Population dynamics, food habits, seasonal habitat use, and spatial relationships of bighorn sheep, mule deer, and feral horses in the Pryor Mountains, Montana/Wyoming
by Robert E. Kissell, Jr

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
Seasonal habitat use, seasonal food habits, interspecific behavior, and population dynamics of bighorn sheep (Ovis canadensis) mule deer (Odocoileus hemionus) and feral horses (Equus Caballus) in the Pryor Mountains, Montana, centered on the Pryor Mountain Wild Horse Range and adjacent rangelands, were examined during 1993-1995. Bighorn sheep used mountainmahogany, juniper, and mountainmahogany/juniper complexes most frequently at elevations < 2200 m on northeast and southeast aspects. Most slopes used were <45°° and at distances > 100 m from escape terrain.' Mule deer used juniper and mountainmahogany/juniper complexes on the winter range and sagebrush and conifer on the summer range. Elevations used on the winter range were < 1800 m and on the summer range varied from 1400 - 2200 m. Southeast and southwest aspects. dominated use in winter and northeast in summer. Slopes <31°° were commonly used on both summer and winter range. [Feral horses used juniper and grasslands most frequently, and use varied in elevation depending upon the season and portion of the herd. Winter was spent at elevations < 1800 m and summer elevation use included elevations > 2300 m and < 1800] All aspects were used equally, except northwest which was used least.

Bighorn sheep diets were dominated by browse (34.0% - 93.8%) in all seasons except spring, when grass was the dominant (58.6% - 66.0%) forage class. Mule deer diets showed winter to summer seasonal trends, with browse as the major winter, summer, and fall dietary component and forbs as the major spring dietary component. Feral horses consumed primarily grasses (66.95% - 96.35%) during all seasons and exhibited a high level (>20%) of browse use in the fall. Morista's similarity index suggested substantial dietary overlap between bighorn sheep and mule deer during fall and winter and substantial dietary overlap between bighorn sheep and feral horses during spring and summer.

Twenty-one interspecific interactions were observed during the study. Ifhorses were involved in an encounter and there was a dominant species, horses were the dominant species; bighorn sheep and mule deer were not observed exhibiting dominant or subordinate actions towards one another during the study.

The bighorn sheep population peaked at an estimated 211 animals in 1994 and declined in 1996 to an estimated 125 animals. Lamb production by bighorn sheep was sufficient to increase the population size; however, mean recruitment of yearlings was only sufficient to maintain the population in each year except 1995, when recruitment fell below the maintenance level. The mule deer population peaked at an estimated 780 animals during 1995 and decreased to an estimated 143 animals in 1996. Mean mule deer recruitment increased each year from 1994-1996, from 37 fawns: 100 does to 44.8 fawns to 100 does. The feral horse-population peaked at a minimum of 177 animals during 1994. Removal of 51 feral horses yielded a minimum of 143 animals in 1995. Population growth rates for feral horses were estimated at a maximum of 16.5%, 23.8%, and 21.2%, during 1993, 1994,-and 1995, respectively. Population structure of bighorn sheep and mule deer indicated inadequate nutrition for lambs and

fawns, respectively. Feral horse population growth indicated adequate nutrition. -

POPULATION DYNAMICS, FOOD HABITS, SEASONAL HABITAT USE, AND SPATIAL RELATIONSHIPS OF BIGHORN SHEEP, MULE DEER, AND FERAL HORSES IN THE PRYOR MOUNTAINS, MONTANA/WYOMING

by

Robert E. Kissell, Jr.

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

of

Doctor of Philosophy

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

December 1996

APPROVAL

of a thesis submitted by

Robert E. Kissell, 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.

Lynn R. Irby ____________ (Signature) 17 Dec 96 (Date)

Approved for the Department of Biology

Ernest R. Vyse ____________ (Signature) 12/17/96 (Date)

Approved for the College of Graduate Studies

Robert L. Brown ____________ (Signature) 1/20/97 (Date)

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a doctoral degree at Montana State University-Bozeman, I agree that the Library shall make it available to borrowers under rules of the Library. I further agree that copying of this thesis is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for extensive copying or reproduction of this thesis should be referred to University Microfilms International, 300 North Zeeb Road, Ann Arbor, Michigan 48106, to whom I have granted "the exclusive right to reproduce and distribute my abstract in any format in whole or in part."

Signature Robert E. Kissell Jr.

Date 18 December 1996

ACKNOWLEDGMENTS

I convey my deepest gratitude to Elizabeth, my wife, who supported and provided me with encouragement throughout my entire degree program. I wish to express my sincere appreciation to Dr. Lynn R. Irby who generously gave of his time when requested and provided advice, encouragement, and freedom during manuscript preparation and with related topics. I am indebted to Drs. Richard J. Mackie, Carl L. Wambolt, Jay J. Rotella, Robert G. White, and Earl Skogley, Montana State University, for reviewing the manuscript. I wish to recognize the many individuals who assisted in capture and collaring animals. I would also like to acknowledge Mr. Keith Iverson, Montana Department of Fish, Wildlife & Parks, Mr. Robert Hawkins, Mr. Rick Sanford, Mr. Rick Schwartz, and Mr. Kent Potter for their excellent flying during relocation and population survey flights. My appreciation is extended to Mr. Mark Thompson and Mr. Toby Swank for summer field assistance. I thank Mr. James T. Peters and Mr. Jack Lindsey for use of office space. I am indebted to the Barton, Carroll, Bassit, Schwend, Snell, Sintec, and Tillet families, and the Crow Tribe Indian Reservation for their hospitality. I thank F. Schwieger for assistance concerning the horse population. I also extend my appreciation to Dr. David E. Worley, Montana State University, for processing and analyzing samples for lungworm larvae counts. I am also grateful to the staff of the Geographic Information and Analysis Center, Montana State University. I wish to express my appreciation to the National Park Service, Bureau of Land Management, National Forest Service, and Montana Department of Fish, Wildlife & Parks for funding the study.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES
(continued)

LIST OF FIGURES

LIST OF FIGURES
(continued)

LIST OF FIGURES
(continued)

LIST OF FIGURES
(continued)

LIST OF FIGURES
(continued)

LIST OF FIGURES
(continued)

ABSTRACT

Seasonal habitat use, seasonal food habits, interspecific behavior, and population dynamics of bighorn sheep (Ovis canadensis), mule deer (Odocoileus hemionus), and feral horses (Equus caballus) in the Pryor Mountains, Montana, centered on the Pryor Mountain Wild Horse Range and adjacent rangelands, were examined during 1993-1995. Bighorn sheep used mountainmahogany, juniper, and mountainmahogany/juniper complexes most frequently at elevations < 2200 m on northeast and southeast aspects. Most slopes used were < 45° and at distances > 100 m from escape terrain. Mule deer used juniper and mountainmahogany/juniper complexes on the winter range and sagebrush and conifer on the summer range. Elevations used on the winter range were < 1800 m and on the summer range varied from 1400 - 2200 m. Southeast and southwest aspects dominated use in winter and northeast in summer. Slopes < 31° were commonly used on both summer and winter range. Feral horses used juniper and grasslands most frequently, and use varied in elevation depending upon the season and portion of the herd. Winter was spent at elevations < 1800 m and summer elevation use included elevations > 2300 m and < 1800 m. All aspects were used equally, except northwest which was used least.

Bighorn sheep diets were dominated by browse (34.0% - 93.8%) in all seasons except spring, when grass was the dominant (58.6% - 66.0%) forage class. Mule deer diets showed winter to summer seasonal trends, with browse as the major winter, summer, and fall dietary component and forbs as the major spring dietary component. Feral horses consumed primarily grasses (66.95% - 96.35%) during all seasons and exhibited a high level (>20%) of browse use in the fall. Morista's similarity index suggested substantial dietary overlap between bighorn sheep and mule deer during fall and winter and substantial dietary overlap between bighorn sheep and feral horses during spring and summer.

Twenty-one interspecific interactions were observed during the study. If horses were involved in an encounter and there was a dominant species, horses were the dominant species; bighorn sheep and mule deer were not observed exhibiting dominant or subordinate actions towards one another during the study.

The bighorn sheep population peaked at an estimated 211 animals in 1994 and declined in 1996 to an estimated 125 animals. Lamb production by bighorn sheep was sufficient to increase the population size; however, mean recruitment of yearlings was only sufficient to maintain the population in each year except 1995, when recruitment fell below the maintenance level. The mule deer population peaked at an estimated 780 animals during 1995 and decreased to an estimated 143 animals in 1996. Mean mule deer recruitment increased each year from 1994-1996, from 37 fawns:100 does to 44.8 fawns to 100 does. The feral horse population peaked at a minimum of 177 animals during 1994. Removal of 51 feral horses yielded a minimum of 143 animals in 1995. Population growth rates for feral horses were estimated at a maximum of 16.5%, 23.8%, and 21.2%, during 1993, 1994, and 1995, respectively. Population structure of bighorn sheep and mule deer indicated inadequate nutrition for lambs and fawns, respectively. Feral horse population growth indicated adequate nutrition.

INTRODUCTION

According to fossil records (Buechner 1960, Martin and Guilday 1967, Wallmo 1981, McFadden 1992), bighorn sheep (Ovis canadensis canadensis), mule deer (Odocoileus hemionus hemionus), and horses (Equus spp.) were all present on the North American continent prior to 8,000 years ago. Bighorn sheep evolved in Asia, apparently moved across the Bearing land bridge during the Pliestocene (Buechner 1960), and expanded southward throughout the Rocky Mountain range as far south as present day Mexico (Lawson and Johnson 1982). The evolution of mule deer on the continent is unclear and still debated; nonetheless, mule deer have been present in North America for at least 10,000 years and probably evolved from a cervid line that originated in Asia (Wallmo 1981, Mackie et al. 1982, Geist 1994). Equus evolved on the North American continent during the Pliocene (Simpson 1951, McFadden 1992), but along with many other large mammals (Simpson 1951, Martin 1967, Grayson 1989, McFadden 1992) became extinct on the North and South American continents between 8,000 and 13,000 years ago. Prior to that great megafaunal extinction all three genera had distributions encompassing the present day Pryor Mountains (Cowan 1940, Simpson 1951, Buechner 1960, McFadden 1992).

Bighorn sheep were numerous and widely distributed in western North America prior to European settlement (Buechner 1960), occurring in the Pryor Mountains and surrounding area before 1850 (Hamilton 1910). Distribution and numbers of bighorn sheep in the Pryor Mountains declined from the early 1800's to about 1860, when sheep were extirpated (Gordon et al. 1974). The Montana Department of Fish, Wildlife & Parks (MDFWP) reintroduced a total of 77 bighorn sheep in 1971 and 1974 to the Pryor Mountains (Gordon et al. 1974). In 1973, the Wyoming Game and Fish Department (WGFD) transplanted 39 sheep to the Porcupine drainage (Helms 1973) of the Bighorn Mountains, which empties into the Bighorn River. Genetic profiles (FitzSimmons 1992) and visual observations (Simmons and Stewart 1977, Coates and Schemnitz 1989) indicated sheep from both reintroductions contributed to establishment of the present Pryor Mountain bighorn sheep herd.

Mule deer were a very common ungulate in Montana before European settlement of the area (Burroughs 1961). With growing numbers of settlers, collapse of the fur trade, expansion of the livestock industry, loss of habitat, and unlimited harvest, the mule deer population declined prior to 1900 and did not rebound until the 1940's (Egan 1971). Since the early 1960's, the Pryor Mountain mule deer herd has experienced periodic increases and decreases in harvests (Ellig 1960, Townsend 1964, Foss and Whitney 1966, Foss et al. 1969, Simmons and Stewart 1979) which are assumed to reflect population size (Wood et al. 1989).

