



Ecology of a prairie mule deer population
by Alan Keith Wood

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

Montana State University

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Abstract:

The ecology of a mule deer (*Odocoileus hemionus*) population inhabiting an eastern Montana prairie, was studied during 1975-1986, using periodic aerial surveys and radioed and neckbanded deer. Spring population size increased by 29%/year from 1976 to 1983, stabilized at approximately 1,080 deer during 1983-1984, and declined 61% during 1984-1986. An average of 42% of the adult females successfully weaned > 1 fawn, resulting in autumn, winter, and spring fawn:doe ratios averaging 56:100, 55:100, and 35:100, respectively. Annual mortality rates for fawns, adult females, and adult males averaged 70%, 23%, and 63%, respectively; harvest rates averaged 3%, 19%, and 59%, respectively. Deer distribution was highly aggregated across the area. Mixed groups of males and females were uncommon, though distributions of males and females overlapped significantly. Individual females exhibited 1 of 3 movement patterns: yearlong residency, spring and autumn migration, or late summer and late autumn migration. Annual home ranges averaged 4.4 km². Females and mature, males demonstrated a high degree of fidelity to traditional herd ranges, but yearling males did not. Areas of topographic diversity in winter, and mesic sites in summer were preferred. Interspersion of habitat complexes influenced both distribution and home range size. Environmental variability caused specific responses by mule deer, and was reflected in variable fawn recruitment rates. Population regulation seemed to be influenced by the limited availability of high, quality forage during late summer. Spring population size of white-tailed deer (*O. virginianus*) peaked at 335 deer. Population dynamics of both species were similar, except during 1984, when 60% of the female whitetails were harvested. Significant interspecific overlap occurred, and the 2 species demonstrated no intrinsic avoidance mechanisms. Whitetailed deer preferred areas with overhead cover adjacent to agricultural fields, used larger annual home ranges (9.98 km²) and showed much less home range fidelity than mule deer. Pronghorn antelope (*Antilocapra americana*) occurred on the area at densities similar to white-tailed deer, used open habitats, and had little impact on the mule deer population.

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APPROVAL

of a thesis submitted by

Alan Keith Wood

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.

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ABSTRACT

The ecology of a mule deer (Odocoileus hemionus) population inhabiting an eastern Montana prairie, was studied during 1975-1986, using periodic aerial surveys and radioed and neckbanded deer. Spring population size increased by 29%/year from 1976 to 1983, stabilized at approximately 1,080 deer during 1983-1984, and declined 61% during 1984-1986. An average of 42% of the adult females successfully weaned ≥ 1 fawn, resulting in autumn, winter, and spring fawn:doe ratios averaging 56:100, 55:100, and 35:100, respectively. Annual mortality rates for fawns, adult females, and adult males averaged 70%, 23%, and 63%, respectively; harvest rates averaged 3%, 19%, and 59%, respectively. Deer distribution was highly aggregated across the area. Mixed groups of males and females were uncommon, though distributions of males and females overlapped significantly. Individual females exhibited 1 of 3 movement patterns: yearlong residency, spring and autumn migration, or late summer and late autumn migration. Annual home ranges averaged 4.4 km². Females and mature males demonstrated a high degree of fidelity to traditional herd ranges, but yearling males did not. Areas of topographic diversity in winter, and mesic sites in summer were preferred. Interspersion of habitat complexes influenced both distribution and home range size. Environmental variability caused specific responses by mule deer, and was reflected in variable fawn recruitment rates. Population regulation seemed to be influenced by the limited availability of high quality forage during late summer. Spring population size of white-tailed deer (O. virginianus) peaked at 335 deer. Population dynamics of both species were similar, except during 1984, when 60% of the female whitetails were harvested. Significant interspecific overlap occurred, and the 2 species demonstrated no intrinsic avoidance mechanisms. White-tailed deer preferred areas with overhead cover adjacent to agricultural fields, used larger annual home ranges (9.98 km²) and showed much less home range fidelity than mule deer. Pronghorn antelope (Antilocapra americana) occurred on the area at densities similar to white-tailed deer, used open habitats, and had little impact on the mule deer population.

INTRODUCTION

Rocky Mountain mule deer (Odocoileus hemionus hemionus) occur across a broad spectrum of habitats, from the Great Plains, through shrublands, woodlands and forests of the Rocky Mountains, and desert scrub of the Great Basin (Wallmo 1981). Although various aspects of mule deer biology and ecology have been intensively studied in many of these habitats, relatively little research has been directed towards mule deer inhabiting nontimbered prairie environments of the northern Great Plains.

Past studies of mule deer in prairie habitats have focused primarily on range-habitat relationships. These include evaluations of range relationships between mule deer and cattle (Dusek 1975), movements and habitat use patterns of adults (Severson and Carter 1978), habitat use and mortality rates of fawns (Steigers 1981), winter habitat use patterns (Swenson et al. 1983), and the effects of hunting on habitat use (Swenson 1982). Studies of population dynamics as they relate to habitat characteristics are lacking.

In September 1975, the Montana Department of Fish and Game initiated a series of studies to evaluate factors influencing mule and white-tailed deer populations in several different habitats, including an eastern Montana

prairie. Although designed as a long-term, intensive study, detailed field work was conducted in the prairie habitat only from September 1975 through May 1976 (Hamlin 1976). From May 1976 through March 1980, efforts were limited to autumn (September-October), winter (December-January), and spring (March-April) aerial surveys to monitor population trends (Hamlin 1977-1980). Field work was suspended during 1980-1981.

The work was revived with my studies, under which full-time field work was conducted during July-September 1982, January-March 1983, and June 1983-December 1984, and part-time through April 1986. Objectives were to evaluate population dynamics, home range, movement, and habitat use patterns of mule deer occupying this prairie habitat. Additional data were also collected on white-tailed deer, pronghorn antelope, and cattle, which shared this range with mule deer, to evaluate their potential influences on the mule deer population or its use of the area.

METHODS

Field Methods

Existing classification and delineation of major cover types within the study area (unpubl. rpt., BLM, Proj. 208-76-B, 1979) were employed with 2 minor modifications. A "grassland" type was divided into 2 cover types (mixed grass prairie and bunchgrass prairie), and the closed canopy and open canopy broadleaf tree types were combined into a single hardwood draw cover type.

All native cover types were sampled to quantitatively describe the vegetation. The cover type map was arbitrarily divided into 10 units of approximately equal size, and the largest area of each cover type within each of the 10 units was identified for sampling. Sample sites were then identified on aerial photographs, based on the mapping unit description (unpubl. rpt., BLM, Proj. 208-76-B, 1979).

At each sample site 40, 2 x 5 dm quadrats were spaced at 5 m intervals along a transect line, and the frequency of each plant species in each quadrat was recorded to estimate a ubiquity index (frequency x constancy, Curtis 1959:81). In addition, percent coverage of grasses, forbs, shrubs, litter, and bare ground was determined in alternate quadrats following procedures described by Daubenmire (1959). Transects in narrow cover types were oriented at a

45° angle to the flow of the drainage to provide samples from the edge. When an outer edge of the type was encountered, another line was established at 90° from the previous line but still at 45° to the drainage until 200 m were covered. All other cover types were sampled along a straight 200 m line. Vegetation measurements were completed during July 1983. Plant taxonomy followed Hitchcock and Cronquist (1981).

During January and February 1983 and 1984, 151 mule deer (110 females and 41 males) were captured using a drive net (Beasom et al. 1980) or a hand held net-gun (Barrett et al. 1982). An additional 13 animals were captured with the net-gun in February 1986. Deer were manually restrained, ear tagged, and marked for individual identification. Fifty-three females were equipped with radio transmitters (150-151 megahertz) the remainder with colored, plastic neckbands. Ages were determined by tooth replacement and wear (Robinette et al. 1957). A blood sample was collected from females for pregnancy diagnosis (Wood et al. 1986b). An additional 34 white-tailed deer (29 females and 5 males) were captured and handled in a similar manner. Sixteen females were fitted with radio transmitters, the remainder with neckbands.

Aerial population surveys were conducted during autumn (September-October), winter (December-January), and spring (March-April) of each year from a Piper Super Cub. One

aerial survey was also conducted during summer (July 1983). Survey flights were completed during morning and evening hours and followed topographic features to ensure complete coverage of the study area. Morning flights began at daylight and were terminated when activity levels of deer decreased, usually within 2 hours after sunrise. Afternoon flights began as activity levels increased (approximately 2 hours before sunset) and were terminated shortly after sunset.

During aerial population surveys, deer were classified by age and sex, locations were plotted on 1:24000 topographic maps, and cover types occupied were recorded. Individuals were classified as mature males (2-years or older), yearling males (1-year old), adult females (1-year or older), and fawns (<1-year old) during all surveys except spring when deer were classified as adults or fawns. All marked deer observed during the survey were also recorded. The same data were recorded for all white-tailed deer and pronghorn antelope observed, except that pronghorn groups were not classified. Pastures occupied by livestock were also recorded during aerial surveys.

The entire area was surveyed from a vehicle, during mornings and evenings immediately prior to each aerial survey and at 10-day intervals from mid-July to mid-October. Group composition, cover type used, and identification and location of all marked deer were

recorded. During the July-December surveys, yearling males were classified as spikes (at least one unbranched antler) or 2-points (2 or more points per antler) for both mule and white-tailed deer.

Spotlight counts of deer in five alfalfa fields were conducted weekly during July-October, 1983 and 1984 to evaluate nocturnal habitat use patterns. Counts were made approximately 1.5 hours after sunset using a 300,000 candle power white light. Total number of deer, and identification and location of any marked deer observed in each field were recorded.

Radioed females were located on alternate weeks throughout the year from a Piper Super Cub equipped with a single, 3-element directional antenna attached to the wing strut. The timing of locations varied among seasons. During summer (June-September), 378 (60%) of 645 locations were made 0-3 hours after sunrise. During autumn (October-November), 115 (50%) of 230 were made 2-4 hours after sunrise. During winter (December-March), 358 (56%) of 640 were made between 1100-1300 hours. All other locations, including those in spring (April-May), were made uniformly throughout the remaining daylight hours. Location, cover type used, and group composition were recorded for each radioed, and all neckbanded deer observed during the flights. These data were also recorded for any observations of marked deer. Deer were classified as

yearling males, mature males, adult females, or fawns during June-January, adults or fawns during February-April, and were unclassified during May. All deer were assigned an arbitrary birthday of June 1.

Data on the physical condition of deer harvested during the hunting season were collected during field checks of hunters in 1983 and 1984 and at checking stations operated on opening day of the hunting seasons in 1982 and 1985. Ages (based on tooth replacement and wear), and weights were recorded. In addition, diastema length of yearlings (Swenson and Stewart 1982), and antler beam length and beam diameter (2.5 cm above the bur) (French et al. 1956, Swenson and Stewart 1982) were recorded for males. When a kill site was located, a 1-liter sample of rumen contents was taken for food habits analysis (Wilkins 1957) and both kidneys were collected to calculate a kidney fat index (Riney 1955). Similar data were collected from all dead deer found throughout the year, and an estimated cause of death was assigned.

Microenvironmental conditions were measured at 57 sites used by deer during January-February and November-December 1984 similar to the procedure described by Staines (1976). Undisturbed deer were observed, and the site was classified as a feeding site (n=26) or bedding site (n=31) based on the behavior of most deer in the group. Average snow depth, wind direction and speed (using a hand-held

anemometer), air temperature, and slope aspect were recorded at each site. Measurements were taken at 50 cm above the ground at bedding sites, and at 100 cm above the ground at feeding sites, to reflect conditions experienced by deer. Similar readings were taken at the nearest possible adjacent site that was completely exposed to the wind.

Analytical Methods

Population estimates for 1975-1980 were based on aerial survey data collected by Hamlin (1976-1980). Total number of adult females was estimated by assuming that 85% of the females in the population were observed. Although this was somewhat higher than the 58-86% observability of marked animals obtained during 1983-1986 (Appendix, Table 41), different survey methods justified the use of higher observability estimates during earlier years. During 1976-1978, areas which normally held deer were repeatedly searched until animals were observed (K. L. Hamlin, pers. comm.): whereas after 1982, each area was flown only once. Estimates of fawn and adult male numbers were based on observed fawn:female:male ratios and were added to female population estimates to determine total population size.

Base population estimates during 1983-1986 were derived using a Lincoln index (Davis and Winstead 1980) with an average of 9% of the population marked (range 4-

13%) during all surveys. Only those marked deer known to be alive and on the survey area were used. The Lincoln index estimates were then adjusted based on mortality rates of marked deer so that mortality rates based on population estimates and on the marked sample agreed as closely as possible.

The population estimate for September 1982 was back-calculated from the January 1983 estimate using change-in-ratio procedures (Davis and Winstead 1980) to estimate harvest rates. The April 1981 and 1982 estimates were extrapolated from the spring estimates of 1980 and autumn estimates of 1982, respectively. July estimates were based on spring population estimates, mortality rates of marked deer from April to July, pregnancy rates, and July fawn-at-heel counts.

Seasonal and annual rates of population change were first calculated as exponential rates of change, then converted to finite rates of change for reporting (Caughley 1977). Correlation analysis was used to determine factors influencing population dynamics using exponential rates of change, finite rates of change, and observed fawn:female and fawn:adult ratios as dependent variables.

The age structure of the mule deer population during 1983 and 1984 was estimated by the proportion of marked adult deer in each age class and fawn:adult ratios in December, assuming a 50:50 sex ratio among fawns. Age

structures in 1985 and 1986 were calculated from 1984 data using mortality and fawn recruitment data. Age structures for white-tailed deer were calculated in a similar manner except that ages of all deer trapped, and shot by hunters were used.

Interspecific distribution and habitat overlap between mule deer and white-tailed deer and mule deer and pronghorn antelope were evaluated using 2x2 independence chi-square tests, as was sexual segregation within the mule deer population. The area was divided into 25 ha blocks and the number of blocks with each sex or species present and absent was determined. A determination of overlap did not require concurrent occupancy, just occupancy at some time during the period of analysis. Thus, the analysis tested for spatial segregation and not temporal segregation.

The effects of cattle on mule deer distribution were evaluated by comparing the number of deer observed in pastures with and without cattle. The test of the null hypothesis that deer were distributed independently of cattle was done with a goodness of fit chi-square test using the proportion of the area occupied and unoccupied by cattle as a measure of availability.

Climate data from 1958 to 1980 were compiled from the Buffalo Rapids weather service reporting station (Climatological Data 1958-1986) near Terry. Data from 1980 to 1986 were obtained from the Terry NE station because

recent records were more complete. Weather data from the 2 stations were highly correlated ($r=0.96$, $P<0.01$). A modified Lamb index of winter (November-March) severity, and an index of climatic conditions over 18 months (July-December) were calculated as described by Picton (1979). A modified Leckenby index of winter severity was also calculated for the months of November-March following the concepts of Leckenby and Adams (1986) but using daily rather than hourly climatological data.

Locations of mule deer, white-tailed deer, and pronghorn antelope observed during aerial surveys, and locations of all marked deer were plotted on 1:24000 topographic maps and converted to Universal Transverse Mercator coordinates recorded to the nearest 100 m. Seasonal and annual estimates of average activity radii (AARs) (Robinette 1966) and convex polygon areas (Mohr 1947) were calculated using the TELDAY computer program (T. N. Lonner and D. E. Burkhalter, Users manual for the computer program TELDAY, Mont. Dept. of Fish, Wildl., and Parks, unpubl. 15 pp.). Home range and distribution plots were also obtained using TELDAY. Single points which fell outside of the normal cluster of locations were excluded from calculations of seasonal and annual home range sizes.

AARs were used as an index of home range size in all statistical analyses because they are less sensitive to outlying locations than convex polygons (MacDonald et al.

1980). They also more nearly approximate a normal distribution because of the central limit theorem (Zar 1984). Differences in summer and winter AARs were evaluated with a paired-sample t test. Differences between AARs for groups of mule deer within seasons, were evaluated by analysis of variance (ANOVA) with differences between means identified by a least significant difference (LSD) test. Seasonal differences between species were evaluated with ANOVA and LSD tests on the ranks of AARs (Conover and Iman 1981), because variances were not equal between species. The determination of which months to include in each season was based on major changes in monthly patterns of movements and habitat use.

Monthly AARs were calculated as described by Dusek and Wood (1986) for radioed female and neckbanded male mule deer. Observations of neckbanded females were excluded because an analysis of variance indicated significant differences in average monthly AARs due to the interaction of band type (neckband or radio) and month. Adult females were assigned to one of three migration categories indicated by observed movement pattern. Differences in the AARs between months and migration classes were evaluated using ANOVA. All marked females were used in the evaluation of monthly movements of white-tailed deer.

Cover type availability was determined by calculating the percent of the total study area in each type.

