and to mule deer over the entire study. Diet composition for elk, bison, feral horses, mule deer, and white-tailed deer was determined from fecal microhistological analysis. Total elk diets were most correlated to total feral horse diets, but were not significantly correlated to the diets of any ungulate species for major forage items. Diet composition, distribution, and vegetative production were used in a computer model to determine the optimum carrying capacity for elk, bison, feral horses, and mule deer. Winterfat (Ceratoides lanata) was the forage item that most limited ungulate numbers.

THE ECOLOGY OF REINTRODUCED ELK IN THEODORE ROOSEVELT NATIONAL PARK, NORTH DAKOTA

by

Jerry Allen Westfall, Jr.

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

October 1989

APPROVAL

of a thesis submitted by

Jerry Allen Westfall, Jr.

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Oct 16, 1989 — Robert P. Eng
Date — Chairperson, Graduate Committee

Approved for the Major Department

16 October 1989 — Robert S. Moore
Date — Head, Major Department

Approved for the College of Graduate Studies

October 20, 1989 — Henry L. Parsons
Date — Graduate Dean

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University, I agree that the Library shall make it available to borrowers under rules of the Library. Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of source is made.

Permission for extensive quotation from or reproduction of this thesis may be granted by my major professor, or in his absence, by the Dean of Libraries when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission.

Signature J. Westfall, Jr.

Date 16 October 1989

ACKNOWLEDGEMENTS

I would like to thank my committee members, Drs. Lynn Irby, Clayton Marlow, Harold Picton, and Robert White for their helpful comments and suggestions. Classes by Drs. Marlow and Picton were instrumental in my educational experience at Montana State University and provided me with a deeper understanding and appreciation of my profession. I especially would like to thank Dr. Lynn Irby who provided assistance throughout the project, yet allowed me the flexibility to pursue my own ideas.

Thanks go to the faculty and staff of the Biology, and Animal and Range Science Departments. I am indebted to my fellow graduate students for their friendship and for providing an environment where learning was important.

A special thanks goes to the personnel at Theodore Roosevelt National Park, especially Jeff Bradybaugh, Bob Powell, Jim and Karla Zahradka, Jim Cutler, Shirley Norton, Melvin Haynes, and Marilyn Sahlstrom. A heartfelt appreciation is extended to the fine people of the town of Medora, too numerous to mention, who truly made Medora my "home away from home." Carl and Pearl Zilsdorf extended their home and their friendship to me, which I will always remember.

This project was funded by the National Park Service and Theodore Roosevelt National Park.

TABLE OF CONTENTS

Page

LIST OF TABLES viii

LIST OF FIGURES xiv

ABSTRACT xv

INTRODUCTION 1

STUDY AREA 4

- Geology 4
- Climate 6
- Vegetation 6

METHODS 9

- Daily and Seasonal Movements 9
- Habitat Use and Activity Patterns 10
- Ungulate Interactions 12
- Human Impacts 13
- Population Dynamics and Carrying Capacity 13
  - Population Censuses 13
  - Forage Allocation 14
    - Number of Hectares of PTs 15
    - Amount of Time in Region 15
    - Ungulate Diets 16
    - Production of Major Dietary Items 17
    - Growing Season Forage Intake 17
    - Percent Allowable Use 18

RESULTS AND DISCUSSION 19

- Distribution 19
- Pellet Group Survey 21
- Herd Organization 23
- Seasonal Distribution and Home Range 25
  - Summer 1987 25
  - Winter 1988 31
  - Spring 1988 33
  - Summer 1988 34
- Population Dynamics 35

TABLE OF CONTENTS—Continued

Page

Food Habits..40
Elk Diets..40
Comparison of Ungulate Diets....................................44
Activity Patterns..46
Habitat Use..54
Sex/Age Classes..54
Overall and Seasonal Habitat Use...............................57
Feeding Areas..58
Bedding Areas..62
Calving and Rutting Areas......................................64
Ungulate Interactions..65
Elk - Bison Interactions.......................................65
Elk - Feral Horse Interactions.................................68
Elk - Mule Deer Interactions...................................69
Dominance Hierarchy..71
Human Impacts..72
Optimum Carrying Capacity......................................74

CONCLUSIONS AND RECOMMENDATIONS.................................82

REFERENCES CITED...85

APPENDICES...93

APPENDIX A - Description of Physiographic Types and Habitat Types/Mapping Units/Complexes in TRNP.............94

APPENDIX B - Percent elk activity in Physiographic Types and Habitat Types/Mapping Units/Complexes for each season and time period.......................99

APPENDIX C - Ungulate interactions and reaction of elk to human caused disturbances by distance category...109

APPENDIX D - Percent vegetative species composition identified in fecal analysis of elk, bison, feral horses, mule deer, and white-tailed deer in TRNP.113

APPENDIX E - Percent composition, hecterage and vegetative production of Habitat Types/Mapping Units/ Complexes in the Upland Grassland Physiographic Type for the South Unit of Theodore Roosevelt National Park.................................123

LIST OF TABLES

Table Page

1. Verified reports of elk leaving and later returning to TRNP from 1985-1988. Reports for 1985-1986 are from Sullivan (1988)....21

2. Seasonal home range sizes (km^2) for radio-collared and uncollared elk in TRNP....31

3. Population dynamics of adult male and female (≥2 years), yearling male and female (1 year), and calf elk in TRNP. Data for 1986-1987 are from Sullivan (1988)....36

4. Male:female ratios and logarithmic growth rates based on elk within and outside TRNP, and calf:cow ratios based potential breeding females within TRNP during previous years....40

5. Seasonal percent elk diet composition of graminoids, forbs, and browse comprising ≥3% of any seasonal diet....42

6. Spearman's rank correlations (r_S) of total diets (TOT) and diets of 11 major forage items (MAJ) for elk, bison, feral horses, mule deer (MD), and white-tailed deer (WTD)....45

7. Season lengths and number of observation-minutes recorded for elk during each season....47

8. Feeding to bedding ratios of elk during diurnal hours in each season, and the time period designation for morning (AM), midday (MD), and evening (PM)....48

9. Percent elk activity for each season and adjusted activity for the spring 1988 and summer 1987-1988 seasons. Adjusted activities are in parentheses....52

10. Percent feeding (F), bedding (B), and total activities (TOT) by adult male, yearling male, female, and calf elk in Physiographic Types (PTs) of TRNP....55

11. Percent feeding (F), bedding (B), and total activities (TOT) by adult male, yearling male, female, and calf elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes of TRNP....56

LISTS OF TABLES—Continued

Table | Page

12. Percent utilization of Physiographic Types (PTs) by elk during summer 1987-1988, winter 1988, spring 1988, the growing season (summer 1987-1988 and spring 1988) and over the entire study, and the percent of Physiographic Types available.....58

13. Percent utilization of Habitat Types (HTs), Mapping Units (MUs), and Complexes by elk during summer 1987-1988, winter 1988, spring 1988, the growing season (summer 1987-1988 and spring 1988) and over the entire study, and the percent of HTs, MUs, and Complexes available.....59

14. Percent activity of elk within Physiographic Types (PTs) during the entire study and during the growing season (spring 1988, and summer 1987-1988). Growing season values are in parentheses.....60

15. Percent activity of elk within Habitat Types (HTs), Mapping Units (MUs), and Complexes during the entire study and during the growing season (spring 1988, and summer 1987-1988). Growing season values are in parentheses.....62

16. Percent bedding, unknown, and adjusted bedding activities during midday hours by elk in Physiographic Types (PTs) for spring 1988 and summer 1987-1988.....63

17. Percent bedding, unknown, and adjusted bedding activities during midday hours by elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes for spring 1988 and summer 1987-1988.....64

18. Total percent utilization of Physiographic Types (PTs) by ungulates. Utilization is based on observation-minutes for elk and on sightings for bison, feral horses, mule deer (MD), white-tailed deer (WTD). Sample sizes are in parentheses.....67

19. Percent utilization of Physiographic Types (PTs) by ungulates and percent feeding by elk during the growing season. Utilization is based on observation-minutes for elk and on sightings for bison, horse, mule deer (MD), white-tailed deer (WTD). Sample sizes are in parentheses.....67

LISTS OF TABLES—Continued

Table Page

20. Spearman's rank correlations (r_S) of Physiographic Types (PTs) used during the entire study (TOT) and during the growing season (GRO) by elk, bison, feral horses, mule deer (MD), and white-tailed deer (WTD) 68

21. Percent reaction of other ungulate species to elk with mean displacement distance 70

22. Percent reaction of elk to other ungulate species with mean displacement distance 70

23. Percent reaction of elk to human caused disturbances with mean displacement distance 74

24. Percent utilization of regions in TRNP by elk, bison, feral horses, and mule deer (MD) during the growing season (spring 1988 and summer 1987-1988). Utilization is based on observation-minutes for elk and on sightings for the other ungulates 75

25. Population estimates, weights of the typical animal, daily intake, and forage intake over the growing season for elk, bison, feral horses, and mule deer (MD) 75

26. Typical animal intake (kg) during the growing season (spring and summer) by elk, bison, feral horses, and mule deer (MD) of the 11 major forage items used in the Ungulate Resources Allocation Model 77

27. Optimum carrying capacity of elk in a 6-region area of TRNP based on utilization patterns for each region, population levels for bison (200), feral horses (50), and mule deer (312), and limiting forage species 78

28. Population levels, densities, and stocking rates for elk, bison, feral horses, and mule deer at the optimum carrying capacity for a 6-region area (123.9 km^2) of TRNP 79

29. Exchange rate coefficients of ungulate species 1 for species 2, based on predetermined optimal population levels from winterfat intake 81

LISTS OF TABLES—Continued

Table Page

30. Description of Physiographic Types in TRNP (Norland 1984).....95

31. Description of Habitat Types, Mapping Units, and Complexes in TRNP (Norland 1984, Sullivan 1988).........................96

32. Percent activity of elk in Physiographic Types (PTs) during winter 1988...100

33. Percent activity of elk in Physiographic Types (PTs) during spring 1988...100

34. Percent activity of elk in Physiographic Types (PTs) during summer 1987-1988....................................101

35. Percent feeding by elk in Physiographic Types (PTs) for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988........101

36. Percent bedding by elk in Physiographic Types (PTs) for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988........102

37. Percent utilization of Physiographic Types (PTs) by elk for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988........102

38. Percent activity of elk in Habitat Types (HTs), Mapping Units (MU), and Complexes during winter 1988..................103

39. Percent activity of elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes during spring 1988................104

40. Percent activity of elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes during summer 1987-1988.............105

41. Percent feeding by elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988..106

42. Percent bedding by elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988..107

LISTS OF TABLES—Continued

Table Page

43. Percent utilization of Habitat Types (HTs), Mapping Units (MUs), and Complexes by elk for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988....108

44. Percent reaction of other ungulate species to elk within distance categories. Sample sizes are in parentheses....110

45. Percent reaction of elk to other ungulate species within distance categories. Sample sizes are in parentheses....111

46. Percent reaction of elk to human caused disturbances by distance category. Sample sizes are in parentheses....112

47. Percent vegetative species composition identified in fecal samples of elk during spring 1988 and summer 1987-1988 and during the growing season (spring 1988 and summer 1987-1988)....114

48. Percent vegetative species composition identified in fecal samples of bison during spring 1988 and summer 1988 and during the growing season (spring 1988 and summer 1988)....116

49. Percent vegetative species composition identified in fecal samples of feral horses during spring 1988 and summer 1988 and during the growing season (spring 1988 and summer 1988)..118

50. Percent vegetative species composition identified in fecal samples of mule deer during spring 1988 and summer 1988 and during the growing season (spring 1988 and summer 1988)....119

51. Percent vegetative species composition identified in fecal samples of white-tailed deer during spring 1988 and summer 1988 and during the growing season (spring 1988 and summer 1988)....121

52. Percent composition and hecterage of Habitat Types (HTs), Mapping Units (MUs), and Complexes in the Upland Grassland Physiographic Type (PT) for the South Unit of Theodore Roosevelt National Park....124

LISTS OF TABLES—Continued

Table | Page

53. Vegetative production (kg/ha) for Habitat Types (HTs), Mapping Units (MUs), and Complexes within the Upland Grassland Physiographic Type (PT). Production figures are from Marlow et al. 1984, Norland 1988[a] and Sullivan 1988 125

LIST OF FIGURES

Figure   Page

1. Map of the South Unit of Theodore Roosevelt National Park......5

2. A view of the Physiographic Types within an idealized landform of the South Unit of Theodore Roosevelt National Park. From Norland (1984)......8

3. Elk pellet group survey in Theodore Roosevelt National Park, 1988. Numbers in sections = pellet groups per km. Map drawn by Sullivan (1988)......22

4. Locations of adult male and female elk during summer 1987.....26

5. Locations of adult male and female elk during winter 1988.....27

6. Locations of adult male and female elk during spring 1988.....28

7. Locations of adult male and female elk during summer 1988.....29

8. Percent observation-minutes spent feeding, bedding, standing, moving, and other by elk during summer 1987-1988....49

9. Percent observation-minutes spent feeding, bedding, standing, moving, and other by elk during winter 1988.........50

10. Percent observation-minutes spent feeding, bedding, standing, moving, and other by elk during spring 1988.........51

ABSTRACT

The ecology of a population of Rocky Mountain elk (Cervus elaphus nelsoni), reintroduced into the South Unit (SU) of Theodore Roosevelt National Park (TRNP) in 1985, was studied from 1987-1988. Eight elk, previously equipped with radio-collars, were relocated daily during 4 seasons. At each observation, location, activity, habitat use, and behavior were noted. The population grew at a logarithmic growth rate of 0.31 over 4 years. Elk were segregated into a bull and a cow-calf group that only associated during the rut. Home ranges were largest in winter for the cow-calf group (62.6 km^2) and in summer for the bull group (80.0 km^2). Adult and yearling males preferred more rugged habitats than females. Elk exhibited crepuscular activity during spring and summer but remained active throughout diurnal hours in winter. Elk fed primarily in upland grasslands in all seasons. Rocky Mountain juniper (Juniperus scopulorum), in breaks habitats, was used as overhead cover during midday hours in spring and summer. Elk did not use overhead cover in winter but bedded near foraging areas. Humans on foot were more disturbing to elk than stationary vehicles or horseback riders. Elk did not respond to humans >1,000 m away, but always displaced when approached <100 m. A dominance hierarchy of bison (Bison bison) > feral horses (Equus caballus) > elk > mule deer (Odocoileus hemionus) was observed at TRNP. Elk habitat selection was most correlated to horses during the growing season and to mule deer over the entire study. Diet composition for elk, bison, feral horses, mule deer, and white-tailed deer was determined from fecal microhistological analysis. Total elk diets were most correlated to total feral horse diets, but were not significantly correlated to the diets of any ungulate species for major forage items. Diet composition, distribution, and vegetative production were used in a computer model to determine the optimum carrying capacity for elk, bison, feral horses, and mule deer. Winterfat (Ceratoides lanata) was the forage item that most limited ungulate numbers.

INTRODUCTION

With the recession of glaciers at the end of the Wisconsin glacial stage 10,000 years ago, elk spread south and east from non-glaciated Alaskan refugia to inhabit prairies, parks, and open forests. Elk became the most widely distributed North American cervid, extending their range as far south as northern Mexico, Louisiana, and Alabama (Hall and Kelson 1959, Curren 1977, and Boyd 1978). By the end of the Wisconsin glacial stage, elk were segregated into 4 geographic regions: 1) the northwestern Pacific coast; 2) western and central California; 3) the southwestern United States and northern Mexico; 4) the area east of the Cascade and Sierra Nevada ranges (Guthrie 1966).

The ranges of three presently recognized subspecies of the North American elk: Rocky Mountain elk, Manitoban elk (C. e. manitobensis), and Eastern elk (C. e. canadensis), overlapped in the area of the Northern Great Plains (Guthrie 1966). Guthrie (1966) suggested that a distinct subspecies uniquely adapted to the environment of the Great Plains may have been forming. However, Bryant and Maser (1982) asserted that elk in the Northern Great Plains were Manitoban elk. With the extirpation of elk in the eastern 2/3 of the continent, any subspeciation that may have been occurring was forever halted.

In North Dakota, elk were abundant before European settlement. Audubon, Lewis and Clark, and Alexander Henry all reported seeing vast herds along the Missouri River. Remington Kellogg hypothesized, based on reports of early explorers and settlers of the region, that elk migrated to river bottoms in the fall and back to the open prairies in late spring (Bryant and Maser 1982). Riparian areas presumably provided ideal winter range, with thermal cover and abundant browse. However, the last reported elk killed in North Dakota occurred in Cavalier County in 1883, precluding any further research into this phenomenon (Kruckenberg 1973).

In 1942, 25 Rocky Mountain elk were released in the Killdeer mountains, western North Dakota, by the North Dakota Department of Game and Fish (Bryant and Maser 1982). This transplant failed and future reintroductions were not attempted. In 1979, however, a small herd of elk escaped from a holding pen on an Indian reservation into river breaks near the North Unit (NU) of TRNP (Sullivan 1988). Within a few years this herd had grown in size to allow a limited hunt (25-30 animals per year) by the North Dakota Department of Game and Fish.

Plans to reintroduce elk into the SU of TRNP were initiated in 1984, in an attempt to restore one of the major ungulate species native to the area. Pronghorn (*Antilocapra americana*), bison, and California bighorn sheep (*Ovis canadensis california*) were reintroduced into the SU in 1951, 1956, and 1959, respectively. Mule deer and white-tailed deer (*O. virginianus*) were present in the Park since its inception. Feral horses, from a variety of sources, have established themselves in the Park, and are currently being managed according to Park goals (TRNP 1984). An elk reintroduction would complete the historic ungulate assemblage in the badlands ecosystem

(TRNP 1984). In March 1985, 47 Rocky Mountain elk were acquired from Wind Cave National Park, South Dakota and released in the SU of TRNP on Buck Hill (Fig. 1).

This study represents the second phase of a 4-year investigation of the dynamics and ecology of a reintroduced elk population. M. Sullivan conducted research during phase 1 of this project from 1985-1986. Specific objectives of phase 2 (1987-1988) were:

1. Description of daily and seasonal movements of elk.

2. Description of the population dynamics of elk and determination of elk population levels that are consistent with Park management objectives.

3. Identification of seasonally important Habitat Types/Mapping Units/Complexes and Physiographic Types used for feeding, cover, mating, and calving.

4. Description of interactions between elk and other ungulates and identification of interactions that could detrimentally affect individual ungulate species.

5. Determination of human impacts on elk behavior and distribution in the Park.

STUDY AREA

The study was conducted in the SU of TRNP in southwestern North Dakota (Fig. 1). The Park was originally created as Theodore Roosevelt Memorial Park on 25 April 1947, but the name was changed to Theodore Roosevelt National Park in 1978. The Park is divided into two units, the SU near the town of Medora, and the NU, 80 km to the north. The SU of TRNP is bordered by U. S. Interstate Highway 94 to the south, private landholdings to the north and east, and USFS Little Missouri National Grasslands to the west. The SU covers 18,756 ha, and is bisected north to south by the Little Missouri River.

Geology

The SU of TRNP is part of the Missouri River Plateau of the Great Plains Province (Fenneman 1931). Soil substrates are from the Paleocene, Fort Union Group of the Tongue River Formation (Leonard 1930). Although TRNP was unglaciated during the last ice age, glacial diversion caused an eastern shift in the route of the Little Missouri River, which caused extensive downcutting in areas along the river channel creating an unique topography known as the badlands. The badlands are characterized by considerable erosion leaving resistant layers of sandstone, shale, and lignite.

Often when partially exposed lignite beds became heated, they would bake overlying clay beds, forming a red, slaglike clinker

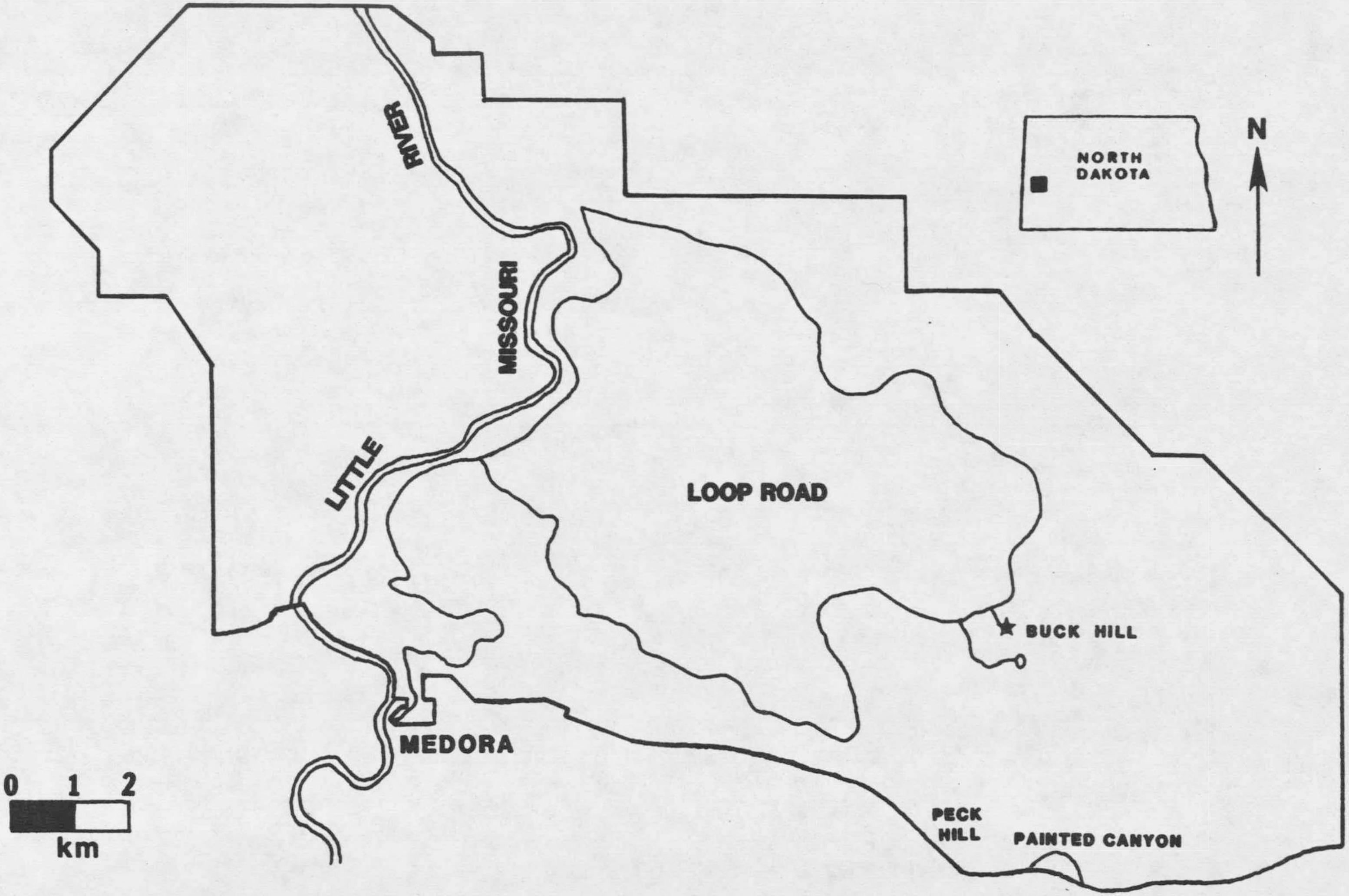

Figure 1. Map of the South Unit of Theodore Roosevelt National Park.

locally known as "scoria" (Hanson et al. 1980). Scoria, which was more resistant to erosion than surrounding material, became the caps to small hills and buttes. Relics of the upland prairie can be found atop these buttes and on grassland plateaus (Sullivan 1988).

Climate

The climate of TRNP is semi-arid, continental, typical of the Northern Great Plains (Hirsch 1985). Long, cold winters and short, dry summers typify seasonal weather patterns. Over 70% of the annual precipitation occurs during the growing season (April through September), with 25% of the total precipitation as snow (Ramirez 1973). Annual precipitation averages 36 cm (TRNP 1984).

Vegetation

Vegetation in TRNP has been described as mixed prairie. Small, scattered stands of deciduous trees or Rocky Mountain juniper exist in ravines with mesic microenvironments. A large portion (≈30%) of TRNP is unvegetated or covered only by scattered shrubs (Marlow et al. 1984). Detailed descriptions of the vegetation in TRNP are found in Nelson (1961), Whitman (1978), Hanson et al. (1980), Girard (1985), and Hirsch (1985).

Habitat classification used in this study followed the 2-tiered Physiographic Type and Habitat Type/Mapping Unit/Complex classification scheme developed by Norland (1984). Large areas of TRNP were classified by Norland (1984) as Physiographic Types (PTs) based on topography and physiography, landform origin, and gross structure of associated vegetation. Classification of Habitat Types (HTs) within PTs (Norland 1984) were based on the vegetation assemblages that could eventually develop on the site, given the climate and substrate (Daubenmire 1968).

The actual classification of these sites followed similar HTs identified by: the Soil Conservation Service (range site guidelines for the North Dakota badlands), Whitman (1978), Hanson et al. (1980), Girard (1985), and Hirsch (1985) in and around TRNP. Mapping Units (MUs) were created by Norland (1984) to describe vegetative assemblages which had been disturbed by natural or anthropogenic forces, or were in the early stages of succession. Complexes were identified as assemblages of Habitat Types too small to map (Norland 1984). The area of individual HTs/MUs/Complexes and their composition in each PT was measured from aerial photographs by Marlow et al. (1984).