Cortez, on March 13, 1519, unloaded 16 horses from his ships near Vera Cruz, Mexico and introduced the first horses to inhabit North America in at least 8,000 years (Wyman 1946, Martin and Guilday 1967, McFadden 1992). During the following 3 centuries numerous other horses were brought to the continent where trading by Native Americans, ranchers, and missions facilitated the expansion of horses throughout the United States

(Simpson 1951). "Wild" horses of today are descendants of horses that escaped or were released by ranchers, missions, or Native Americans to range freely.

The time of arrival of horses in the Pryor Mountains is uncertain. Hamilton (1910) did not mention the presence of free-ranging horses in the Bighorn Basin in 1848 or 1849. Others suggest that free-ranging horses may have occupied south-central Montana since the 1700's (Wyman 1946). Regardless, feral horses occurred in the Pryor Mountains and the surrounding area, apparently in great numbers (Wyman 1946), until the 1930's. In the early 1930's, because of potential competition with livestock, stockmen sponsored round-up efforts. By 1939, these efforts were sufficiently effective that few feral horses were still free-ranging in Montana (Wyman 1946). Feral horses became re-established in the Pryor Mountains (Thomas 1979) prior to or during the 1960's and numbered approximately 200 by 1968 (BLM 1984).

As public support for protection of feral horses grew in the western United States, both national and local pleas for preservation increased. The Pryor Mountain Wild Horse Range (PMWHR) was established in 1968 by the Department of Interior (Federal Register Document 68-11056). Subsequent passage of the Wild Free-Roaming Horses and Burros Act (Public Law 92-195) in 1971 ended commercial exploitation of feral horse herds on public lands in the United States.

Condition of rangeland across the majority of the PMWHR and adjacent areas during the last half of this century has been described as poor or very poor (Firebaugh 1969, Gordon and Coop 1973, Hall 1973, BLM 1984, BLM 1992) with high potential for soil loss (Cleary and MacIntyre 1973). This, together with a steady increase in the bighorn sheep herd (Coates and Schemnitz 1989), fluctuating mule deer numbers as indicated by highly variable harvests (MDFWP, unpubl. data), and consistent high levels of reproduction of feral horses (Garrott and Taylor 1990), provided impetus for this study.

The study was designed to address the following objectives and hypotheses [given in brackets] on and around the PMWHR: 1) determine seasonal habitat use for bighorn sheep, mule deer, and feral horses [H_0: there is no significant overlap in habitat use among ungulates by season]; 2) determine seasonal diets for bighorn sheep, mule deer, and feral horses [H_0: there is no significant overlap in diets of ungulates by season]; 3) determine if population structure of bighorn sheep, mule deer, or feral horses indicated adequate nutrition [H_0: there is no difference between population structure of healthy populations and population structures of ungulates in the Pryor Mountain Study Area]; 4) estimate the population size trends for bighorn sheep, mule deer, and feral horses during 1993-1995; and, 5) determine if behavioral interactions among bighorn sheep, mule deer, and feral horses influence distribution or habitat use patterns [H_0: there is no difference in distribution given the presence or absence of another species].

STUDY AREA

The Pryor Mountain Study Area (PMSA) is located approximately 75 km south of Billings in Bighorn county, Wyoming, and Bighorn and Carbon counties, Montana (45° 00' N latitude, 108° 15' W longitude). The study area (Figure 1) encompassed approximately 700 km^2 that included the PMWHR and adjacent lands managed by the Bureau of Land Management (BLM), portions of the Bighorn Canyon National Recreation Area (BCNRA), the Custer National Forest (CNF), the Crow Tribe Indian Reservation (CTIR), and privately owned properties.

Topoedaphic Features

Topographic features (Figure 1) consisted of vertical canyon walls, steep talus slopes, and gently rolling hills and meadows intersected by canyons. Elevation varied from 1109 m to 2660 m. Steep slopes (> 45°) were primarily located along the Bighorn and Crooked Creek Canyons. Many creeks traversed the area, but perennial streams were rare and most water courses were intermittent (Figure 2). Soils were composed of sandstone, limestone, shale, dolomite, and alluvial deposits (Richards 1955, Blackstone 1975). Soil depth varied but has been described as severely depleted (Cleary and MacIntyre 1973).

Vegetation

Vegetation (Figure 3) was classified into 9 principal types (Knight et al. 1987, McCarthy 1996). Juniper woodlands were dominated by Utah juniper (Juniperus osteosperma). Mountainmahogany woodlands were dominated by curlleaf mountainmahogany (Cercocarpus ledifolius). Juniper/mountainmahogany woodlands were composed of a mixture of both Utah juniper and curlleaf mountainmahoghany. Riparian habitat was dominated by cottonwoods (Populus spp.) and fragrant sumac (Rhus aromatica). Desert shrubland was characterized by saltbush (Atriplex canescens, A. confertifolia), black greasewood (Sarcobatus vermiculatus), rubber rabbitbrush (Chrysothamnus nauseosus), big sagebrush (Artemisia tridentata), broom snakeweed (Gutierrezia sarothrae), bluebunch wheatgrass (Agropyron spicatum), threeawn (Aristida fendleriana and A. longiseta), and needle-and-thread (Stipa comata). Sagebrush steppe included both big sagebrush and black sagebrush (Artemisia nova) communities, the latter on limestone derived soils. Grasslands were dominated by bluebunch wheatgrass, blue grama (Bouteloua gracilis), needle-and-thread, broom snakeweed, Hooker sandwort (Arenaria hookeri), fringed sagebrush (Artemisia frigida), and Hood phlox (Phlox hoodii), alpine bluegrass (Poa alpinum), alpine timothy (Phleum alpinum), Ross sedge (Carex rossii), bluebunch wheatgrass, annual fescue (Festuca octoflora), silky lupine (Lupinus sericeus), grouse whortleberry (Vaccinium scoparium), paintbrush (Castilleja pulchellum), tufted fleabane (Erigeron caespitosus), tufted phlox (Phlox caespitosa), and goldenrod (Solidago radiata). Coniferous woodlands were characterized by limber pine (Pinus

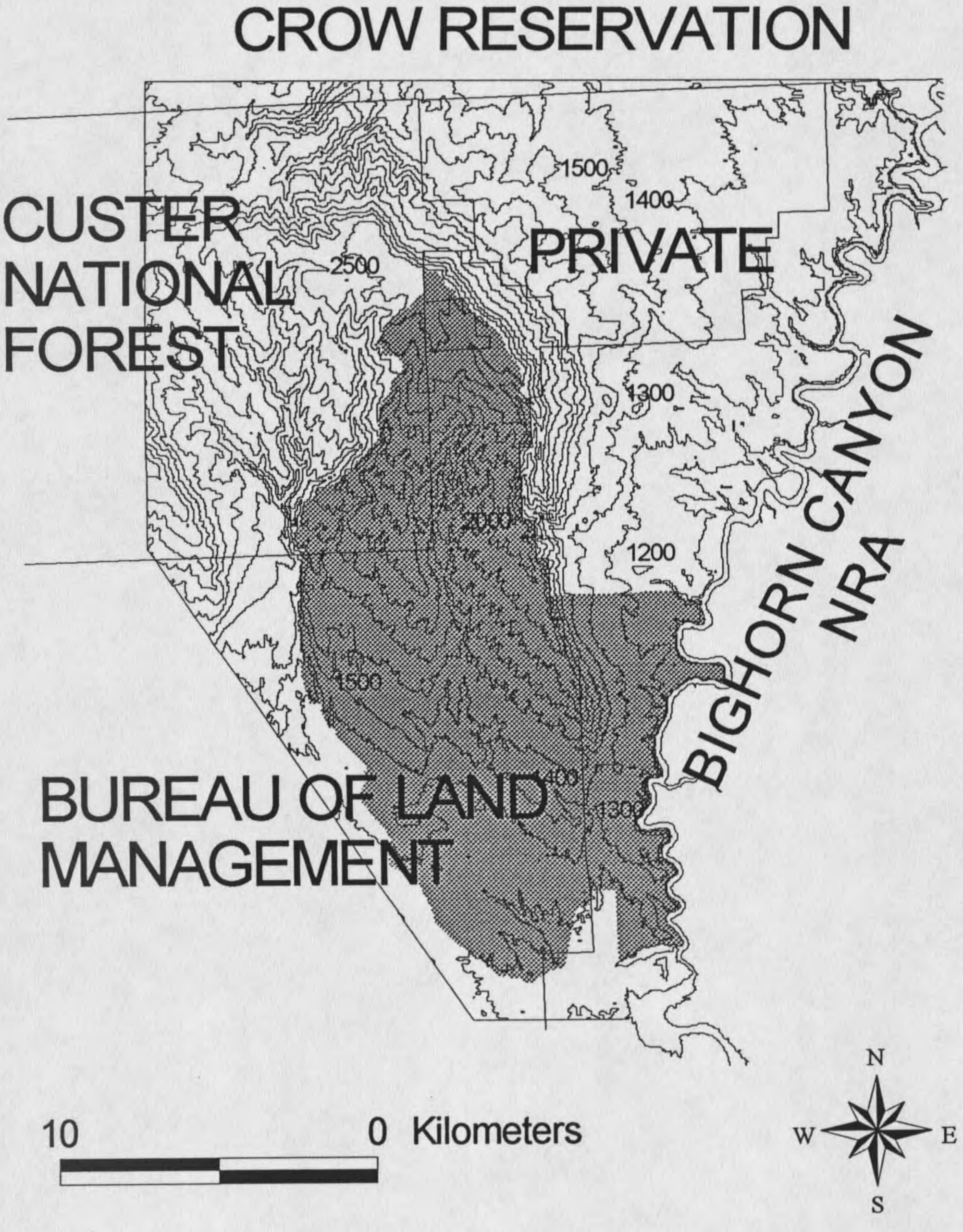

Figure 1. Pryor Mountain Study Area, associated ownership, and topography. The Pryor Mountain Wild Horse Range (shaded area) represents an approximate boundary.