Availability for the analysis of survey data was based on the types within predefined survey area boundaries. Cover type availability used in the analysis of data from marked deer was measured over a larger area determined by the movements of marked deer. Tests for cover type selection (use greater than availability) or avoidance (use less than availability) were conducted using goodness of fit chi-square tests as described by Byers et al. (1984).

Evaluation of cover type selection or avoidance based on point locations could only determine which types were important. To evaluate interactions between habitat characteristics and interspersions, and distribution and movements of deer, the 25 ha blocks mentioned previously were used. The amount of area and the meters of edge per ha of each cover type, and a Shannon-Weiner diversity index (Krebs 1978:455) were calculated in each block.

Comparisons were then made on the basis of migration class, season, home range size, and intensity of use (high use=3 or more observations per block, low use=1 observation per block). Because only occupied blocks were used, the analysis should identify habitat factors which influenced deer use or movement patterns. Analysis of both home range size and intensity of use should identify parameters which influence distribution and density because if a home range is small or a block is intensively used, then the area must contain a higher quantity or quality of resources that

would also affect density.

Habitat variables which were important in differentiating among groups were determined by stepwise discriminate analysis and field experience. These variables were then tested for statistical significance using a Wilcoxon test. Unless tests on survey data were specified, all habitat analyses were conducted on the locations of females as determined by radio telemetry. Similar methods were used to evaluate movement and habitat use data for white-tailed deer. Habitat characteristics in areas of interspecific overlap and exclusive use were also calculated using 25 ha blocks.

Wind chill, a measure of conductive heat loss in man, was calculated using the formula presented by Staines (1976). Differences between wind speed, wind chill, and temperature at deer sites (feeding and bedding sites) and adjacent sites were evaluated using t tests. The relationship between slope aspect at deer sites and wind direction at adjacent sites was evaluated by a goodness of fit chi-square test. The shelter index was calculated as the percent reduction of free wind speed at deer sites by the formula: $\text{shelter index} = (1 - \text{wind speed at deer site} / \text{wind speed at adjacent site}) \times 100$.

Unless otherwise stated, all statistical analyses were conducted using the Statistical Analysis System (Ray 1982) following procedures described by Zar (1984).

STUDY AREA

General Description

The Cherry Creek study area was located in eastern Montana (Figure 1) at 47° North Latitude and 106° West Longitude, approximately 20 km northwest of the town of Terry, in extreme northern Prairie County, Montana. It encompassed 520 km² and extended a maximum of 40 km east to west and 23 km north to south. Land ownership was 55% Federal administered by the USDI Bureau of Land Management (BLM), 39% private, and 6% State, arranged in a checkerboard pattern. The 61% public ownership on the Cherry Creek area represented a greater proportion of public land than the 25% public and 75% private reported by Eustace and Swenson (1977) for southeastern Montana.

Physical Features

The area was bisected from southwest to northeast by the drainage divide of the Yellowstone and Missouri Rivers. The most prominent geographic feature was Big Sheep Mountain which rises 90 m above the adjacent divide to an elevation of 1096 m. The terrain sloped gradually on either side of the divide to the lowest point of elevation (771 m) in the southeast corner, a maximum elevational change of only 325 m over 29 km.

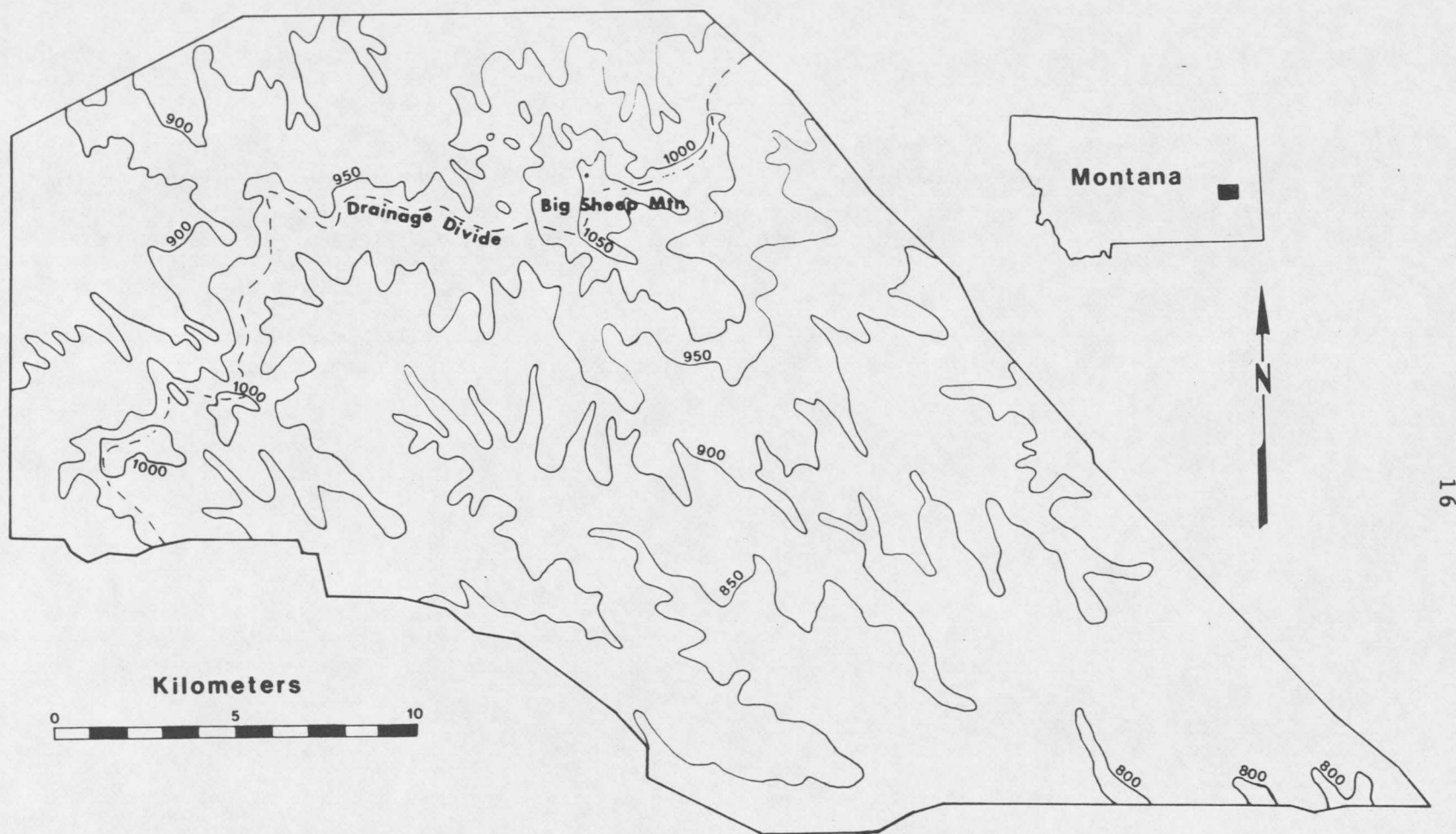


Figure 1. A map of the Cherry Creek study area showing the study area boundaries, drainage divide, Big Sheep Mountain, and 50 m elevation contours.

Water sources were widely scattered and ephemeral, with most of the drainages flowing water only during early spring snowmelt and intense summer thundershowers. Natural pits within drainages held water for variable lengths of time following any runoff. A few widely scattered springs were located on the study area. Most flowed only during spring and summer with a few flowing throughout the year. The majority of the water used by livestock was provided by wells and stock ponds. Most well pumps were turned off when livestock were absent and many of the smaller ponds went dry in late summer.

Geology

The study area was located in an unglaciated portion of the mixed-grass prairie zone (Weaver and Clements 1938) on the Tongue River member of the Fort Union formation which developed during the Paleocene Epoch. The Fort Union formation consists of alternating beds of sandstone and shale with intermixed seams of coal. This formation is distinguished by hard, reddish material locally known as scoria which resulted from baking of the overburden by heat generated from burning coal seams. Because scoria is very hard and not easily eroded it often caps small buttes scattered through the prairie (Perry 1935, Veseth and Montagne 1980).

The soils developed from the yellowish gray lenticular sandstones, yellow-gray siltstone, and gray claystone and

shale of the Fort Union formation, or from alluvium derived from them (Veseth and Montagne 1980). Ten different soil series have been identified on the study area: Bigsheep, Cabbart, Cambert, Cambeth, Chinook, Hedstrom, Kremlin, Lihen, Lonna, and Wabek (J. Setera, unpubl. data, USDA, Soil Conservation Service, Miles City, Montana).

Climate

The climate of the area is semi-arid and continental, marked by extreme fluctuations in seasonal and annual temperature and precipitation. Mean annual temperature at the Buffalo Rapids weather station, located approximately 15 km south of the study area, is 6.4 °C. Total annual precipitation averages 28.7 centimeters (cm), over 70% of which falls from May through September when temperatures are adequate for plant growth (Figure 2). The average frost-free season is about 110 days with the last frosts of spring occurring in May and the first frosts of autumn occurring in September (Climatological Data 1958-1986). Annual precipitation was more variable than annual temperature and was below normal during 1983-1986, the 3 years of intensive study (Figure 3).

Wind was an almost continual aspect of this environment. Wind speeds ranged from 0-88 km/hr and averaged 21 km/hr for 57 measurements taken during January, February, November, and December 1984.

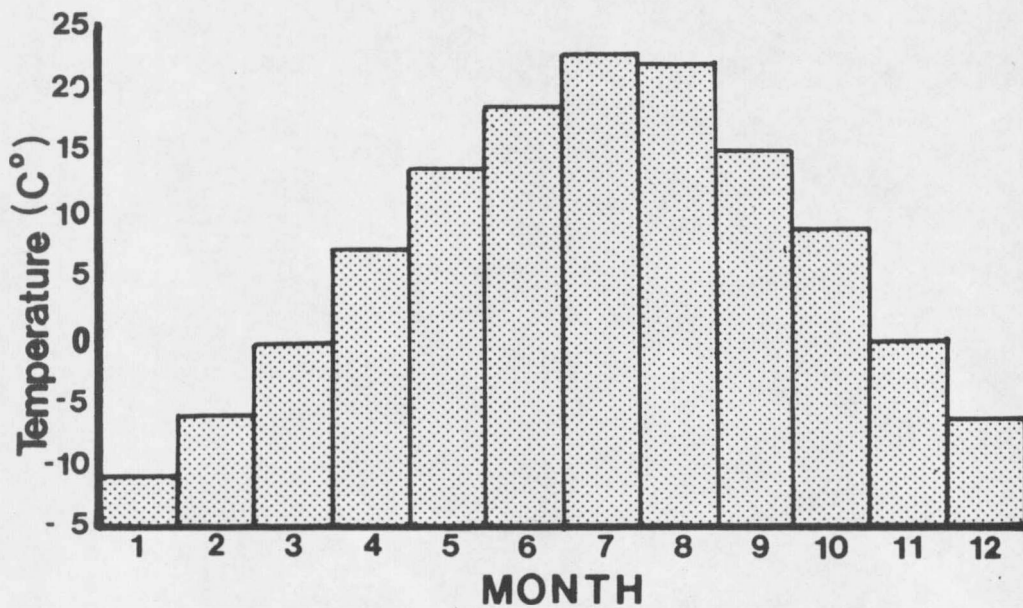
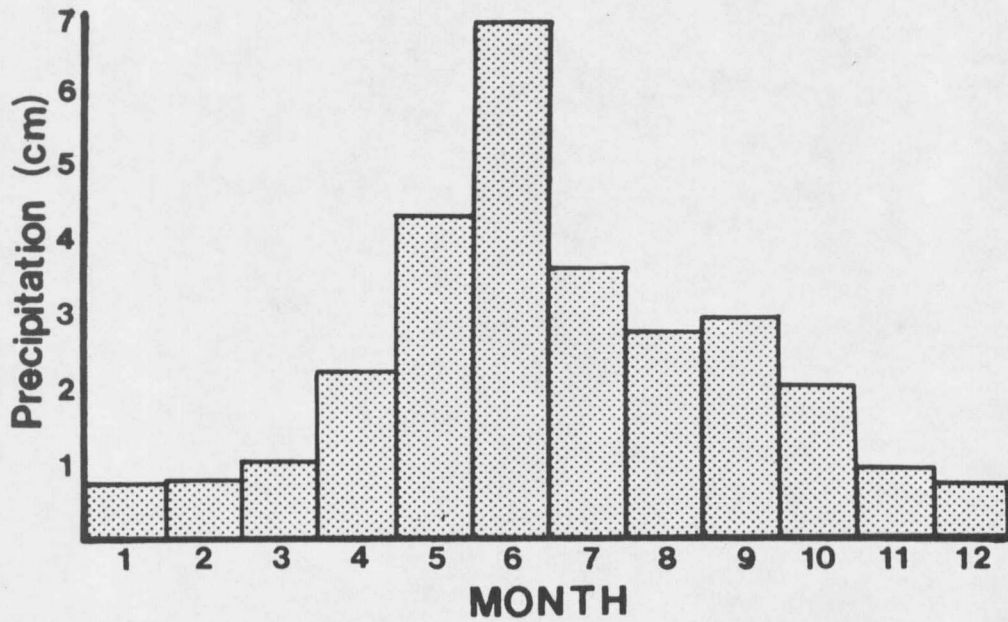


Figure 2. Average monthly temperature and precipitation patterns (1958-1985) from the Buffalo Rapids weather station located 15 km south of the Cherry Creek study area.

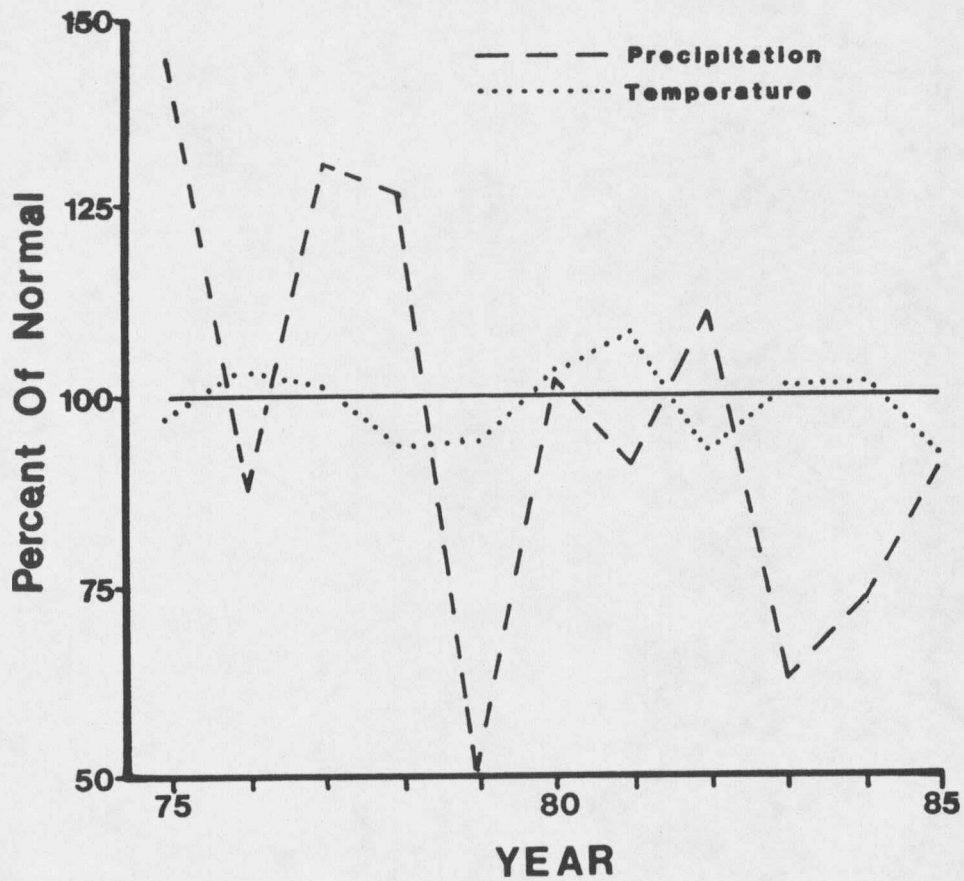


Figure 3. Annual precipitation and temperature patterns at the Buffalo Rapids weather station during 1975-1985 recorded as a percentage of the 28 year average. One standard deviation equalled $\pm 28\%$ of the mean precipitation and $\pm 4\%$ of the mean temperature.