Vegetative production (the addition of vegetative tissue in 1 growing season), for major graminoid and shrub species in several HTs/MUs/Complexes in and around TRNP were reported by the Soil Conservation Service (range site guidelines for the North Dakota badlands), Whitman (1978), Hanson et al. (1980), Norland (1984), Marlow et al. (1984), Girard (1985), and Hirsch (1985). These production figures were later collected and revised by Norland (1988a).

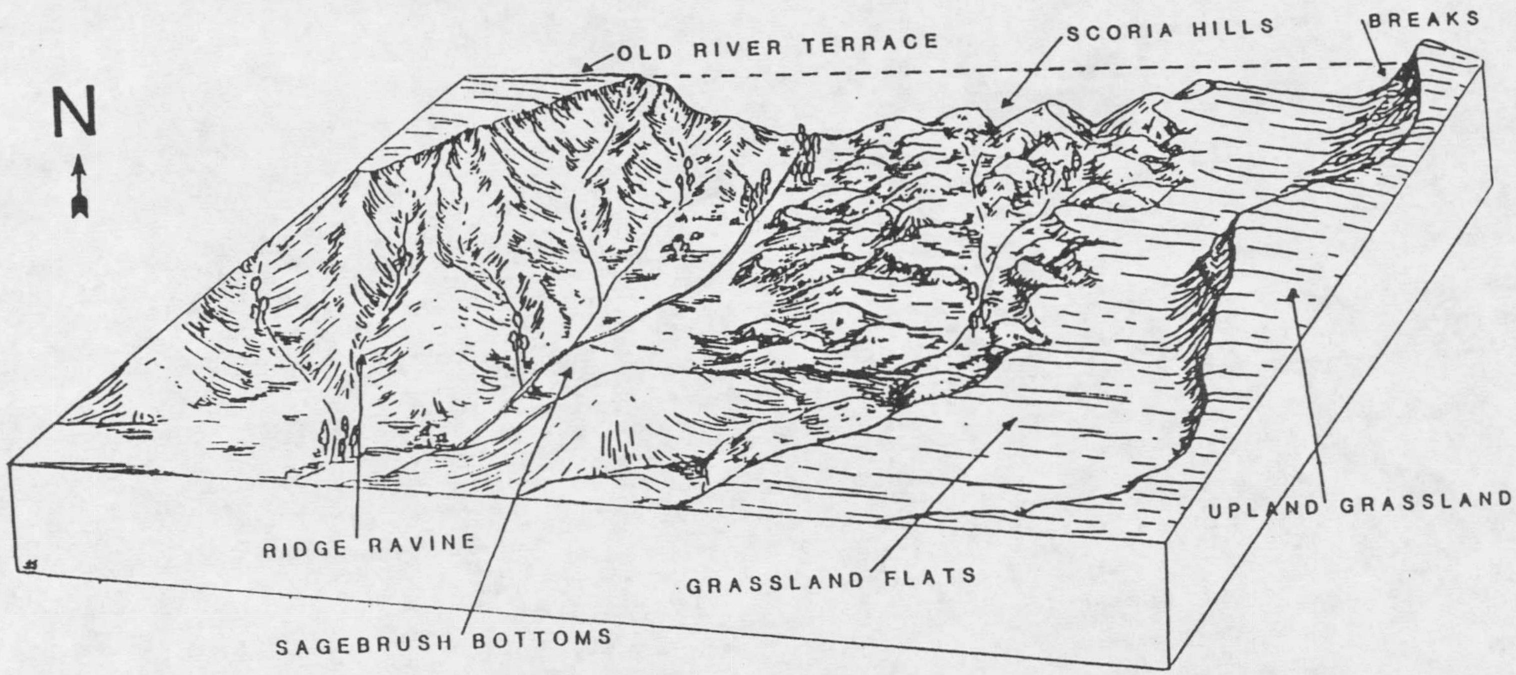

Figure 2. A view of the Physiographic Types within an idealized landform of the South Unit of Theodore Roosevelt National Park. From Norland (1984).

METHODS

Daily and Seasonal Movements

Eight elk, 3 males and 5 females, were equipped with radio-collars during phase 1 of the study. These animals were relocated with a radio receiver and a hand-held, 3-element, yagi antenna during phase 2. Most relocations were confirmed visually with 7x35 mm field binoculars and a 15-60X spotting scope. Locations of these elk groups were plotted on 1:24,000 topographic maps and Universal Transverse Mercator (UTM) coordinates were determined.

Seasonal home range sizes were determined for radio-collared and uncollared animals using McPaal, a computer software package (Stuwe and Blohowiak 1985). McPaal has several options for generating home range sizes, one of which uses the minimum convex polygon method (Mohr 1947) to determine the area within a polygon formed by connecting the outermost locations. Home ranges for females and males were found by combining all locations for each sex.

General information on elk distribution within the Park was based on elk pellet group transects walked along major hiking and game trails within TRNP in August 1988. The number of pellet groups were counted along 2-m strip transects in 9 geographical divisions (sections) delineated by Sullivan (1988). A minimum transect length of 6.0 km was walked in each section. All elk pellet groups along transects were counted regardless of age or condition of the group.

Sectional elk use indices were calculated by dividing the number of pellet groups seen in each section by the number of km walked in that section.

Habitat Use and Activity Patterns

Elk habitat use was quantified using the two-tiered PT and HT/MU/Complex system discussed in the Vegetation section. Descriptions of these PTs and HTs/MUs/Complexes are found in Appendix A, Tables 30 and 31. Information concerning the landform and vegetational features of areas used by elk were noted in the field and used to identify PTs and HTs/MUs/Complexes on respective overlay maps of the SU of TRNP created by J. Norland.

Considerable effort was made to avoid disturbing elk, so observations were conducted at distances where I could not be spotted by the animals. Observations were logged on the first group of elk that were spotted. Elk were observed during diurnal hours for 1-7 hr periods. At each observation period the following information was collected: 1) the location of the elk group (plotted on 1:24,000 topographic maps); 2) the number of adult males (≥2 years), yearling males (1 year), females (≥1 year), and calves in each PT and HT/MU/Complex; and 3) the activity of each animal (recorded as feeding, bedding, standing, moving, other, or unknown). Calves were difficult to distinguish from yearling females after 7 months, so this class was recorded as "female" for observations beginning 15 January. Other activities included: interactions with other ungulates, mating activities, grooming, nursing, and other social behavior.

The activity of 1 animal recorded at the beginning of each 5-min interval was labeled an observation-minute. A minimum of 12 consecutive observation-minutes for 1 animal, or ≥6 consecutive observation-minutes for ≥2 animals was considered the minimum for inclusion of an observation period in the analysis.

Unknown activity was recorded when elk were known to be in a particular HT/MU/Complex even though they were not visible. This activity class was recorded most often during the spring and summer midday hours when elk were in wooded draws. If elk entered these draws and could not leave without the observer noticing, observation-minutes were recorded as unknown within that PT and HT/MU/Complex. The unknown category was necessary to determine relative diurnal habitat use.

When radio-collared animals were within wooded draws during spring/summer midday hours, the signal was checked at 15-min intervals for 30 sec to determine if the animal was active. Distinct changes in the strength of the signal during the 30-sec time period signal was identified as an "active" observation-minute. The number of observation-minutes recorded as unknown activity were multiplied by the percentage of radio-signal checks recorded as "inactive" to obtain adjusted diurnal activity and habitat utilization values. Irby (1976) reported that this technique was 89% effective in estimating activity in an ungulate study in Africa.

Data were collected for 4 seasons during phase 2. Each season was divided into 3 time periods (morning, midday, and evening). The lengths of these time periods were determined from natural breaks in the feeding:bedding ratios during diurnal hours. The percentage of activities occurring in PTs and HTs/MUs/Complexes was calculated for each time period. Time was recorded as Mountain Standard Time for comparison between seasons.

Ungulate Interactions

PT utilization was determined for elk, bison, feral horses, mule deer and white-tailed deer over the entire study and during the growing season (spring and summer seasons). Spearman's Rank Correlation Coefficients (r_S) were used to compare PT selection. Similarities in PT selection were considered significant at $p \leq 0.05$.

Interactions between elk, and bison, feral horses, and mule deer were noted during the study. The frequencies of no reaction, awareness, alarm, aggression, or displacement exhibited by elk or the other ungulates were recorded for 5 distance categories. The distance between elk and the other ungulates was estimated when these animals were first observed. Additional interaction notes were taken only if the distance between these animals changed abruptly, or if the reactions were different than when animals first came into contact. Displacement included slow, gradual movement away from another species or an immediate withdrawal. The distance animals withdrew, or distance to where they were last observed was also estimated. A mean displacement distance was calculated for elk and the other ungulates when displacement occurred.

Human Impacts

The reactions of elk to humans on foot, horseback, and in stationary vehicles were noted during the study. The frequencies of no reaction, awareness, alarm, or displacement were recorded for 4 distance categories. Both the distance of elk from humans during the time of disturbance and displacement distance, if any, were estimated. Displacement distance included the distance moved to cover or the distance to where the elk were observed no longer to be fleeing from the disturbance. A mean displacement distance was calculated for each type of human caused disturbance when displacement occurred.

Population Dynamics and Carrying Capacity

Population Censuses

A complete ground count of all elk in TRNP was taken in September 1987, and a complete ground count of the calf crop and adult bulls was taken in September 1988. Ground censuses could only be conducted in late August/early September when the entire herd had coalesced for pre-rutting activities. Census data for 1985-1986 were from Sullivan (1988).

Population age structures were calculated for each year of the 4-year study from estimated ages of the transplanted elk and from elk born in the Park from 1985-1988. Because a few elk of unknown ages left the Park, the age structures represent approximations. Calf:cow ratios were determined in September from the previous year's adult

(≥2 years) and yearling (1 year) females and from adult females alone, to determine herd productivity.

The population growth rate was determined from the linear regression (least squares method) of the $\log_e$ of the population counts each year from transplant to 1988. The slope of the regression line was assumed to be an approximation of r_a, the Actual Rate of Increase for a population (Caughley and Birch 1971, Caughley 1977, Gogan and Barrett 1987). The growth rate generated was compared to growth rates in the literature. Annual growth rates (r) were generated by the formula $r = \log_e(\text{count}_{t+1}/\text{count}_t)$ after Caughley (1977).

Forage Allocation

Forage was allocated for 4 ungulate species in the SU of TRNP (elk, bison, feral horse, and mule deer) using the Ungulate Resources Allocation Model developed by Norland (1988b). Pronghorn and white-tailed deer also occurred at TRNP, but these species had limited distributions and were not considered in the model. The model utilizes LINPRO, a linear programming software package, which solves optimization problems using the simplex solution technique (James 1981). An objective function is formulated which defines how the resource (forage) will be efficiently allocated among the competing decision variables (the ungulates). The objective function is then solved within the constraints (forage available) arriving at an optimal solution (number of ungulates) from an infinite number of feasible solutions (Norland 1988b).

Six inputs were used in the model:

1. Hectares of each PT within TRNP.
2. The amount of time spent in each region (defined below) by the various ungulates during the growing season (spring 1988, summer 1987-1988).
3. The diet (food habits) of each ungulate.
4. The production of the major dietary items within each PT, HT/MU/Complex, and region.
5. The average forage intake during the 6-month growing season for a typical animal of each ungulate species.
6. The percent allowable use of each dietary item.

<u>Number of Hectares of PTs</u>. Physiographic Types (PTs) used in this study were delineated by Norland (1984). A digitizing board was used to calculate areas of PTs outlined in aerial photographs (Marlow et al. 1984). Descriptions of these PTs are found in Appendix A, Table 30.

<u>Amount of Time in Region</u>. For analytical purposes, the Park was divided into 9 geographical regions, and the area of each measured by Marlow et al. (1984). A 6-region area (123.9 km^2) of TRNP, excluding the Cottonwood Forest and Old River Terrace PTs, was the only area used by elk. This area, hereafter referred to as the "Target Area", was the only area included in the model. Utilization of regions was based on observation-minutes for elk and on sightings for the other ungulates. Data collected during the growing season (summer 1987-1988, and spring 1988) were used. Utilization was only determined during the growing season because this is the time when plants are most susceptible to grazing damage (Sampson 1952, Bell 1973).

Ungulate Diets. Twenty fecal samples of elk, bison, feral horses, mule deer, and white-tailed deer were collected during late spring (15 May - 14 June) 1988, and late summer (1 August - 5 September) 1988, and 10 samples were collected for elk in early summer (15 June - 31 July) 1987. Each sample was collected from fresh fecal piles throughout the Target Area. These samples were shipped frozen to the Wildlife Habitat Laboratory in Pullman, Washington for microhistological identification of shrub, forb, and graminoid species composition. A reference collection of 104 plant species, collected in TRNP during phase 1 of the study (Sullivan 1988), was used to help identify forage items. Spearman's Rank Correlation Coefficients (r_S) were used to compare the similarities of growing season diets. Similarities in diet composition were considered significant at $p \leq 0.05$.

Microhistological analysis of food items in animal stomachs was first described by Baumgartner and Martin (1939) and later refined by Dusi (1949). Analyses of fecal samples follow similar procedures (Sparks and Malechek 1968, Ward 1970, Dearden et al. 1975). Forbs, which are the most digestible and least identifiable forage class, are often under-represented, and graminoids and browse over represented, in ungulate diet estimates using this technique (Bergerud and Russell 1964, Dearden et al. 1975, Vavra et al. 1978). Hanley and Hanley (1982) concluded that this analysis was sufficient for gross diet comparisons of ungulates. Accuracy could be improved by using digestion coefficients for individual forage species, but these coefficients were not available for most of the major forage species in TRNP.

<u>Production of Major Dietary Items</u>. Production for major forage species was determined for selected HTs/MUs/Complexes by Norland (1988<u>a</u>), and the percentage of HT/MU/Complex composition for the various PTs in TRNP was determined by Marlow et al. (1984). Production for the major forage species in each region and in the Target Area were estimated from the percent composition of PTs in each region (Marlow et al. 1984).

<u>Growing Season Intake</u>. Forage intake rates during the growing season were determined for a "typical animal" (based on the mean body size for a population) of each ungulate species from reported live weights, population estimates, sex ratios, and reported daily intake rates. Estimates of live weights for adult male elk (317 kg), adult females (236 kg), and calves (100 kg) were from Sullivan (1988). Feral horse weights for stallions, mares, and colts were visually estimated at 522 kg, 454 kg, 181 kg, respectively, by researchers at TRNP (L. Gagnon, pers. comm. 1989). Estimates of mule deer weights were from R. Mackie, pers. comm. 1989. Estimates of typical animal size, daily intake, and growing season intake for bison were from Marlow et al. (1984).

Intake rates have been calculated for elk (Murie 1951, Nelson and Leege 1982), and deer (French et al. 1955). Sex ratios and population censuses of feral horses were recorded by Park personnel in 1989 (J. Bradybaugh, pers comm. 1989). Population estimates and buck:doe:fawn ratios of mule deer were from aerial surveys conducted in 1988 by the North Dakota Department of Game and Fish.

<u>Percent Allowable Use</u>. Production values for the forage species used in the model were multiplied by an Allowable Use Factor (AUF) of 0.35 (35%). Sullivan (1988) chose an AUF of 0.35 when estimating the carrying capacity for elk in TRNP during phase 1. Marlow et al. (1984) adopted an AUF of 0.40 when determining the optimum carrying capacity for bison in TRNP. Long-term herbage production was reported to have substantially declined after season-long grazing by cattle at 35-50% utilization levels in the Central Great Plains (Kipple 1964).

RESULTS AND DISCUSSION

Distribution

Since the reintroduction, elk have expanded their range from the southeast corner of TRNP (Sullivan 1988) to include northcentral and southcentral areas. The region within the Park Loop Road (Fig. 1) appeared to receive heavier use by elk during phase 2 than was noted by Sullivan (1988) during phase 1. The Loop Road received considerable vehicular traffic during the tourist season, but the terrain within this loop was highly dissected and provided seclusion from human disturbance. The expansion of elk within TRNP can be attributed to an increased familiarity of areas with preferred forage and security cover, but the slow rate in which it occurred suggests that elk were conservative in selecting new habitats. Dispersal of individuals typically occurs under high density dependent pressures (Caughley 1970) and should not be expected to occur immediately following the introduction of animals into a relatively unrestricted environment.

Elk had not used areas west of the Little Missouri River extensively as of summer 1988, although forage and developed water sources were abundant. Elk were observed west of the river only once, when a Park employee saw two adult bulls 0.75 km west of the river in August 1988. As the elk population grows, this area should receive greater use and could potentially lessen relative grazing pressure in the eastern 2/3 of the Park.

Most elk have remained within TRNP since the reintroduction. A 2.3 m fence, which enclosed TRNP to prevent bison damage to surrounding private property, may have acted as a partial barrier to elk emigration. Vehicular traffic along an interstate highway which paralleled the Park's southern boundary and oil well activity along the northern boundary may have deterred elk from leaving TRNP. However, some elk were reported in areas outside TRNP, and these absences were reflected in population censuses.

Four reports of animals outside the Park were filed in 1987-1988 (Table 1). Two bulls (1 radio-collared in March 1987, identification number 0926, and 1 unmarked bull) left the Park in spring 1987. Reports of two adult bulls, including 1 with a radio-collar, were received throughout summer and fall 1987, at distances of 160-515 km east of the Park. The radio-collared bull was observed in TRNP on 18 January 1988 unaccompanied by the other bull.

On 4 November 1987, ≈20 cow and calf elk evidently leveled a 10-20 m section of fence on the eastern boundary and grazed on cropland adjacent to the Park for a short period of time before being herded into TRNP by Park rangers. Additional elk have been seen in the same area by Park employees during 1989. Fifteen to 17 elk were reported 18 km southeast of TRNP and 2-3 bulls 50 km east of TRNP during June 1988 (J. Bradybaugh, pers. comm. 1988). It was not determined whether the latter two groups were from TRNP.

Sullivan (1988) reported 3 incidences of elk leaving TRNP during 1985-1986 and noted that several other reported sightings outside the Park could have involved elk from a herd established ≈150 km to the north. All verified reports of elk leaving TRNP or missing from population censuses during the 4-year project are presented in Table 1.

Table 1. Verified reports of elk leaving and later returning to TRNP from 1985-1988. Reports for 1985-1986 are from Sullivan (1988).

Season	Number leaving	Age/sex	Number returning
Summer 1985	1	cow	0
Summer 1985	1	calf	0
Summer 1985	2	bulls	1
Fall 1986	5	cows	0
Winter 1986	1	cow	0
Spring 1987	2	bulls	1
Fall 1988	20	cows/calves	20
Total	32		22

Pellet Group Survey

In August 1988, an elk pellet group survey was conducted on major hiking and game trails within sections delineated by Sullivan (1988), to assess elk distribution within TRNP. Pellet group distribution roughly followed elk distribution based on observations (Fig. 3). However, this association was not exact because: 1) elk use of game trails may have varied among seasons; 2) the habitats used by elk during times of high defecation rates may have been over or under sampled; 3) feces decomposition and elk distribution varied by season; 4) the spatial distribution of elk along pellet group transects.

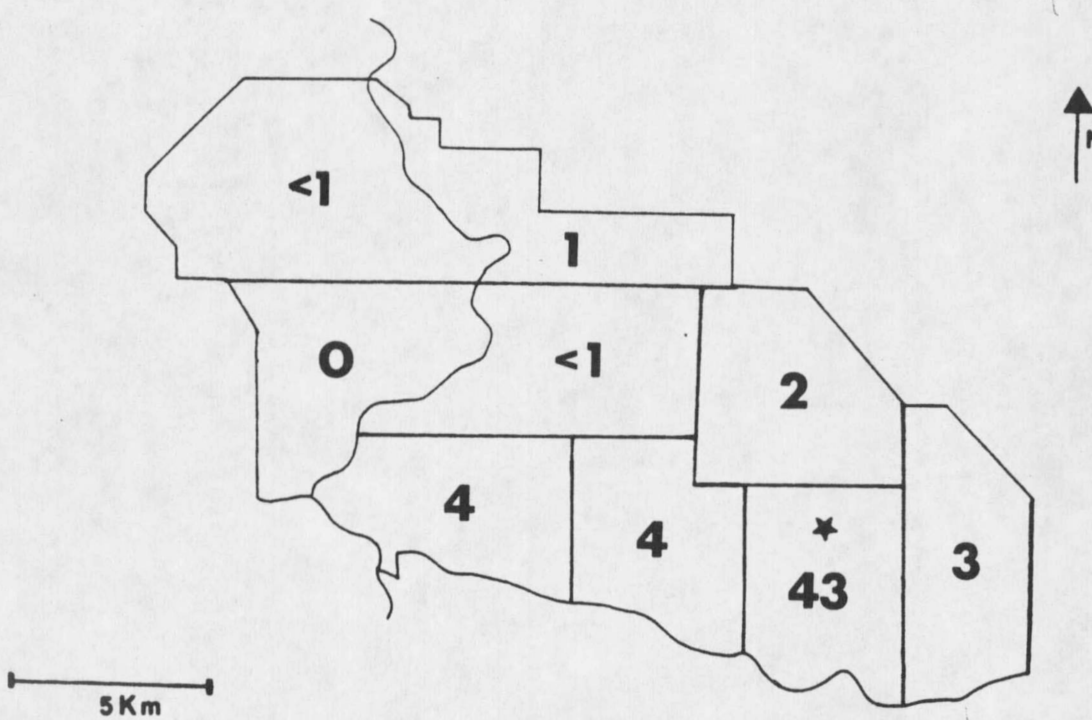

Figure 3. Elk pellet group survey in Theodore Roosevelt National Park, 1988. Numbers in sections = pellet groups per km. Map drawn by Sullivan (1988). ★ = release site of elk.

Transects were also walked along fencelines in several regions to determine if elk had been outside the Park. Three pellet groups were found outside the fenceline of the northernmost section east of the Little Missouri River. Apparently elk were occasionally using these areas, sites of active oil wells and livestock but no human residences, and returning to the Park. The fence in this area is as low as 1.5 m in some places, relative to the terrain, and may have been easily cleared by elk. Movement out of the Park probably occurred at night since there were no reports of elk north of TRNP during phase 2.

Herd Organization

Elk were sexually segregated into a bull and a cow-calf group for most of the year and only associated in late summer and early fall with the onset of rutting activities. Cow-calf groups consisted of adult females (≥2 years), yearling females (1 year), calves and occasionally yearling males. Although temporary divisions in the cow-calf group occurred, no permanent discrete units formed. These divisions occurred sporadically, and the associations between individuals were ephemeral. Craighead et al. (1973) noted that elk cow-calf groups in Yellowstone National Park were in a constant state of flux, with individuals moving often between groups.

The cow-calf group numbered 107 animals (excluding yearling males) at the last population census in 1988 but still appeared relatively stable, with all females associating frequently. In Wind Cave National Park, the origin of the transplanted elk at TRNP, 3 discrete cow-calf groups were observed that numbered 170, 90, and 40 animals, respectively (Varland et al. 1978). Wind Cave National Park is 114 km^2 (about 3/5 the size of TRNP) yet the home ranges of these cow-calf groups seldom overlapped (Varland et al. 1978). Based on cow-calf group sizes in Wind Cave National Park, the cow-calf group at TRNP may reach 170 animals before becoming unstable and dividing into discrete groups.

Yearling males were forced from the cow-calf group by adult females both before and after calving, although a few remained on the periphery of the group throughout the year. Franklin and Lieb (1979) found that yearling males, but not yearling female elk, were forced from cow-calf groups by their dams. Geist (1982) hypothesized that yearling bulls must leave cow-calf groups to seek higher quality forage because of their more demanding nutritional requirements compared to yearling females.

Most yearling bulls began a period of increased wandering, often in small groups of 2-3, after leaving the cow-calf group in summer. This continued throughout the year, except for a brief period of association with the cow-calf group in late August, when all animals coalesced for pre-rutting activities. Yearling males were first recorded with the bull group on 5 March 1988, when 9 of 12 yearling males were seen traveling with adult bulls. Three or 4 yearling males frequently associated with the cow-calf group until late May.

Adult males (≥2 years) segregated from the cow-calf group during most of the year. The ranges of adult bulls and cows seldom overlapped (Figs. 4-7). Geist (1982) suggested that adult bulls become more solitary after the rut to regain depleted fat reserves by feeding on more nutritious forage than what is selected by the cow-calf population. Sexual segregation has been identified in red deer (Darling 1937, Raesfeld and Vorreyer 1964) and elk (Flook 1970, Knight 1970, Franklin and Lieb 1979) populations.

The single bull group was often divided into subgroups with animals forming loose associations. However, because the home ranges of all adult bulls overlapped extensively and because all bulls were seen in 1 group on several occasions, only 1 group was recognized. Varland et al. (1978) identified 3 discrete bull groups in Wind Cave

National Park, with the largest numbering 35 individuals. During an aerial survey of the TRNP elk herd in winter 1989, all 25 adult bulls were observed in 1 group. Based on bull group sizes in Wind Cave National Park, it is conceivable that the bull group in TRNP will become unstable and segment with the addition of the 1988 yearling male cohort.

Seasonal Distribution and Home Range

The seasonal distribution of the bull (Male) and cow-calf (Female) groups are shown in Figures 4-7. Yearling male locations were recorded as "adult male" locations when these animals were with the bull group or isolated from the cow-calf group. Home range sizes were derived for all radio-collared and uncollared elk within TRNP for each season (Table 2). The home range of animal 0926 was impossible to determine over some of the study due to the animal temporarily leaving the Park. Radio transmitters for animals 1200 and 1251 worked only intermittently throughout the study and precluded large relocation sample sizes. Additionally, there is some evidence that these animals may have been using areas outside the Park.