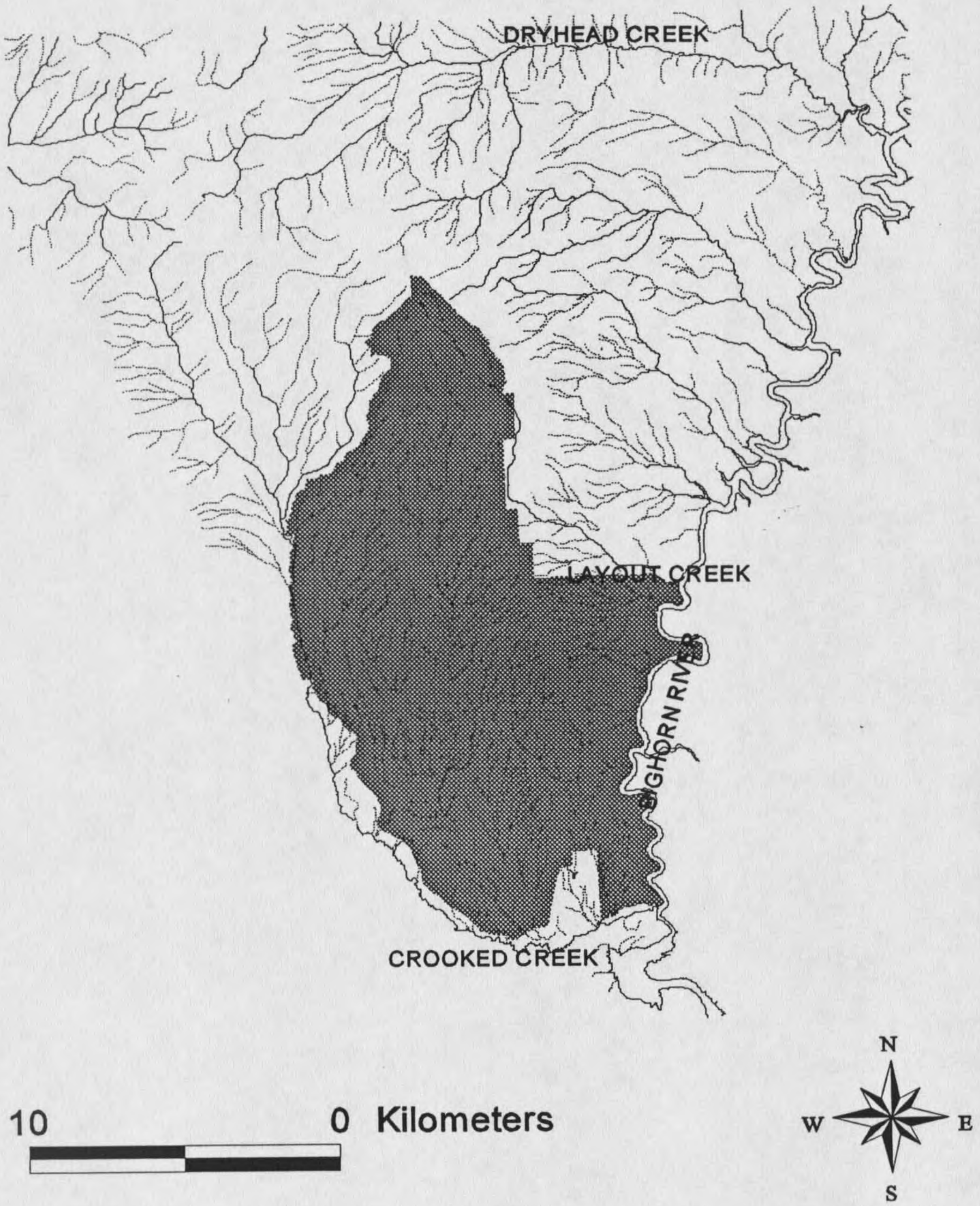

Figure 2. Permanent (solid lines) and ephemeral (dotted lines) streams on the Pryor Mountain Study Area as related to the Pryor Mountain Wild Horse Range (shaded area).

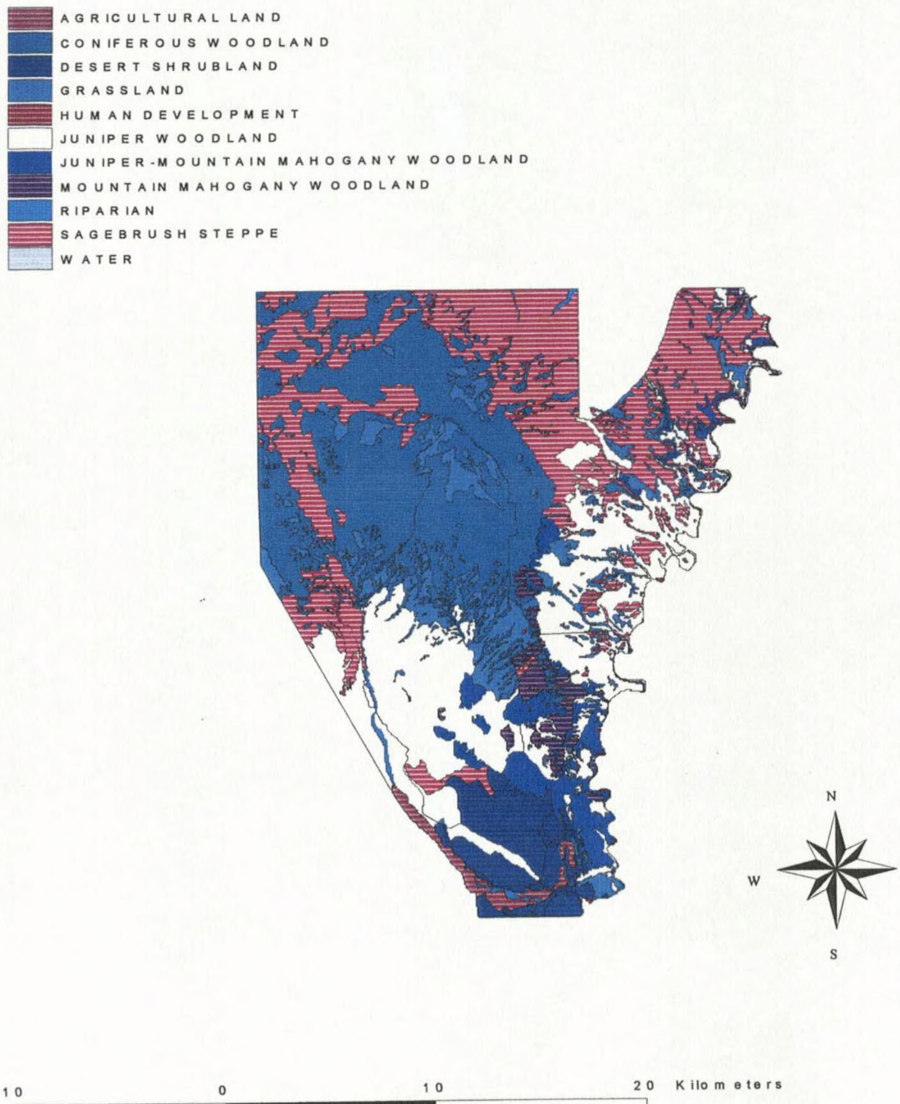

Figure 3. Distribution of vegetation on the Pryor Mountain Study Area. Southern and eastern portions were provided by Knight et al. (1987), and western and northern portions were developed during this study.

flexilis), ponderosa pine (P. ponderosa), Douglas fir (Psuedotsuga menziesii), and a spruce (Picea engelmannii) - fir (Abies lasiocarpa) mix. Agricultural areas were dominated by alfalfa (Medicago spp.).

Climatic Features

Climate varies from hot, dry, semi-arid to cold, dry, mesic conditions. Mean summer temperature in Lovell, WY (approximately 10 km SSW of the study area, measured at the Western Sugar Company (an official National Oceanic and Atmospheric Administration reporting station, recorded since 1920), was 21.1 °C with extremes exceeding 40°C. Mean maximum monthly winter temperature was -6.3 °C with extreme lows exceeding -34°C (Figure 4). December and January were the coldest months with average high temperatures of 0.5 °C and -0.7 °C. July and August were the hottest months with average high temperatures of 29.0 °C and 28.7 °C, respectively. Mean summer precipitation (June - August) was 2.13 cm and mean winter precipitation was 0.74 cm (Figure 5). Precipitation varies monthly with single rainfall events producing amounts ranging from a trace to > 5 cm covering portions or all of the Pryor Mountains.

Land Uses

The BLM, NPS, CNF, and MDFWP properties were most often used for wildlife and horse viewing, hunting, or fishing. Access was limited to a few main roads (Figure 6). Deer hunting was allowed on the study area, and deer were harvested following the regular season regulations of Wyoming and Montana. MDFWP issued 2 bighorn sheep

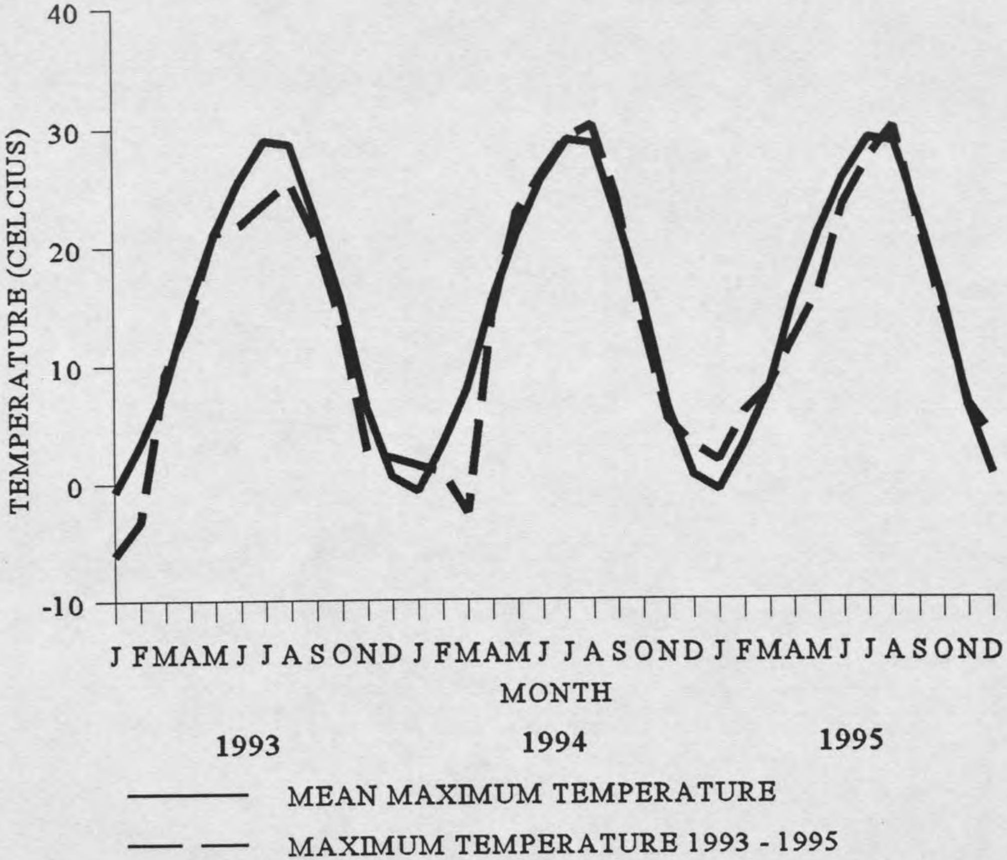

Figure 4. Maximum monthly temperatures for the Pryor Mountain Study Area from 1993 - 1995 in relation to mean monthly maximum temperatures (based on a 20 year average) at Lovell, WY.

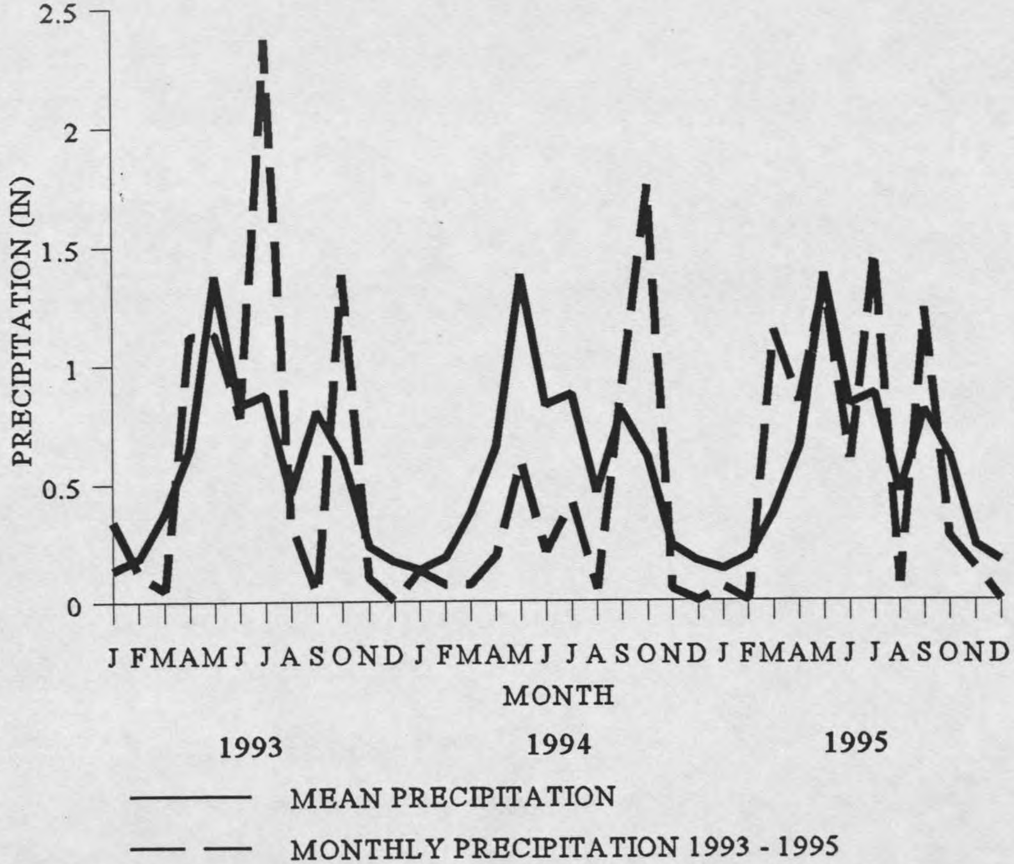

Figure 5. Mean monthly precipitation (based on a 20 year average) for the Pryor Mountain Study Area from 1993 - 1995 in relation to monthly precipitation at Lovell, WY.