Land Use

Early land use was dominated by livestock grazing which became established following the extermination of bison (Bison bison) by the late 1880's. One large cattle ranch (the XIT brand) established a headquarters on the eastern border of the Cherry Creek study area in 1890 and ran cattle over 8100 km² of surrounding rangeland. Domestic sheep grazing increased at the turn of the century, and forced a decrease in cattle grazing because of competition for available forage (Duke and Frantz 1961, p. 152). Sheep numbers peaked in the early 1940's, and have subsequently declined. Cattle numbers increased from 1940 to 1970 and thereafter, remained relatively stable (Montana Agric. Stat., Mont. Crop and Livestock Report Serv., Helena, 1984)

Homesteading began in 1909 and peaked during 1915-1920, when approximately 1 homestead could be found on every 5 km² (Prairie County Historical Society 1974). Droughts in the 1920's and 1930's forced abandonment of most of the farmlands. Though subsequently reclaimed by the BLM, the boundaries of many old fields remain evident in existing vegetation patterns. The density of occupied human dwellings was approximately 1.7/100 km² during the study.

Land use during the study was dominated by cattle grazing. One ranch in the southwest corner of the area

grazed sheep and cattle, all others grazed only cattle. Of 17 operating ranches, 6 grazed under allotment management plans specifying some type of rest-rotation, while others rotated cattle between seasonal pastures used traditionally each year. According to the Soil Conservation Service (1976), 75% of the rangeland on the study area was in good to excellent condition and 25% was in poor to fair condition. Nearly 4% of the area was dryland farmed for small grains (3% of the area) or legume hay.

Recreation, the second most common use of the area, was concentrated during the deer and pronghorn antelope hunting seasons in October and November. Other types of recreation occurred only rarely.

No private lands on the study area were posted against trespass, and numerous permanent roads and trails allowed vehicle access to within 2.3 km of any point on the area. Because of the gentle terrain, many temporary roads were created by hunters driving in search of game. These temporary roads allowed vehicle access to within 720 m of any point on the study area. There were only 3 areas where terrain prevented vehicle access to within 500 m. These ranged in size from 2.5 to 3.0 km² and comprised only 1.5% of the total study area.

Vegetation

The study area was dominated by broad, relatively flat areas of prairie. Badlands, characterized by rough

dissected topography that was sparsely vegetated and actively eroding, were scattered along the divide and in other locations where sudden elevational changes occurred. Heads of drainages were often dominated by snowberry (Symphoricarpos occidentalis) and chokecherry (Prunus virginiana) which progressively gave way to green ash (Fraxinus pennsylvanica), silver buffaloberry (Shepardia argentea), and eventually silver sagebrush (Artemisia cana) in the lower portions of drainages (Figure 4). Similar prairie habitats were described by Severson (1981).



Figure 4. A general overview of the Cherry Creek study area looking west from Big Sheep Mountain, along the drainage divide.

Eight cover types were identified: 1) mixed-grass prairie, 2) small grain, 3) legume hayfield, 4) sagebrush-grassland, 5) bunchgrass prairie, 6) badlands, 7) mesic shrub, and 8) hardwood draw. A list of species occurring in each native cover type and their relative abundance is recorded in Appendix, Table 42.

Mixed-grass prairie covered 64% of the area and occurred on areas with flat to gently rolling topography. Grasses, principally western wheatgrass (Agropyron smithii) and needle-and-thread grass (Stipa comata), provided 71% ground coverage (Table 1).

The bunchgrass prairie type occurred on moderately steep slopes and ridgetops over 7% of the study area. Threadleaf sedge (Carex filifolia) and bluebunch wheatgrass (Agropyron spicatum) dominated the vegetation (Table 1). Percent bare ground was greater than that in the mixed grass prairie. This type resembled the Agropyron spicatum/A. smithii habitat type described by Jorgensen (1979) except threadleaf sedge replaced Parry sedge (Carex parryana) as a subdominant on the Cherry Creek area.

The sagebrush-grassland type covered 4% of the area and occurred on both upland and floodplain sites. Western wheatgrass and silver sagebrush dominated the vegetation. Upland stands were similar to mixed-grass prairie except for an increased shrub component. Floodplain stands were similar to upland stands but also included cottonwoods

Table 1. Dominant species, Shannon-Wiener diversity index, number of species, and coverage values for the six native cover types on the Cherry Creek study area recorded as means $\pm$ 95% confidence intervals.

	Mixed grass	bunch- grass	Sage- Grassl.	Badlands	Mesic Shrub	Hard- wood
Dominants	Agsm Stco	Cafi Agsp	Agsm Arca	Agsp Gusa	Syoc Popr	Frpe Syoc
No. Spp.	53	74	67	78	64	70
Diversity	2.3	2.7	2.7	3.2	2.6	2.9
% Grass	71.1 $\pm$ 2.8	45.4 $\pm$ 3.5	57.2 $\pm$ 3.5	5.0 $\pm$ 1.4	49.7 $\pm$ 4.9	25.2 $\pm$ 4.2
% Forbs	5.5 $\pm$ 1.3	8.0 $\pm$ 1.3	4.6 $\pm$ 0.8	6.8 $\pm$ 1.3	11.8 $\pm$ 1.9	15.6 $\pm$ 2.8
% Shrubs	0.2 $\pm$ 0.2	1.5 $\pm$ 1.1	19.9 $\pm$ 3.4	8.7 $\pm$ 2.6	48.4 $\pm$ 4.3	23.8 $\pm$ 3.8
% Litter	88.8 $\pm$ 1.8	60.9 $\pm$ 4.1	85.2 $\pm$ 2.9	15.0 $\pm$ 3.2	95.1 $\pm$ 1.7	92.6 $\pm$ 2.0
% Bare Grd.	7.2 $\pm$ 1.2	27.5 $\pm$ 3.4	8.9 $\pm$ 2.2	72.8 $\pm$ 3.7	0.8 $\pm$ 0.5	3.0 $\pm$ 1.3

(Populus deltoides) scattered along the water channel.

This cover type was similar to the silver sage type (Hanson and Whitman 1938), sagebrush type (Nelson 1961), and Artemisia cana/Agropyron smithii type (Jorgensen 1979, Hansen et al. 1984) reported in other studies.

Badlands were characterized by rugged, highly dissected, and sparsely vegetated terrain and comprised 18% of the study area. Dominant plant species were bluebunch wheatgrass and snakeweed (Gutierrezia sarothrae). Seventy-three percent of the area sampled was bare ground. Live plant coverage was almost equally distributed between grasses, shrubs, and forbs. The badlands also had the greatest number of species and the highest species diversity of any cover type sampled (Table 1). They contained numerous small inclusions of other native cover types too small to map or sample individually. Brown (1971) studied similar badlands but divided them into 7 community types which demonstrates the complexity of this cover type.

The mesic shrub cover type, dominated by snowberry and Kentucky bluegrass (Poa pratensis), was generally found in long, narrow bands both above and below the hardwood draw cover type. It encompassed 1% of the study area. Shrubs associated with this type were generally found where soil moisture was greater than that associated with the prairie and less than that associated with the hardwood draws

(Severson 1981). The mesic shrub cover type had the greatest amount of litter coverage and the least amount of bare ground of all cover types (Table 1). Hansen et al. (1984) described a similar Symphoricarpos occidentalis community in western North Dakota.

The hardwood draw cover type was identified by the dominance of deciduous trees, particularly green ash, and occupied 2% of the study area. The vegetative composition of this cover type met the criteria presented by Nelson (1961) which indicated a history of moderate grazing pressure. Chokecherry and silver buffaloberry were commonly found surrounding green ash stands. Overhead canopy coverage, as measured by a densiometer, averaged 88% which was comparable to that reported by Nelson (1961). The cover type was similar to the Fraxinus pennsylvanica/Symphoricarpos occidentalis habitat type reported by Hansen et al. (1984).

Two dryland crop types, legume hayfields and small grains, occurred on the area. Legume hayfields were composed of alfalfa or yellow sweetclover, from which a single crop was usually harvested in July. Upland hayfields, planted on areas that were originally occupied by mixed-grass prairie, produced very little growth after harvest. Hayfields located in drainages originally dominated by sagebrush-grassland, received extra moisture from runoff during summer thundershowers or subirrigation,

and normally remained green until autumn frosts. Legume hayfields were small, generally less than 20 ha and covered less than 1% of the study area.

Grainfields covered 3% of the area and typically were larger than hayfields, averaging about 130 ha with some exceeding 260 ha. Small grain crops were primarily winter wheat with some spring wheat, barley, and oats and were generally planted on sites which were originally mixed grass prairie. Fields of both crop types were scattered throughout the study area.

Although fairly distinct boundaries existed between adjacent cover types, a coefficient of similarity (Gleason 1920) indicated some similarities among types (Table 2). The understory of the hardwood draw cover type was similar to the mesic shrub cover type. The bunchgrass type was intermediate between the mixed-grass prairie and the badlands cover type. The sagebrush-grassland was similar to the mixed-grass prairie type except that it contained an increased shrub component and a corresponding decrease in grass coverage. The hardwood draw and badlands cover types were the most dissimilar, the former being the most mesic and the latter the most xeric of all cover types on the area. However, small inclusions of hardwood draws could be found within the badlands.

Table 2. Coefficients of similarity comparing plant species occurrence among native cover types on the Cherry Creek study area. The coefficient ranges from 0 (complete dissimilarity) to 1 (complete similarity).

With	COVER TYPE ¹				
	MGP	SG	BGP	BAD	MS
SG	0.65				
BGP	0.61	0.57			
BAD	0.44	0.46	0.70		
MS	0.38	0.55	0.32	0.30	
HD	0.31	0.45	0.24	0.19	0.66

¹Cover types: MGP=mixed-grass prairie, SG=sagebrush grassland, BGP=bunchgrass prairie, BAD=badlands, MS=mesic shrub, and HD=hardwood draws

POPULATION CHARACTERISTICS AND DYNAMICS

Population SizeHistoric Trends

Mule deer apparently were common to abundant in portions of the northern great plains during most of the 1800's (Burroughs 1961, Severson 1981), but declined with increasing human presence. The first regulations to eliminate yearlong deer hunting in eastern Montana were established in 1872. Thereafter, hunting was increasingly restricted until the deer season was closed in 1923. Although the season was reopened in 1937, few mule deer were shot and hunting was again prohibited from 1938 to 1941. By 1945, deer were becoming abundant in the vicinity of the study area (Hamlin 1976) and by 1950, mule deer were sufficiently abundant in many parts of the state to damage agricultural crops (Egan 1971).

Mule deer harvests from the same 7,750 km² area, which included the Cherry Creek study area, ranged from 846 to 2,530 during 1960-1975, with peaks occurring in 1962 and 1973 (Figure 5). Although harvest statistics may not be directly correlated with mule deer abundance, they would seem to indicate that populations in the vicinity of the study area fluctuated dramatically in size over these years.

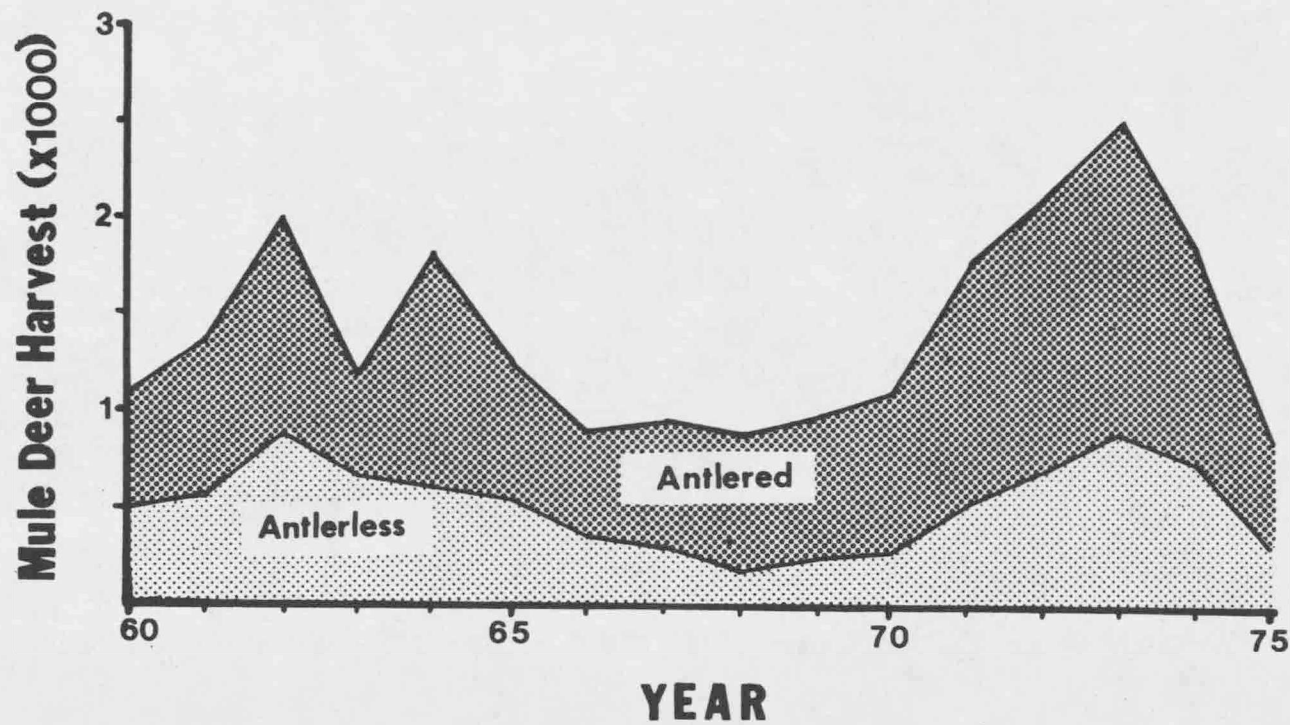


Figure 5. Trends in mule deer harvests reported by the Montana Department of Fish and Game from 1960 to 1975, over a constant geographic area which included the Cherry Creek study area.

Recent Trends

The mule deer population on the Cherry Creek study area (Table 3) was at a low of 183 animals during the spring of 1976. Spring populations increased steadily to a peak of about 1,080 deer in 1983 and 1984, but subsequently declined to 421 animals in the spring of 1986. Other seasonal population estimates followed a similar pattern, though summer and autumn populations peaked in 1983 and declined to 1985. Population size reached a maximum of 1,818 deer during July 1983. The number of adult females ranged from 118 to 768, adult males from 8 to 339, and fawns from 57 to 735 during 1975-1985. Trends in harvest data and population estimates over the last 30 years suggested a pattern of cyclic abundance occurred at approximately 10-11 year intervals.

Productivity

Pregnancy rates of marked females based on serum assays (Wood et al. 1986b) differed among age classes ($P < 0.01$). Five (56%) of 9 2-year-olds, 35 (97%) of 36 aged 3-7, and 7 (88%) of 8 aged 8-years or older, at the time of fawning, were pregnant (Table 4). These rates and differences between age classes were similar to those reported for mule deer elsewhere. Pregnancy rates for 2-year-old females from several habitats averaged 73% (range

Table 3. Mule deer population estimates on the Cherry Creek Study Area from December 1975 to April 1986.

<u>DATE</u>	<u>TOTAL</u>	<u>ADULTS</u>	<u>FAWNS</u>	<u>FEMALES</u>	<u>MALES</u>	
					MATURE	YEARLING
Dec. 75	183	126	57	118	1	7
Apr. 76	183	126	57	118	1	7
Dec. 76	263	177	86	130	25	22
Mar. 77	263	177	86	130	25	22
Jan. 78	348	222	126	170	27	25
Mar. 78	300	210	90	161	25	24
Jan. 79	474	245	229	206	21	18
Mar. 79	409	233	176	196	20	17
Jan. 80	608	318	290	284	17	17
Mar. 80	546	318	228	284	17	17
Apr. 81	700	420	280	---	--	--
Apr. 82	858	478	380	---	--	--
Jul. 82	1538	858	680	655	77	126
Sep. 82	1252	841	411	642	77	122
Dec. 82	1127	710	417	634	31	45
Mar. 83	1083	710	373	634	31	45
Jul. 83	1818	1083	735	744	151	188
Oct. 83	1558	1064	494	735	151	178
Dec. 83	1257	806	451	672	41	93
Apr. 84	1074	776	298	647	39	90
Jul. 84	1722	1074	648	768	129	177
Oct. 84	1441	1031	410	747	129	155
Dec. 84	795	571	224	472	38	61
Mar. 85	595	536	59	443	36	57
Jul. 85	996	595	401	467	107	21
Sep. 85	775	590	185	465	107	18
Dec. 85	538	405	133	340	56	9
Apr. 86	421	360	61	305	47	8

Table 4. Age specific pregnancy rates, autumn fawn recruitment rates (% success and fawns:producing female), and projected fawns:100 total females in autumn for marked female mule deer on the Cherry Creek area, 1983-1985. Sample sizes are recorded in parentheses.