Summer 1987

Most individuals of the cow-calf group were located near the Peck Hill area (Fig.1) during calving in early June. Cows were segregated into small nursery groups ($\approx$4-5 adult females) near calving areas following parturition. Larger groups of yearling males and females were assembled on the peripheral ranges of these nursery groups and

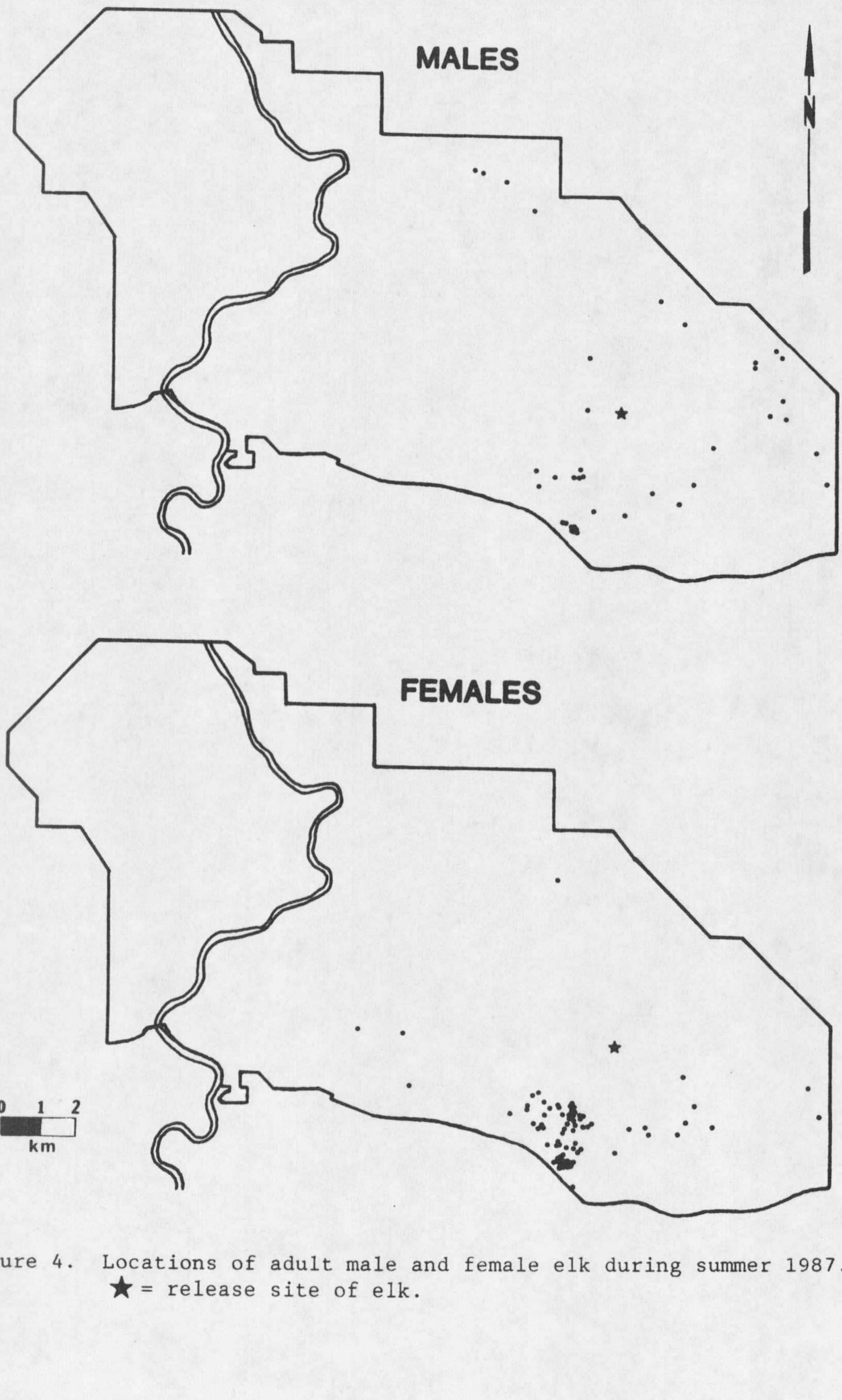

Figure 4. Locations of adult male and female elk during summer 1987.
★ = release site of elk.

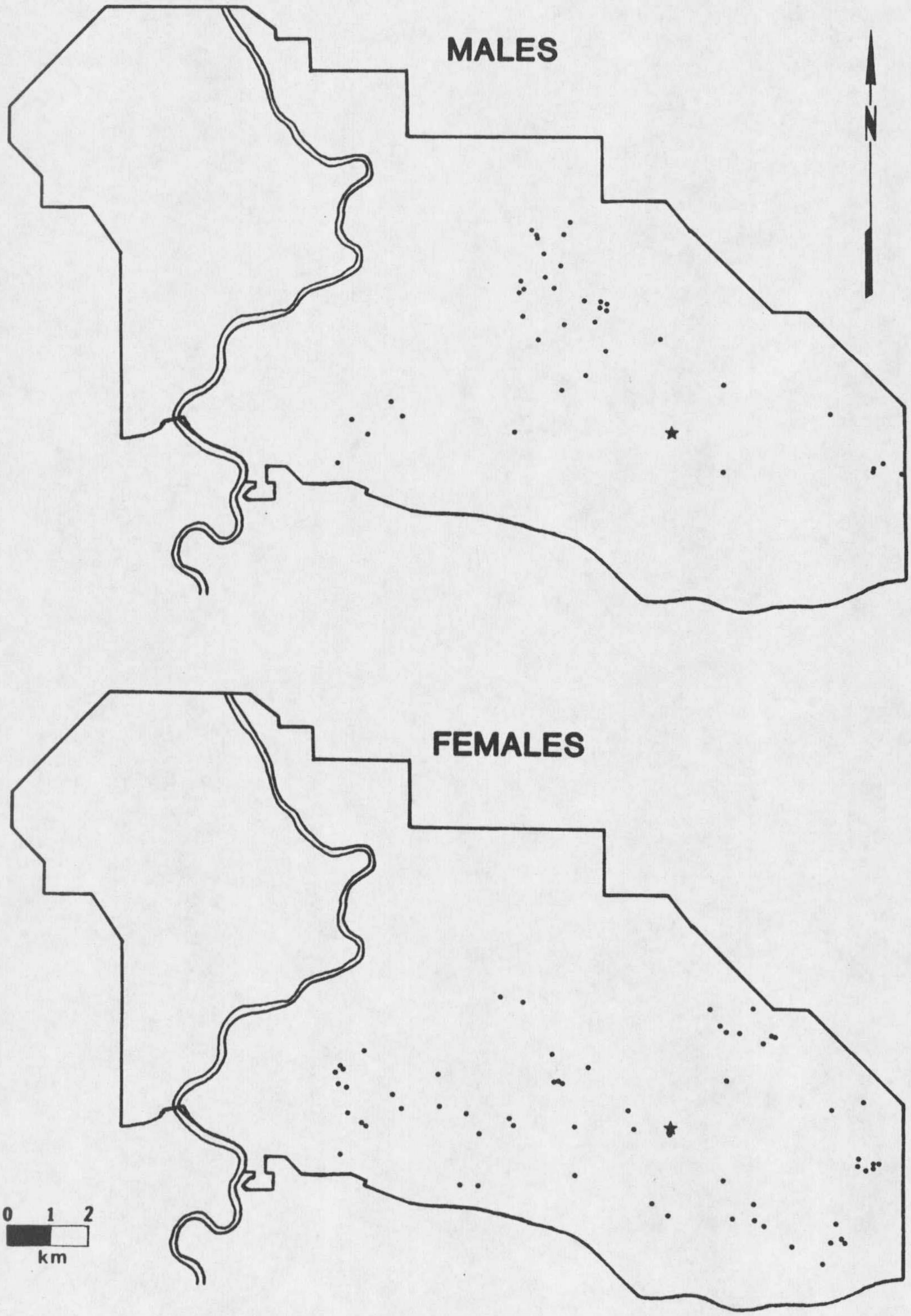

Figure 5. Locations of adult male and female elk during winter 1988.
★ = release site of elk.

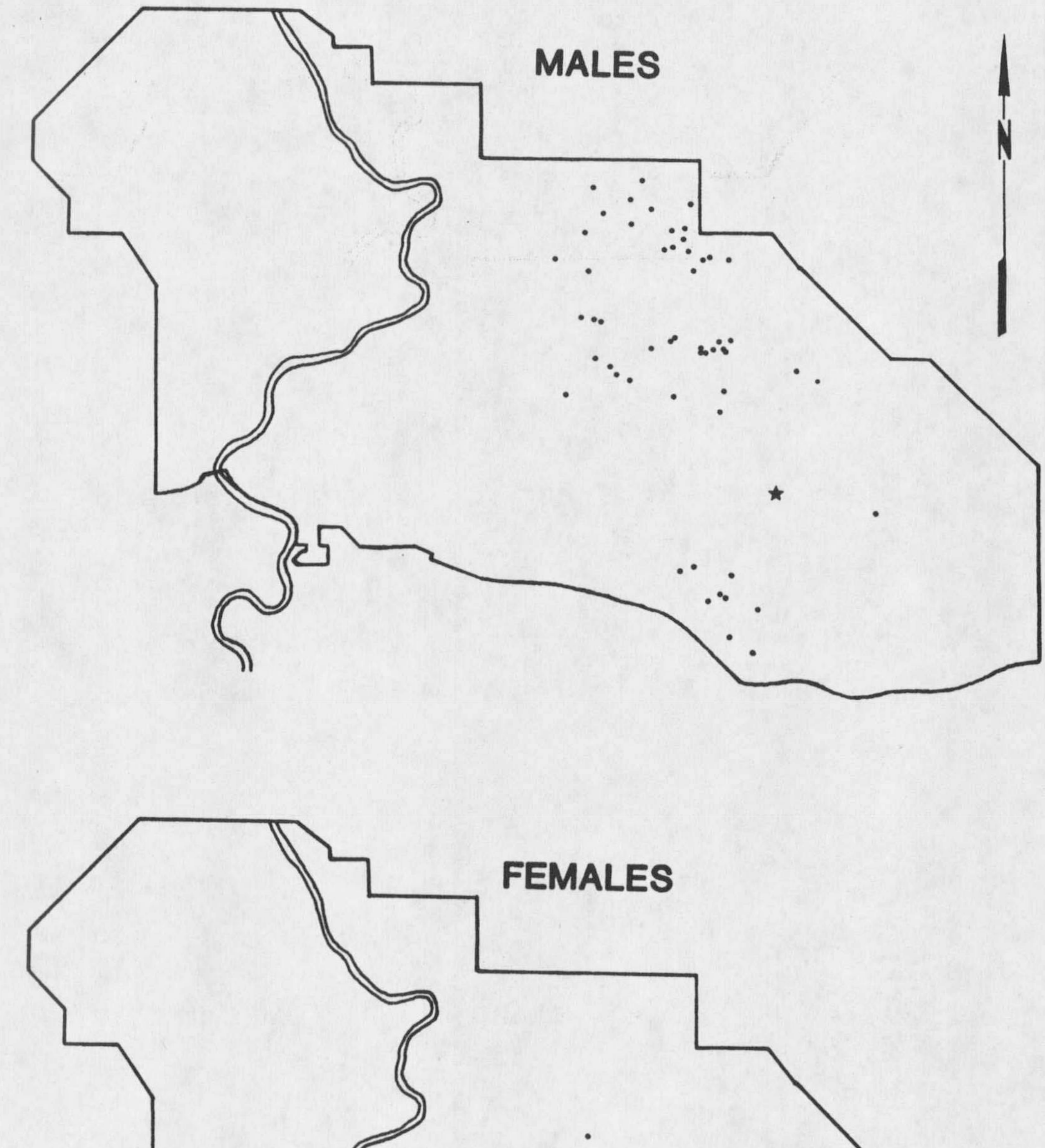

Figure 6. Locations of adult male and female elk during spring 1988.
★ = release site of elk.

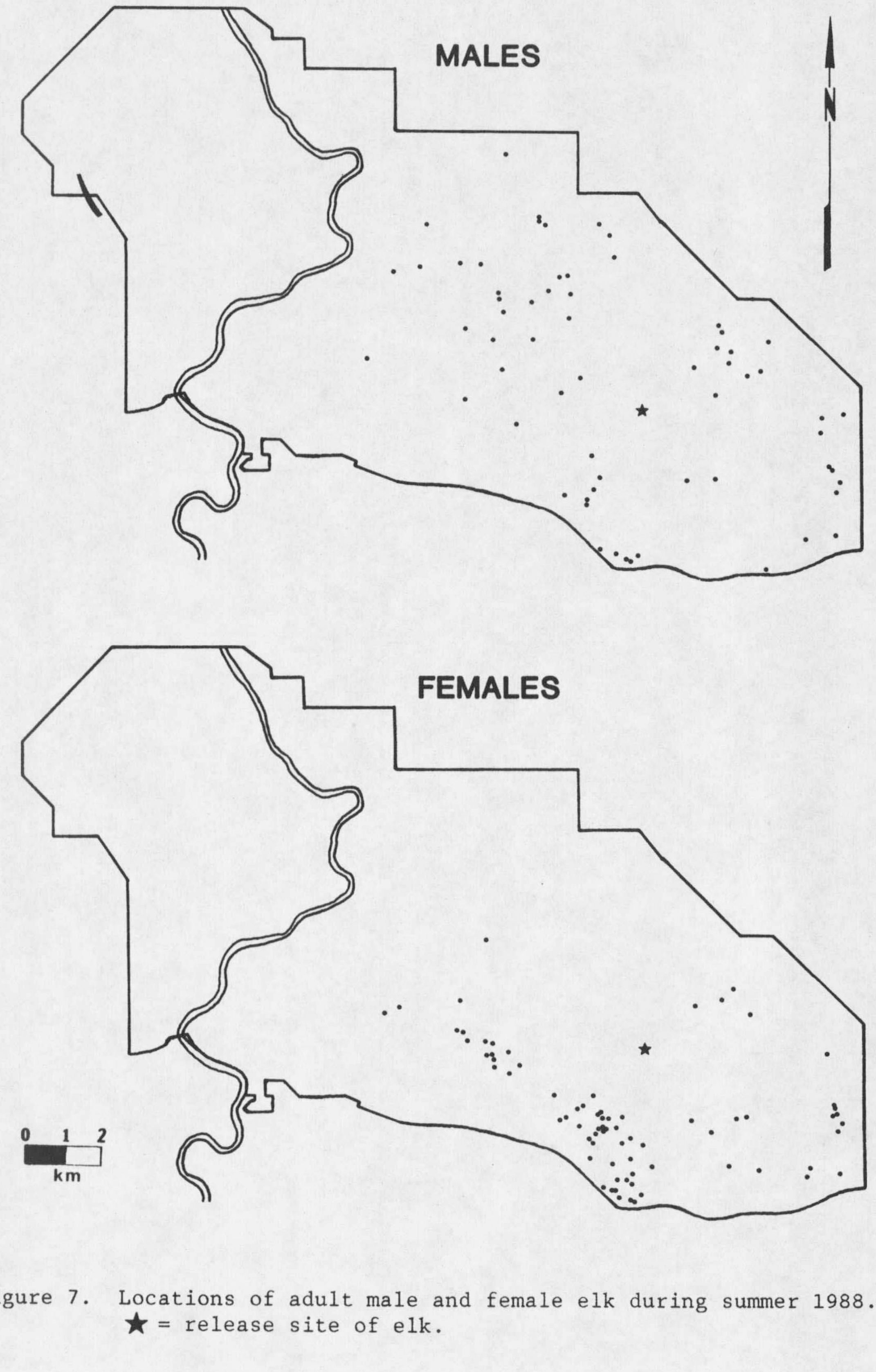

Figure 7. Locations of adult male and female elk during summer 1988. ★ = release site of elk.

occasionally associated with them. Nursery groups began coalescing by late June, and by 26 June, the cow-calf group was once again united.

After the nursery groups united, the cow-calf distribution was concentrated in the southcentral area of TRNP. Yellow sweetclover (<u>Melilotus officinalis</u>), a biennial forb, was very abundant in 1987 and seemed to be the preferred forage of the cow-calf group. Upland grassland plateaus in this area provided the highest concentration of yellow sweetclover in TRNP. Because of these concentrated foraging areas and the use of a single calving area, home range sizes were lowest for females during summer 1987. Home ranges of radio-collared females were similar to one another (9.8 - 20.9 km^2) and to the cow-calf group overall (25.8 km^2). The entire cow-calf group relocated to the eastern boundary of TRNP on 24 August, where pre-rut activities (bugling, sparring, and attempted harem formation by adult bulls) were first observed.

The bull group was observed most frequently in the northeastern and northcentral portion of TRNP in early summer 1987. Most adult bulls remained apart from the cow-calf group, although a raghorn bull (probably a 2-year-old) was observed with the cow-calf group throughout the summer. Larger bulls were infrequently seen with the cow-calf group for 1-3 days at a time starting in late July until the onset of pre-rutting activities on 24 August. After this time, the dominant adult bull (a large 6-point animal) was always seen with the cow-calf group, with satellite bulls often on the periphery of the group. Because of this association with females, home range size for the bull group was large during summer 1987 (49.2 km^2). Home range sizes varied greatly between the two radio-collared bulls in TRNP. Animal 0926, who had left the Park in spring 1987, was still outside TRNP in summer 1987.

Table 2. Seasonal home range sizes (km^2) for radio-collared and uncollared elk in TRNP.

Animal I.D.	Sex	Age[a]	Summer 1987 Size	N	Winter 1988 Size	N	Spring 1988 Size	N	Summer 1988 Size	N
0888	F	A	20.9	34	60.1	32	32.9	35	42.1	39
0980	F	A	15.4	41	54.3	24	27.0	48	36.0	40
0999	F	A	12.2	44	60.9	34	38.6	47	43.9	49
1055	F	A	9.8	46	55.6	30	47.1	45	23.7	37
1350	F	A	12.1	52	50.4	19	16.1	24	23.8	29
0926	M	A			47.1	21	38.2	30	53.2	25
1200	M	A	44.7	18	5.7	14	20.9	18		
1251	M	A	15.6	14	2.3	8	26.7	19	29.8	15
Cow-calf group			25.8	76	62.6	62	51.7	123	51.1	75
Bull group			49.2	38	50.4	38	39.7	53	80.0	62

[a] Adult = ≥2 years.

Winter 1988

The cow-calf group was most gregarious and cohesive during the winter season. The entire group was often seen feeding and bedding in large assemblages and traveled as a unit. The cow-calf group was also most mobile during the winter season, with daily movements from 0 (rarely) to 3 km. In January, the month with the greatest average movement, cows moved an average of 1.2 km / 24 hours. The winter 1988 home ranges were the largest for the cow-calf group (62.6 km^2) and for individual females during the entire study. Varland et al. (1978) recognized no major seasonal shifts in home range for 3 established cow-calf groups in Wind Cave National Park. Mackie (1970) found elk in the Missouri River Breaks, Montana to be most dispersed during the winter season, with constant "wandering" in search of forage which was locally abundant or had received little previous use by livestock.

Cows extended their range westward during the winter season. The western edge of their winter range brought them within sight of the Little Missouri River. An increased distribution and movement pattern may have been a strategy to utilize forage which had received little previous use. Elk in TRNP during winter 1988 frequently moved to isolated wind-swept buttes to graze. Although snowfall was minimal during winter 1988, it was energetically efficient for elk to graze in areas with the least snowfall and in areas that had little ungulate use during the spring and summer. Additionally, low snow cover during December 1987 - March 1988 probably allowed more extensive movement than was observed in winter during phase 1 by Sullivan (1988).

The bull group was most sedentary during the winter season, with its distribution concentrated in the rugged breaks and scoria hills in the northcentral part of TRNP. Bull movement was least during the winter season, with home range sizes for animals 1200 and 1251 only 5.7 and 2.3 km^2, respectively. Marked bulls in Wind Cave National Park did not make long-range movements during winter (Varland et al. 1978). All adult bulls (≥2 years) in TRNP closely associated during winter, and were often seen in 1 group. Varland et al. (1978) recorded the largest mean sizes for the bull groups in Wind Cave National Park during the winter season.

The adult bull home range increased dramatically when animal 0926 returned to TRNP on 18 January 1988 after being outside the Park for

10 months. Upon entering TRNP, animal 0926 associated with the cow-calf group and traveled with them throughout the southern portion of the Park. Most of the southern winter relocations for adult males (Fig. 5) were attributed to this animal. Animal 0926, along with several yearling males, joined the bull group on 5 March, but were low in hierarchal status, as was indicated by their submissive behavior in encounters with other adult males.

Spring 1988

The cow-calf group continued to function as a single unit during the early part of the spring 1988 season. Home range size for the cow-calf group remained high in spring 1988 (51.7 km^2). Occasionally, small subgroups would separate from the main group for 1-3 days, often relocating 1-5 km away, but would invariably return. Travel was considerably reduced compared to the winter season, and areas in the southcentral and southeastern part of TRNP were used more extensively.

Cows began dispersing on 11 May, with the onset of calving season, and by 17 May, 4 of 5 radio-collared females had relocated to within the Loop Road (Fig. 1), the area of most calving in 1988. Cows became solitary during the calving season. The radio collar on animal 1350 ceased to operate during spring 1988, and most relocations for this animal were when it accompanied other radio-collared females. This was also the only radio-collared female to calve east of the Loop Road in 1988, which accounts for the small home range of this animal (16.1 km^2). Small nursery groups formed near calving areas ≈2 weeks following the presumed peak calving time (1 June).

The bull group, which included most of the yearling males by early March, occupied the same area during early spring as during the winter season. In late spring, daily movement and range increased slightly compared to winter. Most bulls increased their home range in spring 1988 (20.9 - 38.2 km^2). Antler drop, which occurred from 13 April - 22 April, was accompanied by decreased tolerance among adult bulls (Geist 1982) and led to the breakup of the bull group into subgroups. Several subgroups roamed the southern portions of TRNP occasionally associating with groups of immature males and females on the periphery of female calving grounds. Bulls remained in these subgroups throughout the spring season.

Summer 1988

Cow nursery groups began to coalesce in late June, but remained near the calving grounds. Two large cow-calf groups, the largest inside the Loop Road and a smaller one in the southcentral portion of the Park near Peck Hill (Fig 1.), formed from the combined nursery groups and persisted throughout June and the first half of July. The cow-calf home range in summer 1988 was similar in size (51.1 km^2) to spring 1988 because of the extended period of time that nursery groups remained on the calving grounds.

On 18 July, the cow-calf groups reunited east of the Loop Road and remained united throughout the summer. The late reunion of cow-calf groups following calving in summer 1988 compared to summer 1987 was due to the greater distance between calving areas and, possibly, to a hesitancy to leave available water during a drought year. This separation following calving may become prolonged in the future and lead to a permanent division in cow-calf group.

Bull distribution and home range (80.0 km^2) was greatest during the summer 1988 season because: 1) bulls remained intolerant of each other throughout early summer; 2) bulls had gained a greater familiarity with the Park than during earlier seasons; 3) bulls began associating and traveling with the cow-calf group in August, and the cow-calf group had increased their distribution from summer 1987 to summer 1988. Adult bulls did not associate with the cow-calf group in July, as in summer 1987, and were first seen with females on 13 August. Pre-rutting activities were first observed on 25 August, when several bulls joined the cow-calf group on the eastern boundary of TRNP. Most bulls followed the cow-calf group as it moved to the southcentral portion of TRNP.

Population Dynamics

The population dynamics of the TRNP elk herd was recorded for each year of the 4-year project (Table 3). The number of yearling animals for 1985 and 1986 were extrapolated from earlier census data of Sullivan (1988). Sullivan (1988) noted 5 females of unknown age in summer 1986 and 1 in winter 1986 were missing from population censuses, and reported that local hunters and ranchers had observed 5-6 animals outside of TRNP about that time. It was assumed in this study that these animals left TRNP and, for the purposes of population modeling and cow:calf ratios, that these were 3 adult (≥2 years) and 3 yearling (1 year) females.

Table 3. Population dynamics of adult male and female (≥2 years), yearling male and female (1 year), and calf elk in TRNP. Data for 1986-1987 are from Sullivan (1988).

	Phase 1			Phase 2	
Sex/Age class	(Transplant) Mar 1985	Sept 1985	Aug 1986	Sept 1987	Sept 1988
Adult females	33	35	35[a]	40	53
Yearling females	3	2	6[a]	13	17[b]
Adult males	0	7	8	13	25
Yearling males	8	1	7	12	16[b]
Calves (male:female)	3 (1:2)	16 (7:9)	25 (12:13)	33 (16:17)[b]	37 (18:19)[c]
Total	47	61	81	111	148

[a] Extrapolated from censuses by Sullivan (1988).
[b] Estimates based on near complete censuses during phase 2.
[c] Estimated during phase 2.
[d] Elk leaving and entering TRNP in Table 1.

Complete censuses were obtained for calves and adult bulls in 1988, but only "near complete" censuses were obtained for adult females and yearling animals. Only one instance of mortality was verified during the study, when an adult bull was found dead after falling into a sinkhole in spring 1988. Therefore, because of the relatively young age of the herd, and because extensive groundwork revealed no other elk carcasses, I assumed that no other mortality had occurred between 1987 and 1988. Because previous calf crops at TRNP yielded ≈50:50 sex ratios (slightly favoring females), and other researchers have found near equal sex ratios in calf elk (Johnson 1951, Picton 1961), the calf crops in 1987 and 1988 were estimated to be 16 male : 17 female and 18 male : 19 female, respectively.