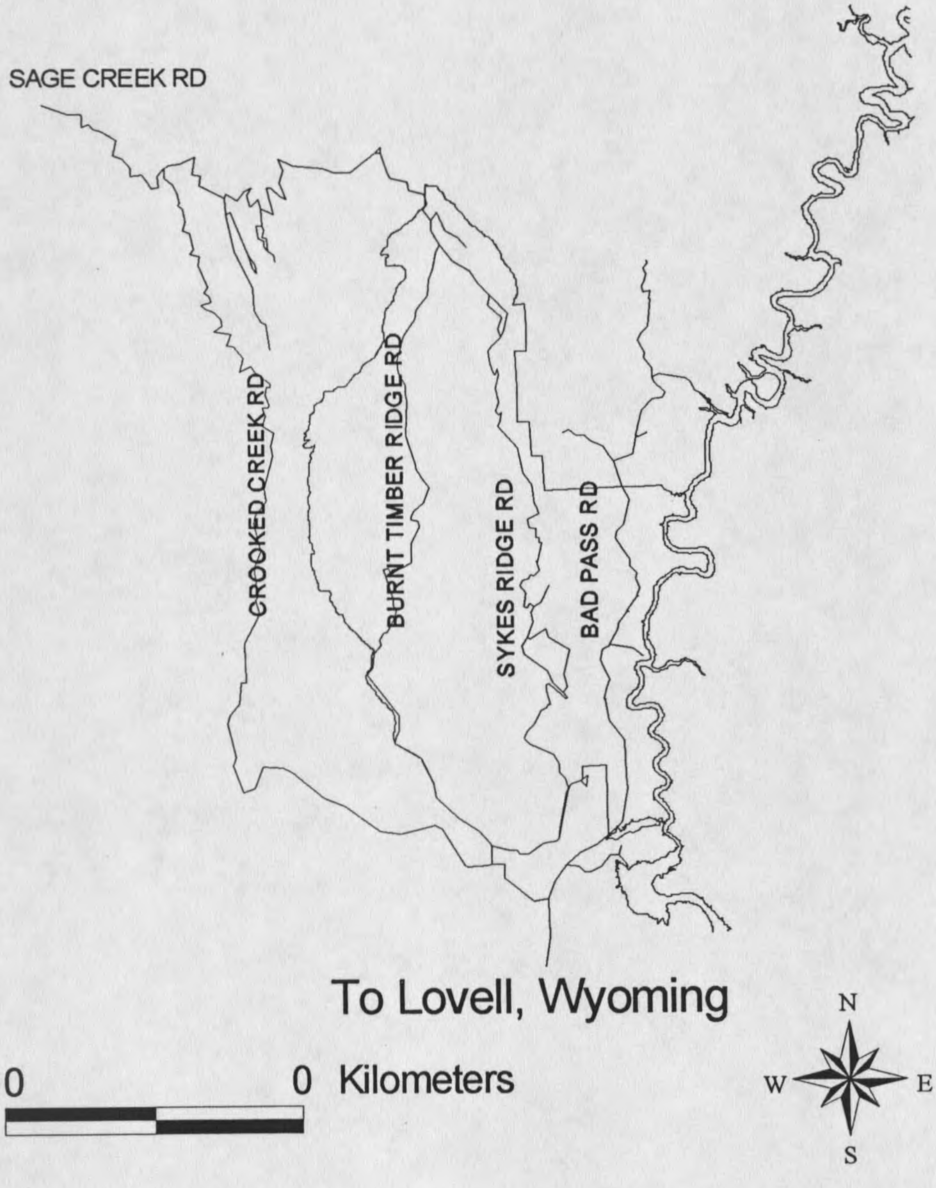

Figure 6. Main roads of the Pryor Mountain Study Area in relation to the Pryor Mountain Wild Horse Range (bold line).

permits annually in 1991 - 1993, and 4 permits were issued annually in 1994 - 1995. There were no bighorn sheep permits issued by WGFD for the area. Horses were gathered and the population was culled in fall 1992 and fall 1994.

Adjacent land uses included cattle ranching and farming. Cattle were maintained on portions (< 25%) of the study area throughout the spring and summer months on the CNF, the CTIR, and adjacent private lands. Alfalfa was the only agricultural crop grown during the study, occurring only in fields along the southern boundary of the study area.

METHODS

Animal Capture and Marking

Bighorn Sheep

Twenty-two female and 4 male bighorn sheep were captured and marked in September 1992, January 1993, April 1994, and June and July 1995 (Appendix, Table 14). Bighorn sheep were captured using a hand-held net gun fired from the ground or from a Hughes 500C helicopter following techniques described by Andryk et al. (1983). A concerted effort was made to distribute radiocollars among different bands to sample the population as broadly possible. Upon capture, the time and location were noted, the animal was blindfolded, and its legs were bound. Blood samples, nasal and pharyngeal swabs, and fecal samples were taken. Age was estimated for bighorn sheep using tooth wear and replacement (Cowan 1940, Deming 1952). Bighorn sheep males ≥ 4 years of age and females > 2 years of age were considered adults, male bighorns > 1 year and < 4 years of age were considered juveniles, and bighorns of both sexes < 1 year of age were considered young of the year (YOY) (Geist 1971). Thirteen of 22 (59%) ewes were adults at the time of capture and 3 of 4 (75%) rams were adults at the time of capture. Each bighorn sheep was fitted with an individually recognizable radiocollar (150.000-151.999 MHz) and tagged in each ear with a numbered, metal tag provided by MDFWP. Handling time was < 10 minutes per animal, and animals were released at the site of capture.

Mule Deer

Twenty-five mule deer, 19 does and 6 bucks, were captured and marked during January 1993 and January and February 1994 (Appendix Table 15). Mule deer were captured using a net gun fired from a Hughes 500C helicopter following techniques described by Barrett et al. (1982) or with Clover traps (Clover 1954) baited with alfalfa hay. An effort was made to distribute radiocollars as broadly as possible across the deer population. Upon capture, the time and location were noted, the animal was blindfolded, and its legs were bound. Only blood samples were taken from mule deer. Age of each individual was estimated to the nearest 6 months using tooth wear and replacement (Robinette et al. 1957). Mule deer ≥ 2 years of age were considered adults, deer > 1 year and < 2 years of age were considered yearlings, and deer < 1 year of age were considered YOY (Wallmo 1981). At the time of collaring, 2 of 6 (33%) bucks were adults, 3 (50%) were yearlings, and 1 (15%) was a YOY. Sixteen of 19 (84%) does were adults and 3 of 19 (16%) does were YOY at the time of capture. Each mule deer was also fitted with an uniquely marked radiocollar (150.000-151.999 MHz) and tagged in each ear with a numbered, metal tag provided by MDFWP. Handling time was < 10 minutes per animal, and animals were released at the site of capture.

Horses

Feral horses were not captured or radiocollared and no tissue samples or other biological materials were taken from horses prior to or during the study. Based on coat color and pattern, 20 readily recognizable horses, 14 females and 6 males, were used as "marked" animals (Appendix Table 16). At the time of identifying marked females, only 1 was a juvenile (7%).

Radiotracking and Visual Observation

Locations were determined for 3 time periods: morning (0500-0959 hrs); midday (1000 - 1559 hrs); and evening (1600-2300 hrs). Aerial locations of radiocollared bighorn sheep and mule deer were obtained using a portable TR-2 receiver (Telonics, Inc., Mesa, AZ) and 2, 2-element H-antennas attached to the wing struts of a Super Cub, or 1 pivotal, 3-element yagi antenna mounted beneath the fuselage. Aerial locations were typically obtained during the morning time block. Aerial locations were recorded on 1:24000 United States Geological Survey (USGS) topographic maps from January 1993 to January 1994; thereafter, a Garmin 95XL geographic positioning system (GPS) or a Garmin 45 Personal Navigator™ GPS unit (Garmin Inc., Lenexa, KS) was used to record aerial locations.

Radiocollared mule deer and bighorn sheep were located from the ground using a portable receiver and a hand-held, 2-element H-antenna for triangulation. Two bearings were obtained from routinely used telemetry stations (Nams and Boutin 1991), or by homing in on the marked animal. All locations were recorded from a 1:24000 USGS topographic map or determined by a Garmin 45 Personal Navigator™ GPS unit. Additional locations obtained by chance were recorded in a similar manner.

An attempt to locate radiocollared animals was made once each week from the ground and twice per month from the air between 15 February 1993 and 30 June 1993. From 1

July 1993 to 30 August 1995, radiocollared animals were aerially located once per month if conditions permitted. An attempt was also made to locate all radiocollared animals from the ground 3 times every 2 weeks during field seasons (Table 1). To obtain independence of observations within seasons, days and time blocks were randomly assigned to species and individual radiocollared animals, respectively. Feral horses were located during weekly ground surveys.

Usable telemetry or visual locations for bighorn sheep, mule deer, and feral horses totaled 2,512 (Table 2) from January 1993 through February 1996.

Table 1. Field seasons during which data were collected on the Pryor Mountain Study Area.

	YEAR		
SEASON	1993	1994	1995
WINTER	X	X	
SPRING	X	X	
SUMMER	X	X	X
FALL	X		

Coordinate Transformation

Universal Transverse Mercator (UTM) coordinates were obtained from telemetry data for each estimated location using a program written in SAS (SAS Inst., Inc. 1987). Locations determined using bearings having a difference of $< 30°$ or $> 150°$ were omitted, as these data resulted in unacceptable error polygons (White and Garrott 1990). Telemetry locations were transferred into ARC/INFO using the GENERATE subcommand. Visual locations recorded on 1:24000 USGS topographic maps were digitized and projected into real world coordinates using PROJECTDEFINE,

Table 2. Number of usable locations by season and species recorded from January 1993 - August 1995.

SEASON	SPECIES		
	BIGHORN SHEEP	MULE DEER	FERAL HORSES
WINTER	227	179	122
SPRING	322	199	165
SUMMER	492	132	276
FALL	226	95	77

PROJECT, and TRANSFORM subcommands in ARC/INFO. All locations were attributed in ARC/INFO.

Bearing Error

Bearing error was quantified by locating transmitters placed in unknown locations (n = 44) at varying distances (400, 600, 800, and 1500 m) from routinely used telemetry stations. The difference between observed and true bearings was recorded for each bearing taken.

An analysis of variance was used to determine if there was a difference between mean bearing error at different distances. Confidence intervals were calculated for each distance to determine if error was $\leq 5°$. A standard deviation of $\leq 5°$ was considered acceptable. Any deviation $> 5°$ would have resulted in error polygons being unacceptably large.

No significant differences were found in bearing errors (Table 3) at different distances (Table 4); therefore, error was assumed to remain the same at any distance. The mean error across all distances was 0.636° ± 2.96° and the average arc between bearings was 71.4°.

Table 3. Mean bearing error in degrees and the associated standard deviation for bearings taken for radiocollars placed at unknown locations at varying distances from routinely used telemetry stations on the Pryor Mountain Study Area.