Age at fawning	% Pregnant	% Rearing ≥ 1 fawn	Fawns: female	Fawns: 100 females
2	56 (9)	41 (17)	1.00	41
3-4	100 (15)	61 (23)	1.15	70
5-7	95 (21)	72 (25)	1.53	110
8+	88 (8)	50 (14)	1.14	57

0-100%), those of prime aged females 97%, (range 93-100%), and those of females 8 years or older, 94% (range 88-100%) (Anderson 1981, Beasom and Wiggers 1984).

Among marked females, fawn rearing success from birth to autumn was not dependent on age ($P > 0.05$). Differences in pregnancy rates apparently accounted for differences in the number of females that successfully reared at least 1 fawn to weaning age (Table 4). However, fawn:100 female ratios in autumn revealed that the highest reproductive rates were by females 5-7 years of age (Table 4). The lack of fetal production data made it impossible to determine whether age-specific differences in fawn production resulted from different rates of fetal production or fawn survival.

Although estimates of age-specific fawn production (fawns:100 females) were based on small samples of marked females, they seemed representative of the entire population. The mean fawn:doe ratio calculated for marked deer during 1983 and 1984 (58 fawns:100 females) was intermediate to the 67 fawns:100 females and 55 fawns:100 females observed in autumn of those years. Increased fawn:doe ratios reported for 1977 to 1981 must have resulted from increased yearling pregnancy rates, fetal production, and/or fawn survival over summer.

Mortality

Fawns

Seasonal fawn mortality rates (Table 5) were highest in winter (43%) and summer (41%), and lowest in autumn (21%). However, because the seasons were not of equal length, seasonal rates were not directly comparable. On a monthly basis, mortality rates decreased as fawns matured, averaging 16% from July through September and 12% from October through April. Although fawn mortality during June was not determined, substantial losses can occur during the first month of life (Hamlin et al. 1984). Therefore, higher monthly mortality rates during summer with lower rates during autumn and winter was probably the general pattern for mule deer fawns during most years.

Table 5. Finite seasonal mortality rates (percent) for mule deer on the Cherry Creek area during 1982-1986.

Season	Total Adult	Fawn	Adult Female	Adult Male
04/82-04/83	17	46	3	63
04/82-10/82	2	40 ¹	2	2
10/82-12/82	16	0	1	62
12/82-04/83	0	11	0	0
04/83-04/84	28	59	13	62
04/83-10/83	2	33	1	3
10/83-12/83	24	9	9	59
12/83-04/84	4	34	4	4
04/84-04/85	50	91	42	70
04/84-10/84	4	37	3	7
10/84-12/84	45	45	37	65
12/84-04/85	6	74	6	6
04/85-04/86	40	85	35	57
04/85-10/85	1	54	0	2
10/85-12/85	32	28	27	48
12/85-04/86	11	54	10	15
Mean				
Annual	34	70	23	63
Apr.-Sep.	2	41	2	4
Oct.-Nov.	29	21	19	59
Dec.-Apr.	5	43	5	6

¹Rates for fawns are calculated from July-September

During autumn, the rate of natural mortality of fawns was probably higher than hunter harvest. Fawns comprised 16 (8%) of 205 harvested mule deer examined from 1982 to 1984 while comprising from 32-38% of the population. Based on fawn:doe ratios of deer observed in hunter's possession and population estimates, natural mortality rates for fawns during autumn were 0, 8, 23, and 21% for individual years, from 1982 to 1985; corresponding hunting harvest rates were 0, 1, 22, and 7%, respectively.

Adult Females

Annual mortality rates of adult females in the population averaged 23% (Table 5). Hunting harvest was the greatest cause of death, averaging 19% over the 4 years of intensive study (1982-1986). Natural mortality rates throughout the rest of the year averaged 7%.

The annual mortality rate for marked adult females was estimated at 20%. Twelve (20%) of 60 adult females deaths resulted from causes other than hunting (Table 6). Two of these were study related, resulting from deer getting a front foot entangled in their collars. Mortality rates related to stress induced by trapping and handling were very low for the trapping techniques used in this study (Wood et al. 1986a). With these 2 animals removed from the calculations, 17% of all deaths resulted from natural causes and 83% were harvest related.

Table 6. Number of marked mule deer lost from the Cherry Creek Study area population during 1983-1985 by cause, season, and age class. A=accident, C=cripple loss, E=emigration, H=harvest, I=illegal kill, M=malnutrition, P=predation, T=trap related, U=undetermined.

Age Class	Number Alive	FEMALE LOSSES			
		Annual	Autumn	Winter	Summer
0	28	4	0	1M 3U	0
1	39	6	3H 1I	1M 1T	0
2	41	9	7H	1T	1E
3	42	7	4H	1M 1U	1U
4	44	8	7H	0	1A
5	38	7	3C 3H	1U	0
6	33	9	1C 1I 6H	1M	0
7	21	4	3H	0	1P
8	15	5	4H 1I	0	0
9	10	3	2H	1P	0
10+	11	2	2H	0	0
Total	322	64	48	12	4
Age Class	Number Alive	MALE LOSSES			
		Annual	Autumn	Winter	Summer
0	26	2	0	2U	0
1	32	18	2H	0	16E
2	16	6	6H	0	0
3	9	4	4H	0	0
4+	10	2	2H	0	0
Total	93	32	14	2	16

Causes of natural mortality among females varied. During winter, 4 cases of malnutrition and 1 coyote (Canis latrans) kill were confirmed. Five marked females disappeared during winter and were probably winter related mortalities. During summer, 1 dispersal, 1 coyote kill, and 1 automobile collision were confirmed, while 1 marked female disappeared (Table 6).

No natural mortality of marked or unmarked deer was documented among adult females during autumn. Seven (15%) of 48 marked females which died during autumn were documented crippling losses or illegal kills which were included in the calculation of total harvest rates (Table 6).

Adult Males

Annual mortality rates of adult males averaged 63%. Hunting related mortality was the leading cause of death, averaging 59%. Natural mortality rates averaged 10%. The only cause of death identified for marked adult males was hunting (Table 6). Nine marked mature males were shot and reported by hunters; 3 others disappeared during hunting season and were assumed shot. Two yearling males also disappeared during the hunting season and were assumed shot.

The percentage of marked males in the population increased from 7% to 14% over the 1984 hunting season, indicating a selective harvest of unmarked males by

hunters. No cases of crippling loss or illegal kill were documented for marked males, although 12 unmarked males were found dead of those causes.

Three yearling males were known to have dispersed, 13 others disappeared during the summer and were assumed to have dispersed. Emigrating yearling males were apparently replaced by immigrants because there were no changes in population size commensurate with a nonreplaced loss of 16 (67%) of 24 yearling males.

Distribution

Mule deer were distributed in scattered aggregations across the study area. Overall, from 1975 to 1986, deer were observed in only 37% of the 25 ha blocks during survey flights. Seasonally, only 20%, 19%, and 15% of the blocks were occupied during autumn, winter, and spring, respectively. Density patterns also indicated an aggregated distribution. Density averaged 2.3 deer/km² across the entire study area in December 1983, but local concentrations ranged from 5 to 33 deer/km². The same general pattern was observed during all seasons and years.

Mule deer appeared to exist in semi-isolated subpopulation units on the Cherry Creek study area. A few subpopulations were apparent because they were separated by up to 7 km of unoccupied habitat. Other subpopulation units were suggested on the basis of the patchy

distribution of deer across the area and the distribution and movements of marked deer.

Effects of Density

No major changes occurred in the distribution of deer over the study area in response to increasing population density. If deer had widely expanded their distribution into previously unoccupied habitats in response to increasing population density, a large number of 25 ha blocks unoccupied during lows would have been occupied during highs. However, this was not the case. During all seasons, deer occurred in the same blocks during population highs and lows more than expected, and in newly occupied blocks during population highs less than expected based on chance alone ($P < 0.05$). Thus, changes in distribution resulted more from differences in the relative abundance of deer within subpopulation units across the study area than from expansion of deer distribution into previously unoccupied habitats (Figure 6).

Studies of white-tailed deer have indicated that female fawns are recruited into (Nelson and Mech 1985) or adjacent to (Ozoga et al. 1982) areas used by their mothers, resulting in a traditional pattern of distribution through time. This phenomenon might also explain the consistency in distribution of female mule deer on the Cherry Creek area. Dispersal of males (Robinette 1966, Severson and Carter 1978, Nelson and Mech 1984) has the

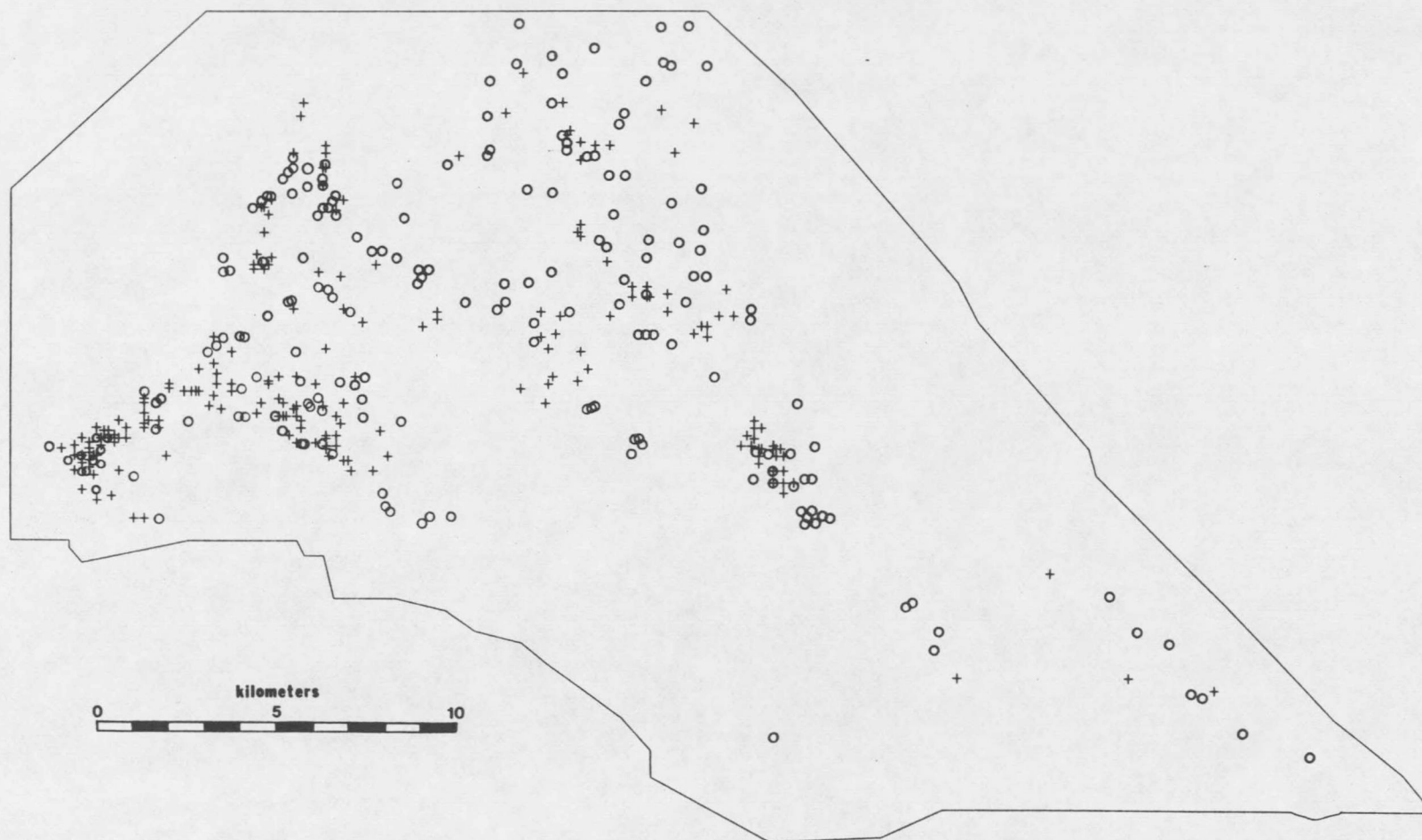


Figure 6. Winter distribution of mule deer groups on the Cherry Creek study area during low populations (+, 1976-1980) and high populations (o, 1982-1983).

potential to change distribution. However, the small number of males and their high mortality rate apparently minimized any such effect. Apparently, the availability of suitable habitat was sufficiently restricted and the deer density during 1975-1976 sufficiently low to result in a nearly 6-fold increase in mule deer numbers within the originally occupied habitat.

Effects of Cattle

Cattle grazing did not seem to broadly influence the distribution of mule deer during any season (Figure 7). The occurrence of mule deer in occupied cattle pastures was not different from expected based on the proportion of the study area occupied by cattle ($P > 0.05$). Cattle generally grazed drainage bottoms and rolling prairies and either avoided or made relatively minor use of the rougher terrain in badlands and along drainages which deer preferred (see habitat use). This limited the opportunity for cattle to affect mule deer distribution over an entire pasture.

There was one case, however, where a deer seemed to avoid occupied cattle pastures. This involved a radio-equipped, female mule deer whose home range overlapped 3 adjacent pastures. Pastures 1 and 2 were part of a rest-rotation grazing system and were grazed rather intensively for 40 and 50 days in early and late summer, respectively. Pasture 3, part of another allotment, was grazed

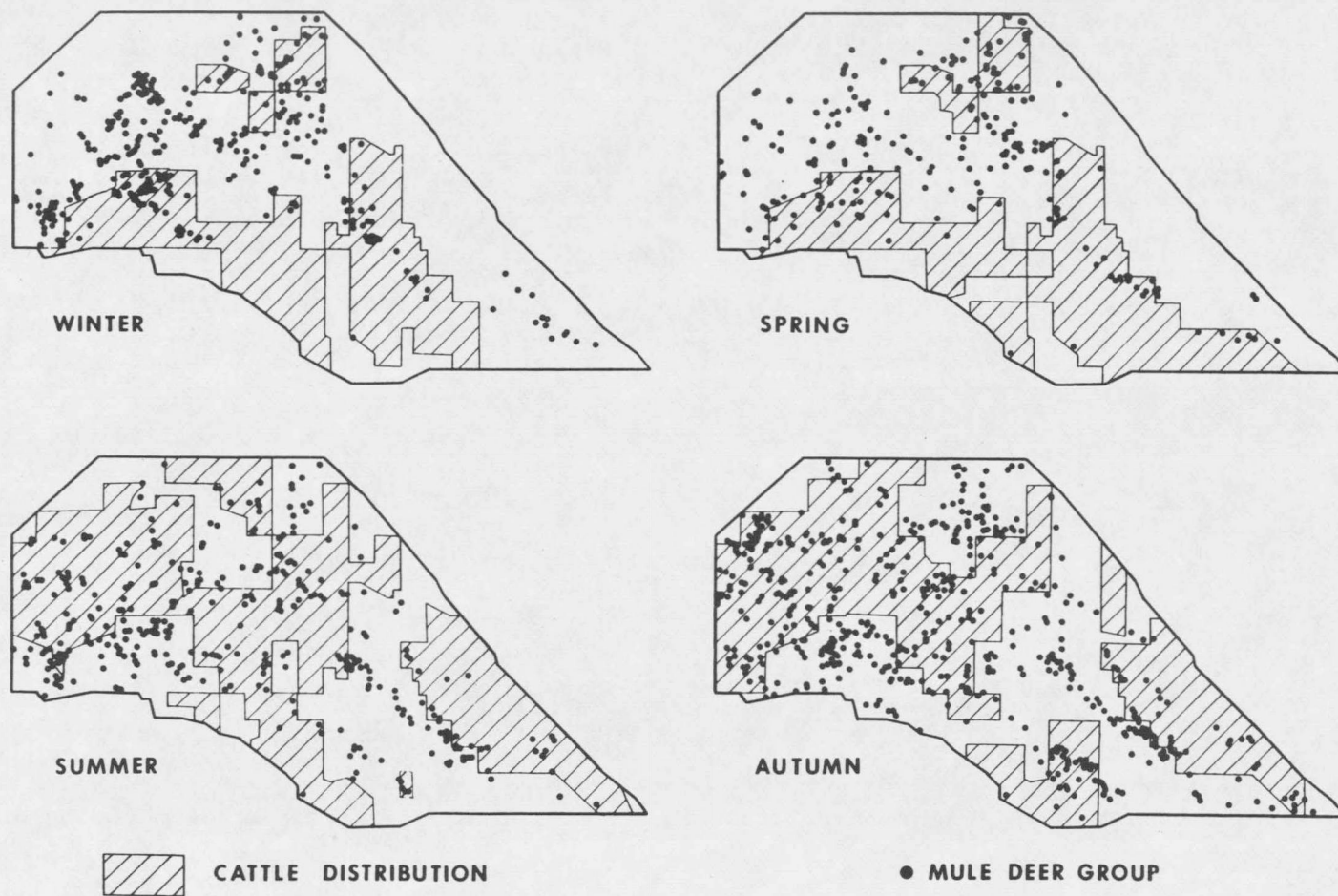


Figure 7. Seasonal distribution of mule deer and cattle on the Cherry Creek study area, 1982-1985.

continuously for 184 days by relatively fewer cattle (Figure 8). When livestock were placed in pasture 1, this deer appeared to spend less time there and more time in pasture 2 which remained ungrazed. When the cattle were later moved to pasture 2, she apparently spent more time in pasture 3 which was grazed all summer at a lower rate.