Population dynamics of elk in TRNP during 1985-1988 (Table 3) were indicative of a healthy, rapidly expanding population. Male antler development during 1987-1988 indicated bulls were receiving near optimal nutrition. Five out of 14 (36%) bulls 2 1/2 to 4 1/2 years of age had antlers with 6 points in 1987. Only 1 of the 14 (7%), probably a 2 1/2 year old, had antlers with <5 points. Nine out of 12 (75%) yearling bulls had 2 points on 1 or both antlers. Only 28% of the yearling bulls examined in Colorado by Boyd (1970) had 2 or more tines per antler.

Population growth rates and sex ratios were calculated from all known animals in the TRNP herd (Table 4). Only 10 elk (3 males and 7 females) were known to have emigrated from TRNP during the 4-year study. The fates of these individuals were not known, but they were included in the growth rate and sex ratio estimates to better understand the biological characteristics of the herd.

The male:female ratio of elk at TRNP increased from 24:100 for the original transplanted herd to 65:100 in September 1988 (Table 4), including those animals which left the Park (Table 1). A preponderance of females were introduced into TRNP to rapidly build up the population and because it is traditionally more difficult to capture, contain, and transport males during a reintroduction (J. Bradybaugh, pers. comm. 1989). Elk sex ratios of established populations, such as reported by Flook (1970) in Banff National Park

(36:100) and by Cole (1969) at the National Elk Refuge, Wyoming (31:100), are often low because of excessive mortality in adult males resulting from rutting injuries and/or from hunting in unprotected areas near reserves. Because of the near even calf sex ratios observed at TRNP, the overall sex ratio should continue to rise until mortality becomes a factor, and then decline, approaching the level of established herds (Peek 1982).

The Actual Rate of Increase of elk at TRNP (r_a), approximated by the least squares method (linear regression), was 0.31 over the 4-year study. Annual growth rates (r) varied from 0.33 from 1985-1986 to 0.26 from 1987-1988, the last year of the study. An aerial survey of the Park in September 1989 produced a count of 176 elk, indicating that the population is still increasing at a rapid rate.

Few studies have documented growth rates for liberated or naturally colonizing populations of elk in North America. A captive herd of Rocky Mountain elk on an ammunition storage depot in Missouri grew at 0.29 over an 8-year period (Murphy 1963). The growth rates of 2 reintroduced populations of Tule elk (*C. e. nannodes*) in southern California differed significantly, at 0.31 and 0.17, over a 6-year period (Gogan and Barrett 1987). McCorquodale et al. (1988) estimated the rate of increase in a colonizing population of Rocky Mountain elk in the shrub-steppe region of southcentral Washington to be 0.30 over a 4-year period beginning 9 years after colonization. The highest reported rate of increase in elk, 0.37, occurred 6 years after a reintroduction project on Afognak Island, Alaska (Burris and McKnight 1973).

Calf:cow ratios were calculated for each year of the 4-year study for all females ≥1 year and for adult females ≥2 years of the previous year (Table 4). Overall ratios were high, 66:100, when yearling females were included, and 77:100, when they were excluded. The decline in the calf:cow (≥1 year) ratio in 1988 was due to the growth of the yearling population segment. However, the calf:cow (≥2years) ratio in 1987 and 1988 were similar, at 94:100 and 93:100, respectively, indicating that the herd remained productive and did not suffer from density dependent factors.

Calf:cow (≥1 year) ratios at TRNP exceeded those of most established populations, which range from 18:100 (Cole 1969) to 71:100 (Boyd 1970). Craighead et al. (1973) found calf-cow (≥1 year) ratios in a non-migratory, non-exploited elk herd in Yellowstone National Park at 31 and 38:100 over 2 summers. These values were considered normal to low productivity for that area. Calf:cow ratios recorded during an aerial census of elk at TRNP in September 1989 also exceeded 90:100.

Calf:cow ratios at TRNP were similar to reported values in other newly established elk herds in North America. Gogan and Barrett (1987) recorded calf:cow (≥2 years) ratios of 64:100 and 87:100 for two reintroduced populations of Tule elk over 6 and 7 years, respectively. McCorquodale (1988) recorded calf:cow ratios of 76:100 (including yearlings) and 91:100 (excluding yearlings) for a colonizing Rocky Mountain elk population.

Table 4. Male:female ratios and logarithmic growth rates based on elk within and outside TRNP, and calf:cow ratios based potential breeding females within TRNP during previous years.

Year	Total population[a]	Male: 100 females	Growth rate (r)[b]	Calves : 100 cows All cows (≥1 year)	Calves : 100 cows Adult cows (≥2 years)
1985[c]	47	24	--	--	--
1985	64	36	0.31	47	52
1986	89	48	0.33	68	71
1987	122	58	0.32	80	94
1988	158	65	0.26	70	93
			r_a = 0.31	$\bar{X}$ = 66	77

[a] Total population of elk within and outside TRNP.
[b] $r = \ln(count_{t+1}/count_t)$.
[c] Transplant.
[d] r_a = Actual Rate of Increase over 4 years.

Food Habits

Plant species composition in the fecal samples of elk, bison, feral horses, mule deer, and white-tailed deer was determined for late spring 1988 and late summer 1988 (Appendix D, Tables 47-51). Plant species composition in elk feces was also determined for samples collected in early summer 1987 (Appendix D, Table 47). Plant species composition for the growing season (spring and summer seasons) was calculated from the mean of seasonal percentages. Percent species composition in fecal samples was assumed to be approximately equivalent to diet composition.

Elk Diets

Forage items which composed ≥3% of elk diets in any seasonal sample are listed in Table 5. In late spring (15 May - 15 June) 1988 graminoids and forbs were selected in roughly equal proportions, with browse being less important. A wide variety of forbs were selected but only scarlet gaura (Gaura coccinea), wild bergamot (Monarda fistulosa), and scarlet globemallow (Sphaeralcea coccinea) were >3% of the spring diet composition. Western wheatgrass (Agropyron smithii) and sedges (Carex spp.) were the most abundant graminoids in fecal samples during late spring 1988.

Other studies have shown the importance of western wheatgrass (Mackie 1970) and carices (Wydeven and Dahlgren 1983, Sullivan 1988) in the diets of elk in the Northern Great Plains. Spring elk diets in TRNP had a higher percentage of forbs than reported in most studies (Kufeld 1973). Precipitation was below normal during spring and summer 1988, and low precipitation and high temperatures typically advance plant phenology (Bell 1973). In spring 1988, elk in TRNP may have shifted to a typical summer diet (i.e. high in forbs) (Kufeld 1973) early because of the drought.

In early summer (16 June - 31 July) 1987, browse was the most abundant forage class in fecal samples. Winterfat and snowberry (Symphoricarpos occidentalis) were the major browse species in elk diets during early summer. Female elk observed at TRNP increased their browsing prior to calving in both years of the study and continued to browse heavily throughout the early summer. Elk need high levels of protein during this time for gestation, lactation, and body growth (Nelson and Leege 1982). Flowers and succulent stems of woody vegetation were evidently the best source of available protein in TRNP.

Table 5. Seasonal percent elk diet composition of graminoids, forbs, and browse comprising ≥3% of any seasonal diet.

Plant species	Late spring 1988	Early summer 1987	Late summer 1988
Graminoids			
Agropyron smithii	7.8	3.4	4.2
Bromus inermis	5.7	1.2	1.0
Carex spp.	7.2	2.4	
Poa spp.	1.1	9.5	0.3
Schizachirium scoparium	3.8		
Stipa viridula	5.4	8.7	4.8
Total graminoids	36.3	26.4	12.5
Forbs			
Gaura coccinea	3.6	1.6	4.2
Lactuca spp.	1.3	3.2	0.3
Monarda fistulosa	3.3	2.8	3.2
Sphaeralcea coccinea	4.5	6.0	21.5
Total forbs	38.8	25.4	45.9
Shrubs			
Artemisia frigida	0.3	1.6	4.9
Ceratoides lanata	2.2	18.1	17.5
Prunus virginiana	3.5	6.8	4.6
Rhus trilobata	4.0	4.8	2.1
Ribes spp.	1.6	1.2	3.5
Rosa spp.	3.1		2.0
Shepherdia argentea	4.7		0.5
Symphoricarpos occidentalis	3.1	14.3	5.0
Total shrubs	24.9	47.0	41.6

Cool season grasses were selected in early summer, with bluegrass (*Poa* spp.) and green needlegrass (*Stipa viridula*) constituting the majority of the graminoids eaten. In summer 1987, TRNP received above average precipitation, and the proportion of forbs to graminoids selected by elk was roughly equivalent to late spring 1988, a drought year. The major forb species selected were also similar to late spring 1988, except for the increased importance of wild lettuce (Lactuca spp.). Although yellow sweetclover did not appear as a major dietary item, observational data indicated that elk were selecting for yellow sweetclover and were often seen in concentrated stands. Elk fed mostly on the flowers of yellow sweetclover, the most digestible and least identifiable structure in microhistological analysis. This may explain the limited amount of yellow sweetclover in elk feces collected during early summer. Mackie (1970) found yellow sweetclover to comprise over 1/2 the total summer diets of elk in the Missouri River Breaks, Montana.

In late summer (1 August - 5 September) 1988, elk diets were composed mostly of forbs and browse with minimal graminoids. As graminoids begin to mature and desiccate in late summer, elk in several studies have been reported to switch to forbs and the succulent twigs and leaves of browse (Nelson and Leege 1982). Scarlet globemallow was once again an important food component, comprising 21.5% of the total late summer elk diets. Sullivan (1988) found scarlet globemallow to be the only forb to constitute >3% diet composition for elk at TRNP during any season. Scarlet gaura, a forb of dietary significance in late spring 1988, also received substantial use by elk in late summer 1988.

Winterfat was the most common browse species, constituting 17.5% of the estimated elk diets in late summer 1988. Sullivan (1988) found winterfat to be the most important browse species in elk diets for every season at TRNP. Fringed sage (Artemisia frigida), snowberry, and chokecherry (Prunus virginiana) were also important browse species in late summer 1988. Elk evidently still preferred cool season grasses over warm season grasses in late summer. Cool season grasses at TRNP are mostly associated with moist sites and may produce some regrowth in late summer.

Comparison of Ungulate Diets

Comparisons of ungulate diets during the growing season were based on all items identified in fecal analysis (62 items) (Appendix D, Tables 47-51), and on the percentages of graminoid and browse species which composed ≥3% of any growing season diet and for which production was available (11 items) (Tables 6 and 26). Comparisons of growing season diets assessed potential competition for forage species regardless of the plant phenology or seasonal ungulate preference.

In comparisons of total diets, elk diets were most closely correlated with feral horses diets (r_S=0.49 $p<0.01$), followed by bison diets (r_S=0.39 $p<0.01$). These correlations were significant but not very strong because bison and feral horses tended to use more grass and elk more forbs during the growing season. When the relative utilization of the 11 major forage items was compared, elk were negatively correlated, but not significantly, to both bison and feral horses.

Table 6. Spearman's rank correlations (r_S) of total diets (TOT) and diets of 11 major forage items (MAJ) for elk, bison, feral horses, mule deer (MD), and white-tailed deer (WTD).

	Bison		Horse		MD		WTD	
	TOT	MAJ	TOT	MAJ	TOT	MAJ	TOT	MAJ
Elk	0.39 p<0.01	-0.25 p=0.44	0.49 p<0.01	-0.11 p=0.76	0.32 p=0.01	0.25 p=0.46	0.21 p=0.10	0.23 p=0.48
Bison			0.82 p<0.01	0.94 p<0.01	-0.14 p=0.29	-0.66 p=0.03	-0.14 p=0.29	-0.47 p=0.14
Horse					0.07 p=0.60	-0.60 p=0.05	0.08 p=0.55	0.87 p=0.19
MD							0.48 p<0.01	0.87 p<0.01

Total elk and deer diets were not closely correlated, due to a greater use of browse by deer, utilization of different forbs, and greater use of graminoids by elk. When use of the 11 major forage items were compared (Table 6), elk were positively, but nonsignificantly, correlated with both mule deer and white-tailed deer. Sullivan (1988) found significant, positive correlations between elk and mule deer diets in summer, fall, and spring and felt that competition may become acute for certain browse species. In this study, the most selected browse item by elk, winterfat, was not eaten by mule deer or white-tailed deer in spring or summer. Based on feeding site data, Mackie (1970) found mule deer diets to consist of 48% browse during the spring and summer seasons combined, while elk diets included only 10% browse.

The correlation between total bison and feral horse diets was very high (r_S=0.82 p<0.01). Bison and feral horses fed primarily on graminoids. Forbs were somewhat more important in bison diets. Graminoid species, such as western wheatgrass, sedges, and bluegrass, were important in both diets. One shrub, winterfat, was also of dietary significance. When diet composition of the 11 major forage items was compared, bison and feral horse diets were almost identical (r_S=0.94 $p<0.01$).

Total diets of mule deer and white-tailed deer were significantly similar, although this correlation was not strong (r_S=0.48 $p<0.01$). Although both herbivores selected mostly for browse, the forb and browse species found in white-tailed deer diets were associated with the more mesic river bottom sites. Two browse species, chokecherry, used heavily by white-tailed deer, and silver buffaloberry (Shepherdia argentea), used mostly by mule deer, were important in both diets. Chokecherry, and to a lesser extent buffaloberry, were found to be important in white-tailed deer diets in eastern Montana (Allen 1971). Mackie (1970) found chokecherry second in importance to skunkbush sumac (Rhus trilobata) as primary browse in mule deer diets in the Missouri River Breaks, Montana. The correlation between mule deer and white-tailed deer diets was much higher (r_S=0.87 $p<0.01$) when the 11 major forage items were compared.

Activity Patterns

Season lengths and the number of observation-minutes of elk are noted in Table 7. Activity was similar for summer 1987 and summer 1988 (r_S=0.82 $p<0.01$) so these seasons were combined for analysis. Hours of each season were divided into morning, midday, and evening time periods based on distinct breaks in feeding:bedding ratios (Table 8). Percentage elk activity recorded for each diurnal hour during summer 1987-1988, winter 1988, and spring 1988 is shown in Figs. 8-10.

Table 7. Season lengths and number of observation-minutes recorded for elk during each season.

Season	Starting date	Ending date	Observation-minutes
Summer 1987[a]	June 15	Sept. 5	21,284
Winter 1988	Jan. 15	March 15	23,008
Spring 1988	March 16	June 14	32,073
Summer 1988[a]	June 15	Sept. 5	29,249

[a] These seasons were combined for analyses.

Elk exhibited crepuscular peaks in feeding in spring 1988 (hours 5 and 18) and summer 1987-1988 (hours 4-6 and 16-20). Bedding was the dominant activity during midday hours in spring and summer. Bedding reached daily highs during hours 9, 11, and 13 in spring and hours 11 and 13 in summer. Standing and other activities were minimal throughout the day during each season. Moving occurred most often in the morning and evening as animals moved to and from feeding and bedding areas. Spring and summer patterns were roughly similar, but elk exhibited a slightly stronger crepuscular pattern in spring than summer. Sullivan (1988) noted similar spring and summer activity patterns during phase 1 but found elk to be slightly more active during midday hours than was observed in this study.

During the winter 1988 season, elk also exhibited morning and evening peaks of activity but fed throughout the day. Diurnal feeding may have been an energy conservation strategy in that elk could reduce heat loss by concentrating activity during the warmer diurnal hours and seeking thermal shelter during the colder nocturnal hours (Beall 1974). Bedding showed similar, but less dramatic, patterns to spring and summer. Bedding reached a midday high at hours 10 and 11, and daily lows at hours 7 and 18. Elk were more gregarious during the winter season than the spring and summer seasons; and because elk tend to conform to herd activity patterns (Craighead et al. 1973), showed less variation in hourly activities than during spring and summer.

Table 8. Feeding to bedding ratios of elk during diurnal hours in each season, and the time period designation for morning (AM), midday (MD), and evening (PM).

	Feeding:bedding ratio					
Hour	Winter 1988		Spring 1988		Summer 1987-1988	
4			3.07	AM	3.22	AM
5			10.70	AM	2.07	AM
6	3.00	AM	2.29	AM	1.89	AM
7	17.70	AM	0.68	MD	0.37	MD
8	1.38	AM	0.27	MD	0.30	MD
9	0.43	MD	0.06	MD	0.14	MD
10	0.43	MD	0.23	MD	0.26	MD
11	0.51	MD	0.07	MD	0.30	MD
12	0.63	MD	0.13	MD	1.03	MD
13	0.72	MD	0.04	MD	0.19	MD
14	1.28	MD	0.99	PM	0.78	MD
15	0.70	MD	1.40	PM	0.66	MD
16	1.66	PM	2.55	PM	2.75	PM
17	1.19	PM	3.56	PM	1.86	PM
18	72.00	PM	9.11	PM	3.87	PM
19			6.62	PM	3.74	PM
20					3.65	PM

When elk were in cover during spring and summer midday hours they were recorded as being inactive 76% and 70% of the time, respectively, based on radio-signal checks. New diurnal activity percentages were

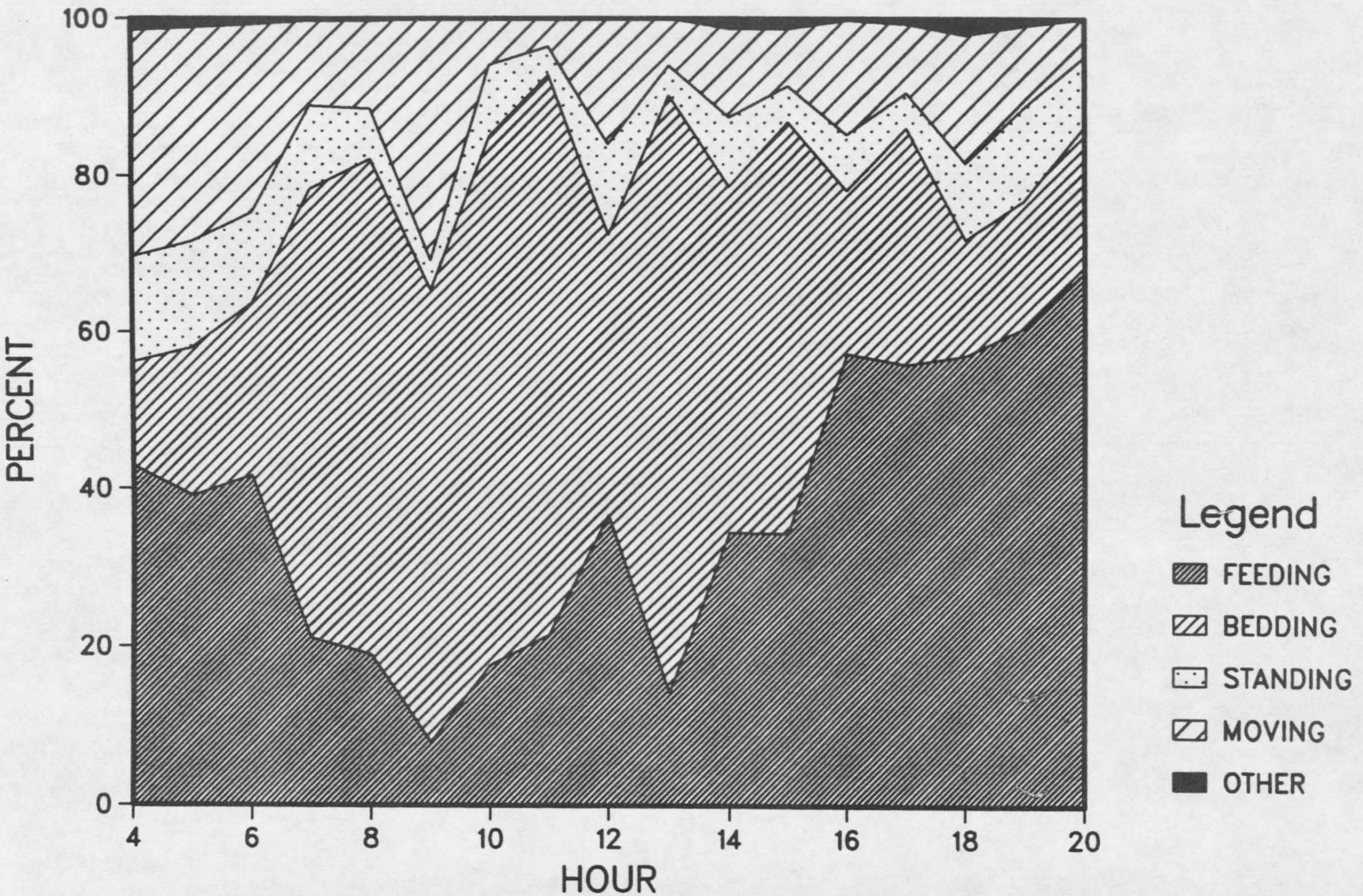

Figure 8. Percent observation-minutes spent feeding, bedding, standing, moving, and other by elk during summer 1987-1988.

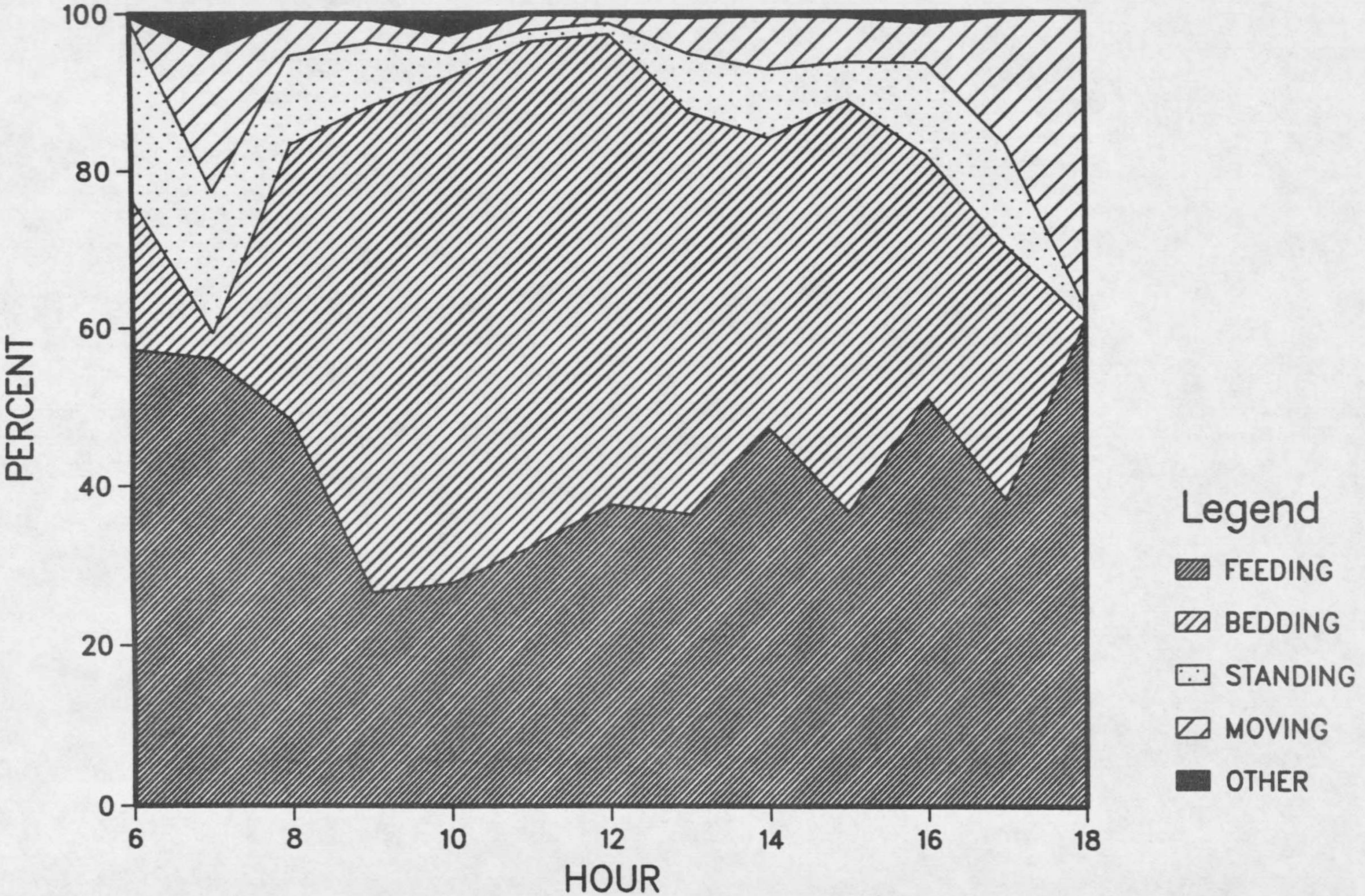

Figure 9. Percent observation-minutes spent feeding, bedding, standing, moving, and other by elk during winter 1988.