Distance (m)	Mean (degrees)	Standard deviation (degrees)
400	0.727	2.91
600	0.455	2.40
800	0.727	1.03
1500	0.636	1.12

Table 4. Analysis of variance results testing the effect of distance (400 m, 600 m, 800 m, and 1500 m) on bearing error from routinely used telemetry stations on the Pryor Mountain Study Area from 1993-1995.

Source	D.F.	Sum of Squares	Mean Square	F-Value	Pr > F
Model	3	0.5454545	0.1818182	0.02	0.9963
Error	40	375.63636	9.3909091		
Total	43	376.18182			

Error Polygons Based on Telemetry, GPS, and Visual Data

Using the standard deviation calculated from the bearing error trials, degrees were added to and subtracted from the observed bearing, such that 97.5% error arcs were obtained about each bearing. The intersection of the 2 error arcs provided the 95% error polygon (Nams and Boutin 1991) for each location. UTM coordinates were obtained from telemetry data for each error polygon.

Locations recorded by GPS units were presumed to be within 100 m 100% of the time (Garmin Int. 1994). To account for this GPS error, a circle with a radius of 100 m around recorded locations was created using the BUFFER subcommand in ARC/INFO. Visual locations recorded on 1:24000 USGS topographic maps were treated in the same manner.

Average distance from telemetry stations to estimated locations determined by telemetry was 1,869 m. The average error polygon size, based on distance from test collars and the standard deviation of bearings, was 6.92 ha. Error polygon size was 3.14 ha for visual or GPS locations.

Seasonal Habitat Use

Determining Use of Habitat Variables

Seasons were defined as winter: 23 December - 20 March; spring: 21 March - 21 June; summer: 22 June - 23 September; and, fall: 24 September - 22 December. Habitat was defined by the following variables: elevation, slope, aspect, vegetative type, distance to permanent water, distance to main roads, and distance to escape terrain (for sheep only). Elevation was partitioned into 100 m intervals (1000 m - 2600 m). Slope was segregated into 5 categories (≤ 15°, 16°-30°, 31°-45°, 46°-60°, > 60°). Aspect was divided into 9 categories (flat, NNW, NNE, ENE, ESE, SSE, SSW, WSW, WNW). Vegetation was separated into 9 types (see Study Area for description). Distance to permanent water and distance to main roads were arranged into 8 intervals (0 - 50 m, 50 - 100 m, 101 - 300 m, 301- 500 m, 500 - 750 m, 750 m -1 km, 1km - 1.5 km, and > 1.5 km). Because escape terrain is considered an important parameter aiding in predator avoidance and evasion for bighorn sheep (Geist 1971), it was defined as areas having slopes > 30° (Fairbanks et al. 1987, Tilton and Willard 1982). Distance from escape terrain was divided into the same intervals as distance to permanent water and main roads. Use was determined by telemetry and visual locations.

Analytical Procedures

For each habitat variable, a chi-square test was used to determine distributional differences among ungulates. To assess spatial overlap, the study area was divided into 25 ha (500 m X 500 m) cells (Figure 7). The number of grid cells common to 2-species pairs was used to determine the minimum percent overlap (Porter and Church 1987, Wood et al. 1989, Fritzen 1995). Spatial overlap of one species by another was relative to the number of cells occupied by the other. For instance, if bighorn sheep occupied 100 cells, horses 50, and there were 25 cells common to each, bighorn sheep overlapped horses 50% and horses overlapped sheep 25%.

Seasonal Diets

Field Procedures

Pellet groups observed to be dropped by bighorn sheep and mule deer were collected within 1-48 hrs after defecation. The time delay was sometimes necessary to avoid

Figure 7. Grid cells overlaying the Pryor Mountain Study Area used to assess spatial overlap among bighorn sheep, mule deer, and feral horses during winter 1993 - summer 1995.

behavioral disturbance. Entire, or nearly entire, pellet groups were collected for bighorn sheep and mule deer; only one pellet from each fecal deposit from horses was collected. Samples were air-dried before being analyzed by an independent laboratory (Wildlife Habitat Lab, Washington State University). Two composite samples, each containing pellet groups from 10-20 individuals of the same species, were collected during winter, spring, summer, and fall during 1993, winter, spring, and fall during 1994, and winter and summer 1995.

Diet composition was determined using microhistological techniques to identify epidermal fragments to species when possible; otherwise, identification was made to the most detailed level possible (e.g., genus). Eight slides and 25 views per slide were used to determine percent diet composition. Nomenclature of all dietary items followed Scott and Wasser (1980).

Analytical Procedures

Food habits of each species were presented seasonally as percent occurrence by plant species or genera within 4 major forage classes or groups (grasses, forbs, browse, and other). Grasses included grasses and grass-like plants; forbs were non-woody, non-grass or grass-like plants; browse included leaves, current annual growth, buds and stem tissues from trees, shrubs, and half-shrubs; and, other included unknown items. For each season, comparisons of each forage class between years was performed using a Wilcoxon 2-sample test if 2 years were represented and a Kruskal-Wallis test if 3 years were represented. Only major food items ($\geq$ 3%) were used as data for each comparison. If no differences existed, the data were pooled to represent annual food habits.

Interspecific similarity of diets was determined using Morista's (1959) similarity index as modified by Hardin (1966). This was not a statistical test but yielded the percent overlap in the diet. Dietary overlap of > 50% during any season was considered substantial.

Behavioral Interspecific Interactions

Field Procedures

An attempt was made to observe each marked animal and its associates twice per season, once during morning and once during afternoon hours. Randomly chosen days within a season and randomly chosen individual radiocollared animals were selected for observation. Observations of horses were conducted by chance. An observation consisted of a 1-hour session during which behavior (feeding, bedded, standing, moving) was recorded every 5 minutes for both the focal animal and the majority (> half of the group) of animals present. Observations were made using a 15-60 X spotting scope or 7-21 X 50 binoculars. During each session, the number of hetero- and conspecifics visible in the area, estimated distance of hetero- and conspecific groups from the focal group, estimated distances moved at 15-minute intervals by the focal animal and the group associated with it, and social responses (dominant, submissive, or indifferent) of an encounter (i.e., when different species were in close proximity (<200 m) to one another) were noted. Dominant behavior included displays, such as head bowing by horses or horn displays by sheep, chases, or usurping of an area. Submissive behavior was characterized by vacating an area with the approach of another species or a change of behavior when near another species; for instance, walking slowly until within a given distance of a heterospecific individual or group and running past until at a tolerable distance, then returning to a walk. Indifference was recorded when neither species exhibited dominant or submissive behavior.

Analytical Procedures

Behavioral data by season were pooled across years and percentages of different categories of behavior recorded were presented by hour and season. An analysis of variance was performed to assess differences in timing of interspecific behaviors. Data were arcsine-square root transformed to achieve homogeneity of variance, and hours were used as replicates for both the morning and afternoon time periods.

Population Structure and Population Size Estimation

Field Procedures

Population structure was described in terms of the numbers of young of the year (YOY; lambs, fawns, or foals) and numbers of adult males (rams, bucks, or stallions) per 100 adult females (ewes, does, or mares) observed from ground or aerial surveys. Age and sex ratios were obtained during the first 3 flights of winter population surveys during 1993-1994, 1994-1995, and 1995-1996. The ratio of YOY:100 adult females during winter was used as an indicator of recruitment of young to adult population based on the assumption that no differential mortality of young occurred during the remainder of winter or spring.

To estimate population sizes, I counted numbers of marked and unmarked animals observed during aerial transect surveys (Figure 8) flown in a Hiller 12-E or a Bell 47 helicopter during winter, 1993-1995 (Table 5), with each transect replicated 5 times. Four flights were conducted during January and February 1996, in a Hiller 12-E or a Hughes 500C. These included 2 complete area coverage surveys and 2 replicate transect flights.

In all years, transects varied in length (0.8 km - 10.8 km), were separated by approximately 0.8 km, and were typically flown during morning hours (Table 5). Transects were flown ≥ 40 m above the ground and at 40 - 60 km/hr using geographic landmarks and compass bearings for guidance. The date, time, species, number of animals, number of marked animals, the identification of each marked animal, sex, age (adult, juvenile, or YOY), and location were noted during each survey. To prevent double counting, bighorn sheep and mule deer groups were hazed in the opposite direction of the progression of the survey; feral horses were not intentionally disturbed. During surveys conducted in the winters of 1992-1993 and 1993-1994, locations were recorded on 1:24000 USGS topographic maps using landmarks and the flight path to determine locations. During the winters of 1994-1995 and 1995-1996, locations were recorded using a Garmin 95XL™ GPS unit (Garmin Inc., Lenexa, KS).

Figure 8. Transects flown during winter population surveys in relation to the Pryor Mountain Wild Horse Range (shaded area).

Table 5. Date, time, pilot, aircraft, flight time, and type of coverage used during population surveys conducted on the Pryor Mountain Study Area during winters of 1993-1996.

SURVEY YEAR	DATE	PILOT	AIRCRAFT	FLIGHT TIME	COVERAGE
1993	11 FEB	HAWKINS	HILLER	0700-1200	TRANSECT
1993	17 FEB	HAWKINS	HILLER	1230-1630	TRANSECT
1993	22 FEB	HAWKINS	HILLER	0800-1100	TRANSECT
1993	1 MAR	HAWKINS	HILLER	0745-1230	TRANSECT
1993	8 MAR	HAWKINS	HILLER	0745-1115	TRANSECT
1994	29 NOV	IVERSON	BELL 47	0815-1345	TRANSECT
1994	6 DEC	IVERSON	BELL 47	0800-1315	TRANSECT
1994	13 DEC	IVERSON	BELL 47	0745-1245	TRANSECT
1994	11 FEB	IVERSON	BELL 47	0730-1100	TRANSECT
1994	17 MAR	IVERSON	BELL 47	0700-1130	TRANSECT
1995	24 FEB	IVERSON	BELL 47	0845-1330	TRANSECT
1995	1 MAR	IVERSON	BELL 47	0900-1415	TRANSECT
1995	3 MAR	IVERSON	BELL 47	0845-1215	TRANSECT
1995	26 MAR	SANFORD	HILLER	1000-1400	TRANSECT
1995	6 APR	SANFORD	HILLER	0915-1345	TRANSECT
1996	23 JAN	SANFORD	HILLER	0930-1515	TOTAL AREA
1996	6 FEB	SANFORD	HILLER	0815-1315	TOTAL AREA
1996	13 FEB	SANFORD	HUGHES	0745-1130	TRANSECT
1996	17 FEB	SANFORD	HUGHES	0745-1100	TRANSECT

Analytical Procedures

A Wilcoxon 2-sample test was used to compare median age ratios for bighorn sheep and mule deer populations against other populations described as increasing, and therefore thought to have adequate nutrition (Keating 1982). Comparison of the feral horse population with other feral horse populations was made using population growth rates, as age and sex ratios were not common statistics reported for this species. While age ratios for bighorns and deer or population growth rates for horses were the only data available to use as a measure of adequate nutrition, it should be noted the relationship between these factors is not known. Other possible methods of assessing this relationship include urinary indicators of nutritional status (DelGiudice 1995; however, see Saltz et al. 1995), measurements of kidney fat, marrow fat, and blood related indices (Harder and Kirkpatrick 1996).

Estimates of population size were calculated using the joint hypergeometric maximum likelihood estimator (Bartmann et al. 1987, Bear et al. 1989, White and Garrott 1990, Neal et al. 1993, White 1996) from the NOREMARK program (White 1996). If the minimum number known alive (MNKA) was greater than the lower confidence interval bound, the MNKA was used as the lower bound. This method is a modified form of the Lincoln-Peterson mark-recapture model based on the hypergeometric distribution (Chapman 1951, Chapman 1952). The model has 5 assumptions (White and Garrott 1990, White 1996): 1) marking of animals is by simple random sampling without replacement; 2) the population is closed, both geographically and demographically; 3) equal sighting probability for each animal, but sighting probabilities can vary from one survey to another; 4) the correct number of marked animals is known; and, 5) double counting does not occur.