PASTURE 1

260 cattle (77/km²)

June 12 - July 21

May 29
Jun. 27
Aug. 23

PASTURE 2

260 cattle (46/km²)

July 21 - September 8

May 10
May 17
Jun. 5
Jul. 10

PASTURE 3

300 cattle (9/km²)

May 15 - November 15

May 2
Jul. 20
Sep. 11
Sep. 19
Sep. 30

Figure 8. Movements of a radioed mule deer in response to livestock grazing on the Cherry Creek study area during 1984. Below livestock density and grazing periods are dates on which this deer was located in each pasture.

Although not conclusive, these data suggested that deer avoided close association with cattle, and that grazing patterns and stocking rates can affect how deer respond to cattle as discussed by Mackie (1981).

Results of other studies on the effects of livestock grazing on deer distribution have varied greatly. McMahan (1966), Dusek (1975), and Edwards (1977) reported deer avoid pastures occupied by livestock. Knowles (1975) suggested that, while summer and autumn cattle grazing did not exclude deer from an area, it did cause them to move more widely. Komberec (1976) found little effect on mule deer distribution resulting from winter and spring grazing. Livestock grazing has also been reported to directly increase mortality rates (McMahan and Ramsey 1965, Knowles 1975) or affect the availability of preferred feeding areas (Austin and Urness 1986).

Hardwood draws, an important cover type for deer during summer (Severson and Carter 1978, and see habitat use section), are also heavily used by livestock for feed and shade. When hardwood draws are uncommon, even lightly stocked pastures can be subject to damage by rubbing, grazing, and soil compaction (Severson and Carter 1978). This type of impact could cause decreased cover for fawn rearing even if it did not directly affect deer distribution or forage availability.

Hamlin et al. (1984) reported that fawn production in central Montana was not limited by the availability of hiding cover. However, fawns on that area used patches of dense cover on steep slopes which cattle avoided. On the Cherry Creek area most of the rugged terrain had little available vegetative cover to hide young fawns. The best hiding cover occurred in the drainage bottoms that were also used for feeding and loafing by cattle. Thus, cattle had the potential to limit the availability of fawn rearing sites by direct exclusion, or destruction of cover and forage.

Sexual Segregation

Mature males and adult females were least associated in common groups during summer and autumn (see group size section) which maximized chances for a sexually segregated distribution of deer across the study area during those seasons. However, even though they were not closely associated in common groups, their distributions overlapped. During July-September, mature males and adult females occurred in the same 25 ha blocks more than expected and in different areas less than expected compared to a random distribution ($P < 0.05$). Male concentration areas (more than 2-times as many mature males as females) were uncommon, comprising only 35% of the blocks in which mature males occurred.

Exclusive use of areas by adult females was observed but was not evidence for sexual segregation because females were relatively more abundant. Mature males comprised only 12% of the adult population during summer and autumn.

Sexual segregation apparently occurs in other environments. Mackie (1970) reported the existence of "buck" habitats for a mule deer population in central Montana as did Bowyer (1984) for southern mule deer (O. h. fuliginatus) in California. The lack of buck habitats on the Cherry Creek area probably resulted from the relatively few mature bucks in the population, the high mortality rate of mature males, and the concentration of all animals on only a fraction of the total study area. If lower mortality rates were maintained, buck habitats might also form on the Cherry Creek area.

Population Structure

Composition

Fawn production was relatively high throughout most of the study. During 1975-1986, fawn:doe ratios averaged 69:100 in autumn and winter and ranged from 39 to 111:100 (Table 7). Fawns comprised an average 33% (range 24-45%), 36% (range 25-48%), and 32% (range 10-44%) of the population during autumn, winter, and spring, respectively. The percentage of fawns in spring generally increased from 1976 to 1982, and decreased from 1983 to 1985.

Table 7. Observed mule deer buck:doe:fawn ratios and percent bucks, does, and fawns during autumn, winter, and spring on the Cherry Creek study area, 1975-1986.

Year	AUTUMN				WINTER				SPRING			
	Ratio buck:doe:fawn	Percent buck doe fawn			Ratio buck:doe:fawn	Percent buck doe fawn			Ratio buck:doe:fawn	Percent buck doe fawn		
1975-76 ¹	30:100:43	17	58	25	7:100:48	5	64	31	7:100:48	5	64	31
1976-77 ¹	42:100:67	20	48	32	36:100:66	18	49	33	36:100:66	18	49	33
1977-78 ¹	51:100:79	22	44	34	31:100:74	15	49	36	30:100:56	16	54	30
1978-79 ¹	-----	--	--	--	19:100:111	8	44	48	19:100:90	9	48	43
1979-80 ¹	17:100:97	8	47	45	12:100:102	5	47	48	12:100:80	6	52	42
1980-81 ²	36:100:84	16	46	38	-----	--	--	--	-----	--	--	40
1981-82 ²	45:100:90	19	43	38	-----	--	--	--	-----	--	--	44
1982-83	31:100:64	16	51	33	12:100:66	7	56	37	12:100:59	7	59	34
1983-84	45:100:67	21	47	32	20:100:67	11	53	36	20:100:46	12	60	28
1984-85	38:100:55	20	52	28	21:100:47	13	59	28	21:100:13	16	74	10
1985-86	27:100:40	16	60	24	19:100:39	12	63	25	18:100:20	13	72	15

¹Data from Hamlin, 1976-1980

²Unpub. data, Mont. Dept. Fish, Wildl., and Parks, Fed. Aid Proj. W-130-R.

Buck:doe ratios were relatively high in autumn, averaging 36:100 (range 17-51) but dropped to 20:100 (range 7-36) following the hunting season. Post-season buck:doe ratios were highest following the 1976 and 1977 hunting seasons and lowest following the 1975, 1979, and 1982 seasons.

Population composition was estimated with fair precision. During summer, fawn:doe ratios increased steadily from mid-July to late August then stabilized through October. Replicate classification surveys from late August to mid-October (5 in 1983 and 4 in 1984) resulted in coefficients of variation ranging from 4%-6% for fawn:doe ratios and 10%-17% for buck:doe ratios. Robinette et al. (1977) also reported greater precision in estimating fawn:doe ratios as compared to buck:doe ratios.

Ratios from replicated surveys in winter and spring were also fairly consistent. The difference between the fawn:adult, fawn:doe, and buck:doe ratios determined from the air and ground, ranged from 5 to 26% of the overall mean determined for the 2 independent samples. Much of the discrepancy between air and ground classification surveys was attributable to the misclassification of small yearling bucks as does during winter, and large fawns as yearlings during spring. Deer surveys conducted from the ground had the advantage of providing more accurate

classifications while aerial surveys provided more representative samples across the population.

Age Structure

The age structure of the female segment of the population was heavily skewed toward younger age classes during 1983-1984 when harvest rates were low, but shifted toward an older age structure concurrent with increased harvest rates during 1985-1986, as a result of decreased fawn recruitment (Table 8). Approximately 53-55% of the females were 2 years or younger during 1983 and 1984. By 1986, this group comprised only 32% of the females. The percentage of females 8 years or older increased from 6% to 12% over the same time period. The percentage of prime age females (3-7 years old) showed less variation, increasing from 41% to 56% during 1984-1986.

The male segment of the population was more heavily skewed toward younger age classes than the female segment (Table 8). Fawns comprised 69% of all males during 1983, while bucks older than 4 years were uncommon. The lack of older males in the population was also indicated by harvest data in which only 8 (10%) of 78 antlered mule deer examined were 4 years or older, and only 5 (6%) were 5 years or older.

Table 8. Percentage of mule deer estimated in each age class on the Cherry Creek study area during spring 1983-1986. Percent of males recorded in age class 4 represents all males 4 and older.

Age Class	YEAR							
	FEMALES				MALES			
	83	84	85	86	83	84	85	86
0	24	20	6	9	69	61	24	36
1	17	18	18	6	17	25	46	15
2	14	15	17	17	9	9	20	29
3	12	13	14	15	4	3	7	13
4	11	12	12	13	1	2	3	7
5	8	8	11	11				
6	4	4	8	10				
7	4	4	4	7				
8	3	3	4	4				
9	1	1	3	3				
10+	2	2	3	5				
Number of deer	760	794	472	335	323	280	123	86

Group Size and Composition

Average group size for a given season was not correlated with population size ($P > 0.05$). Therefore, data on group size and composition were combined from 1975 to 1986.

The average number of deer per group for all groups containing adult females, mature males, and yearling males increased through the summer, peaked in January and February, then declined (Figure 9). Males occurred in larger groups than females during all months when individuals in the group could be classified. Increased female group size through summer may have resulted from reestablishment of family groups following parturition (Hawkins and Klimstra 1970) but the continued increase from October through February was also affected by the increased use of common areas as described by Mackie (1970). Studies of black-tailed deer (*O. h. columbianus*) by Dasmann and Taber (1956) and white-tailed deer by Hawkins and Klimstra (1970) and Gavin et al. (1984) indicated a temporary breakup of doe groups during the rut. This phenomenon was not observed on the Cherry Creek area.

Over 49% of the females occurred in groups with other females, with fawns, or alone from July through January (Table 9). Females alone were most common in July, but groups including 2 or more females with fawns were most

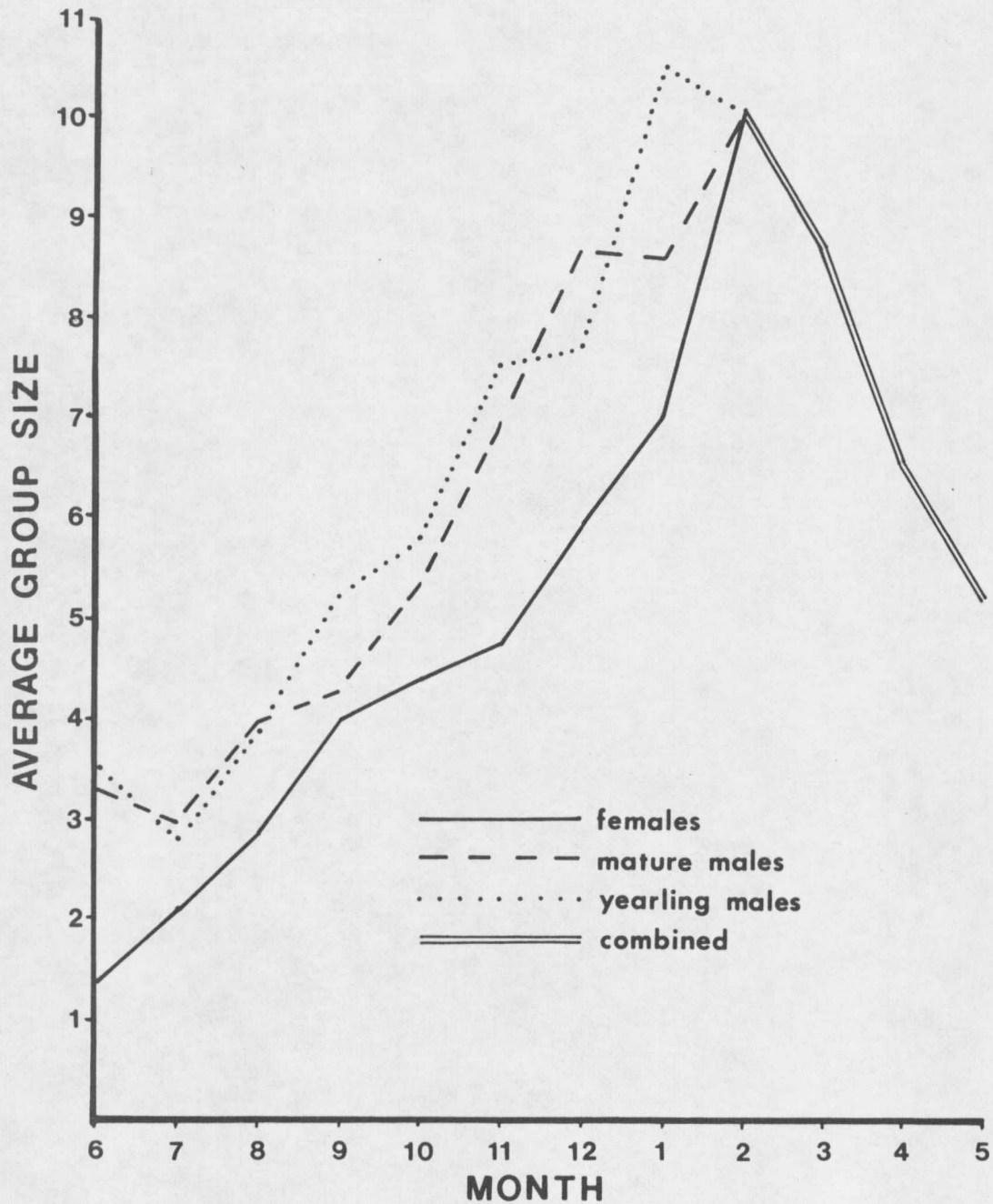


Figure 9. Average total group size of mule deer groups on the Cherry Creek study area that contained adult females, yearling males, and mature males during 1975-1985. Sexes were combined from February through May.

Table 9. Group composition of mule deer on the Cherry Creek study area during July-January, 1976-1986. Data are percentage of all females, mature males, and yearling males which occurred in each category.

	MONTH						
	7	8	9	10	11	12	1
FEMALES							
Alone	35	20	7	6	4	2	1
In groups/no fawns	17	12	13	7	8	4	1
Alone with fawns	12	13	8	7	5	4	5
In female/fawn groups	10	27	40	40	39	41	43
With mature males	9	4	7	9	16	22	8
With yearling males	12	17	19	22	14	18	20
In mixed groups	5	7	6	9	14	9	22
Number observed	606	1008	1821	1085	494	1793	674
MATURE MALES							
Alone	21	12	12	14	6	5	6
Mature male groups	20	29	32	26	0	5	14
With females	27	25	14	23	60	63	29
With yearling males	17	15	17	19	0	5	10
In mixed groups	15	19	25	18	34	22	41
Number observed	144	173	285	140	50	153	79
YEARLING MALES							
Alone	25	18	10	10	9	7	3
Yearling male groups	12	8	9	7	0	2	0
With females	38	51	47	53	57	56	50
With mature males	13	7	12	13	0	5	8
In mixed groups	12	16	22	17	34	30	39
Number observed	122	218	303	166	44	161	77

prevalent by August. Even during the breeding season (November-December), no more than 22% of all adult females were observed with mature males.

Mature males were observed with females almost as frequently as with other mature males during July-October (Table 9). Most mature males were associated with other mature males or in mixed groups during September. During October, mature males were in groups with any other deer. During November and December, over 60% of the mature males were associated with females during the breeding season. The fact that less than 22% of the females were attended by mature males reflected the low male:female ratios (Table 7). From November through January, mature males were most often associated with females or in mixed groups of females, mature males, and yearling males. Geist (1981) suggested that mixed groups of mule deer should be common during winter when the availability of winter range is limiting and when the chances of males successfully reproducing in consecutive years are limited. Data from this study support that hypothesis.

The majority of yearling males occurred with females from July to January. Yearling males alone, with other yearling males, or with mature males were relatively uncommon from September through January. Because yearling males begin dispersing in summer (Robinette 1966, and see home range and movements section) and may establish new

home ranges by November (Nelson and Mech 1984), they were probably associating with females other than their mother.

Females with fawns tended to occur in smaller groups than females without fawns. The number of females per group during December and January decreased as December and January fawn:doe ratios increased ($P < 0.01$, $r = -0.83$, $n = 9$). Also, fawn:doe ratios were highest for females that were not accompanied by other adult females and generally decreased as the number of adult females per group increased (Table 10) over all years. Female white-tailed deer that lose their fawns seek the company of other deer soon after their fawns death (Ozoga et al. 1982). Thus, it appears that does with fawns prefer isolation but, except for a brief period around parturition (Ozoga et al. 1982), and under some conditions (Miller 1974), they do not enforce their isolation through aggression. Under this hypothesis, increased group size results from nonproductive does joining with a producing doe and possibly her fawns from the previous year.