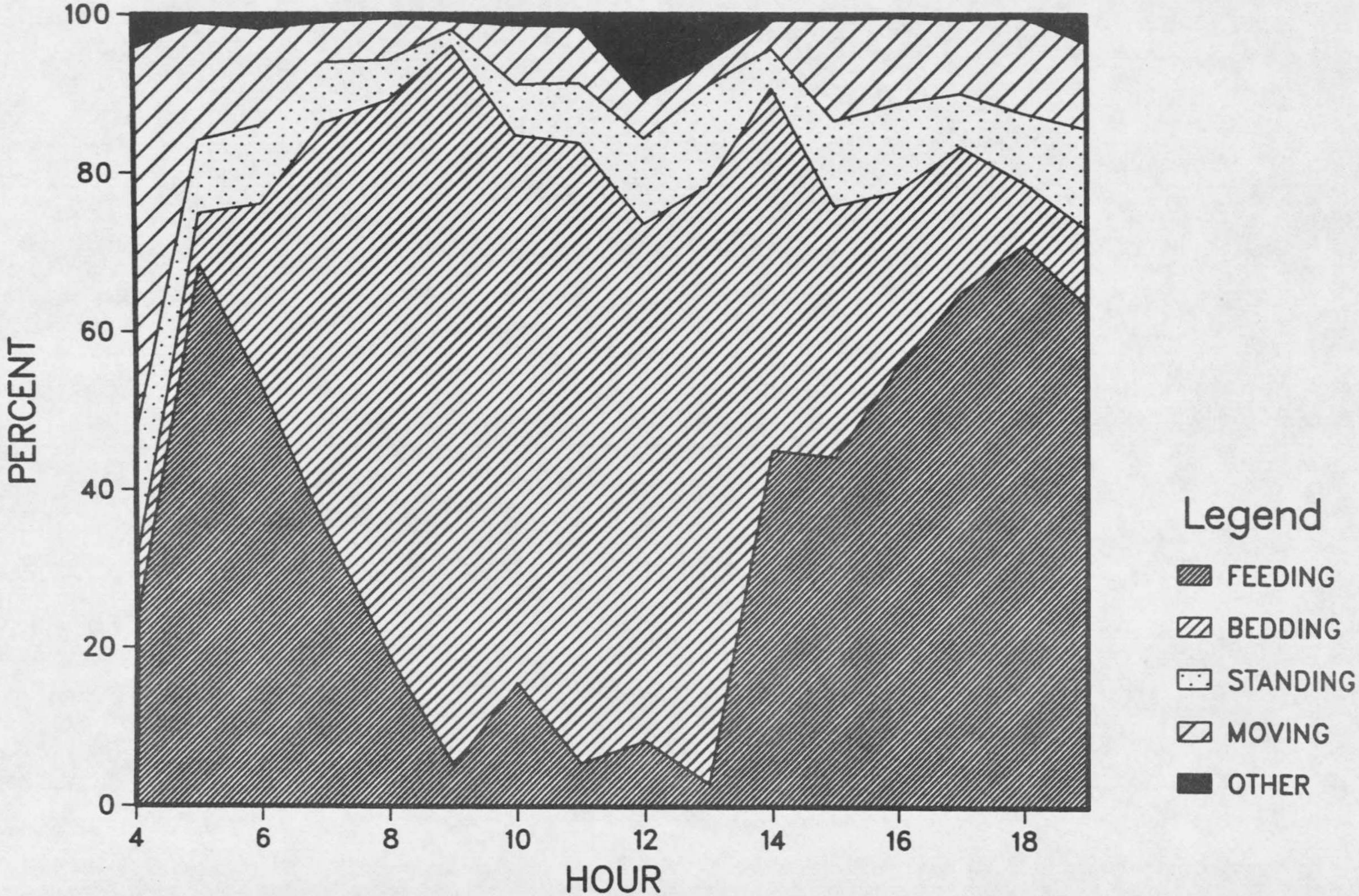

Figure 10. Percent observation-minutes spent feeding, bedding, standing, moving, and other by elk during spring 1988.

calculated using these figures (Table 9). Percent bedding was more realistically expressed, but the amount of feeding, standing, moving, and other activities that occurred in cover could not be accurately estimated.

Table 9. Percent elk activity for each season and adjusted activity for the spring 1988 and summer 1987-1988 seasons. Adjusted activities are in parentheses.

	Activity				
Season	Feeding	Bedding	Standing	Moving	Other
Winter 1988	40	46	7	5	1
Spring 1988	46 (38)	35 (47)	8 (7)	10 (8)	1 (1)
Summer 1987-1988	46 (37)	26 (40)	10 (8)	17 (14)	1 (1)
Total	44 (38)	34 (44)	9 (7)	12 (10)	1 (1)

Over the course of the study, elk were observed feeding and bedding 44% and 34%, respectively. When activity figures were adjusted, bedding became the dominant diurnal activity, at 44%, followed by feeding at 38%. Craighead et al. (1973), when monitoring the 24 hour activities of 7 female elk in Yellowstone National Park (recorded as feeding, bedding, and moving) also found bedding to be the dominant activity, at 46%, followed by feeding at 44%. Sullivan (1988) observed elk in TRNP feeding and bedding 49% and 41%, respectively, but noted that feeding, which occurred mostly in open grassland habitats, might be overestimated.

In summer 1987-1988, adjusted bedding (40%) was slightly higher than adjusted feeding (37%). Because the amount of feeding that occurred in wooded draws could not be observed, it is possible that true diurnal percentages of feeding and bedding were near equal. Craighead et al. (1973) noted that feeding and bedding by elk occurred in similar proportions in summer, at 40% and 41%, respectively. In TRNP, adjusted moving was highest in summer (14%) than in any other season because of extensive movement between feeding and bedding areas in the late morning and early evening. Craighead et al. (1973) also noted traveling (moving) to be highest during the summer season.

Bedding was the dominant diurnal activity (46%) in the winter 1988 season. Midday cover was not used, and elk bedded in open areas. Feeding in winter, at 40%, was higher than adjusted feeding in spring and summer. However, Craighead et al. (1973) noted that elk adopted a conservative strategy during winter, feeding less and bedding more during the nocturnal and diurnal hours than in other seasons. Standing, moving, and other activities were minimal for elk at TRNP during the winter diurnal hours.

During the spring 1988 season, adjusted bedding (47%) was the dominant activity. Craighead et al. (1973) found feeding to be dominant spring activity because of a response to newly available food sources. The changes in seasonal forage availability is less dramatic in the Northern Great Plains than in the Rocky Mountains because of substantially less snow accumulation. Elk at TRNP followed similar activity patterns in the early spring as in the winter, until high midday temperatures forced elk to seek cover.

Habitat Use

Sex/Age Classes

Adult males were most often observed in Breaks (50%) and Scoria Hills (35%) PTs (Table 10), mostly the Steep Scoria Complex (Table 11). Females selected for Breaks (39%) and Scoria Hills (18%) PTs, but used the less precipitous Rolling Scoria Complex. Calf use of PTs closely followed that of females. Males selected for more rugged habitat than females throughout the year, except during the rutting season when sexes were together. Adult males were most often sighted in the northern regions of TRNP where highly dissected terrain and large expanses of juniper cover (JUSC/ORMI HT) were most prevalent. Juniper draws provided shade during the hot midday hours of spring and summer which minimized evaporative cooling by elk. Males made greater use of wooded draws during all seasons than females.

Other researchers have also found male elk to utilize rougher terrain and higher elevations than females (Flook 1970, Franklin and Lieb 1979). Geist (1982) attributed differences in habitat selection between males and females to the need of males for protected areas with high quality forage to gather nutrients, recuperate from the rut, and avoid predators. Raesfeld and Vorreyer (1964) noted that red deer males selected heavily wooded areas following the rut, and Franklin and Lieb (1979) found Roosevelt elk (C. e. roosevelti) to exhibit this same pattern.

Yearling bull PT selection differed from females and adult males. Because cow-calf groups may be able to subsist on lesser quality forage than yearling males (Geist 1982), young bulls should leave female home ranges to seek areas with more nutritional food. Yearling males are also harassed by their dams at calving and begin a period of increased wandering following the birth of new calves (Altman 1952, Lowe 1966, Franklin and Lieb 1979). During the late winter and spring seasons, yearling males were often seen with or in close proximity to the bull group, although a few remained with the cow-calf group throughout the year.

Table 10. Percent feeding (F), bedding (B), and total activities (TOT) by adult male, yearling male, female, and calf elk in Physiographic Types (PTs) of TRNP.

Physiographic Type	Adult males			Yearling males			Females			Calves		
	F	B	TOT	F	B	TOT	F	B	TOT	F	B	TOT
Bottom Grasslands	5	1	3	10	10	8	13	9	10	7	9	6
Breaks	30	43	50	13	29	36	25	41	39	24	37	43
Sagebrush Bottoms	tr[a]	tr	tr	1	tr	1	1	tr	1	2	tr	1
Upland Grasslands	20	10	10	42	31	25	41	27	29	38	30	21
Prairie Dog Towns			0			0	tr	0	tr	tr	tr	tr
Ridge & Ravine	4	tr	2	tr	tr	tr	2	6	3	0	0	0
Old River Terrace			0			0			0			0
Scoria Hills	40	45	35	34	30	31	18	17	18	29	24	28

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

Habitat Type (HT) selection was more similar than PT selection among sex/age classes (Table 11). Juniper draws (JUSC/ORMI HT), which occurred mostly in the Breaks PT, was heavily used by all sex/age classes but females. This HT was used most for midday cover. Females, which lived in large aggregations and were presumably less vulnerable to ambush by predators or displacement by other ungulates

(Geist 1982), may have felt more secure and, therefore, were willing to spend a greater proportion of diurnal hours in open habitats. The heavy use of AGSM/STVI HT, an open prairie HT which occurs in both the Upland and Bottom Grassland PTs, was important to all sex/age classes, but was especially preferred by females.

Table 11. Percent feeding (F), bedding (B), and total activities (TOT) by adult male, yearling male, female, and calf elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes of TRNP.

HTs, MUs, and Complexes	Adult males			Yearling males			Females			Calves		
	F	B	TOT	F	B	TOT	F	B	TOT	F	B	TOT
AGSM/STVI	10	8	6	16	30	17	27	34	25	11	24	14
AGSM/STCO			0	1	0	tr[a]	1	tr	1			0
STCO/BOGR	6	5	4	3	1	2	5	4	4	3	6	3
SCSC	8	4	6	4	9	5	12	10	10	7	12	7
SCSC/JUHO	0	0	tr	1	4	1	tr	4	1	tr	2	1
ARTR/ATCO	3	1	2	5	7	5	8	13	9	4	2	4
ARTR/BOGR	tr	0	tr	tr	2	1	1	2	1	0	0	tr
ARCA	tr	tr	tr	1	tr	1	2	tr	1	2	tr	1
JUSC/ORMI	2	14	30	1	4	19	tr	3	11	tr	2	21
POTR/BEOC	0	0	tr	tr	0	tr	tr	0	tr	tr	0	tr
Hardwood Draws	2	2	3	3	4	6	3	7	7	10	15	16
Brush			0	tr	0	tr	1	tr	tr	tr	tr	tr
Rolling Scoria	18	18	11	25	18	19	13	11	11	24	18	15
Steep Scoria	19	24	17	8	11	8	4	5	4	3	4	3
Introduced Grass	12	1	4	33	8	14	21	4	11	32	15	13
Prairie Dog Towns			0			0	tr	0	tr	tr	tr	tr
Man-Managed	tr	0	tr	tr	0	tr	1	0	tr	1	tr	tr
Unvegetated Areas	19	24	15	tr	1	1	1	3	2	1	tr	1

[a] tr = <0.5%.
[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

Feeding by adult bulls was observed primarily in the unvegetated areas, but this was sporadic and mostly during the late morning, midday, or early evening when bulls were moving to and from bedding sites. Active feeding in the early morning and late evening, and presumably overnight, was in the AGSM/STVI HT, similar to the cow-calf group. The low frequency of observed feeding by bulls during daylight hours suggested that they relied heavily on nocturnal feeding. Feeding during nocturnal hours was possibly a energy conservation strategy to minimize activity during warm diurnal hours.

Overall and Seasonal Habitat Use

Even though differences in habitat selection existed among the sex/age classes, the data were collected for these classes in proportions similar to the occurrence of each class in the population. Therefore, observational data were pooled for further analyses. Habitat selection was similar between summer 1987 and summer 1988 (r_S=0.81 p<0.01) so observational data for these seasons were combined.

Elk were observed in the Breaks PT 40% of the time during the study (Table 12). Use of this PT was much greater than its proportionate occurrence in the Park, indicating a strong preference of elk for sloping, timbered habitat. Sullivan (1988), in phase 1 of the study, also found that elk selected for the Breaks PT 40% of the time during diurnal hours. The Upland Grasslands PT was second in overall importance, and also used much greater than which it occurred in TRNP. Upland grasslands received considerable use in every season, but were most important in the winter (Table 12). The Scoria Hills PT, which ranked third in total utilization in phase 2, was found by Sullivan (1988) to be only of minor importance during phase 1. This change occurred because elk expanded their range to include western areas of the Park, where the Scoria Hills PT was more prevalent.

The AGSM/STVI HT received the highest proportion of elk use of any HT/MU/Complex in winter, spring, and over the entire study (Table 13). This HT makes up a substantial part of TRNP, and its proportionate use was similar to its proportionate availability in all seasons except winter 1988. In winter, elk increased use of this HT above proportionate availability. Juniper draws (JUSC/ORMI HT) ranked first in summer use and second in spring use. This Habitat Type was most important during the midday hours of both seasons (Appendix B, Table 43).

Table 12. Percent utilization of Physiographic Types (PTs) by elk during summer 1987-1988, winter 1988, spring 1988, the growing season (summer 1987-1988 and spring 1988) and over the entire study, and the percent of Physiographic Types available.

Physiographic Type	Winter 1988	Spring 1988	Summer 1987-88	Growing season	Total use	Percent available
Bottom Grasslands	14	6	8	7	9	15.64
Breaks	19	56	40	46	40	25.16
Sagebrush Bottoms	0	1	1	1	1	11.09
Upland Grasslands	38	23	24	24	27	0.69
Prairie Dog Town	0	0	tr[a]	tr	tr	7.45
Ridge & Ravine	8	1	0	1	2	34.91
Old River Terrace	0	0	0	0	0	4.04
Scoria Hills	21	13	26	21	21	1.02

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

Feeding Areas

The Upland Grasslands PT was the PT most used by elk for feeding during the growing season (Table 14) and during the spring 1988 and

Table 13. Percent utilization of Habitat Types (HTs), Mapping Units (MUs), and Complexes by elk during summer 1987-1988, winter 1988, spring 1988, the growing season (summer 1987-1988 and spring 1988) and over the entire study, and the percent of HTs, MUs, and Complexes available.

HTs, MUs and Complexes	Winter 1988	Spring 1988	Summer 1987-88	Growing Season	Total Use	Percent Available
AGSM/STVI	44	18	15	16	22	16.98
AGSM/STCO	1	1	0	tr[a]	tr	1.69
STCO/BOGR	8	4	2	3	4	1.67
SCSC	9	13	6	9	9	4.79
SCSC/JUHO	0	2	1	2	1	1.87
ARTR/ATCO	11	11	5	7	8	2.44
ARTR/BOGR	tr	3	tr	1	1	0.89
ARCA	tr	1	1	1	1	3.67
JUSC/ORMI	tr	17	18	18	14	2.26
POTR/BEOC	0	tr	tr	tr	tr	0.01
Hardwood Draws	1	5	13	10	8	1.82
Brush	0	1	tr	tr	tr	0.07
Rolling Scoria	12	7	15	12	12	10.29
Steep Scoria	8	4	4	4	5	19.22
Introduced Grass	0	11	16	14	11	1.48
Prairie Dog Towns	0	0	tr	tr	tr	0.69
Man-Managed	0	1	tr	tr	tr	0.23
Unvegetated Areas	6	1	1	1	2	29.93

[a] tr = <0.5%.
[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

summer 1987-1988 seasons individually (Appendix B, Tables 33 and 34). Although production of graminoids was slightly lower for this PT than the most productive Bottom Grasslands PT (Marlow et al. 1984), the production of forbs was higher. Forbs were the dominant forage class in late spring 1988 and late summer 1988 elk diets (Table 5) indicating that elk at TRNP sought areas of greater forb concentration for feeding areas during most of the growing season. Other researchers have found that forbs contribute significantly to summer elk diets (Rouse 1958, Mackie 1970, Knowles 1975, Singer 1975).

Vegetative production for HTs/MUs/Complexes in the Upland Grasslands PT is listed in Appendix E, Table 53, and the proportion of HT/MU/Complex occurrence in the Upland Grasslands PT is shown in Appendix E, Table 52.

Upland grasslands were often the first to produce new growth in spring. Smooth brome (Bromus inermis), and sedges, which were early growing species that contributed greatly to late spring elk diets (Table 5), were found in the highest densities in the upland grasslands. Upland grasslands were used for feeding in both the morning and evening time periods in spring, but mostly in the evening time period in summer (Appendix B, Table 41).

Table 14. Percent activity of elk within Physiographic Types (PTs) during the entire study and during the growing season (spring 1988, and summer 1987-1988). Growing season values are in parentheses.

Physiographic Type	Activity					
	Feeding	Bedding	Standing	Moving	Other	Unknown
Bottom Grasslands	12 (10)	9 (8)	8 (8)	13 (10)	6 (6)	1 (1)
Breaks	25 (26)	40 (54)	39 (41)	35 (38)	31 (33)	73 (74)
Sagebrush Bottoms	1 (2)	tr[a] (tr)	3 (4)	2 (2)	1 (2)	tr (tr)
Upland Grasslands	40 (40)	27 (18)	22 (20)	22 (22)	32 (35)	6 (6)
Prairie Dog Towns	tr (tr)	tr (tr)	tr (tr)	0 (0)	0 (0)	0 (0)
Ridge & Ravine	2 (1)	4 (tr)	2 (1)	1 (1)	1 (tr)	tr (tr)
Old River Terrace	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Scoria Hills	21 (21)	19 (20)	26 (26)	27 (27)	29 (25)	19 (18)

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

During the winter 1988 season the Upland Grasslands PT was most used for feeding (Appendix B, Table 32), especially during the morning and midday time periods (Appendix B, Table 35). Upland grasslands were swept free of snow by wind action. Although TRNP did not receive enough snow during winter 1988 to hinder elk movement, it was more energy efficient for elk to graze in areas with minimal or no snow cover (Geist 1982). Breaks and Scoria Hills PTs were next in importance as winter feeding areas. These PTs were highly dissected, had southern slopes which were free of snow, and provided some topographic relief from high winds. Mackie (1970) noted that elk in the Missouri River Breaks used steep, snow-free slopes during winter. Elk at TRNP used the Breaks PT in higher proportions during the evening time period (Appendix B, Table 35) to possibly take advantage of a warmer microclimate (Moen 1968).

During the growing season, the most important HT/MU/Complex for feeding was the Introduced Grass HT (Table 15), which occurred entirely in the Upland Grasslands PT. An abundance of early-growing introduced grasses in the spring and forbs in the summer evidently made this a favored feeding site. The AGSM/STVI HT was an also important feeding area in spring and summer. Although the AGSM/STVI HT did not have the highest overall vegetative production for HTs/MUs/Complexes (Appendix E, Table 53), it did have the highest concentration of western wheatgrass and green needlegrass combined, the most preferred graminoid species by elk during the growing season (Appendix D, Table 47).

During winter 1988, the AGSM/STVI HT was the major HT/MU/Complex selected for feeding (Appendix B, Table 38). This HT occurred mostly in the Upland and Bottom Grasslands PTs. The Rolling Scoria Complex and ARTR/ARCO HT, which occurred mostly in the Scoria Hills and Breaks

PTs, respectively, were selected next as feeding areas during winter 1988.

Table 15. Percent activity of elk within Habitat Types (HTs), Mapping Units (MUs), and Complexes during the entire study and during the growing season (spring 1988, and summer 1987-1988). Growing season values are in parentheses.

HTs, MUs and Complexes	Activity					
	Feeding	Bedding	Standing	Moving	Other	Unknown
AGSM/STVI	25 (19)	32 (23)	22 (18)	23 (19)	16 (13)	3 (3)
AGSM/STCO	1 (1)	tr[a] (tr)	1 (1)	1 (tr)	tr (tr)	tr (tr)
STCO/BOGR	5 (4)	4 (2)	3 (2)	5 (5)	2 (2)	2 (1)
SCSC	11 (11)	10 (11)	12 (11)	11 (11)	8 (9)	2 (2)
SCSC/JUHO	tr (tr)	3 (5)	1 (1)	1 (1)	tr (tr)	tr (tr)
ARTR/ATCO	8 (6)	11 (12)	14 (13)	11 (11)	11 (9)	2 (2)
ARTR/BOGR	1 (1)	1 (2)	1 (1)	2 (2)	1 (1)	tr (tr)
ARCA	2 (2)	tr (tr)	3 (3)	2 (2)	1 (1)	tr (tr)
JUSC/ORMI	tr (tr)	4 (6)	3 (4)	5 (5)	5 (6)	64 (64)
POTR/BEOC	tr (tr)	0 (0)	0 (0)	tr (tr)	0 (0)	tr (tr)
Hardwood Draws	4 (5)	8 (11)	5 (6)	4 (5)	5 (6)	19 (20)
Brush	tr (1)	tr (tr)	tr (tr)	tr (tr)	tr (tr)	tr (tr)
Rolling Scoria	15 (15)	12 (14)	16 (17)	16 (16)	17 (16)	3 (2)
Steep Scoria	5 (4)	6 (4)	7 (6)	7 (8)	9 (6)	2 (2)
Introduced Grass	22 (29)	6 (9)	8 (10)	8 (9)	21 (27)	2 (2)
Prairie Dog Towns	tr (tr)	tr (tr)	tr (tr)	0 (0)	0 (0)	0 (0)
Man-Managed	1 (1)	tr (tr)	1 (1)	1 (1)	tr (tr)	0 (0)
Unvegetated Areas	2 (1)	3 (1)	5 (4)	4 (4)	3 (3)	1 (tr)

[a] tr = <0.5%.
[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

Bedding Areas

The percentage of diurnal bedding areas selected during the spring and summer seasons were adjusted using midday radio-signal checks during each season (Table 16 and 17). In spring and summer the Breaks PT was used most for bedding and adjusted bedding activities (Table 16), especially during the midday time periods (Appendix B, Table 36). Elk sought overhead cover in juniper draws (JUSC/ORMI HT), which occurred mostly in the Breaks PT, for adjusted bedding activities in spring and summer (Table 17). Juniper draws allowed elk to maintain their body temperature within the thermal neutral zone (Moen 1973), and functioned as shelter from high winds and biting insects, and as hiding/escape cover. Mackie (1970) observed elk in the Missouri River Breaks of Montana, an environment similar to TRNP, bedding in Pinus-Juniperus and Pseudotsuga-Juniperus Habitat Types during hot midday hours.

Table 16. Percent bedding, unknown, and adjusted bedding activities during midday hours by elk in Physiographic Types (PTs) for spring 1988 and summer 1987-1988.

	Spring			Summer		
Physiographic Type	Bedding	Unknown	Adjusted bedding	Bedding	Unknown	Adjusted bedding
Bottom Grasslands	6	1	1	10	1	5
Breaks	66	79	84	43	71	57
Sagebrush Bottoms	0	tr[a]	0	tr	tr	tr
Upland Grasslands	10	9	3	25	5	15
Prairie Dog Towns	0	0	0	tr	0	tr
Ridge & Ravine	tr	1	tr	0	0	0
Old River Terrace	0	0	0	0	0	0
Scoria Hills	18	9	11	22	23	22

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

During the winter 1988 season, elk rarely entered juniper or hardwood draws and bedded in open areas when feeding bouts ended. Upland Grasslands PTs were selected most by elk for bedding during the entire winter season (Appendix B, Table 32), and during each time period (Appendix B, Table 36). Topographic relief was apparently used to dampen the effects of wind-chill or to maximize thermal insulation.

Decreased use of cover in the winter season is a common phenomenon in most elk populations (Skovlin 1982). Sullivan (1988) also identified this pattern during phase 1, but observed elk bedding mostly in the Bottom Grasslands PT rather than the Upland Grasslands PT.

Table 17. Percent bedding, unknown, and adjusted bedding activities during midday hours by elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes for spring 1988 and summer 1987-1988.

HTs, MUs, and Complexes	Spring			Summer		
	Bedding	Unknown	Adjusted bedding	Bedding	Unknown	Adjusted bedding
AGSM/STVI	23	2	14	23	4	14
AGSM/STCO	tr[a]	tr	tr	0	0	0
STCO/BOGR	1	4	tr	2	tr	1
SCSC	8	3	6	14	1	7
SCSC/JUHO	6	tr	3	4	tr	2
ARTR/ATCO	22	4	20	2	tr	1
ARTR/BOGR	5	1	4	0	tr	tr
ARCA	0	tr	0	tr	tr	tr
JUSC/ORMI	7	63	35	5	65	34
POTR/BEOC	0	0	0	0	tr	tr
Hardwood Draws	5	11	8	16	24	20
Brush	tr	1	tr	tr	0	tr
Rolling Scoria	11	3	8	16	2	10
Steep Scoria	5	2	0	4	2	3
Introduced Grass	4	3	tr	13	2	7
Prairie Dog Towns	0	0	0	tr	0	tr
Man-Managed	0	0	0	tr	0	tr
Unvegetated Areas	2	1	2	tr	tr	tr

[a] tr = <0.5%.
[b] Descriptions of HTs, MUs, and complexes and definition of acronyms in Appendix A, Table 31.

Calving and Rutting Areas

Radio locations during summer 1987 placed calving females in the Breaks and Scoria Hills PTs near Peck Hill (Fig. 1). A similar PT utilization pattern was noted in summer 1988, but scoria hills, mostly the Steep Scoria HT, were used to a greater extent. Nearly all the cow-calf herd (including 5 of 6 radio-collared females) relocated to the large expanses of steep scoria within the Loop Road (Fig. 1) to calve in 1988. This area had complex topographic relief and offered ground cover concealment (Skovlin 1982). Additionally, it was most removed from the areas frequented by Park tourists.