Assumptions were reasonably met in the study. Radiocollared bighorn sheep did not have consistent associations with other radiocollared bighorn sheep, and I assumed this same random association extended to the entire population. Marked bighorn sheep, therefore, were considered to represent a random sample. Radiocollared mule deer live in matriarchal family and bachelor groups (Mackie et al. 1982) and were assumed to be marked in a simple random fashion as no matriarchal groups had > 1 radiocollar.

The process used to "mark" feral horses violated the assumption of simple random sampling with replacement. Feral horses have a patriarchal social system (Klingel 1974), and in some cases more than one "marked" animal occurred in a social unit, indicating simple random sampling with replacement. Given the unique markings of the feral horses and low sightability (LeResche and Rausch 1974, Bartmann et al. 1986), the MNKA was determined during ground surveys (Frei et al. 1979).

In winter, bighorn sheep and mule deer populations were assumed to be both demographically and geographically closed. No lambing occurred during this time of year, and no known deaths of bighorn sheep were recorded. Geographically, bighorn sheep show strong site fidelity (Geist 1971) and, based on radiocollared animals, did not disperse to new areas during winter. Mule deer were not fawning at this time of year, and even though some carcasses were discovered during the winter, these were few in number and not likely to significantly affect the population estimation. The winter range for mule deer was well defined by climatic, vegetative, and topographic features which limited mule deer movements to a given area, thereby providing geographic closure.

Sightability is known to affect population estimation of large mammals (Samuel et al. 1987, Neal et al. 1993, Bodie et al. 1995). Equal sighting probabilities were assumed to exist among animals but not confirmed. Bighorn sheep favor steep terrain in areas with high visibility (Geist 1971, Wakelyn 1987), and locations in which bighorn sheep were observed were represented by such features. Likewise, in this study, mule deer favored and were observed occupying outcropping terrain in association with curlleaf mountainmahogany or juniper.

Prior to surveys in each year, I determined the number of marked animals available by days or weeks of ground coverage of the study area using telemetry and visual reconnaissance. Marked animals with non-functioning radiocollars that were not observed during.this period were not included in marked samples.

RESULTS

Seasonal Habitat Use

Bighorn Sheep

Bighorn sheep were located at lower elevations (< 1500 m) yearround (Figure 9), with a majority of the locations occurring between 1300 - 1400 m. Less steep slopes (< 31°) contained a majority (> 75%) of locations during each season examined (Figure 10), and only a small percentage of all locations were recorded in very steep terrain. Eastern aspects were used most frequently in all seasons (Figure 11) followed by southern aspects; completely flat aspects were used least. Locations were most often in the mountainmahogany and/or juniper vegetative type during all seasons (Figure 12). Little use of agricultural and desert shrubland was noted. Distance of locations from permanent water varied (Figure 13), but consistent peaks at distances > 500 m were common for each season. Bighorns were often observed along the roads, but frequency of occurrence related to distance to main roads (Figure 14) varied by season and more than 50% were > 200 m during all seasons. Distribution of locations in relation to escape terrain (Figure 15) indicated more than 50% of locations were within 400 m of cliffs or steep slopes regardless of season. However, more than 20% of all seasonal locations occurred at distances > 500 m from escape terrain.

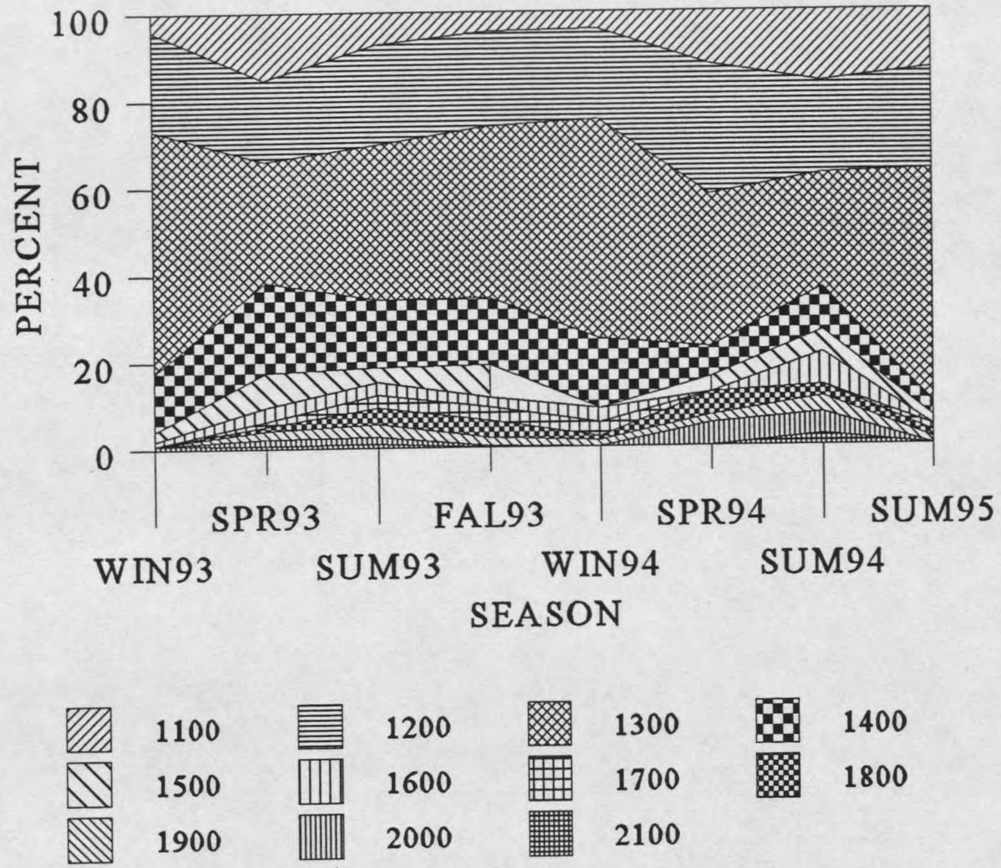

Figure 9. Percent of all locations of bighorn sheep that occurred at various elevations (< 1100 m - > 2100 m) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

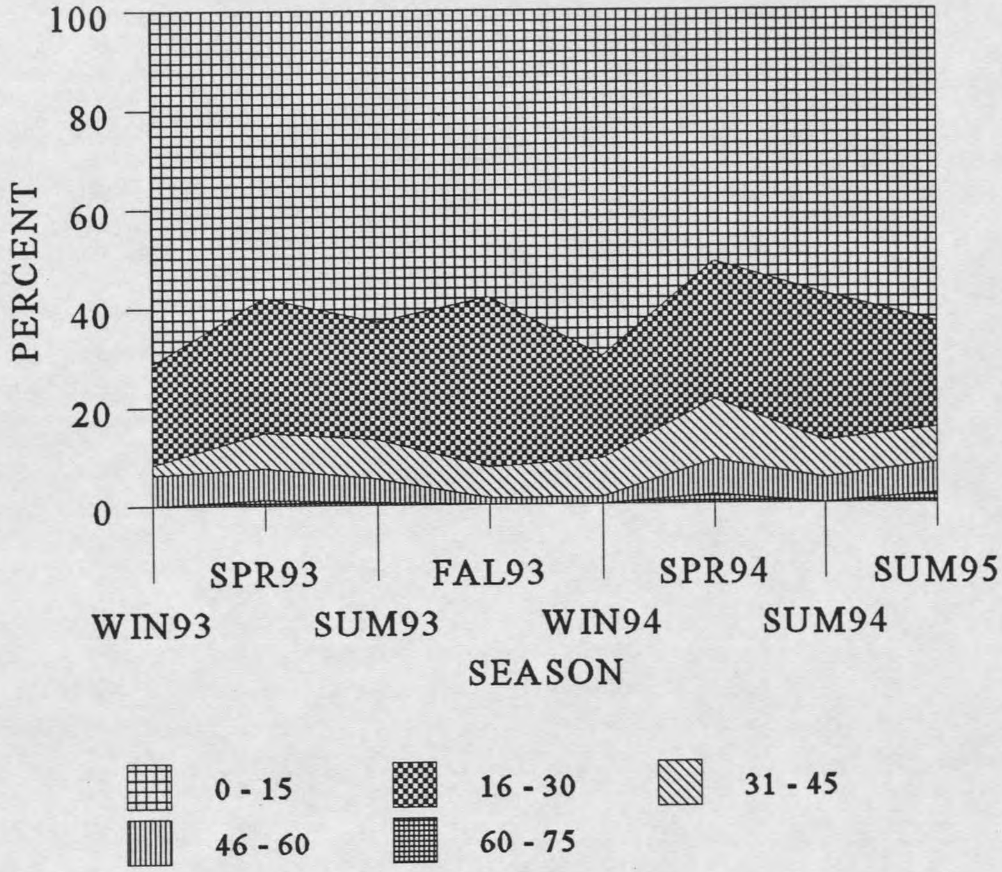

Figure 10. Percent of all locations of bighorn sheep that occurred at various slopes (0 - 60°+) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

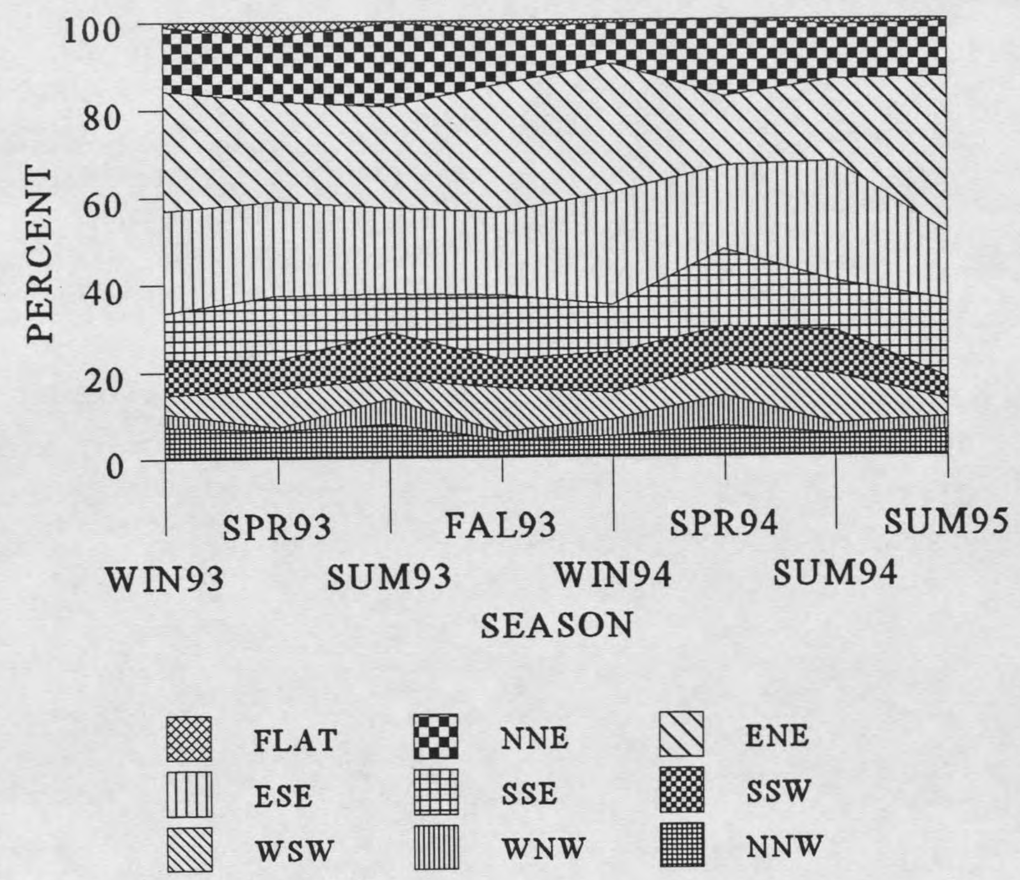

Figure 11. Percent of all locations of bighorn sheep that occurred on various aspects (flat, NNE, ENE, ESE, SSE, SSW, WSW, WNW, NNW) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