Average mule deer group size on the Cherry Creek study area was larger than in other areas of Montana (K. L. Hamlin and D. F. Pac, pers. comm.) and Utah (Robinette et al. 1977). Geist (1981:219) suggested that large group size was an antipredator adaptation of mule deer occupying open habitats. A similar relationship has also been postulated for bighorn sheep (Ovis canadensis) (Bailey

Table 10. Number of females and fawns, and fawn:doe ratios for groups with 1 to 7 or more mule deer females per group on the Cherry Creek study area during 1975-1986.

Females/group	September-October			December-January		
	Fem.	Fawns	Ratio	Fem.	Fawns	Ratio
1	493	363	0.74	176	188	1.07
2	600	386	0.64	312	270	0.87
3	459	231	0.50	279	206	0.74
4	396	175	0.44	368	192	0.52
5	265	115	0.43	215	118	0.55
6	186	54	0.29	252	140	0.56
7+	507	210	0.41	865	398	0.46
Total or Mean	2906	1534	0.53	2467	1512	0.61

1980, Risenhoover and Bailey 1985). If large groups were formed as an antipredator strategy, then those deer most vulnerable to predation (i.e. does with fawns) should form larger groups. Because females with fawns occurred in smaller groups and females associated in smaller groups than males (Figure 9), the hypothesis may not be valid for mule deer in prairie habitats.

Apparently, mule deer social organization is similar to that described for white-tailed deer by Hawkins and Klimstra (1970) and Nelson and Mech (1984). Yearling males

typically disperse from the family unit. As female fawns mature and begin to produce fawns, they separate from their mothers and form their own matriarchal group. This hypothesis would explain why the number of females per group decreased with increasing fawn production and why average group size did not change as the population increased.

Condition Indices

Dressed weights of fawns shot by hunters averaged 20.7 and 22.7 kilograms (kg) for females and males, respectively. Weights of yearling females averaged 33.1 kg, though most were obtained in 1984 when weights of other age classes were minimal and therefore are probably lower than long-term averages. Weights of mature females (2+ years) averaged 38.5 kg (range 32-48 kg), yearling males averaged 39.3 kg (range 32-48 kg), and mature males averaged 56.5 kg. The heaviest (64 kg) and lightest (52 kg) mature males were both 3 years old. Main antler beam length of yearling males averaged 21.4 cm (range 4-28 cm), antler diameter 1.54 cm (range 0.8-2.5 cm), and diastema length 6.45 cm (range 5.9-7.5 cm). Among mature males, beam diameter averaged 2.33 cm (range 1.7-3.2 cm) and beam length averaged 36.7 cm (range 25-48 cm) (Table 11).

Table 11. Hog-dressed weights (kg), antler beam diameters (cm, measured 2.5 cm above the bur), main beam length (cm), and diastema length (cm) of hunter killed mule deer from the Cherry Creek study area. Sample size is recorded in parentheses.

Year	FAWNS		ADULT FEMALES		ADULT MALES						
	Fem. Wt.	Male Wt.	Age (years)		Age (Years)						
			1.5	2+	1.5	Beam diam.	Beam length	Diastema	2+	Beam diam.	Beam length
	Wt.	Wt.	Wt.	Wt.	Wt.	Wt.	Wt.	Wt.	Wt.	Wt.	Wt.
1975 ¹	20(1)	25(2)	--	41(3)	42(4)	1.7(8)	----	---	65(3)	2.6(6)	----
1982	--	--	--	43(2)	43(1)	1.9(5)	23.3(5)	6.5(2)	61(2)	2.7(8)	38.6(8)
1983	18(1)	20(1)	34(1)	40(8)	40(14)	1.5(18)	22.1(18)	6.6(18)	57(10)	2.2(16)	37.4(16)
1984	21(4)	22(5)	33(7)	37(21)	35(5)	1.3(10)	19.1(10)	6.2(10)	51(10)	2.1(17)	35.1(17)
1985	23(1)	24(1)	--	39(7)	36(1)	1.6(1)	----	6.1(1)	68(1)	3.0(2)	----
MEAN	20.7	22.7	33.1	38.5	39.3	1.54	21.4	6.45	56.4	2.33	36.68

¹Data from Hamlin 1976

There seemed to be a decrease in the physiological condition of adult mule deer on the study area during 1983 and 1984. Although dressed weights in 1983 were comparable to those in earlier years, antler growth had decreased (Table 11). In 1984, body weights of both sexes, and antler growth of males decreased. Weights for males in 1975 and 1982 were comparable to those collected from throughout Montana (Mackie 1964), but were 18-22% less by 1984. The percentage of yearling males that were spikes (at least 1 unbranched antler) increased from 1983 (38%) to 1984 (52%).

Although sample sizes were small, and there was no statistically significant decrease in either weights or antler measurements, other data supported the hypothesis of a decline in physical condition. The dentary bone is a priority growth area in young mammals (Reimers 1972). Diastema measurements of yearling males decreased significantly ($P < 0.05$) from 1983 to 1984. Also, kidney fat indices (KFI) were very low, averaging 39% ($n=9$) and 66% ($n=7$) for adult females and males, respectively in 1984. Although samples were collected during October and November, a time when fat reserves peak (Anderson et al. 1972), they were nearly at levels where utilization of marrow fat begins (Ransom 1965).

The first effects of reduced physical condition in species that typically have multiple births is a decrease

in the mean litter size (Caughley 1976). During July, 1982-1985, a decrease in the number of fawns-at-heel per producing female (1.50, 1.43, 1.29, and 1.27, respectively), also indicated a general decrease in the physiological condition over those years. Fawn-at-heel ratios in 1986 (1.54) indicated that the increase in body weights and antler growth of deer harvested in 1985 reflected a trend of improving condition. Although no single index was adequate to conclusively demonstrate physical condition, taken collectively they all indicated a decline in physical condition beginning in 1983 and extending to summer, 1985.

Factors Influencing Population Dynamics

Density

The finite rate of population increase from 1976 to 1982 averaged 29% per year ($SE=0.92\%$), indicating that population growth remained relatively constant over the period. From 1976 to 1982, the size of the population in any given year could be estimated simply by knowing the population size from the previous year and the average rate of increase ($r=0.997$, $P<0.001$) during the period.

Fawn mortality rates during summer increased as the number of fawns, females, and total deer present during summer decreased ($P<0.03$), which was opposite to the density dependent response normally reported for ungulates

(Caughley 1976). There were no other significant correlations between population size and seasonal or annual natural mortality rates ($P > 0.2$).

Natural mortality rates of adults were not related to density. The strongest correlation found was between the mortality rate of adult females in summer and female abundance from 1982 to 1986, but the relationship was not significant ($r = 0.77$, $P = 0.23$).

Adult female mortality due to natural causes remained fairly stable over the study period, similar to other ungulate populations (Caughley 1970, Skogland 1985). Skogland (1983) proposed that high density ungulate populations suffer decreased physical condition, which Hanks (1981) suggested leads to the following sequential demographic changes: 1) increased juvenile mortality 2) increased age of sexual maturity, 3) declined fecundity of mature females, and 4) increased adult mortality. Mule deer on the Cherry Creek study area progressed through steps 1-3, but apparently not as a simple function of density.

Hunting

Hunting regulations varied from 1975 to 1985 (Table 12) and influenced population size and harvest rates (Table 13) of adult females. From 1976 through 1980, antlerless mule deer were not legal game. From 1980 to 1985, at least

Table 12. Hunting season regulations for the hunting district that included the Cherry Creek study area, 1975-1985. Two types of permits were issued to residents, unlimited permits that all licensed hunters could purchase, and limited permits which were issued through drawings.

YEAR	Unlimited Permits	Limited Permits
1975	1 ES ¹ ES. + 1 ES WT	
1976 ²	1 ES WT	50 ES MD
1977	1 ES WT	200 antlered MD
1978	1 ES WT or antlered MD	none
1979	1 ES WT or antlered MD	200 antlerless WT
1980	1 ES WT or antlered MD	200 antlerless ES.
1981	1 ES ES.	200 antlerless WT
1982 ²	1 ES ES.	none
1983	1 ES ES.	200 antlerless ES.
1984 ²	1 ES ES. + 5 antlerless WT	5000 antlerless ES.
1985	1 ES ES. + 1 antlerless WT	4000 antlerless ES.

¹ES = either sex deer, ES. = either species of deer, WT = white-tailed deer, MD = mule deer

²Hunting district boundaries were changed so number of permits issued was not comparable to previous years.

Table 13. Estimated percentage of the preseason population of mule deer which disappeared from the Cherry Creek area during the hunting season, 1982-1985.

Year	Total	Fawns	Adult Fem.	Adult Males			
				All	Mat.	Yearl.	(2pt. Spike)
1982	10	0	1	62	60	63	(-- --)
1983	19	9	9	59	73	48	(87 15)
1984	45	45	37	65	71	61	(80 36)
1985	31	28	27	48	48	50	(-- --)

some hunters could legally shoot antlerless mule deer. Regulations during 1982 resulted in a 1% harvest of adult females (Table 13) which allowed the population to increase by 26%. From 1983 to 1985, special regulations were implemented (Table 12) to increase the harvest of antlerless mule deer. During 1983, 200 hunters were allowed to shoot an antlerless deer of either species (a "B" deer tag, 6.2 tags sold/100 km²) in addition to their regular "A" tag, which resulted in a 9% harvest (Table 13). During 1984, the size of the hunting district was increased and 5000 "B" tags (27.7 tags/100 km²) were sold. A maximum of 6 tags (1 "A" and 5 "B") could be purchased by each hunter which resulted in a 37% harvest. In 1985, 4000 "B" tags (22.2/100 km²) were sold resulting in a 27% harvest of adult females. Apparently, the smaller population size and

the extremely severe weather during the last 2 weeks of the season resulted in a decreased harvest rate compared to 1984. The more liberal regulations during 1983-1985 increased harvest rates.

The harvest rates of adult males reflected intense selection by hunters for males with the largest possible antlers as described by Taber and Dasmann (1957), Robinette et al. (1977), and Barlow and McCullouch (1984). Yearling males with at least 2 points on each antler were harvested at a rate of 80-87%, while those with at least 1 unbranched antler (spikes) were harvested at a rate of 15-36% (Table 13). The increase in the harvest of spikes during 1984 resulted mainly from their harvest as "antlerless" deer, because small spikes are difficult to see at long distances or on running deer.

Harvest rates of adult males on the Cherry Creek study area were similar to the 56% harvest rate reported by Robinette et al. (1977) and were much higher than the 15% reported by Barlow and McCullouch (1984). Annual mortality rates of males were only slightly higher than the 57% reported by White and Bartmann (1983), and were much higher than the 24-29% reported by Taber and Dasmann (1957). Harvest rates for adult females on the Cherry Creek area were comparable only to the 19% reported in Utah (Robinette et al. 1977). Only studies of deer in enclosures have reported annual harvest rates higher than these. Nellis

(1968) reported a 50% annual harvest of adult deer on the National Bison Range in western Montana.

The decline in the number of adults from 1984 to 1986, resulted from a decrease in the number of yearlings in the population concurrent with an increase in hunting harvests (Figure 10). Total number of yearling recruits peaked in 1982. A combination of 5% natural mortality and 24% hunter harvest of adults, along with a late spring population consisting of 28% fawns (Table 7), resulted in a stable population from 1983 to 1984. The fact that the 1984 harvest exceeded the number of yearling recruits in the population along with the severe decrease in yearling recruitment during 1985, resulted in a 43% decrease in the autumn 1985 population size. The 1985 harvest also exceeded recruitment, resulting in a further decrease in the population size to the spring of 1986. Eustace and Swenson (1977), and Swenson (1978) suggested that the mule deer population decline which occurred in eastern Montana from 1971 to 1975 also resulted from a combination of declining recruitment and heavy hunting pressure.

Harvest rates of adult females exceeded recruitment rates of fawns into the adult population during 1984 and 1985 and was therefore not sustainable. From 1976 to 1980 the population averaged 36% fawns in spring, providing for an annual rate of population growth of 24% in adult females. If fawn production during 1983-1985 had been

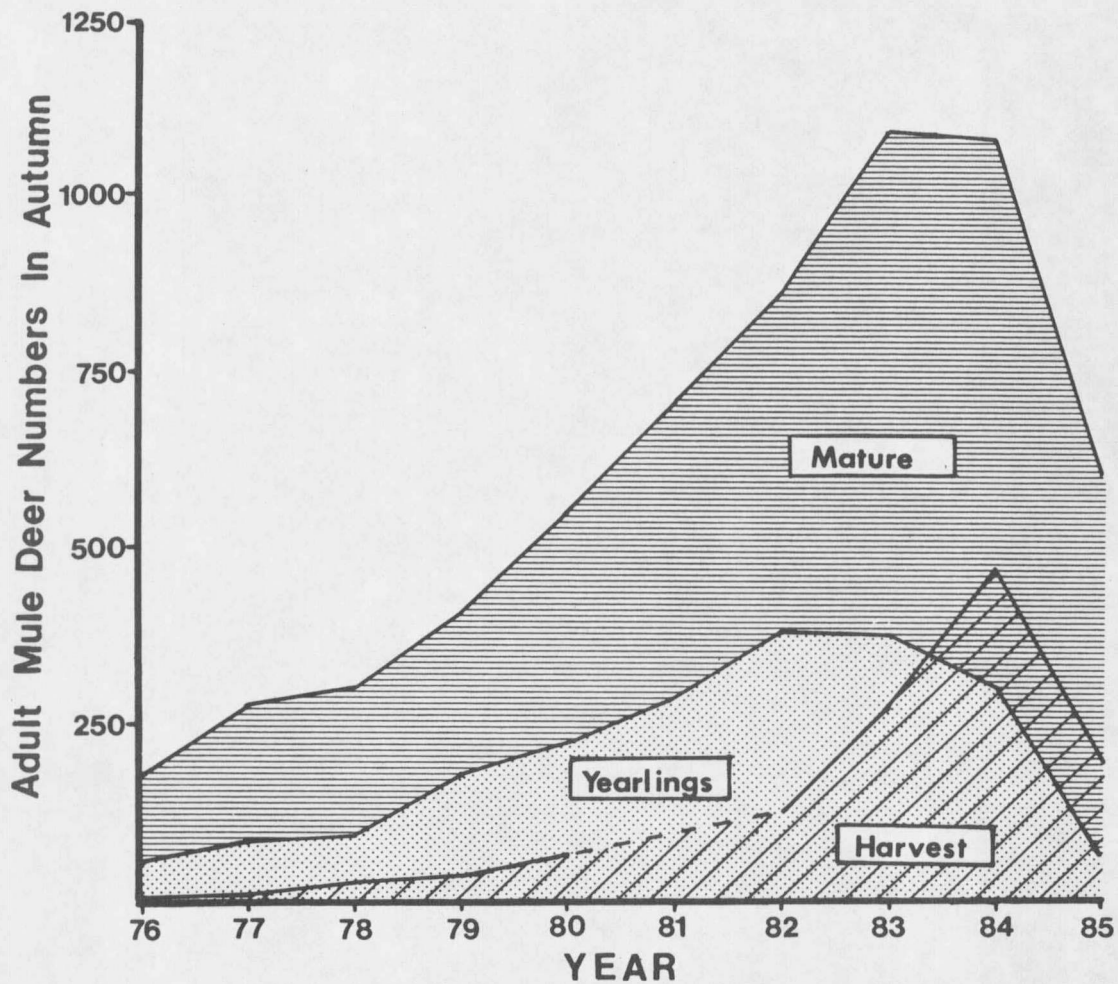


Figure 10. Number of yearling and mature mule deer in the Cherry Creek population during autumn, and total autumn harvest of adults, 1976-1985.

sustained at the same rate as 1976-1980, the average harvest rate experienced from 1982 to 1986 (19%) might also have been sustained.

Autumn hunting mortality and annual natural mortality appeared to be additive for adult females, for which natural mortality tended to increase with increasing

harvest rates ($r=0.86$, $P=0.07$). Compensatory decreases in natural mortality rates with increasing harvests are a common assumption of wildlife management, and have been proposed for North American big game by McCullough (1979) and Houston (1982). However, even if compensatory mortality can be demonstrated it is unreasonable to assume that hunting mortality could completely eliminate natural mortality in wild ungulate populations (Caughley 1976).

The number of adult males harvested on the study area was influenced primarily by adult male density from 1982 to 1985 ($r=0.987$, $P<0.01$). From 1977 to 1982 the total mule deer harvest on a $7,750 \text{ km}^2$ area which included the study area was also related to the density of adult mule deer on the study area at the start of the hunting season ($r=0.982$, $P<0.01$). Swenson (1982) also reported a similar relationship between deer harvest and observed deer density in all nonforested hunting districts in southeastern Montana. Factors such as hunting pressure, hunting regulations, and weather may also influence hunting harvest (Freddy 1982); however, the findings of this study agree with those of Swenson (1982), and both indicate that mule deer which occupy open habitats are extremely vulnerable to hunters regardless of other factors. The fact that hunters were able to harvest 48% of all adult males on the area despite their low density ($0.18/\text{km}^2$) in 1985 indicated that

any security threshold which may exist is too low to be important in management.