Pre-rutting activities were observed most frequently in the Upland and Bottom Grassland PTs. Adult bulls adjusted their habitat utilization pattern to conform with adult females in late August and early September. Although elk were not observed during the peak of rutting activities in phase 2, Sullivan (1988) identified similar PT utilization patterns during the fall rut in phase 1.

Ungulate Interactions

Comparisons of PT selection during the entire study and during the growing season were made for the 5 ungulates in TRNP (Tables 18-20). Of these species, the behavioral interactions for 4 (elk, bison, feral horses, and mule deer) were quantified. White-tailed deer were limited in distribution, and interactions with other ungulates were seldom observed. The other 4 ungulates species observed shared similar habitats throughout the study, but incidents of agonistic threats or displays were infrequently observed.

Elk - Bison Interactions

The correlation of PT selection between elk and bison was very low and not significant (r_S=0.01 p=0.98). Elk selected mostly for breaks and bison for prairie dog towns (Table 18). However, the chief feeding area preferred by elk during the growing season, the Upland Grasslands PT (Table 19), was of some importance to bison. Some similarities between elk and bison diets were observed (Table 6), principally the common use of some graminoids and winterfat (Appendix D, Tables 47 and 48). The potential for forage competition or "exploitative competition" (Nelson 1982) is low, but if exploitative competition ever occurs between these two species, it is likely to occur in the Upland Grasslands PT.

Elk showed a greater aversion to bison than to any other species and were displaced most frequently by them (Table 22). Elk were displaced by bison 371 m when displacement occurred. Bison were never displaced by elk and were the only species to exhibit active aggression towards elk (Table 21). McHugh (1958) noted that bison were dominant over elk and that bison calves could displace a 6-point bull elk. Other authors have suggested that bison occasionally harass and kill elk calves (Rush 1942, Mahan 1977).

Elk were most often displaced by bison at the upper and lower distance categories (Appendix C, Table 45). Although the number of bison or number of elk were not tallied, observational notes indicate that elk were displaced by large herds of bison when these groups were >50 m apart, but elk would allow a single bull bison to graze within 20 m before displacing. Twenty and 50 m, therefore, appeared to be the threshold distances that elk would allow a single bison or a herd of bison to approach, respectively, without displacing. In Yellowstone National Park, bison and elk have been observed foraging within 10 m of each other, despite their seeming intolerance (Reynolds et al. 1982).

Table 18. Total percent utilization of Physiographic Types (PTs) by ungulates. Utilization is based on observation-minutes for elk and on sightings for bison, feral horses, mule deer (MD), white-tailed deer (WTD). Sample sizes are in parentheses.

Physiographic Type	Ungulate species				
	Elk (105,614)	Bison (4,715)	Horse (809)	MD (2,116)	WTD (196)
Bottom Grasslands	9	13	31	7	7
Breaks	40	3	5	25	3
Sagebrush Bottoms	1	12	2	4	42
Upland Grasslands	27	17	44	15	3
Prairie Dog Towns	tr	25	0	4	28
Ridge & Ravine	2	14	2	15	14
Old River Terrace	0	3	0	4	4
Scoria Hills	21	14	17	27	0

[a] Descriptions of PTs in Appendix A, Table 30.

Table 19. Percent utilization of Physiographic Types (PTs) by ungulates and percent feeding by elk during the growing season. Utilization is based on observation-minutes for elk and on sightings for bison, horse, mule deer (MD), white-tailed deer (WTD). Sample sizes are in parentheses.

Physiographic Type	Ungulate species					
	Elk (82,606)	% Elk Feeding (28,812)	Bison (3,932)	Horse (583)	MD (1,801)	WTD (194)
Bottom Grasslands	7	10	15	30	8	7
Breaks	46	26	2	7	25	3
Sagebrush Bottoms	1	2	14	3	4	42
Upland Grasslands	24	40	11	42	14	3
Prairie Dog Towns	tr	tr	29	0	4	28
Ridge & Ravine	1	1	10	0	15	14
Old River Terrace	0	0	2	0	4	4
Scoria Hills	21	21	16	19	26	0

[a] Descriptions of PTs in Appendix A, Table 30.

Table 20. Spearman's rank correlations (r_S) of Physiographic Types (PTs) used during the entire study (TOT) and during the growing season (GRO) by elk, bison, feral horses, mule deer (MD), and white-tailed deer (WTD).

	Bison		Horse		MD		WTD	
	TOT	GRO	TOT	GRO	TOT	GRO	TOT	GRO
Elk	0.01 p=0.98	-0.02 p=0.96	0.82 p=0.01	0.88 p<0.01	0.85 p<0.01	0.66 p=0.08	-0.66 p=0.08	-0.61 p=0.11
Bison			0.16 p=0.71	0.16 p=0.71	0.06 p=0.90	-0.11 p=0.79	0.09 p=0.83	0.21 p=0.62
Horse					0.63 p=0.10	0.43 p=0.29	-0.56 p=0.15	-0.55 p=0.29
MD							-0.78 p=0.02	-0.74 p=0.04

Elk - Feral Horse Interactions

Elk were most correlated with feral horses in growing season PT use (r_S=0.88 $p<0.01$). Total PT utilization by these two species was also similar (r_S=0.82 $p=0.01$). Horses preferred the Upland Grassland PT, which was also the primary feeding area of elk during the growing season (Table 19). Also, elk were most correlated with feral horses for total diets (Table 6). Therefore, exploitative competition between these two species is a real possibility and may have a direct affect on their future well being.

Besides forage, these ungulate species evidently competed directly for the limited supply of developed water during summer 1988, a drought year. Small bands of horses were frequently seen around wildlife dish tanks in summer 1988. Recently, feral horses have been observed by researchers at TRNP to drive elk from these tanks (L.

Gagnon, pers. comm. 1989). Searches for fecal material around several dish tanks during summer 1988 revealed abundant horse droppings but no fresh elk pellets.

Although elk were observed to displace feral horses (Table 21), it was more common for elk to be displaced by horses (Table 22). Elk were also displaced by horses for greater distances (562 m) than by any other ungulate. This was attributed to the strongly gregarious nature of horses, which were presumably more disturbing to elk than a single bison. Elk were disturbed more frequently by horses at short distances than by any other ungulate (Appendix C, Table 45) but not at longer distances, indicating that elk would allow bands of horses to approach closer than large bison herds before being displaced. Elk may have been tolerant of individual horses, as they were of individual bison, but horses seldom moved as individuals. Apparently, elk had a threshold distance of 20 m for bands of horses, at which the percentage of no reaction decreased and displacement dramatically increased.

Elk - Mule Deer Interactions

Elk and mule deer had the highest correlation in total PT selection among elk and other ungulates (r_S=0.85 p<0.01), but growing season PT selection was less similar and not significant (r_S=0.66 p=0.08). Elk and mule deer had diets which had high amounts of browse, but similarities in forage species composition were minimal (Table 6). Because graminoids made up only a small part of mule deer diets, and because elk preferred graminoids when available (Murie

Table 21. Percent reaction of other ungulate species to elk with mean displacement distance.

Reaction	Ungulate species		
	Mule deer (n=101)	Bison (n=29)	Feral horse (n=16)
No reaction	45	97	88
Awareness	15	0	0
Alarm	2	0	0
Aggression	0	3	0
Displacement	39	0	13
Mean displacement distance (m)	63	0	28

Table 22. Percent reaction of elk to other ungulate species with mean displacement distance.

Reaction	Ungulate species		
	Mule deer (n=101)	Bison (n=29)	Feral horse (n=16)
No Reaction	75	48	56
Awareness	15	17	19
Alarm	0	0	0
Aggression	9	0	0
Displacement	1	34	25
Mean displacement distance (m)	10	371	562

1951), exploitative competition between elk and mule deer was minimal, despite similarities in PT use. Extreme competition between these two species should not occur in the future unless graminoids become overutilized by elk and other grazing herbivores, or elk and mule deer become overpopulated.

Because of habitat similarities, elk and mule deer were often seen in close proximity. Although researchers have noticed social compatibility between elk and mule deer (White 1958, Kirsch 1963), agonistic encounters between elk and mule deer occurred more frequently in TRNP than between any other ungulate pair. Mule deer were most often displaced ≤20 m, and aggression on the part of elk was noticed most at distances ≤20 m (Appendix C, Tables 44 and 45). Therefore, a threshold distance of 20 m existed between elk and mule deer. Because mule deer and elk did not respond to one another at distances ≥20 m, they were more socially compatible than elk with bison or horses.

Dominance Hierarchy

My data corroborates Sullivan's (1988) dominance hierarchy of bison > feral horses > elk > mule deer in the SU of TRNP. The frequency that elk were displaced by these species, and the frequency other ungulates were displaced by elk supports this linear arrangement. McHugh (1958) observed that bison were dominant to elk and elk to mule deer.

Apparently, the dominance of one species over another in TRNP was based on size. However, other factors such as: number of individuals, gregariousness of the species, and age and sex may have affected ungulate interactions. For instance, the only time elk were displaced by mule deer occurred when a yearling bull elk and an adult buck mule deer approached each other to within 10 m. Both quickly retreated (were displaced) 10 m. Individual bison could approach elk very closely without stimulating a reaction by elk, but large herds could not. Mule deer were often seen foraging ≥20 m from elk, but encounters of elk with horses or bison at distances <100 m were rare.

Human Impacts

Three types of human interactions with elk were noted (Table 23). Elk were aware of human presence at distances >1,000 m, but were displaced only at distances <1,000 m (Appendix C, Table 46). Ward and Cupal (1979) found that the range at which elk responded to human disturbances was about 400 m. Flight distance "the distance to which a person can approach a wild animal without causing it to flee" (Altman 1958) is influenced by a number of factors such as: 1) seasonal change in reproduction and nutritional status; 2) type of habitat; and 3) previous experience of the individual or the group to human caused disturbances. Topographic relief may also influence flight distance by providing "line-of-sight" barriers which visually screen elk from human disturbances (Lyon 1979, Lyon et al. 1985).

When elk in TRNP were displaced they traveled 171-502 m, depending on the type of disturbance. Movements involved displacement to cover (most often) and movement away from the disturbance without visual concealment. Coop (1971) found that elk in the Little Belt Mountains, Montana fled an average of 114 m to dense adjacent forest cover when disturbed by humans. Ward et al. (1973) indicated that elk maintain a "buffer zone" of 800 m between themselves and recreationists, and if this space is violated, will exhibit evasive movement to reestablish it.

Disturbances by humans on foot elicited the greatest response on the part of elk. Displacement occurred in 88% of observed incidences. Mean displacement from humans on foot was 471 m. Elk always ran when approached to within 100 m by humans on foot during 1987-1988 (Appendix C, Table 46). By 1989, some elk (animals near the interstate highway and in areas frequented by researchers during a horse study at TRNP) would tolerate humans on foot to approach <100 m.

Stopped motor vehicles alarmed elk at distances of 301-1,000 m but displaced them only at 101-300 m. The elk in TRNP became habituated to traffic on the interstate highway along the southern boundary of the Park. Sightings of elk within 200 m of this highway were common. If vehicles stopped along the interstate or along the Park Loop Road, elk were alarmed and would usually run. Ward (1973) found that elk were easily conditioned to normal activities within their home range, but became alarmed at unusual disturbances. The mean displacement distance from motor vehicles in TRNP, 502 m, was comparable to displacement from humans on foot.

Humans on horseback, based on a small sample size, appeared to be less disturbing to elk than other human activities, when riders did not harass elk. Some riders were observed during phase 1 chasing elk (M. Sullivan, pers. comm. 1989). Observed frequency of displacement of elk from horseback riders was less than that associated with foot-travel and similar to vehicular disturbance. As with other human disturbances, elk were invariably displaced when riders approached ≤100 m.

Table 23. Percent reaction of elk to human caused disturbances with mean displacement distance.

	Type of disturbance		
Reaction	On foot (n=48)	Vehicle (n=23)	Horseback (n=6)
No reaction	2	13	33
Awareness	8	35	17
Alarm	2	4	0
Displacement	88	48	50
Mean displacement distance (m)	471	502	171

Optimum Carrying Capacity

The optimum carrying capacity for elk, bison, feral horses, and mule deer was determined for a 6-region area (the Target Area) of TRNP. Population levels for bison (200) and feral horses (50) were set in the model based on recommendations by the Park (TRNP 1984). Mule deer numbers (312) were derived from population density figures of the 1988 aerial survey of the SU of TRNP conducted by North Dakota Department of Game and Fish. The relative distribution of each ungulate in the Target Area is shown in Table 24. Population estimates, sex ratios, weights of the "typical animal", daily forage intake (percent of body weight) and growing-season forage intake (kg/6 months), for each ungulate species used in the Ungulate Resources Allocation Model is shown in Table 25.

Table 24. Percent utilization of regions in TRNP by elk, bison, feral horses, and mule deer (MD) during the growing season (spring 1988 and summer 1987-1988). Utilization is based on observation-minutes for elk and on sightings for the other ungulates.

Ungulate species	Region 1	2	3	4	5	6
Elk	20	71	3	3	2	tr[a]
Bison	11	11	15	7	4	52
Feral horse	36	39	22	1	2	0
MD	15	25	11	17	8	24

[a] tr = <0.5%.

Table 25. Population estimates, weights of the typical animal, daily intake, and forage intake over the growing season for elk, bison, feral horses, and mule deer (MD).

Ungulate species	Number adult males	Number adult females	Number of juveniles	Weight typical animal (kg)	Average intake rate (% B.W./day)	Forage intake (kg)
Elk	41	70	37	228	2.4	983
Bison	--	--	--	454	1.8	1470
Horses	29	31	12	442	2.5	1988
MD	100	189	177	46	3.7	309

Nine graminoids and 8 browse species contributed ≥3% to the growing season diets of elk, bison, feral horses, and mule deer (Appendix D, Tables 47-51). However, vegetative production figures were inadequate for wild-rye (Elymus spp.), currant/gooseberry (Ribes spp.), silver buffaloberry, and poison ivy (Toxicodendron radicans). Two graminoid species, smooth brome and bluegrass - mostly Kentucky bluegrass (Poa pratensis), were introduced species and considered expendable. Vegetative production figures were unavailable for all forb species. No production figures were available for the JUSC/ORMI HT, POTR/BEOC HT, and Man-Managed MU. Production for only selected shrubs were available for the Hardwood Draws HT.

Typical animal intake of the 11 major forage items used in the model by elk, bison, feral horses, and mule deer is shown in Table 26. The optimum population of elk was determined by allocating 35% of the production for these forage species to each of the other ungulates in the model over the 6-month growing season and then allocating the residual to elk.

Winterfat was the forage species that most limited elk numbers in every region and in the Target Area overall (Table 27), based on present distribution within regions and food habits. The next most constraining forage species were: 2) chokecherry; 3) skunkbush sumac; and 4) green needlegrass. These species are decreasers under moderate to heavy grazing pressure (Lacey 1984) and could be adversely affected in the Park if overutilized.

Sullivan (1988) calculated a carrying capacity for elk in TRNP during phase 1 without consideration of other ungulate species. He listed 8 browse species: winterfat, chokecherry, snowberry, buffaloberry, yucca (Yucca glauca), golden currant (Ribes setosum), water birch (Betula occidentalis), and green ash (Fraxinus pennsylvanica); and 3 graminoids: big bluestem (Andropogon gerardii), little bluestem (Schizachirium scoparium), and bluegrass, that would likely be overutilized at high elk populations.

Table 26. Typical animal intake (kg) during the growing season (spring and summer) by elk, bison, feral horses, and mule deer (MD) of the 11 major forage items used in the Ungulate Resources Allocation Model.

Forage item	Ungulate species			
	Elk	Bison	Horses	MD
Agropyron smithii	54.0	282.5	385.4	3.0
Bouteloua gracilis	9.9	60.0	32.0	0
Carex spp.	33.1	133.4	444.2	1.1
Koeleria pyramidata	5.7	125.1	237.9	0
Stipa comata	0	121.1	317.8	0.6
Stipa viridula	57.1	43.6	49.3	1.7
Artemisia tridentata	0	1.6	0	13.6
Ceratoides lanata	113.1	59.4	111.5	0
Prunus virginiana	45.1	0	0	23.3
Rhus trilobata	33.2	0	0	19.5
Symphoricarpos occidentalis	59.7	0	0	27.6

Although the carrying capacity for the target area was calculated 7 times (once from percent utilization of each region and once from utilization of the Target Area overall, these estimates differed due to ungulate distribution. High population estimates of elk in some regions was due to the low use of these regions in 1987-1988. Considering the increased western distribution of elk over the 4-year study, eastern sections should receive relatively less utilization in the future. Therefore, the final carrying capacity for elk, 243, was based on the estimate of the Target Area as a whole (Table 27). This figure should be considered the optimum population of elk at TRNP, if the number of the other ungulates are kept at the recommended levels. At these population levels, the possibility exists that some HTs may be locally overutilized, but no vegetational communities are likely to be degraded throughout the Park.

Table 27. Optimum carrying capacity of elk in a 6-region area of TRNP based on utilization patterns for each region, population levels for bison (200), feral horses (50), and mule deer (312), and limiting forage species.

Region	Limiting forage species	Optimum carrying capacity
1	1. Winterfat	67
	2. Skunkbush sumac	89
	3. Chokecherry	230
2	1. Winterfat	46
	2. Chokecherry	108
	3. Skunkbrush sumac	157
3	1. Winterfat	1,255
	2. Chokecherry	2,864
	3. Skunkbush sumac	5,746
4	1. Winterfat	2,337
	2. Chokecherry	3,040
	3. Green needlegrass	8,358
5	1. Winterfat	2,476
	2. Chokecherry	4,014
	3. Green needlegrass	9,381
6	1. Winterfat	73,530
	2. Green needlegrass	301,380
	3. Chokecherry	307,273
Total[a] area ($123.9\ km^2$)	1. Winterfat	243[b]
	2. Chokecherry	533
	3. Skunkbush sumac	1,123

[a] Does not include the Cottonwood Forest and Old River Terrace PTs.
[b] Optimum carrying capacity.

At the projected optimum population, elk density in the Target Area would be 1.96 elk/km^2 (Table 28). The densities for the other ungulates would be: bison (1.61/km^2); feral horses (0.40/km^2); and mule deer (2.52/km^2). Wydeven and Dahlgren (1985) found ungulate densities at Wind Cave National Park to be: elk (3.96-4.40/km^2); bison (3.30-3.52/km^2); mule deer (0.70-0.80/km^2); and pronghorn (1.10-1.32/km^2). Researchers at Wind Cave National Park had previously determined the optimum carrying capacity for elk to be 150-300 animals (1.32-2.64/km^2). Periods of extreme high numbers of elk at Wind Cave National Park in the past, 1,100 (9.68/km^2) in 1953 and 800 (7.05/km^2) in 1969 (Varland et al. 1978), may have severely reduced forage and restricted mule deer numbers and distribution (Wydeven and Dahlgren 1985).

Table 28. Population levels, densities, and stocking rates for elk, bison, feral horses, and mule deer at the optimum carrying capacity for a 6-region area (123.9 km^2) of TRNP.

Ungulate species	Population level	Density (no./km^2)	Stocking rate (AUM/ha)	(ha/AUM)
Elk	243	1.96	0.011	93.15
Bison	200	1.61	0.013	73.70
Feral horses	50	0.40	0.004	223.91
Mule deer	312	2.52	0.004	230.60
Total	805	6.50	0.033	30.54

When each herbivore was considered in terms of an Animal Unit Month (AUM), equivalent to the forage consumed by 1 adult domestic cow (<u>Bos</u> spp.) and her calf for 1 month, 405.7 AUMs were generated for each month at the optimum carrying capacity. The stocking rate for all ungulates on the target area would be 0.033 AUM/ha or 30.54 ha/AUM

(Table 28). Since this area consists of 30.2% bare ground (Marlow et al. 1984), the stocking rate on the vegetated areas would be 0.047 AUM/ha or 21.31 ha/AUM. In the USFS Little Missouri National Grasslands, adjacent to TRNP, cattle are grazed 8 months of the year at stocking rates of 0.35 ha/AUM (2.8 ha/AUM) to 0.82 ha/AUM (1.2 ha/AUM) (M. Walker, pers. comm 1989). These stocking rates may be somewhat high, considering the condition of the vegetation in the National Grasslands (M. Walker, pers. comm. 1989). Because of the strong grazing tendencies of domestic cattle, a stocking rate analysis may only be applicable to the chiefly grazing wild herbivores in TRNP: bison, feral horses and elk.

When the modeled numbers of wild herbivores in the target area (123.9 km^2) were applied to the entire SU (183.4 km^2), ungulate densities were: elk (1.32/km^2); bison (1.09/km^2); feral horses (0.27/km^2); and mule deer (1.70/km^2). When the densities calculated for the Target Area were extrapolated to the entire park, numbers of ungulates were: elk (359); bison (295); feral horses (73); and mule deer (462). To support ungulates at these levels without damaging Park resources, the entire Park would have to be fully utilized by all ungulates. This has been observed in bison (Norland 1984) and mule deer, but elk and feral horses have yet to fully utilize all areas of TRNP.

Alternate ungulate population levels for elk, bison, and feral horses are feasible. An exchange rate coefficient was calculated for these animals based on winterfat intake (Table 29). A reduction in 1 species would free forage to support increases in other ungulate species. For instance, if 275 bison are considered more desirable than the modeled number, elk numbers must be reduced to 243 - (75) (0.525) = 204, or feral horses must be reduced to 50 - (75) (0.532) = 10. If Park officials decide to hold elk numbers at 200, then bison numbers could be raised to 200 + (43) (1.904) = 282, or feral horse numbers could be raised to 50 + (43) (1.014) = 94.

Table 29. Exchange rate coefficients of ungulate species 1 for species 2, based on predetermined optimal population levels from winterfat intake.

Species 1	Species 2	Exchange rate coefficient
Elk	Bison	1.904
Elk	Feral horse	1.014
Bison	Elk	0.525
Bison	Feral horse	0.532
Feral horse	Elk	0.986
Feral horse	Bison	1.878

These ungulate exchange coefficients are justified because winterfat limits elk, bison, and feral horses but not mule deer. Care should be taken not to elevate elk numbers much past the optimum carrying capacity because of potential conflict with mule deer over chokecherry and skunkbush sumac. These forage items were predicted to limit elk and mule deer numbers, but not bison or feral horse numbers.

CONCLUSIONS AND RECOMMENDATIONS

Since the reintroduction, elk have extended their range within TRNP to occupy the northcentral and southcentral areas. Ten elk emigrated from the Park, with additional reports of elk infrequently utilizing areas outside TRNP. Elk were sexually segregated over most of the study, with ranges of the bull and cow-calf groups overlapping only during the rut. Calving grounds consistently moved west as elk became more familiar with new areas.

Elk grew in number from the 1985 reintroduced population of 47 to 148 in September 1988. Rapid antler development, high reproductive performance, and low mortality, all indicative of a healthy population, were witnessed at TRNP. The population growth rate, 0.31 over 4 years, is among the highest in the literature.

Differences were noted in habitat selection among sex/age classes, with adult and yearling bulls preferring rougher terrain. All elk foraged in open grassland habitats during crepuscular hours. Overhead cover was sought in juniper draws during warm midday hours of spring and summer but not in winter. Unlike the reports of early elk in North Dakota, the reintroduced population at TRNP did not utilize riparian areas extensively.

Elk were more disturbed by humans on foot than in stationary vehicles or on horseback. No response was elicited by elk when humans were >1,000 m, but elk would always displace when approached <100 m.

Recent reports indicate that elk have become more habituated to tourists than were observed during this study.

Overlap in forage utilization among elk and other ungulates was minimal to moderate. However, stronger correlations were noted in PT utilization, especially between elk and feral horses during the growing season, and elk and mule deer over the entire study. A size-based dominance hierarchy of bison > feral horses > elk > mule deer was observed at TRNP.

An optimum carrying capacity was determined for ungulates in TRNP based on forage intake and availability. The model indicated that winterfat would restrict the number of elk, bison, and feral horses. Chokecherry and skunkbush sumac limited mule deer numbers and were secondary constraints on elk numbers. The level of foraging pressure at the projected optimum carrying capacity is well below that for other reported ungulate densities and stocking rates in the Northern Great Plains.

Recommendations to Park management are:

1. Vegetative production is still needed for the JUSC/ORMI HT, POTR/BEOC HT, and Man-Managed MU. A more complete estimate of production is needed for the Hardwood Draws HT.

2. Estimates of vegetative production for certain plant species are needed, especially for wild-rye, currant/gooseberry, and silver buffaloberry. Production for upland grassland shrub species are lacking, and are nonexistent for forb species.

3. Vegetation transects should be regularly monitored to assess foraging pressure. Winterfat, chokecherry, skunkbush sumac, and green needlegrass were predicted to be most limiting; and therefore, are foraging-level indicator species. An elevated level of browsing may indicate that elk numbers were too high or that a decline in upland vegetation forced elk to switch to browse. Since winter diets were not assessed in this study the amount of winter browsing by elk

is unknown. Elk and mule deer may compete directly for browse, especially if elk are forced to browse because of deep snow in winter.

4. Ungulate food habits should be periodically assessed to refine intake values of each forage species and determine if changes in diets are due to changes in range composition. Because the forage allocation model is food habit based, any changes in ungulate diet selection will alter the optimum carrying capacity.