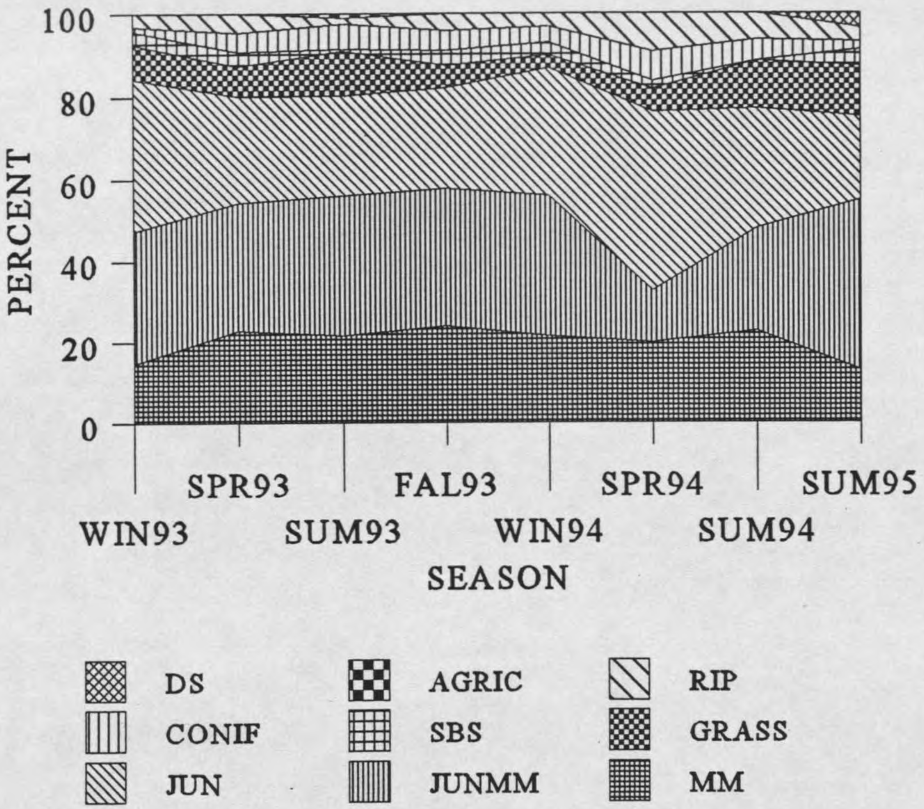

Figure 12. Percent of locations of bighorn sheep that occurred in various vegetative types (MM = Mountain Mahogany Woodland, JUNMM = Juniper-Mountain Mahogany Woodland, GRASS = Grassland, SBS = Sagebrush Steppe, CONIF = Coniferous Woodland, RIP = Riparian, and AGRIC = Agricultural Land) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

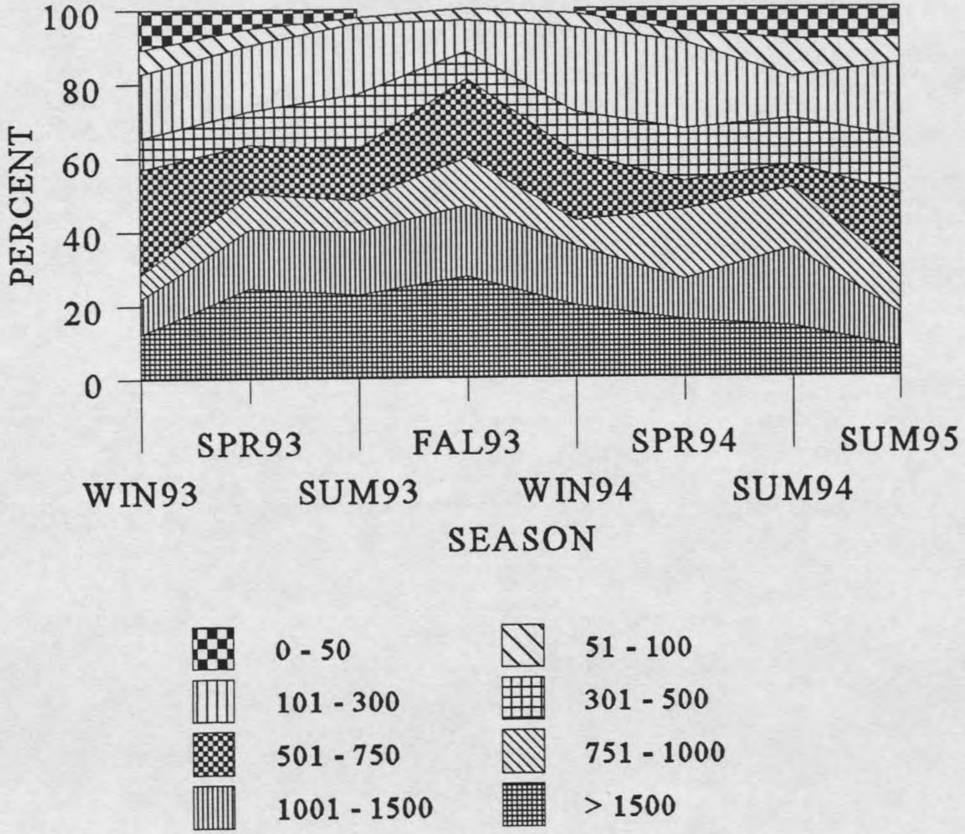

Figure 13. Percent of all locations of bighorn sheep that occurred at various distances to permanent water (0 - 50 m, 51 - 100 m, 101 - 300 m, 301 - 500 m, 501 - 750 m, 751 - 1000 m, 1001 - 1500 m, > 1500 m) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

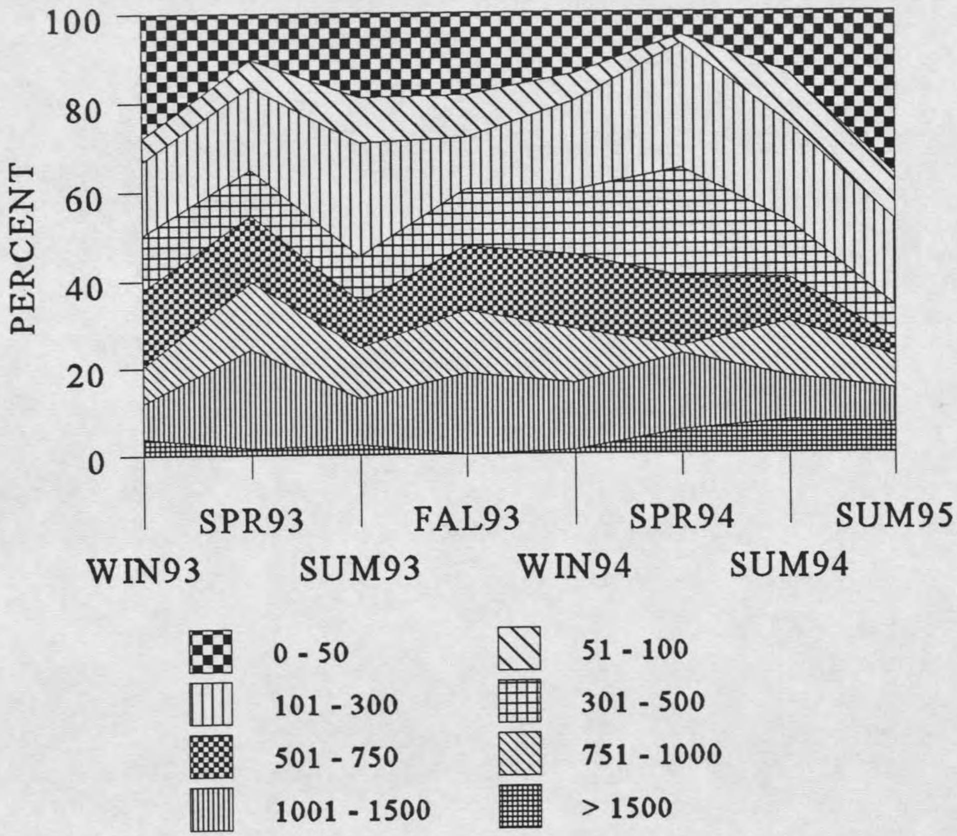

Figure 14. Percent of all locations of bighorn sheep that occurred at various distances to main roads (0 - 50 m, 51 - 100 m, 101 - 300 m, 301 - 500 m, 501 - 750 m, 751 - 1000 m, 1001 - 1500 m, > 1500 m) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

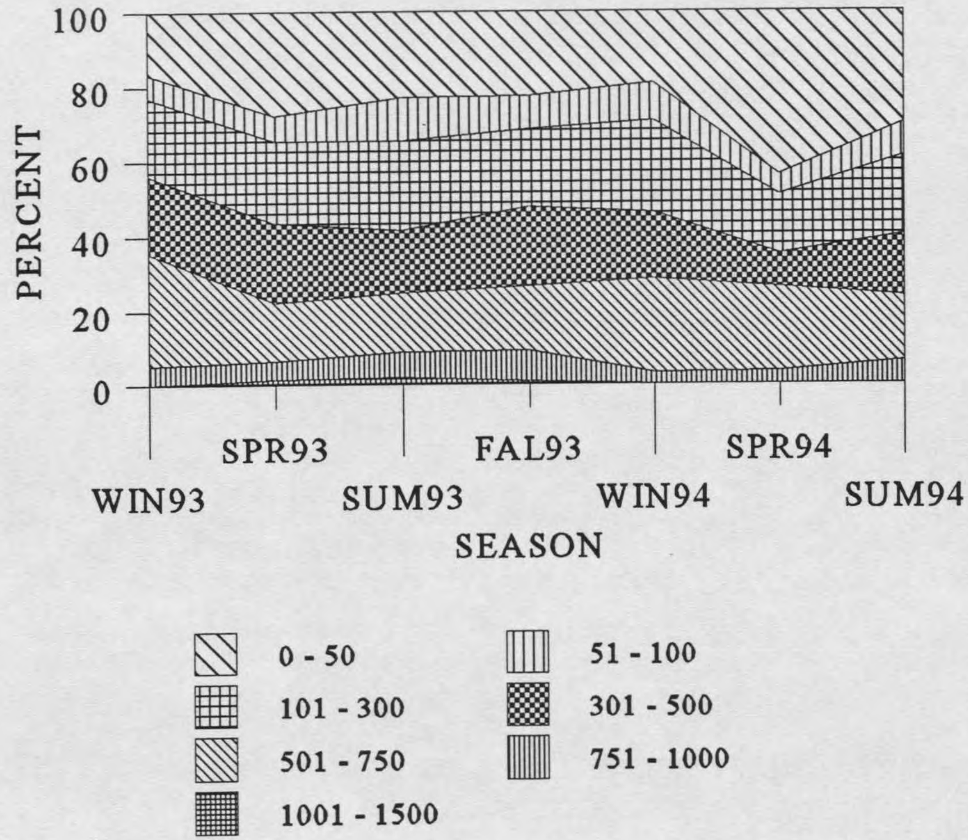

Figure 15. Percent of all locations of bighorn sheep that occurred at various distances to escape terrain (0 - 50 m, 51 - 100 m, 101 - 300 m, 301 - 500 m, 501 - 750 m, 751 - 1000 m, 1001 - 1500 m, > 1500 m) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

Mule Deer

Mule deer occurred over a wide range of elevations (Figure 16), but were most often found at elevations < 1500 m on the PMSA. More than 80% of all locations of mule deer were on slopes < 31°; and slopes > 45° were seldom used (Figure 17). Eastern, southern, and northeastern aspects (Figure 18) were used most regardless of season and completely flat aspects were seldom used. Within the study area, juniper and/or juniper-mountainmahogany vegetation types were used often, as were mountainmahogany, coniferous woodlands, sagebrush steppe, and desert shrubland (Figure 19). Use changed by season with the juniper and mountainmahogany complexes used most in winter and the coniferous woodlands, sagebrush and juniper used in summer. Distance to permanent water (Figure 20) varied depending upon season, but deer appeared to occur at greater distances from water during winter and spring. A majority (> 50%) of locations during fall were within 200 m of main roads (Figure 21). Otherwise, distance to main roads varied depending upon season.