Climate

Overwinter (December-March) fawn mortality rates were influenced by the severity of winter (December-March) weather, but the impact of weather differed during 1975-1980 as compared to 1982-1986 (Figure 11). Overwinter mortality was correlated with a modified Leckenby index of winter severity from 1982 to 1986 ($r=0.94$, $P=0.03$) but not with a modified Lamb index of winter severity during 1975-1980 or 1982-1986 ($P>0.10$), even though the 2 winter severity indices were correlated from 1980 to 1986 ($r=0.83$, $P=0.03$). Physical condition of mule deer decreased from 1982 through 1984 and may have resulted in a more direct relationship between winter severity and overwinter fawn mortality after 1982.

No other climate indices (precipitation prior to fawning season including; July-April, September-April, October-April, April-July, July-July, or a modified Lamb index integrating temperature and precipitation data over 18 months prior to the start of winter) were correlated with productivity or mortality rates of fawns or adults. However, this lack of correlation had biological implications. Severe winter weather can cause the death of adults in poor condition and increased neonatal mortality the following year (Verme 1969) as well as mortality of

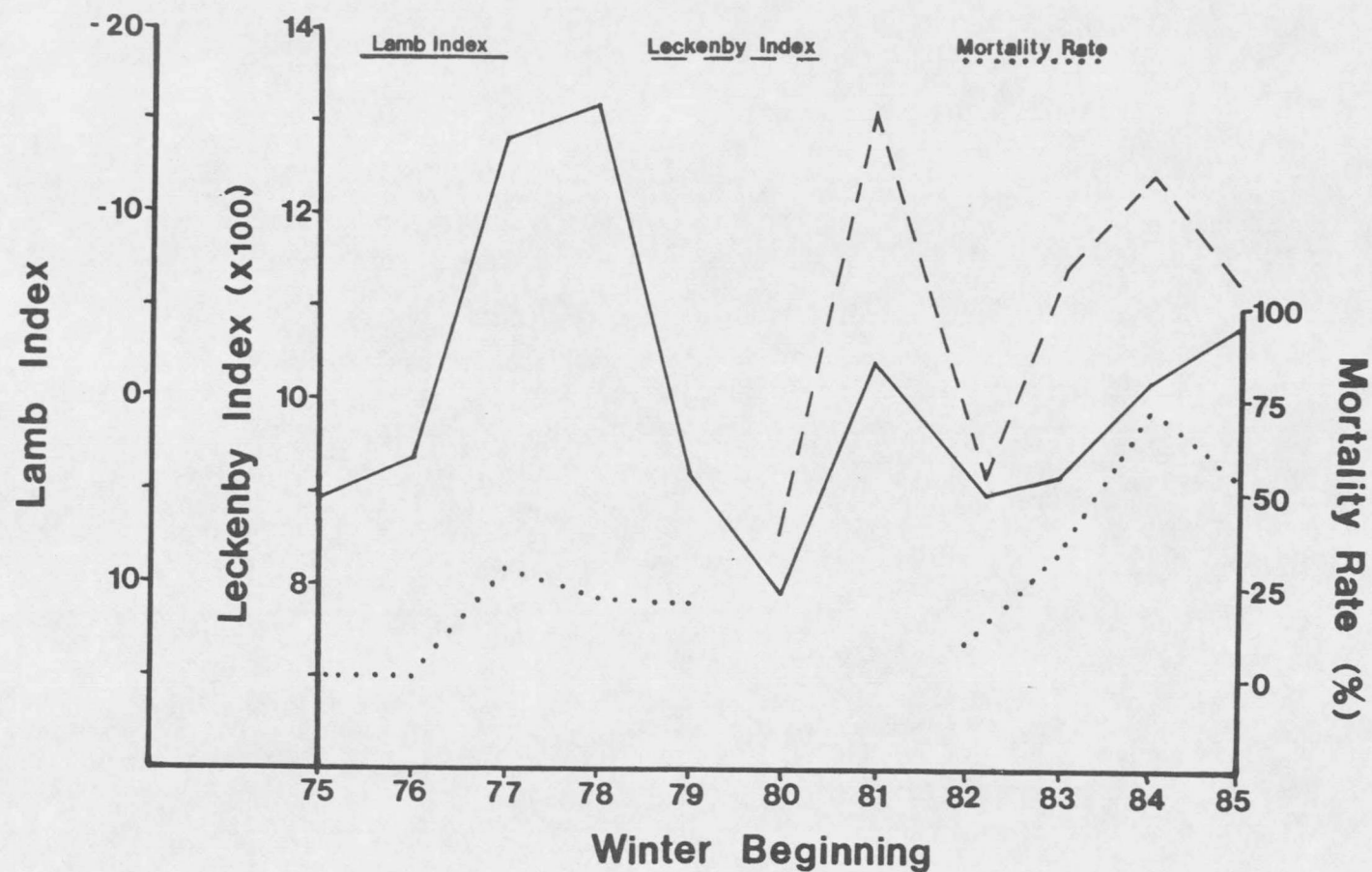


Figure 11. Relationship between winter severity based on modified Lamb and Leckenby winter severity indices, and fawn mortality rate on the Cherry Creek area from November through March, 1975-1986.

fawns born the previous summer (Picton 1979). Although winter weather did influence fawn survival, it had little impact on either adult survival or subsequent fawn production. The 2 coldest and wettest winters which occurred during this study (1977-1978 and 1978-1979, Figure 11) were followed by the highest observed fawn:doe ratios in autumn and early winter (Table 7). Winter mortality of adults was also very low during the study. Apparently, the area provided relatively high quality winter habitat for adults.

Consecutive years of drought appeared to influence population dynamics but a single dry year seemed to have little effect. Although 1979 was the driest year during 1975-1985 (51% of normal precipitation), fawn:doe ratios were above normal in both 1979 and 1980. The second driest year, 1983 (64% of normal precipitation), occurred during peak population levels and average fawn:doe ratios. However, the effects of 2 consecutive years of drought in 1983 and 1984, began to be reflected in lower condition and reproductive success of deer in 1984. The continued drought in 1985 was concurrent with continued poor reproductive success even though population levels had dropped significantly. Although no significant statistical correlations could be developed relating precipitation and fawn production, it appeared that consecutive years of drought can reduce reproductive success. This indicates

that summer range conditions may be important to the dynamics of this population, as reported for other populations (Julander et al. 1961, Anthony 1976, Pederson and Harper 1978).

Time Lags

There was strong evidence suggesting that time lags were involved in the dynamics of the Cherry Creek mule deer population. The population continued to increase in 1983 even though fawn recruitment had begun to decline. Also, the population continued to decline from 1985 to 1986 even though population size was significantly reduced (Figure 12). A similar time lag effect was evident in the cyclic relationship between numbers in year t with numbers in year $t+1$ for females, fawns, and total deer.

Lack of yearling recruitment in 1985 and 1986 drastically altered the age structure of the population (Table 8). Because of this, the population of females in the productive age classes should continue to decline if adult female mortality exceeds 6% during 1986-1987 or 15% during 1987-1988. This type of time lag might provide an explanation for the decreased rate of population growth observed from 1977 to 1978 if the age structure of the population had changed during previous years as a result of poor fawn recruitment.

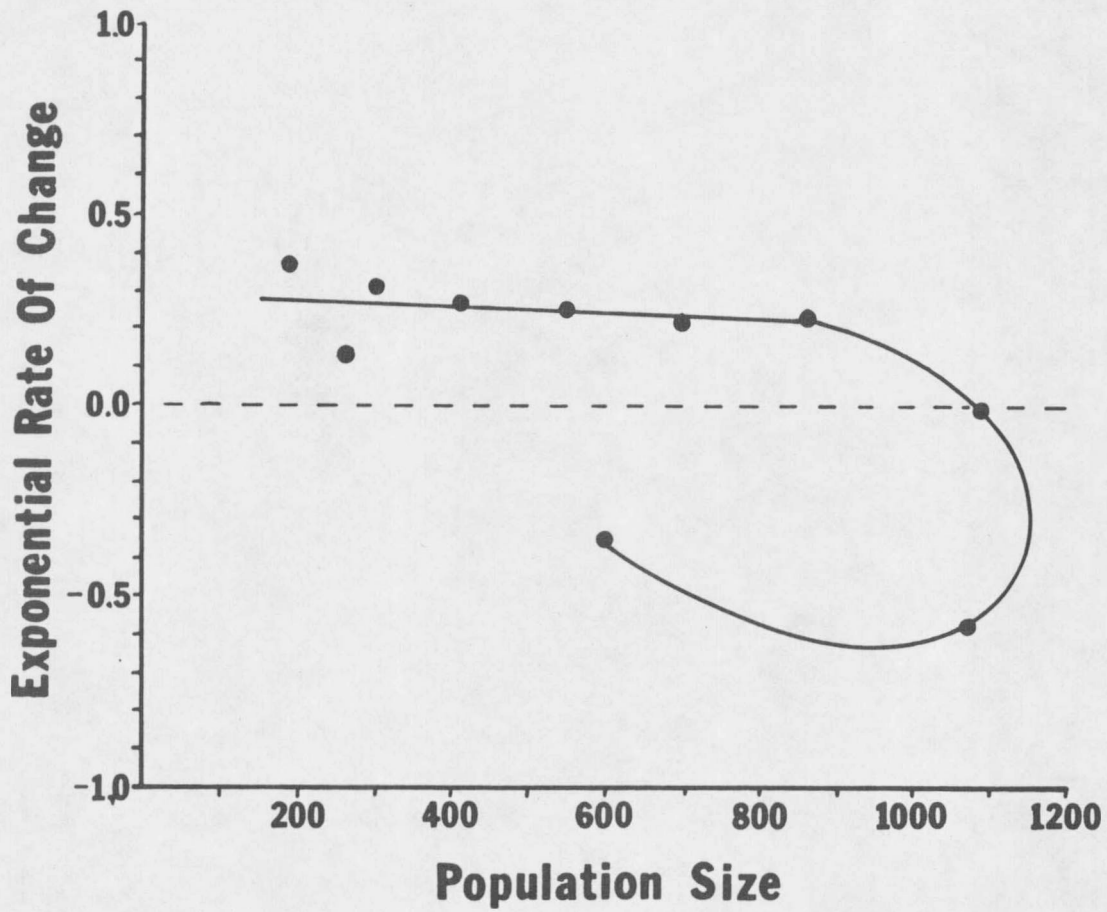


Figure 12. Relationship between population size in spring and the exponential rate of change over the following year for mule deer on the Cherry Creek study area, 1976-1986.

HOME RANGE CHARACTERISTICS AND MOVEMENTS

General Movement Patterns

Among all marked deer on the study area, 86 (78%) of 110 females were observed frequently enough to identify individual movement patterns. Three distinct patterns were identified among these females: 25 (29%) were yearlong residents, 45 (52%) were summer migrants, and 16 (19%) were autumn migrants.

Yearlong residents occupied a single home range area throughout the year. Although individuals used different parts of their home range disproportionately during different seasons, there was no identifiable pattern to these movements which justified delineation of seasonal ranges. These deer did not exhibit any predictable, seasonal shifts in elevation or centers of activity.

Summer migrants, the largest identifiable group, exhibited typical migration movements between distinct summer and winter ranges. The only difference between this migration pattern and that typically described for mule deer in mountainous habitats was the direction and amount of elevational change involved. In spring, summer migrants on the Cherry Creek area moved down (72 m, range 15-130m) from badland dominated winter ranges, to summer ranges containing more of the sagebrush-grassland, mesic shrub,

and hardwood draw cover types. The average distance between individual centers of activity on winter and summer ranges was 5.9 km (range 1-80 km). Martinka (1968) reported similar migration patterns for mule deer in the Bear Paw Mountains of northern Montana but did not quantify the elevational change or distance involved. Spring migration began by mid-March and was usually completed by the end of April. The return to winter range usually began by mid-October and was completed by the end of December. Individual deer completed the migration in less than 8 days, the average interval between relocations. One deer, relocated daily during her migration, completed the move overnight.

Autumn migrants included deer that remained on 1 home range from late autumn through late summer then migrated to an alternate home range occupied from mid-August to mid-October. Average distance between the activity centers of the 2 ranges was 2.9 km (range 1.5-6.0 km). Autumn migrants moved to lower elevation (mean 69 m, range 30-170 m) ranges with an increased component of the mesic shrub and sagebrush grassland cover types in August and returned to higher elevation badlands in October.

Other studies have described similar movements of deer to more mesic habitats (Martinka 1968, Mackie 1970, Dusek 1975), but did not consider them migrational, which led Severson and Carter (1978) to conclude that mule deer

occupying plains habitats were nonmigratory. However, the movements of both summer and autumn migrants on the Cherry Creek area fit Baker's (1978) characterization of migration movements: 1) subsequent return to the original habitat 2) geographical directionality 3) periodicity, and 4) some distance separating the 2 ranges. The discrepancy in the classification of movements as migratory or nonmigratory may have been caused by the relatively short distances moved by deer in prairie environments.

Harestad (1979) observed that black-tailed deer made short duration visits to seasonal home ranges outside of the normal period of permanent seasonal occupancy which fit the definition of a phenomenon Baker (1978) called an exploratory migration. Baker (1978) further hypothesized that an organism makes a determination to migrate based on the quality of the present habitat relative to the expected quality of the new habitat and the total costs incurred during the move. Based on this theory, as the distance between 2 home ranges decreases, the cost involved in moving between them should also decrease and therefore, the probability of an exploratory migration should increase. To test this hypothesis, deer locations were classified as exploratory migrations or seasonal residency. An analysis of covariance indicated that the frequency of exploratory migrations decreased as the distance separating seasonal ranges increased ($r=-0.82$, $P<0.001$), with no difference

($P > 0.2$) between summer and autumn migrants. Therefore, as distance between seasonal ranges decreased, the incidence of exploratory migration increased, which masked the distinction between migrants and nonmigrants over shorter distances. Only by relating temporal similarities between short distance migrants and long distance migrants was it possible to reasonably classify some deer into different migration patterns.

Monthly Movement Patterns

Females classified as yearlong residents, summer migrants, and autumn migrants exhibited significant differences ($P < 0.001$) in monthly average activity radii (Figure 13), suggesting that these groups used different strategies to successfully inhabit this environment. Movements of resident females were essentially stable, with only a slight decrease during the fawning season and increases in September and November. Autumn movements were essentially nondirectional: those in September possibly reflecting increased forage desiccation while those in November probably resulted from disturbance during hunting season.

Movements of autumn migrants increased slightly, though nondirectionally in spring, decreased during the fawning season, and increased again in autumn. The peak in November probably reflected the combined effects of migration and hunting disturbance.