5. New water sources should be established to redistribute ungulates and reduce foraging pressure in certain areas. Also, current water sources may be systematically turned on and off to redistribute ungulates.

6. Production censuses and population censuses should be conducted in summer and winter, respectively, for each ungulate species.

7. Ungulate populations should be maintained within the levels suggested by the Ungulate Resources Allocation Model.

REFERENCES CITED

Allen, E. O. 1971. White-tailed deer. Pages 69-79 in T. W. Mussehl and F. W. Howell, eds. Game management in Montana. Mont. Dept. Fish and Game.

Altman, M. 1952. Social behavior of elk, Cervus canadensis nelsoni, in the Jackson Hole area of Wyoming. Behavior 4:116-143.

———. 1958. The flight distance in free-ranging big game. J. Wildl. Manage. 22:207-209.

Baumgartner, L. L., and A. C. Martin. 1939. Plant histology as an aid in squirrel food-habit studies. J. Wildl. Manage. 3:266-268.

Beall, R. C. 1974. Winter habitat selection and use by a western Montana elk herd. Ph.D. Thesis, Univ. of Mont., Missoula. 197pp.

Bell, N. M. 1973. Rangeland management for livestock production. Univ. of Okla. Press, Norman. 303pp.

Bergerud, A. T., and L. Russell. 1964. Evaluation of rumen food analysis for Newfoundland Carribou. J. Wildl. Manage. 28:52-55.

Boyd, R. J. 1970. Elk of the White River Plateau, Colorado. Colo. Div. Game, Fish, and Parks. 121pp.

———. 1978. American elk. Pages 11-29 in J. L. Schmidt and D. L. Gilbert, eds. Big game of North America. Stackpole Books, Harrisburg, Pa.

Bryant, D. L., and C. Maser. 1982. Classification and distribution. Pages 1-59 in J. W. Thomas and D. E. Toweill, eds. Elk of North America. Stackpole Books, Harrisburg, Pa.

Burris, O. E., and D. E. McKnight. 1973. Game transplants in Alaska. Alaska Dep. Fish and Game Wildl. Tech. Bull. 4. 57pp.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on the Himalayan thar in New Zealand. Ecology 51:52-72.

———, and L. C. Birch. 1971. Rate of increase. J. Wildl. Manage. 35:658-663.

———. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York. 234pp.

Cole, G. F. 1969. The elk of the Grand Teton and southern Yellowstone National Parks. Natl. Park Serv. Res. Rep. GRTE-N-1. 192pp.

Coop, K. J. 1971. Habitat use, distribution, movement, and associated behavior of elk in the Little Belt Mountains, Montana. Mont. Dep. Fish and Game Compl. Rep., Proj. W-120-R-1 & 2. 61pp.

Craighead, J. J., F. C. Craighead, Jr., R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison drainage herd as determined by biotelemetry. Wildl. Monogr. 33. 50pp.

Curren, C. B. 1977. Prehistoric range extension of the elk: Cervus canadensis. Amer. Midl. Nat. 97:230-232.

Darling, F. F. 1937. A herd of red deer. Oxford Univ. Press, London. 215pp.

Daubenmire, R. F. 1968. Plant communities: a textbook of plant synecology. Harper and Row, New York. 300pp.

Dearden, B. L., R. E. Pegau, and R. M. Hansen. 1975. Precision of microhistological estimates of ruminant food habits. J. Wildl. Manage. 39:402-407.

Dusi, J. L. 1949. Methods for the determination of food habits by plant microtechniques and histology and their application to cottontail rabbit food habits. J. Wildl. Manage. 13:295-298.

Fenneman, N. M. 1931. Physiography of the western United States. McGraw-Hill Co., New York. 534pp.

Flook, D. R. 1970. A study in sex differential in the survival of wapiti. Can. Wildl. Serv. Rep. Ser. 11. 71pp.

Franklin, W. L., and J. W. Lieb. 1979. The social organization of a sedentary population of North American elk: a model for understanding other populations. Pages 185-189 in M. S. Boyce and L. D. Hayden-Wing eds. North American elk: ecology, behavior, and management. Univ. of Wyo., Laramie.

French, C. E., L. C. Magruder, N. D. Ingram, and R. W. Swift. 1955. Nutritional requirements of white-tailed deer for growth and antler development. Pa. Agric. Exp. Stn. Bull. 600., University Park. 50pp.

Geist, V. 1982. Adaptive behavioral strategies. Pages 219-277 in J. W. Thomas and D. E. Toweill, eds. Elk of North America. Stackpole Books, Harrisburg, Pa.

Girard, N. M. 1985. Native woodland ecology and habitat type classification of southwestern North Dakota. Ph.D. Thesis, N. D. State Univ., Fargo. 314pp.

Gogan, P. J. P., and R. H. Barrett. 1987. Comparative dynamics of introduced Tule elk populations. J. Wildl. Manage. 51:20-27.

Guthrie, R. D. 1966. The extinct wapiti of Alaska and Yukon Territory. Can. J. Zool. 44:47-57.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America, vol. 2. Ronald Press Co., New York. 1083pp.

Hanley, T. A., and K. A. Hanley. 1982. Food resource partitioning by sympatric ungulates on Great Basin Rangeland. J. Range Manage. 35:152-158.

Hanson, P. L., R. B. Hopkins, and G. R. Hoffman. 1980. An ecological study of the habitat types and their animal components at Theodore Roosevelt National Park, North Dakota. Univ. of S. D., Vermillion 182pp.

Hirsch, K. J. 1985. Habitat type classification of grasslands and shrublands of southwestern North Dakota. Ph.D. Thesis, Univ. of N. D., Fargo. 291pp.

Irby, L. R. 1976. The ecology of mountain reedbuck in southern and eastern Africa. Ph.D. Thesis, Texas A&M Univ., College Station. 248pp.

James, R. L. 1981. Linpro: a linear programming algorithm. Decisions Science Software, Sugarland, Tex. 6pp.

Johnson, D. E. 1951. Biology of the elk calf, Cervus canadensis nelsoni. J. Wildl. Manage. 38:161-174.

Kipple, G. E. 1964. Early- and late-season grazing versus season-long grazing of short-grass vegetation on the Central Great Plains. U. S. For. Serv., Rocky Mountain For. and Range Exp. Stn. Res. Pap. RM-11.

Kirsch, J. B. 1963. Range use, relationship to logging, and food habits of elk in the Little Belt Mountains, Montana. M.S. Thesis, Mont. State Univ., Bozeman. 44pp.

Knight, R. R. 1970. The Sun River elk herd. Wildl. Monogr. 23. 66pp.

Knowles, C. J. 1975. Range relationships of mule deer, elk, and cattle in a rest-rotation grazing system during summer and fall. M.S. Thesis, Mont. State Univ., Bozeman. 111pp.

Kruckenberg, L. 1973. Game management of North Dakota - a summation and review. North Dakota Outdoors. 35:18-27.

Kufeld, R. C. 1973. Foods eaten by the Rocky Mountain elk. J. Range. Manage. 26:106-113.

Lacey, J. L. 1984. Two hundred and fifty plants for range contests in Montana. Mont. State Univ. Agric. Coop. Exten. Ser. Bull. 8402., Bozeman. 4pp.

Leonard, A. G. 1930. The geology of North Dakota. Univ. of N. D. Bull. 11:4-10., Fargo.

Lowe, V. P. W. 1966. Observations on the dispersal of red deer on Rhum. Pages 211-228 in P. A. Jewell and C. Loizos eds. Play, exploration and territoriality in mammals. Academic Press, London.

Lyon, L. J. 1979. Influences of logging and weather on elk distribution in western Montana. U.S. For. Serv. Res. Pap. INT-236. 11pp.

———, T. N. Lonner, J. P. Weigland, C. L. Marcum, W. D. Edge, J. D. Jones, D. W. McCleerey, and L. L. Hicks. 1985. Coordinating elk and timber management: final report of the Montana cooperative elk-logging study 1970-1985. Mont. Dep. Fish, Wildl. and Parks, Fed. Aid. Proj. W-120-R. 53pp.

Mackie, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildl. Monogr. 20. 79pp.

Mahan, B. R. 1977. Harassment of an elk calf by bison. Can. Field. Nat. 91:418-419.

Marlow, C. B., L. R. Irby, and J. E. Norland. 1984. Optimum carrying capacity for bison in Theodore Roosevelt National Park. Mont. State Univ., Bozeman. 83pp.

McCorquodale, S. M., L. L. Eberhardt, and L. E. Eberhardt. 1988. Dynamics of a colonizing elk population. J. Wildl. Manage. 52:309-313.

McHugh, T. 1958. Social behavior of the American buffalo (Bison bison bison). Zoologica 43, part 1. 40pp.

Moen, A. N. 1968. Energy balance of white-tailed deer in winter. Trans. North. Am. Wildl. Conf. 13:224-236.

———. 1973. Wildlife ecology. W. H. Freeman and Co., San Francisco. 458pp.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223-249.

Murie, O. J. 1951. The elk of North America. Teton Bookshop, Jackson, Wy. 376pp.

Murphy, D. A. 1963. A captive elk herd in Missouri. J. Wildl. Manage. 35:658-663.

Nelson, J. R. 1961. Composition and structure of the woody vegetation types in the North Dakota badlands. M.S. Thesis, N. D. State Univ., Grand Forks. 195pp.

Nelson, J. R. 1982. Relationships of elk and other large herbivores. Pages 415-442 in J. W. Thomas and D. E. Toweill, eds. Elk of North American. Stackpole Books, Harrisburg, Pa.

———, and J. L. Leege. 1982. Nutritional requirements and food habits. Pages 323-369 in J. W. Thomas and D. E. Toweill, eds. Elk of North America. Stackpole Books, Harrisburg, Pa.

Norland, J. E. 1984. Habitat use and distribution of bison in Theodore Roosevelt National Park. M.S. Thesis, Mont. State Univ., Bozeman. 131pp.

———. 1988a. Habitat types and annual usable forage production of Theodore Roosevelt National Park: 1988 revision. Natl. Park Ser. Mimeogr. 15pp.

———. 1988b. Ungulate resources allocation model. Theodore Roosevelt Nature and History Association, Medora, N.D. 16pp.

Peek, J. M. 1982. Elk. Pages 851-861 in J. A. Chapman and G. A. Feldhammer eds. Wild mammals of North America: biology, management, economics. The John Hopkins University Press, Baltimore.

Picton, H. D. 1961. Differential hunter harvest of elk in two Montana herds. J. Wildl. Manage. 25:415-451.

Raesfeld, F. V., and F. Vorreyer. 1964. Das rotwildnaturgeschichte: hege und jagd, 5th ed. P. Parey Verlag, Hamburg and Berlin. 368pp.

Ramirez, J. M. 1973. The agro-climatology of North Dakota, part 2. Precipitation: forecasting, probability and rainmaking. N. D. State Univ. Coop. Exten. Serv. and Agric. Exp. Stn. Bull. 16, Fargo.

Reynolds, H. W., R. D. Glaholt, and A. W. L. Hawley. 1982. Bison. Pages 972-1007 in J. A. Chapman and G. A. Feldhammer eds. Wild mammals of North America: biology, management, economics. The John Hopkins Press, Baltimore.

Rouse, R. A. 1958. Wildlife investigations (Dist. 3): elk investigations (elk-livestock relationships). Mont. Dep. Fish and Game, Fed. Aid. Compl. Rep. Proj. W-73-R-3, J-A-2. 3pp.

Rush, W. M. 1942. Wild animals of the Rockies. Harper & Brothers, New York. 296pp.

Sampson, A. W. 1952. Range management: principles and practices. John Wiley and Sons Inc., New York. 570pp.

Singer, F. J. 1975. Wildfires and ungulates in the Glacier National Park area, northwestern Montana. M.S. Thesis, Univ. of Idaho, Moscow. 64pp.

Skovlin, J. M. 1982. Habitat requirement and evaluations. Pages 369-413 in J. W. Thomas and D. E. Toweill, eds. Elk of North America. Stackpole Books, Harrisburg, Pa.

Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscope technique. J. Range Manage. 21:264-265.

Stuwe, M., and C. E. Blohowiak. 1985. McPaal: micro-computer programs for the analysis of animal locations. Smithsonian Inst., Washington, D. C. 20pp.

Sullivan, M. G. 1988. Distribution, movements, habitat use, and food habits of reintroduced elk in Theodore Roosevelt National Park. M.S. Thesis, Mont. State Univ., Bozeman. 94pp.

Theodore Roosevelt National Park. 1984. Natural resources management plan and environmental assessment. Natl. Park. Serv. D-36. 133pp.

Varland, K. L, A. L. Lovaas, and R. B. Dahlgren. 1978. Herd organization and movements of elk in Wind Cave National Park, South Dakota. Natl. Park Serv. Nat. Res. Rep. 13. 28pp.

Vavra, M., R. W. Rice, and R. M. Hansen. 1978. A comparison of esophageal fistula and fecal material to determine steer diets. J. Range Manage. 31:11-13.

Ward, A. L. 1970. Stomach content and fecal analysis: methods of forage identification. Pages 146-158 in Range and wildlife habitat evaluation: a research symposium. U. S. For. Serv. Misc. Pub. 1147.

———. 1973. Elk behavior in relation to multiple uses on the Medicine Bow National Forest. Proc. West. Assoc. State Game and Fish Comm. 53:125-141.

———, J. J. Cupal, A. L. Lea, C. A. Oakley, and R. W. Weeks. 1973. Elk behavior in relation to cattle, grazing, forest recreation, and traffic. Trans. North Amer. Wildl. Conf. 38:327-337.

———, and J. J. Cupal. 1979. Telemetered heart rate of three elk as affected by activity and human disturbance. Pages 47-56 in Dispersed recreation and natural resource management. Symp. Proc. Utah State Univ., Logan.

White, K. L. 1958. Summer range ecology of Rattlesnake Creek mule deer in the spruce-fir zone. M.S. Thesis, Univ. of Mont., Missoula. 95pp.

Whitman, W. C. 1978. Analysis of grassland vegetation on selected key areas in southwestern North Dakota. N.D. Reg. Environ. Program. 72pp.

Wydeven, A. P., and R. B. Dahlgren. 1983. Food habits of elk in the Northern Great Plains. J. Wildl. Manage. 49:805-813.

———, and ———. 1985. Ungulate habitat relationships in Wind Cave National Park. J. Wildl. Manage. 49:805-813.

APPENDICES

APPENDIX A

Description of Physiographic Types and Habitat Types/Mapping Units/Complexes in TRNP.

Table 30. Description of Physiographic Types in TRNP (Norland 1984).

1. Bottom Grasslands: large flat grassed alluvial deposits found on high floodplains of the Little Missouri River and its larger tributaries.

2. Breaks: consists of areas noticeably devoid of vegetation, or if vegetation does exists, it is situated on steep slopes.

3. Sagebrush Bottoms: floodplains dominated by silver sagebrush (Artemisia cana) along with substantial grass cover.

4. Upland Grasslands: level to rolling grasslands found on plains above the river valley. These lands are typical of the Northern Great Plains.

5. Prairie Dog Towns: lands which have been or are being influenced by prairie dogs. At the edges of the towns plants are still characteristic of the former plant community. Nearer the center, vegetation is absent or dominated by unpalatable perennial plant species.

6. Ridge & Ravine: lands highly dissected by watercourses and covered by various grasses, shrubs, and trees.

7. Old River Terrace: level grasslands 200 to 500 feet above the river which are situated on terraces formed before rapid downcutting of the river.

8. Scoria Hills: lands influenced by scoria (a clinker formed from the baking of clays adjacent to burning coal veins) which produce differential weathering of the land. This weathering produces a very rugged topography which is covered by various grasses and shrubs.

Table 31. Description of Habitat Types, Mapping Units, and Complexes in TRNP (Norland 1984, Sullivan 1988).

---

1. Agropyron smithii / Stipa viridula HT (AGSM/STVI HT):

Distinguished by the presence of Stipa viridula in habitats having heavy soil, protected from the wind, or extra moisture from runoff. Agropyron smithii is the primary grass component. Located on well drained, fine textured soils on terraces or gentle uplands with slopes of 0-4%.

2. Agropyron smithii / Stipa comata HT (AGSM/STCO HT):

Agropyron smithii is the major grass component. Bouteloua gracilis is the dominant short grass species. Shrubs are generally not found in this habitat type. Located on loamy to clay soils on uplands and flat terraces with slopes of 0-12%.

3. Agropyron smithii / Bouteloua gracilis / Distichlis spicata HT (AGSM/BOGR/DIST HT):

Characterized by the presence of saline - sodic claypan with scattered bare spots devoid of vegetation. Located on level or hummocky terrain with slopes of 0-6%. Soils have a surface of loamy topsoil with a clay layer 0-25cm below this.

4. Stipa comata / Bouteloua gracilis HT (STCO/BOGR HT):

Canopy cover is dominated by Stipa comata; however, Bouteloua gracilis and Carex spp. contribute substantially to relative basal coverage. Located on gently rolling slopes dominated by sandy uplands with sandy loam or clay loam in the uppermost soil layer.

5. Schizachirium scoparium HT (SCSC HT):

Schizachirium scoparium occurs in bunches and is the primary grass component. Located on moderate steep to steep upland on north, northeast and western exposures with slopes from 18-20%. Soils are shallow, unleached clay loams to sandy loams.

6. Schizachirium scoparium / Juniperus horizontalis (SCSC/JUHO HT):

Vegetation is sparse with soil and exposed rock comprising up to 64% of total coverage. Shrubs are common. Located on hilltops and buttes with very shallow loamy soils and slopes ranging from 20-24%.

Table 31. Continued.

7. Artemisia tridentata / Atriplex confertifolia (ARTR/ATCO HT):

Vegetation is sparse, comprised mostly of low shrubs. Located where barren outcroppings of bentonite clay and/or lignite deposits were obvious. Soils poorly developed and range from silty clay loam to clay loam.

8. Artemisia tridentata / Bouteloua gracilis HT (ARTR/BOGR HT):

Artemisia tridentata abundant above a heavy grass cover comprised mostly of Bouteloua gracilis and Agropyron smithii. Located on upper slopes and stream terraces having shallow, fine textured soils and slopes ranging from 2-20%.

9. Artemisia cana HT (ARCA HT):

Dominated by Artemisia cana, but Symphoricarpos occidentalis frequently also occurs there. Found on flood plains and low terraces. Frequently occupies large flats along streams and creeks. Soils vary due to periodic flooding and new depositions being laid down. Textures range from sandy loams to silt clays.

10. Juniperus scopulorum / Oryzopsis micrantha HT (JUSC/ORMI HT):

Juniperus scopulorum is the dominant upperstory vegetation. The undergrowth is dominated by Oryzopsis micrantha and moss. Located on northwest to north facing hillsides having 35-70% slopes and sandy loam to clay loam soils.

11. Populus tremuloides / Betula occidentalis HT (POTR/BEOC HT):

Characterized by Populus tremuloides as the dominant tree species. Frequently above stands of Fraxinus pennsylvanica - Prunus virginiana. Located on upper slopes facing northwest to east on sandy loam to clay loam soils.

12. Hardwood Draws HT:

Fraxinus pennsylvanica is the dominant tree species in this HT, with Ulmus americana as the codominant in some stands. Prunus virginiana is the dominant understory tree species. Located in ravines in draws or moderately steep north facing slopes having silt loam to clay loam soils.

13. Brush MU:

Small patches of shrubs dominated by Symphoricarpos occidentalis, Prunus virginiana, or Prunus americana. Located on both slopes and grasslands.

Table 31. Continued.

14. Rolling Scoria Complex:

Rolling lands influenced by scoria and composed of the following proportion of habitat types:

.25	SCSC HT
.2	AGSM/STVI HT
.2	STCO/BOGR HT
.15	AGSM/STCO HT
.1	SCSC/JUHO HT
.1	AGSM/BOGR/DIST HT

15. Steep Scoria Complex:

Rolling lands influenced by scoria and composed of the following proportion of habitat types:

.3	SCSC HT
.25	SCSC/JUHO HT
.15	AGSM/STVI HT
.15	STCO/BOGR HT
.1	ARTR/ATCO HT
.05	AGSM/BOGR/DIST HT

16. Introduced Grass MU:

Disturbed areas which have been planted with introduced grasses. The most common grasses occurring at these areas are *Agropyron smithii* and *Bromus inermis*.

17. Prairie Dog Towns MU:

Areas in or around prairie dog towns where the vegetation has been modified by prairie dogs.

18. Man-Managed MU:

Areas where the vegetation has been modified by human disturbance.

APPENDIX B

Percent elk activity in Physiographic Types and Habitat Types/ Mapping Units/Complexes for each season and time period.

Table 32. Percent activity of elk in Physiographic Types (PTs) during winter 1988.

Physiographic Type	Activity					
	Feeding	Bedding	Standing	Moving	Other	Unknown
Bottom Grasslands	18	10	7	33	6	3
Breaks	20	15	32	16	24	17
Sagebrush Bottoms	0	0	0	0	0	0
Upland Grasslands	37	44	31	17	23	15
Prairie Dog Towns	0	0	0	0	0	0
Ridge & Ravine	5	12	6	7	3	7
Old River Terrace	0	0	0	0	0	0
Scoria Hills	20	19	23	26	44	58

[a] Descriptions of PTs in Appendix A, Table 30.

Table 33. Percent activity of elk in Physiographic Types (PTs) during spring 1988.

Physiographic Type	Activity					
	Feeding	Bedding	Standing	Moving	Other	Unknown
Bottom Grasslands	8	6	5	7	5	1
Breaks	36	66	57	43	48	79
Sagebrush Bottoms	1	0	4	1	1	tr[a]
Upland Grasslands	42	10	19	29	17	9
Prairie Dog Towns	0	0	0	0	0	0
Ridge & Ravine	2	tr	3	3	tr	1
Old River Terrace	0	0	0	0	0	0
Scoria Hills	11	18	13	17	30	9

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

Table 34. Percent activity of elk in Physiographic Types (PTs) during summer 1987-1988.

Physiographic Type	Activity					
	Feeding	Bedding	Standing	Moving	Other	Unknown
Bottom Grasslands	12	10	9	11	8	1
Breaks	19	43	33	36	22	71
Sagebrush Bottoms	2	tr[a]	3	3	2	tr
Upland Grasslands	39	25	20	20	47	5
Prairie Dog Towns	tr	tr	tr	0	0	0
Ridge & Ravine	0	0	0	0	0	0
Old River Terrace	0	0	0	0	0	0
Scoria Hills	28	22	34	30	21	23

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

Table 35. Percent feeding by elk in Physiographic Types (PTs) for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988.

Physiographic Type	Winter			Spring			Summer		
	AM	MD	PM	AM	MD	PM	AM	MD	PM
Bottom Grasslands	12	20	17	0	tr[a]	17	9	24	11
Breaks	20	15	37	43	66	20	32	66	6
Sagebrush Bottoms	0	0	0	0	0	2	2	tr	3
Upland Grasslands	50	35	30	51	14	45	16	0	57
Prairie Dog Towns	0	0	0	0	0	0	0	0	tr
Ridge & Ravine	0	8	0	tr	8	1	0	0	0
Old River Terrace	0	0	0	0	0	0	0	0	0
Scoria Hills	18	22	16	5	11	15	40	9	23

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

Table 36. Percent bedding by elk in Physiographic Types (PTs) for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988.

Physiographic Type	Winter			Spring			Summer		
	AM	MD	PM	AM	MD	PM	AM	MD	PM
Bottom Grasslands	tr[a]	11	15	0	2	19	2	13	12
Breaks	5	16	17	76	78	24	45	75	12
Sagebrush Bottoms	0	0	0	0	0	0	tr	0	tr
Upland Grasslands	69	40	48	18	5	24	16	0	55
Prairie Dog Towns	0	0	0	0	0	0	0	0	tr
Ridge & Ravine	0	15	0	0	tr	tr	0	0	0
Old River Terrace	0	0	0	0	0	0	0	0	0
Scoria Hills	25	18	19	6	15	33	37	12	21

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

Table 37. Percent utilization of Physiographic Types (PTs) by elk for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988.

Physiographic Type	Winter			Spring			Summer		
	AM	MD	PM	AM	MD	PM	AM	MD	PM
Bottom Grasslands	7	15	18	0	1	16	7	6	11
Breaks	16	16	32	52	82	26	39	77	11
Sagebrush Bottoms	0	0	0	0	0	2	2	tr[a]	2
Upland Grasslands	53	36	32	39	5	36	15	tr	50
Prairie Dog Towns	0	0	0	0	0	0	0	0	tr
Ridge & Ravine	0	13	tr	tr	2	1	0	0	0
Old River Terrace	0	0	0	0	0	0	0	0	0
Scoria Hills	24	20	18	9	10	20	37	17	25

[a] tr = <0.5%.
[b] Descriptions of PTs in Appendix A, Table 30.

Table 38. Percent activity of elk in Habitat Types (HTs), Mapping Units (MU), and Complexes during winter 1988.

HTs, MUs, and Complexes	Activity					
	Feeding	Bedding	Standing	Moving	Other	Unknown
AGSM/STVI	42	47	33	46	26	7
AGSM/STCO	1	tr[a]	tr	3	0	9
STCO/BOGR	9	9	5	3	3	5
SCSC	9	7	14	10	4	6
SCSC/JUHO	0	0	0	0	0	0
ARTR/ATCO	14	9	15	8	17	3
ARTR/BOGR	tr	0	tr	tr	0	1
ARCA	tr	0	tr	1	0	0
JUSC/ORMI	tr	0	0	1	0	1
POTR/BEOC	0	0	0	0	0	0
Hardwood Draws	tr	2	tr	tr	0	2
Brush	0	0	0	0	0	0
Rolling Scoria	14	10	14	16	22	27
Steep Scoria	5	9	9	7	22	30
Introduced Grass	0	0	0	0	0	0
Prairie Dog Towns	0	0	0	0	0	0
Man-Managed	0	0	0	0	0	0
Unvegetated Areas	5	7	10	3	6	9

[a] tr = <0.5%.