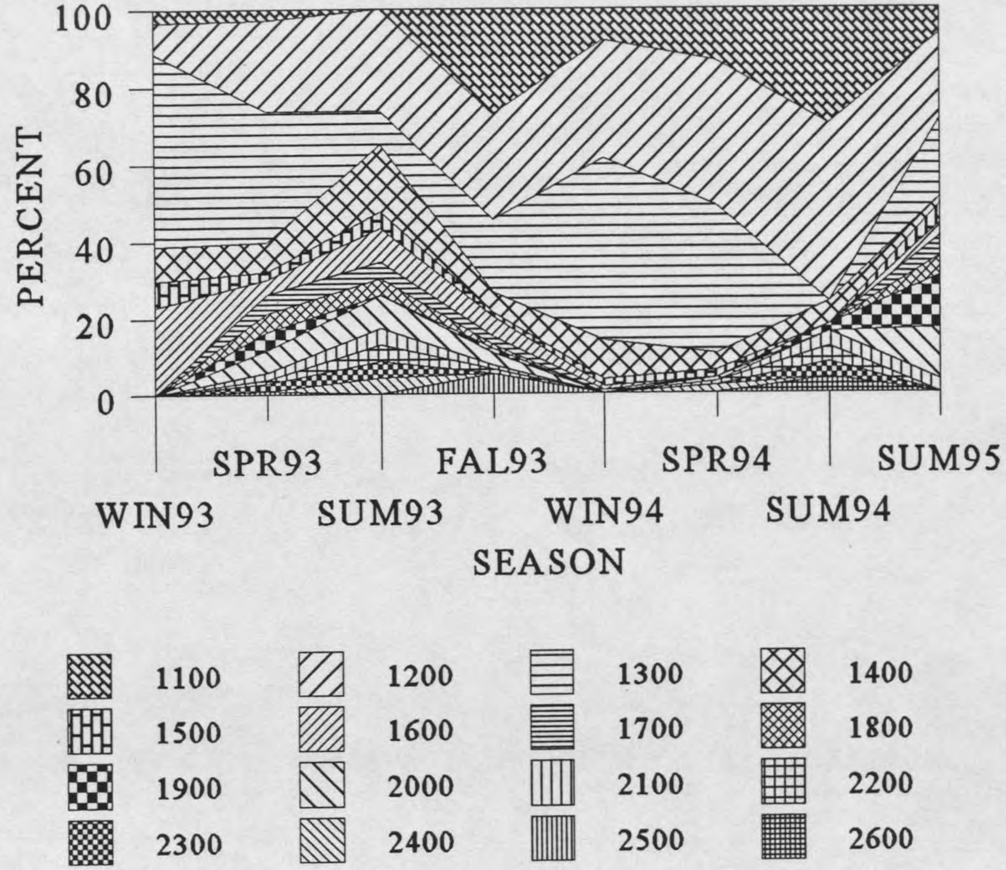

Figure 16. Percent of all locations of mule deer at various elevations (< 1100 - > 2600 m) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

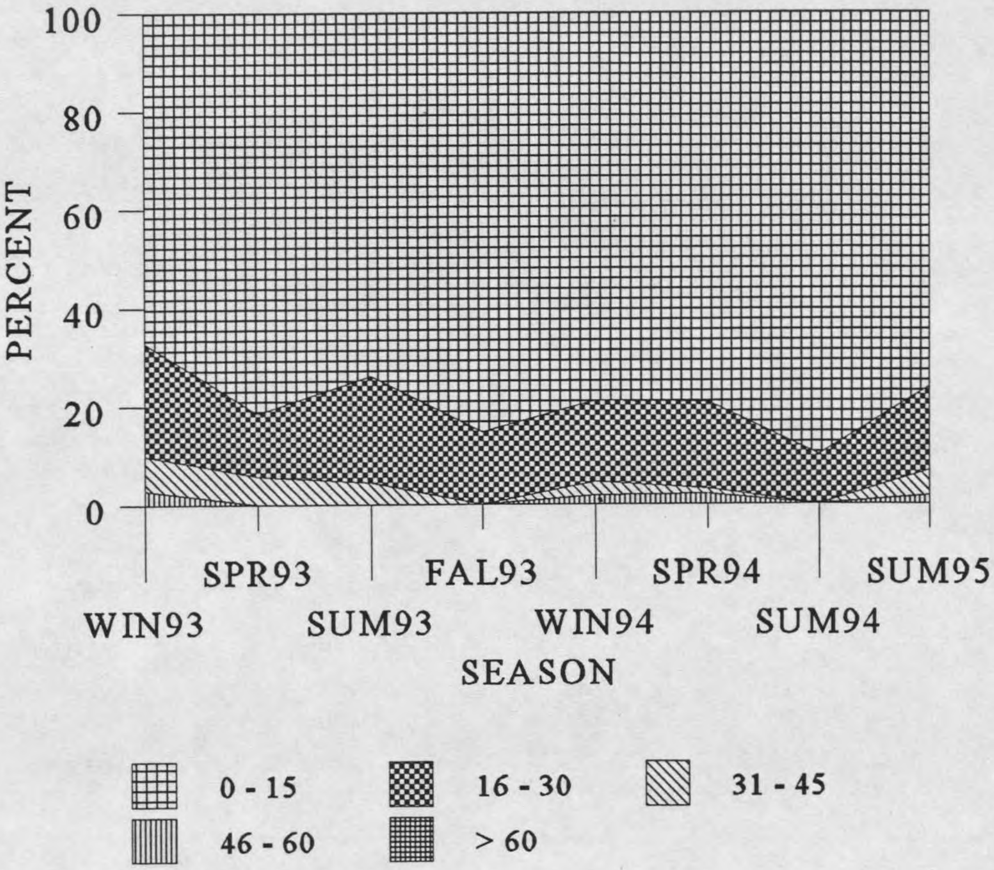

Figure 17. Percent of all locations of mule deer at various slopes (0 - 15°, 16 - 30°, 31 - 45°, 45 - 60°, > 60°) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

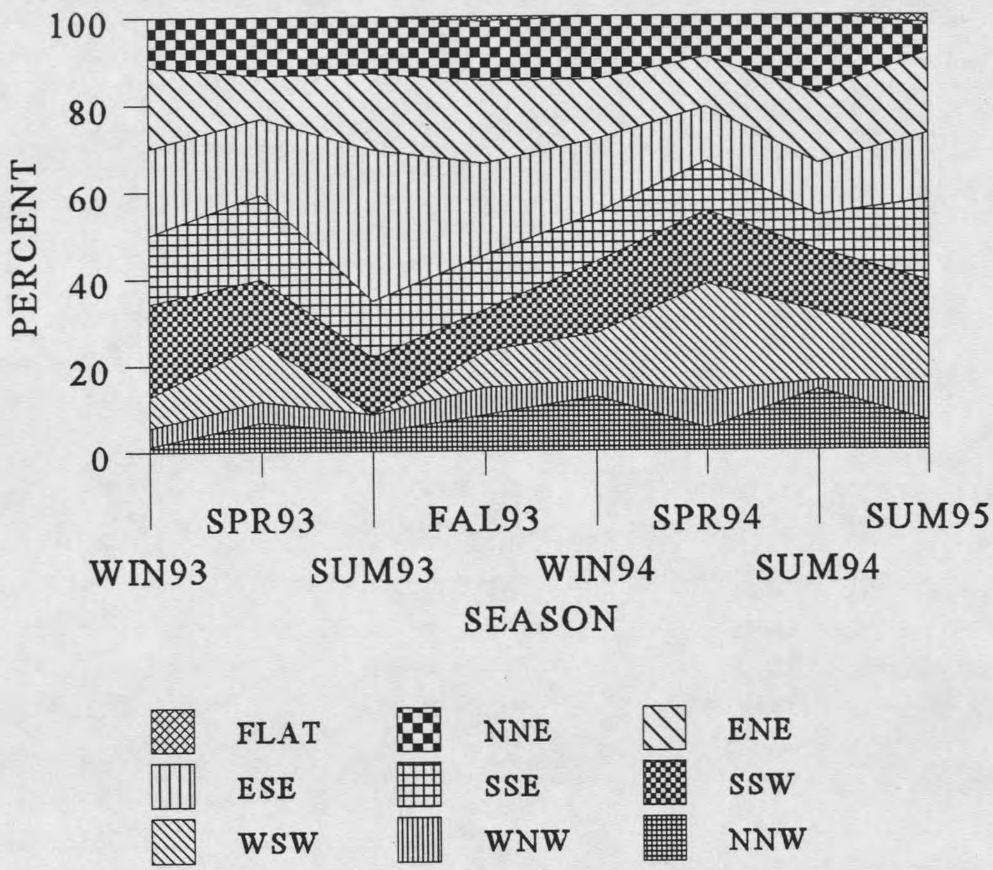

Figure 18. Percent of all locations of mule deer at various aspects (flat, NNE, ENE, ESE, SSE, SSW, WSW, WNW, NNW) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area.

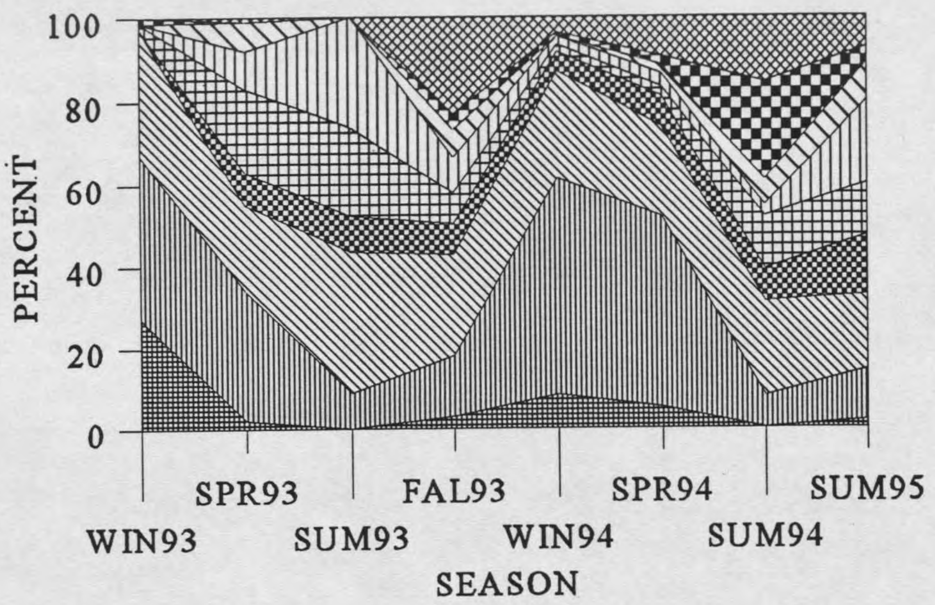

Figure 19. Percent of all locations of mule deer in various vegetation types (MM = Mountain Mahogany Woodland, JUNMM = Juniper-Mountain Mahogany Woodland, GRASS = Grassland, SBS = Sagebrush Steppe, CONIF = Coniferous Woodland, RIP = Riparian, and AGRIC = Agricultural Land) by season and year, winter 1993 - summer 1995, in the Pryor Mountain Study Area. .