[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

Table 39. Percent activity of elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes during spring 1988.

HTs, MUs, and Complexes	Activity					
	Feeding	Bedding	Standing	Moving	Other	Unknown
AGSM/STVI	22	23	21	21	14	2
AGSM/STCO	2	tr[a]	2	1	1	tr
STCO/BOGR	5	1	3	5	3	4
SCSC	21	8	16	16	11	3
SCSC/JUHO	1	6	2	1	tr	tr
ARTR/ATCO	7	22	15	9	16	4
ARTR/BOGR	2	5	3	4	1	1
ARCA	1	0	4	1	1	tr
JUSC/ORMI	tr	7	5	6	14	63
POTR/BEOC	tr	0	0	0	0	0
Hardwood Draws	2	5	6	3	1	11
Brush	1	tr	1	tr	1	1
Rolling Scoria	7	11	6	7	22	3
Steep Scoria	4	5	4	8	5	2
Introduced Grass	22	4	7	13	5	3
Prairie dog towns	0	0	0	0	0	0
Man-Managed	1	0	2	1	1	0
Unvegetated Areas	1	2	3	3	4	1

[a] tr = <0.5%.

[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

Table 40. Percent activity of elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes during summer 1987-1988.

HTs, MUs, and complexes	Activity					
	Feeding	Bedding	Standing	Moving	Other	Unknown
AGSM/STVI	17	23	17	19	13	4
AGSM/STCO	0	0	0	0	0	0
STCO/BOGR	3	2	2	5	1	tr[a]
SCSC	5	14	9	9	7	1
SCSC/JUHO	tr	4	tr	1	tr	tr
ARTR/ATCO	5	2	12	12	4	tr
ARTR/BOGR	tr	0	tr	1	tr	tr
ARCA	2	tr	3	3	2	tr
JUSC/ORMI	1	5	3	5	1	65
POTR/BEOC	tr	0	0	tr	0	tr
Hardwood Draws	7	16	7	6	9	24
Brush	tr	tr	tr	tr	tr	0
Rolling Scoria	21	16	23	20	12	2
Steep Scoria	5	4	7	7	7	2
Introduced Grass	33	13	12	8	42	2
Prairie Dog Towns	tr	tr	tr	0	0	0
Man-Managed	tr	tr	1	1	0	0
Unvegetated Areas	tr	tr	5	5	1	tr

[a] tr = <0.5%.

[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

Table 41. Percent feeding by elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988.

HTs, MUs, and Complexes	Winter			Spring			Summer		
	AM	MD	PM	AM	MD	PM	AM	MD	PM
AGSM/STVI	48	45	27	23	25	20	16	29	16
AGSM/STCO	5	0	0	3	4	0	0	0	0
STCO/BOGR	9	11	0	10	tr[a]	4	3	0	3
SCSC	0	5	35	27	27	13	10	8	2
SCSC/JUHO	0	0	0	1	tr	1	1	2	tr
ARTR/ATCO	13	11	25	2	15	8	7	18	2
ARTR/BOGR	tr	0	tr	0	8	2	tr	0	tr
ARCA	0	1	0	0	0	3	2	tr	2
JUSC/ORMI	0	tr	0	tr	1	tr	tr	1	tr
POTR/BEOC	0	0	0	0	0	tr	0	0	tr
Hardwood Draws	0	tr	0	3	4	1	13	31	1
Brush	0	0	0	2	tr	1	1	tr	0
Rolling Scoria	8	16	13	3	11	8	31	7	18
Steep Scoria	10	5	0	2	tr	6	6	2	5
Introduced Grass	0	0	0	20	0	33	8	0	50
Prairie Dog Towns	0	0	0	0	0	0	0	0	tr
Man-Managed	0	0	0	3	1	tr	1	2	0
Unvegetated Areas	7	6	0	1	2	tr	tr	tr	1

[a] tr = <0.5%.

[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

Table 42. Percent bedding by elk in Habitat Types (HTs), Mapping Units (MUs), and Complexes for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988.

HTs, MUs, and Complexes	Winter			Spring			Summer		
	AM	MD	PM	AM	MD	PM	AM	MD	PM
AGSM/STVI	15	54	24	24	22	23	16	22	30
AGSM/STCO	tr[a]	0	0	0	tr	0	0	0	0
STCO/BOGR	54	4	0	tr	0	4	3	0	4
SCSC	0	3	41	22	8	1	25	10	10
SCSC/JUHO	0	0	0	28	4	1	2	10	tr
ARTR/ATCO	2	10	15	8	28	10	3	2	2
ARTR/BOGR	0	0	0	0	6	5	0	0	0
ARCA	0	0	0	0	0	0	tr	0	tr
JUSC/ORMI	0	0	0	0	9	6	1	10	1
POTR/BEOC	0	0	0	0	0	0	0	0	0
Hardwood Draws	0	3	0	10	6	0	13	35	1
Brush	0	0	0	tr	0	0	tr	tr	0
Rolling Scoria	5	9	19	0	13	12	33	8	13
Steep Scoria	20	8	0	4	0	19	3	1	6
Introduced Grass	0	0	0	2	0	20	tr	0	32
Prairie Dog Towns	0	0	0	0	0	0	0	0	tr
Man-Managed	0	0	0	0	0	0	tr	tr	0
Unvegetated Areas	3	9	0	1	2	0	0	1	tr

[a] tr = <0.5%.
[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

Table 43. Percent utilization of Habitat Types (HTs), Mapping Units (MUs), and Complexes by elk for the morning (AM), midday (MD), and evening (PM) time periods during winter 1988, spring 1988, and summer 1987-1988.

HTs, MUs, and Complexes	Winter			Spring			Summer		
	AM	MD	PM	AM	MD	PM	AM	MD	PM
AGSM/STVI	35	49	29	20	14	20	16	9	20
AGSM/STCO	4	0	0	2	1	0	0	0	0
STCO/BOGR	21	6	0	6	tr[a]	6	2	0	4
SCSC	0	5	35	22	9	10	12	4	4
SCSC/JUHO	0	0	0	4	2	1	1	3	tr
ARTR/ATCO	8	11	20	4	18	9	8	3	3
ARTR/BOGR	tr	0	tr	0	5	2	1	0	tr
ARCA	0	tr	0	0	0	3	2	tr	2
JUSC/ORMI	0	tr	tr	6	32	6	8	49	2
POTR/BEOC	0	0	0	0	0	tr	0	0	tr
Hardwood Draws	0	2	0	8	7	1	13	27	1
Brush	0	0	0	2	tr	1	tr	tr	0
Rolling Scoria	9	12	16	4	8	8	24	3	18
Steep Scoria	15	7	0	4	tr	9	6	1	6
Introduced Grass	0	0	0	14	tr	24	6	0	38
Prairie Dog Towns	0	0	0	0	0	0	0	0	tr
Man-Managed	0	0	0	2	1	tr	1	tr	0
Unvegetated Areas	7	8	0	2	2	tr	1	1	2

[a] tr = <0.5%.

[b] Descriptions of HTs, MUs, and Complexes and definition of acronyms in Appendix A, Table 31.

APPENDIX C

Ungulate interactions and reaction of elk to human caused disturbances by distance category.

Table 44. Percent reaction of other ungulate species to elk within distance categories. Sample sizes are in parentheses.

Reaction	Ungulate species	Distance (m) 0-10	11-20	21-50	51-100	>100
Sample size (n)	Mule deer	(40)	(17)	(15)	(21)	(8)
	Bison	(6)	(4)	(5)	(8)	(6)
	Feral horses	(3)	(1)	(3)	(4)	(5)
No reaction	Mule deer	33	35	53	67	50
	Bison	83	100	100	100	100
	Feral horses	67	100	100	75	100
Awareness	Mule deer	8	12	13	19	50
	Bison	0	0	0	0	0
	Feral horses	0	0	0	0	0
Alarm	Mule deer	3	0	7	0	0
	Bison	0	0	0	0	0
	Feral horses	0	0	0	0	0
Aggression	Mule deer	0	0	0	0	0
	Bison	17	0	0	0	0
	Feral horses	0	0	0	0	0
Displacement	Mule deer	58	53	27	14	0
	Bison	0	0	0	0	0
	Feral horses	33	0	0	25	0

Table 45. Percent reaction of elk to other ungulate species within distance categories. Sample sizes are in parentheses.

Reaction	Ungulate Species	Distance (m) 0-10	11-20	21-50	51-100	>100
Sample size (n)	Mule deer	(40)	(17)	(15)	(21)	(8)
	Bison	(6)	(4)	(5)	(8)	(6)
	Feral horses	(3)	(1)	(3)	(4)	(5)
No reaction	Mule deer	65	82	87	81	75
	Bison	17	75	80	63	17
	Feral horses	33	0	67	75	60
Awareness	Mule deer	15	6	13	19	25
	Bison	33	0	20	13	17
	Feral horses	0	0	0	25	40
Alarm	Mule deer	0	0	0	0	0
	Bison	0	0	0	0	0
	Feral horses	0	0	0	0	0
Aggression	Mule deer	18	12	0	0	0
	Bison	0	0	0	0	0
	Feral horses	0	0	0	0	0
Displacement	Mule deer	3	0	0	0	0
	Bison	50	25	0	25	67
	Feral horses	67	100	33	0	0

Table 46. Percent reaction of elk to human caused disturbances by distance category. Sample sizes are in parentheses.

Reaction	Type of Disturbance	Distance 1-100 m	101-300 m	301-1000 m	>1000 m
Sample size (n)	On foot	(15)	(18)	(13)	(2)
	Vehicle	(6)	(7)	(4)	(6)
	Horseback	(1)	(5)		
No reaction	On foot	0	0	8	0
	Vehicle	0	0	25	33
	Horseback	0	40		
Awareness	On foot	0	11	0	100
	Vehicle	0	29	50	67
	Horseback	0	20		
Alarm	On foot	0	0	8	0
	Vehicle	0	0	25	0
	Horseback	0	0		
Displacement	On foot	100	89	85	0
	Vehicle	100	71	0	0
	Horseback	100	40		

APPENDIX D

Percent vegetative species composition identified in fecal analysis of elk, bison, feral horses, mule deer, white-tailed deer in TRNP.

Table 47. Percent vegetative species composition identified in fecal samples of elk during spring 1988 and summer 1987-1988 and during the growing season (spring 1988 and summer 1987-1988).

Plant species	Late spring 1988	Early summer 1987	Late summer 1988	Growing season total
Graminoids				
Agropyron smithii	7.8	3.4	4.2	5.5
Bouteloua gracilis	1.3	1.2	0.6	1.0
Bromus inermis	5.7	1.2	1.0	2.9
Carex spp.	7.2	2.4		3.4
Koeleria pyramidata	1.5			0.6
Oryzopsis micrantha	2.5		1.6	1.6
Poa spp.	1.1	9.5	0.3	2.5
Schizachirium scoparium	3.8			1.5
Stipa viridula	5.4	8.7	4.8	5.8
Total graminoids	36.3	26.4	12.5	24.8
Forbs				
Achillea millefolium	0.1	0.8	1.0	0.6
Arctium minus		2.0		0.4
Echinacea angustifolia	2.4	1.2	0.6	1.4
Equisetum spp.		0.8		0.2
Erysimum/*Lithospermum*	0.6	0.4	0.7	0.6
Galium boreale	2.9		0.5	1.3
Gaura coccinea	3.6	1.6	4.2	3.5
Lactuca spp.	1.3	3.2	0.3	1.3
Lysimachia ciliata	0.4			0.2
Melilotus spp.	0.3	0.8		0.3
Monarda fistulosa	3.3	2.8	3.2	3.2
Plantago spp.			0.5	0.2
Potentilla spp.	0.4	1.6		0.5
Psoralea spp.	0.1		0.8	0.4
Ranunculus spp.	0.4			0.2
Ratibida columnifera	1.2	1.6	1.3	1.3
Sanicula marilandica	0.4		2.4	1.1
Sphaeralcea coccinea	4.5	6.0	21.5	11.6
Taraxacum officinale	2.0	0.8	1.4	1.5
Thermopsis rhombifolia	0.7			0.3
Tragopogon dubius		0.4		0.1
Unknown forb leaf	9.8	1.6	7.5	7.2
Unknown forb	4.4			1.8
Total forbs	38.8	25.4	45.9	39.0

Table 47. Continued.

Plant species	Late spring 1988	Early summer 1987	Late summer 1988	Growing season total
Total seed		1.2		0.2
Shrubs				
Amelanchier alnifolia		0.4		0.1
Artemisia frigida	0.3	1.6	4.9	2.4
Atriplex confertifolia	0.6		0.5	0.4
Ceratoides lanata	2.2	18.1	17.5	11.5
Fraxinus pennsylvanica	1.4		0.6	0.8
Juniperus spp.	0.3			0.1
Prunus virginiana	3.5	6.8	4.6	4.6
Rhus trilobata	4.0	4.8	2.1	3.4
Ribes spp.	1.6	1.2	3.5	2.3
Rosa spp.	3.1		2.0	2.0
Shepherdia argentea	4.7		0.5	2.1
Symphoricarpos occidentalis	3.1	14.3	5.0	6.1
Yucca glauca	0.1		0.5	0.2
Total shrubs	24.9	47.0	41.6	36.0

Table 48. Percent vegetative species composition identified in fecal samples of bison during spring 1988 and summer 1988 and during the growing season (spring 1988 and summer 1988).

Plant species	Late spring 1988	Early summer 1987	Growing season total
Graminoids			
Agropyron smithii	19.0	19.5	19.2
Bouteloua gracilis	5.3	2.9	4.1
Bromus inermis	2.3	4.0	3.1
Calamovilfa longifolia	2.9	2.3	2.6
Carex spp.	6.3	11.9	9.1
Distichlis spicata	0.3	0.5	0.4
Elymus spp.	5.6	3.4	4.5
Koeleria pyramidata	10.2	6.9	8.5
Muhlenbergia cuspidata	1.4	2.0	1.7
Oryzopsis micrantha	0.3	1.2	0.8
Poa spp.	28.9	7.2	18.0
Schizachirium scoparium	1.8	2.5	2.2
Stipa comata	2.7	13.8	8.2
Stipa viridula	5.5	0.5	3.0
Total graminoids	92.1	78.4	85.2
Forbs			
Achillea millefolium	0.4	0.2	0.3
Arctium minus	0.4		0.2
Erysimum/Lithospermum	0.1		0.1
Galium boreale	0.8	0.8	0.8
Gaura coccinea		0.3	0.2
Lactuca spp.	0.3	0.4	0.3
Melilotus spp.	2.7	1.3	2.0
Monarda fistulosa	0.6		0.3
Psoralea spp.	0.3		0.1
Ranunculus spp.		0.5	0.2
Ratibida columnifera	0.4		0.2
Sphaeralcea coccinea	0.3	5.0	2.7
Taraxacum officinale		0.7	0.4
Tragopogon dubius	0.5	0.7	0.6
Unknown forb leaf	0.3	1.0	0.6
Unknown forb stem	0.1		0.1
Unknown flower		0.5	0.3
Total forbs	7.1	11.4	9.3

Table 48. Continued.

Plant species	Late spring 1988	Early summer 1987	Growing season total
Shrubs			
Artemisia frigida	0.1	0.6	0.4
Artemisia spp.[a]	0.1	0.1	0.1
Atriplex confertifolia		0.2	0.1
Ceratoides lanata	0.3	7.8	4.0
Fraxinus pennsylvanica		0.2	0.1
Rosa spp.	0.3	1.2	0.7
Shepherdia argentea		0.2	0.1
Total shrubs	0.8	10.2	5.5

[a] Includes primarily *Artemisia tridentata* and *A. cana*.

Table 49. Percent vegetative species composition identified in fecal samples of feral horses during spring 1988 and summer 1988 and during the growing season (spring 1988 and summer 1988).

Plant species	Late spring 1988	Early summer 1987	Growing season total
Graminoids			
Agropyron smithii	21.5	17.3	19.4
Bouteloua gracilis	1.7	1.5	1.6
Bromus inermis	3.4	3.3	3.3
Calamovilfa longifolia	0.6	0.3	0.4
Carex spp.	29.1	15.7	22.4
Distichlis spicata	0.7	0.3	0.5
Elymus spp.	0.2		0.1
Koeleria pyramidata	9.9	14.0	12.0
Oryzopsis micrantha		0.9	0.5
Poa spp.	14.0	8.5	11.3
Schizachirium scoparium	1.8	1.4	1.6
Stipa comata	10.2	21.8	16.0
Stipa viridula	4.5	0.5	2.5
Total graminoids	97.5	85.3	91.4
Forbs			
Lactuca spp.	0.2		0.1
Sphaeralcea coccinea	1.1	4.4	2.7
Unknown forb leaf		0.3	0.1
Total forbs	1.3	4.7	3.0
Browse			
Ceratoides lanata	1.2	10.0	5.6
Shepherdia argentea	0.1		0.1
Total shrubs	1.3	10.0	5.6

Table 50. Percent vegetative species composition identified in fecal samples of mule deer during spring 1988 and summer 1988 and during the growing season (spring 1988 and summer 1988).

Plant species	Late spring 1988	Early summer 1987	Growing season total
Graminoids			
Agropyron smithii	0.2	1.7	1.0
Carex spp.		0.7	0.4
Elymus spp.	0.4	0.4	0.4
Poa spp.	0.2		0.1
Stipa comata	0.4		0.2
Stipa viridula	0.4	0.4	0.4
Total graminoids	1.5	3.3	2.4
Forbs			
Achillea millefolium	2.6	0.7	1.6
Aster spp.		2.1	1.0
Astragalis spp.	2.6		1.3
Echinacea angustifolia		1.8	0.9
Erysimum/Lithospermum	2.8	0.4	1.6
Galium boreale	2.3		1.2
Gaura coccinea	3.0		1.5
Lactuca spp.	0.3	1.1	0.7
Linum spp.	2.5	0.7	1.6
Lysimachia ciliata	0.4		0.2
Melilotus spp.	2.1		1.0
Monarda fistulosa	1.4		0.7
Penstemon spp.		0.9	0.4
Ranunculus spp.	0.7		0.4
Ratibida columnifera	2.8	3.2	3.0
Sanicula marilandica	0.9	1.5	1.2
Sphaeralcea coccinea		1.1	0.5
Thermopsis rhombifolia	2.0	0.1	1.0
Tragopogon dubius		0.9	0.4
Vicia spp.	3.1	1.5	2.3
Unknown forb leaf		0.2	0.1
Total forbs	29.3	16.1	22.7
Shrubs			
Amelanchier alnifolia		5.7	2.9
Artemisia frigida	3.2	0.5	1.9
Artemisia spp.[a]	0.1	8.7	4.4

Table 50. Continued.

Plant species	Late spring 1988	Early summer 1987	Growing season total
Shrubs (Continued)			
Fraxinus pennsylvanica		3.0	1.5
Prunus virginiana	5.6	9.5	7.5
Rhus trilobata	5.7	7.0	6.3
Ribes spp.	2.1	5.2	3.7
Rosa spp.	0.7	4.9	2.8
Shepherdia argentea	44.9	11.5	28.2
Symphoricarpos occidentalis	4.9	13.0	8.9
Toxicodendron radicans	2.2	5.9	4.0
Total shrubs	69.2	74.9	72.1

[a] Includes primarily *Artemisia tridentata* and *A. cana*.

Table 51. Percent vegetative species composition identified in fecal samples of white-tailed deer during spring 1988 and summer 1988 and during the growing season (spring 1988 and summer 1988).

Plant species	Late spring 1988	Early summer 1987	Growing season total
Graminoids			
Agropyron smithii	1.1	1.1	1.1
Carex spp.		0.3	0.2
Elymus spp.	2.5	1.0	1.7
Poa spp.	6.4		3.2
Total graminoids	10.0	2.4	6.2
Forbs			
Achillea millefolium	1.1		0.5
Anemone spp.	1.3		0.7
Antennaria spp.	0.2		0.1
Arabis spp.	0.2		0.1
Astragalis spp.	1.3		0.7
Campanula rotundifolia	0.7		0.3
Cystopteris fragilis	0.3		0.2
Erysimum/Lithospermum		0.3	0.2
Galium boreale	1.2	0.2	0.7
Gaura coccinea	2.5		1.3
Lactuca spp.	1.5	0.1	0.8
Melilotus spp.	1.2	0.2	0.7
Monarda fistulosa	3.1	1.8	2.5
Oxalis stricta	2.5		1.3
Psoralea spp.	0.8		0.4
Ranunculus spp.	4.1		2.1
Sanicula marilandica	1.6	2.2	1.9
Smilacena stellata	0.5		0.3
Taraxacum officinale	0.3	1.0	0.7
Thermopsis rhombifolia	0.3		0.2
Vicia spp.	0.7		0.3
Unknown forb leaf	23.8	3.1	13.4
Unknown forb	0.8		0.4
Total forbs	50.0	8.8	29.4
Shrubs			
Artemisia frigida	0.9		0.5
Artemisia spp.[a]	0.2		0.1

Table 51. Continued.

Plant species	Late spring 1988	Early summer 1987	Growing season total
Shrubs (Continued)			
Fraxinus pennsylvanica	2.3	4.1	3.2
Populus spp.	1.9		0.9
Prunus virginiana	0.9	51.3	26.1
Rhus trilobata	3.9	11.2	7.5
Ribes spp.	2.4		1.2
Rosa spp.	4.8	4.1	4.5
Salix spp.	1.5		0.8
Shepherdia argentea	9.9	3.0	6.4
Symphoricarpos occidentalis	5.4		2.7
Toxicodendron radicans	6.1	14.0	10.1
Total shrubs	40.1	87.6	63.8

[a] Includes primarily Artemisia tridentata and A. cana.

APPENDIX E

Percent composition, hecterage and vegetative production of Habitat Types (HTs), Mapping Units (MUs), and Complexes in the Upland Grassland Physiographic Type for the South Unit of Theodore Roosevelt National Park.

Table 52. Percent composition and hecterage of Habitat Types (HTs), Mapping Units (MUs), and Complexes in the Upland Grassland Physiographic Type (PT) for the South Unit of Theodore Roosevelt National Park.

HT/MU/and Complex	Hectares	Percent composition
1. AGSM/STVI	513.5	50.8
2. AGSM/STCO	77.2	7.6
3. STCO/BOGR	192.3	19.0
4. SCSC	25.7	2.5
5. ARTR/ATCO	0.7	0.1
6. Hardwood Draws	0.3	tr[a]
7. Brush	2.6	0.3
8. Introduced Grass	155.7	15.4
9. Unvegetated Areas	42.6	4.2

[a] tr = <0.05%

[b] Description of PTs, HTs, MUs, and Complexes and definition of acronyms in Appendix A, Tables 30 and 31.

Table 53. Vegetative production (kg/ha) for Habitat Types (HTs), Mapping Units (MUs), and Complexes within the Upland Grassland Physiographic Type (PT). Production figures are from Marlow et al. 1984, Norland 1988[a] and Sullivan 1988.

Plant species	HT/MU/Complex			
	AGSM/ STVI	AGSM/ STCO	STCO/ BOGR	SCSC
Agropyron smithii	757	555	191	
Bouteloua curtipendula				64
Bouteloua gracilis	252	369	286	129
Calamovilfa longifolia			286	129
Carex spp.	84	92	191	129
Koeleria pyramidata	84	93	95	64
Muhlenbergia cuspidata				64
Poa spp.	87	25	22	
Schizachirium scoparium				259
Sporobolus cryptandrus			22	
Stipa comata		184	476	194
Stipa viridula	84	92		
Other grasses	210	112	50	64
Forbs	84	185	191	64
Ceratoides lanata	11			28
Rhus trilobata				56
Other shrubs	73	93	95	45
Total	1726	1800	1905	1289

Table 53. Continued.

Plant species	ARTR/ ATCO	HT/MU/Complex Hardwood Draws	Brush	Introduced Grass
Agropyron caninum			104	
Agropyron cristatum				841
Agropyron smithii			20	
Agropyron spp.	84			
Bouteloua curtipendula			11	
Bouteloua gracilis	56		68	
Bromus inermis				280
Calamovilfa longifolia			167	
Carex spp.	28		148	
Distichlis spicata	22			
Elymus canadensis			10	
Koeleria pyramidata			10	
Muhlenbergia cuspidata	28		9	
Muhlenbergia racemosa			26	
Oryzopsis micrantha			20	
Poa pratensis			159	
Poa spp.			19	
Schizachirium scoparium			34	
Stipa comata	28		54	
Stipa spartea			11	
Stipa viridula			21	
Other grasses	39		8	
Forbs	112		39	112
Amelanchier alnifolia		94		
Atriplex confertifolia	56			
Atriplex nuttallii	17			
Artemisia cana	45		3	
Artemisia tridentata	140			
Ceratoides lanata	17			
Chrysothamnus nauseosus	45			
Fraxinus pennsylvanica		559	1	
Juniperus horizontalis			12	
Prunus virginiana		386	82	
Ribes setosum			2	
Ribes odoratum			9	
Rosa spp.		35	1	
Rhus trilobata			10	
Symphoricarpos occidentalis	45	912	856	
Other shrubs	45			
Total	807	1986	1904	1233