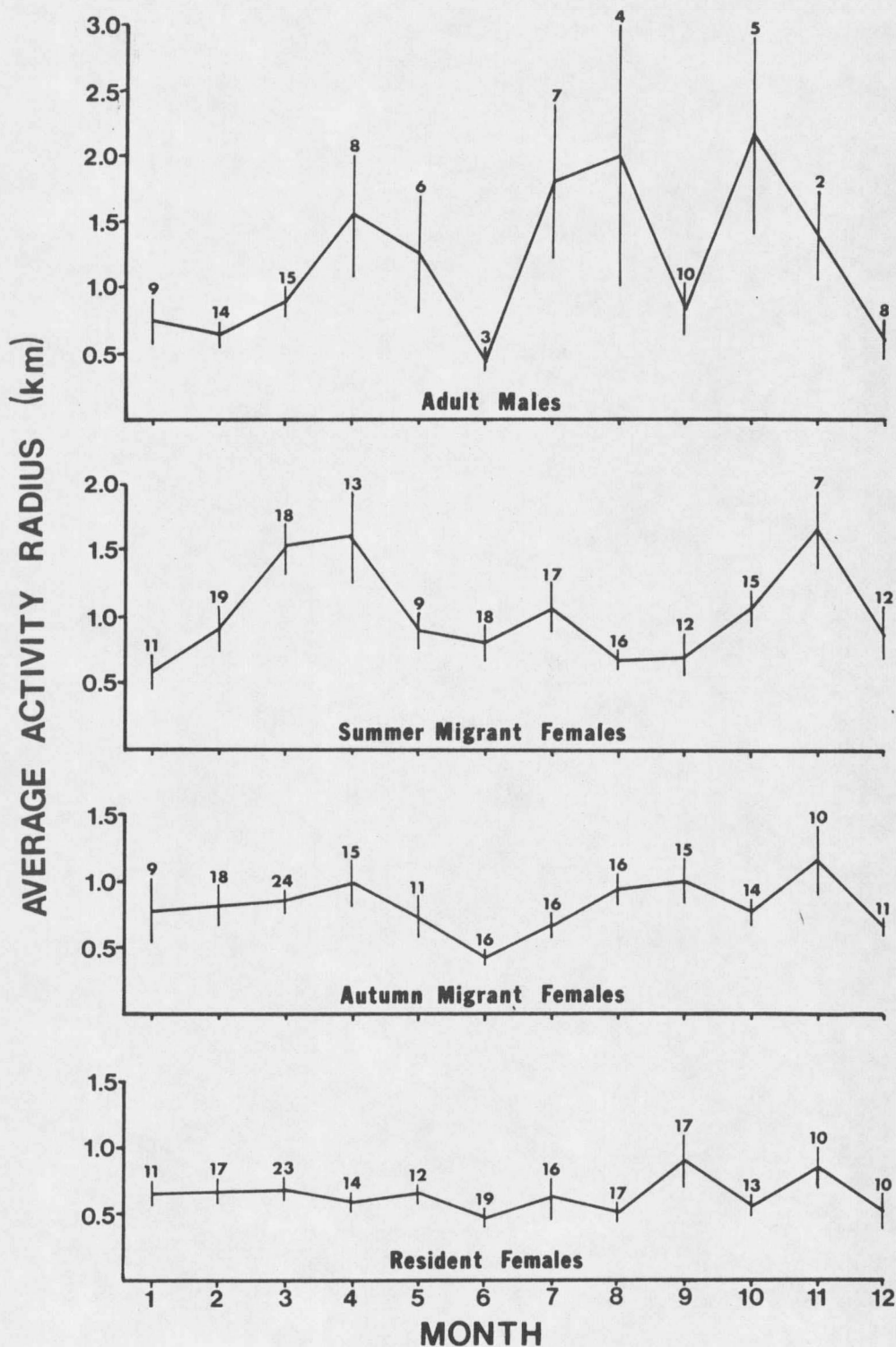


Figure 13. Monthly average activity radius ($\text{km} \pm \text{SE}$) for each female migration class and adult males on the Cherry Creek area, 1983-1985. Number of deer months used to calculate each radius is recorded for each month.

The movements of summer migrants were typical of animals with seasonal migrations. The increase in July resulted from exploratory migrations by 2 yearling females and 2, 2-year-old females in 1983. When these 4 deer were excluded, the pattern for summer migrants in July was a stable average activity radius from May through September.

Data were insufficient to statistically compare movements of females to neckbanded males, so AARs of males were plotted for general comparative purposes only. Males exhibited extreme variation in movement patterns that were similar to females only through the winter and in June. However, the increase in July resulted from long movements by 2 yearling males who later returned to their assumed birth range, and the increase in August from movements associated with dispersal of another yearling male. When these extreme movements were excluded, the resulting pattern was most similar to that exhibited by summer migrant females.

Seasonal and Yearlong Home Range Size

Seasonal home ranges of summer migrants were significantly larger than seasonal home ranges of yearlong residents ($P < 0.05$) during both summer and winter (Table 14). Autumn migrants occupied home ranges that were intermediate in size between summer migrants and yearlong residents during summer, and were comparable to yearlong residents during winter, but were not significantly

Table 14. Estimates of average activity radius (AAR) and polygon home range size for mule deer on the Cherry Creek study area, 1983-1985. Migration classes are: YR=yearlong resident, AM=autumn migrants, SM=summer migrants, and MA=adult males. Within each season, mean AAR's followed by different capital letters were significantly different ($P < 0.05$).

Season		No. pts/deer		AAR (km)			Polygon (km ²)		
Migration Class	No. Deer	Mean	Range	Mean	SE	Range	Mean	SE	Range
Annual									
YR & FM	35	40	19-74	0.82	0.04	0.48-1.57	4.39	0.38	1.79-12.07
Summer									
YR	16	15	10-22	0.63 A	0.05	0.36-1.08	1.63	0.27	0.52-4.83
AM	11	15	9-23	0.74 AB	0.09	0.38-1.16	2.08	0.27	0.65-3.41
SM	17	14	9-26	0.94 B	0.07	0.56-1.76	2.88	0.36	0.70-6.15
Winter									
YR	31	17	10-29	0.74 A	0.06	0.32-1.71	2.29	0.27	0.48-6.36
AM	21	17	11-32	0.75 AB	0.04	0.33-1.13	2.32	0.21	0.64-3.83
MA	10	15	9-23	0.89 AB	0.09	0.50-1.32	3.64	0.72	0.83-8.41
SM	31	16	9-24	0.93 B	0.06	0.44-1.86	3.41	0.54	0.97-13.65

different ($P > 0.05$) than any other classes. There were no differences in the size of summer and winter home ranges of individual mule deer ($P > 0.2$).

Estimates of AARs for males in winter were not significantly different from any group of females. Although comparisons were not made throughout the year, males might be expected to have larger home ranges as reported on other areas (Dasmann and Taber 1956, Robinette 1966, Rodgers et al. 1978, Severson and Carter 1978, Dickinson and Garner 1979) because of differences in resource needs related to differences in the fat cycles (Anderson et al. 1972) between sexes.

Direct comparisons of the home range sizes of adult females between this and other studies were hampered by the multitude of different methods used in calculations. Home range sizes of mule deer on the Cherry Creek area were generally intermediate-to-large, relative to those reported in the literature (Table 15). In general, seasonal home range sizes are relatively small in mountain habitats (Hamlin 1974, Pac 1976, Harestad 1979, Schoen and Kirchhoff 1985), and are relatively large in desert habitats (Rodgers et al. 1978, Eberhardt et al. 1984). However, those reported for the Cherry Creek area were smaller than some mountain environments (Moir 1976, Nyberg 1980, Rosgaard 1981) and larger than some desert habitats (Dickinson and Garner 1979). This makes it difficult to develop any

Table 15. Estimates of mule deer home range size from this study and from the literature. Migration classes for this study were: YR=yearlong residents, AM=autumn migrants, and SM=summer migrants.

PROVINCE ¹	POLYGON HR (KM ²)			AAR (KM)			SOURCE
STUDY AREA	Ann.	Sum.	Win.	Ann.	Sum.	Win.	
Great Plains							
E. Montana							
YR AND AM	4.39	1.81	2.30	0.82	0.67	0.75	This study
SM		2.88	3.41		0.94	0.93	This study
N. Montana	6.97						Hamlin 1978
W. North Dakota	3.38						Wollenberg 1983
W. South Dakota							
Sage Creek				0.79			Severson & Carter 1978
Big Buffalo Crk.				3.82			Severson & Carter 1978
Northern Mountain							
SW. Montana							
E. Bridger Mnt.		3.43	2.26				Rosgaard 1981
E. Bridger Mnt.		2.94	12.85	0.62	1.38		Nyberg 1980
W. Bridger Mnt.		1.07		0.33			Pac 1976
W. Bridger Mnt.				0.36	0.31		Hamlin 1974
N. California			1.55				Loft et al. 1984
Great Basin							
Central Utah				0.36			Robinette 1966
E. Idaho				1.16	0.77		Moir 1976
Coastal Rain Forest							
Vancouver Is. BC		0.39	0.26				Harestad 1979
S. Alaska		0.70	0.83				Schoen & Kirchhoff 1985
Sagebrush steppe							
S. Washington	26.90						Eberhardt et al. 1984
Mojave Sonoran Desert							
S. Arizona				7.25			Rodgers et al. 1978
SW. Texas	2.84	1.63	1.35				Dickinson & Garner 1979

¹After Wallmo 1981

reasonable ecological comparisons across broadly similar habitats, based solely on home range size.

The number of different patterns of migration and home range use exhibited by a population on a given area may be more descriptive of their movement patterns and ecology than a simple description or comparison of home range size. Plains habitats apparently offer a diversity of opportunities for successful occupancy of available habitat and deer seemed to respond by fine-tuning movement strategies to find and utilize available resources. Recent studies (Harestad 1979, Loft et al. 1984, Schoen and Kirchhoff 1985) have revealed that deer in other habitats also use several different strategies to exploit the available resources.

Dispersal

Dispersal was defined following Bunnell and Harestad (1983), as any movement out of an area larger than the home range with no expectation of a subsequent return. Over a total of 157 deer years for females and 47 deer years for males, only 5 dispersals were confirmed (Table 16). However, 13 males, collared as fawns, were also classified as dispersers because they were consistently observed from January to June, then began to disappear during summer, a time when dispersal normally begins (Bunnell and Harestad 1983, Nelson and Mech 1984). All dispersals occurred during the peak population levels of 1983 and 1984. Other

Table 16. Timing and distance of 5 documented dispersals of mule deer from their presumed birth range on the Cherry Creek area.

Sex	Age at Dispersal	Date last observed on birth range	Date first sighted on new range	Dispersal distance (km)
F	1	04-28-83	09-23-83	12
F	2	05-30-84	08-01-84	26
M	1	08-16-83	08-19-83	11
M	1	03-08-83	12-29-83	140
M	1	06-19-83	08-15-83	19

studies have reported few dispersals by fawns (Robinette 1966, Bunnell and Harestad 1983), so fawns marked at approximately 8 months of age were assumed to be within their birth range.

Age specific dispersal rates indicated that the males dispersed as yearlings and females as yearlings and 2-year olds (Table 16). For female mule deer, 1 (3%) of 29 yearlings and 1 (3%) of 32 2-year-olds dispersed. No females older than 2 years dispersed over 96 deer years. For males, 16 (67%) of 24 yearlings dispersed. No males 2 years or older dispersed over 21 deer years. The percentage of males dispersing was within the range of dispersal rates reported by Robinette (1966), Severson and Carter (1978), and Bunnell and Harestad (1983) but the percentage of females dispersing in this study and the 9%

reported by Bunnell and Harestad (1983) were much lower than the 35% reported by Robinette (1966) or the 50% reported by Severson and Carter (1978).

All documented dispersals resulted from observations of marked deer rather than hunter returns of neckbands. Dispersal distances ranged from 12 to 26 km for females and 11-140 km for males (Table 16).

Bunnell and Harestad (1983) summarized dispersal data from Washington and British Columbia and concluded that dispersals greater than 12 km were rare, the longest was 32 km. Similarly, Robinette (1966) reported only 14% of the dispersing males and 9% of the dispersing females moved farther than 10 km. In contrast, Severson and Carter (1978) observed 17 mule deer which dispersed from their South Dakota study area an average of 71 km.

Dispersal distances from the Cherry Creek area (mean 42 km, median 19 km) were most similar to those of Severson and Carter (1978), suggesting that longer dispersals may be more characteristic in areas with widely separated habitat units. Two of the longest dispersal distances ever recorded (240 km by Robinette 1966, and 180 km by Severson and Carter 1978) were across habitats offering little or no cover. Mule deer habitats in the plains are typified by widely scattered areas of rough topography (Severson 1981). When a deer leaves its natal area it may have to travel a great distance before it

reaches other suitable habitat, resulting in long average dispersal distances.

Home Range Fidelity

In this study, dispersal of mule deer females was unusual and fidelity to the herd range and to a single home range within that herd range was the norm. This fidelity was often expressed in the use of only 1 or 2 branches of a drainage system as illustrated by locations of 4 representative deer observed from January 1983 through March 1985 (Figure 14). Though these deer had overlapping winter ranges (upper end of drainage) and made common use of an alfalfa field at the confluence of the 2 branches, each group restricted essentially all of their movements to either the upper or lower branch of the drainage.

Numerous other studies have shown that mule deer have a high degree of fidelity to ancestral ranges. Robinette (1966) reported 1 case where deer temporarily shifted their home range 3-5 km following a wildfire on their winter range and returned when the vegetation recovered. Although these deer apparently adjusted to a habitat disturbance, Robinette (1966) collected no data on the mortality rate of deer which shifted to the new area or the deer density in the new area, both of which may affect survival rates. Taber and Dasmann (1958) indicated that black-tailed deer shifted to areas with high quality forage

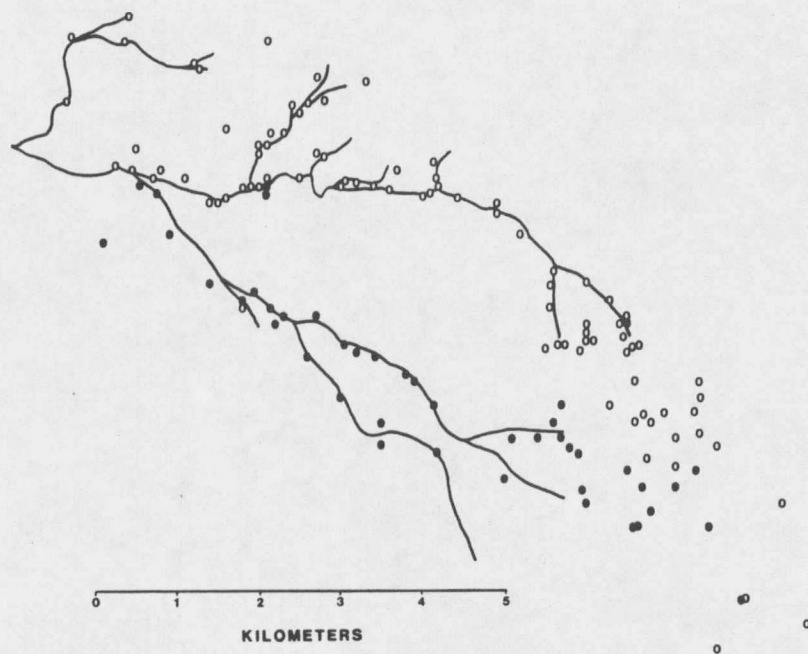


Figure 14. Locations of 4 female mule deer on the Cherry Creek study area from January 1983 to March 1985, illustrating the fidelity of females to individual branches of a drainage system. Solid dots represent locations of 2 deer which resided in the lower fork and open circles the locations of 2 deer which resided in the upper fork of the drainage.

within their home range but would not move to areas outside of their home range "no matter how good the food supply". Based on the degree of fidelity expressed by deer in this study and others, it seemed that any major habitat disturbance within a given herd range could have serious consequences on the welfare of deer within the impacted area.

HABITAT USE

Habitat SelectionAnnual

Overall, radioed mule deer used sagebrush grassland, bunchgrass prairie, badland, mesic shrub, and hardwood draw cover types more than would be expected by chance (selected), and mixed-grass prairie, grainfield, and legume hayfield cover types less than would be expected by chance (avoided) ($P < 0.001$, Table 17, Figure 15). Types avoided by deer provided little topographic relief. Badlands and hardwood draws were the 2 most important cover types, accounting for 1216 (68%) of 1777 diurnal radio locations of mule deer.

The relative importance of cover types, based on a high to low ranking of partial chi-square values, was: 1) hardwood draw, 2) mixed-grass prairie, 3) badlands, 4) mesic shrub, 5) sagebrush-grassland, 6) bunchgrass prairie, 7) small grains, and 8) legume hayfields. The first 3 accounted for 94% of the total chi-square value.

Winter

From December-March, bunchgrass prairie, badland, and hardwood draw types were selected by radioed mule deer; sagebrush grassland and mesic shrub types were used in proportion to their availability; and mixed-grass prairie,

Table 17. Habitat use of mule deer on the Cherry Creek study area based on radio locations (1983-1985) and deer observed during aerial surveys (1975-1986). Data are percentage of observations occurring in each cover type and a selection coefficient indicating avoidance (A), selection (S), and use in proportion to availability (U).

Cover Type	Annual		Spring		Summer		Autumn		Winter	
	Radio Survey		Radio Survey		Radio Survey		Radio Survey		Radio Survey	
Mixed-grass prairie	3 A	6 A*	4 A	10 A*	2 A	5 A*	3 A	7 A*	3 A	4 A
Small grain	0 A	0 A*	0 A	0 A	0 A	0 A	0 A	0 A	0 A	0 A
Legume hayfield	0 A	1 S	0 A	0 A	1 U	3 S	0 A	3 S	0 A	0 A
Sagebrush grassland	9 S	10 S	10 S	6 S*	12 S	19 S*	13 S	20 S*	5 U	4 U*
Bunchgrass prairie	13 S	16 S	24 S	25 S	5 U	10 U*	7 U	9 S*	18 S	15 S*
Badlands	35 S	44 S*	18 U	45 S*	25 S	24 S*	38 S	21 S*	50 S	62 S*
Mesic shrub	6 S	8 S*	8 U	3 S	12 S	15 S*	6 S	21 S*	1 U	2 S
Hardwood draw	34 S	15 S*	36 S	11 S*	43 S	24 S*	33 S	19 S*	23 S	13 S*
Total Observations	1777	10115	262	2958	645	545	230	2773	640	3839

*Indicates significant ($P < 0.05$) differences between the use frequencies of each type.

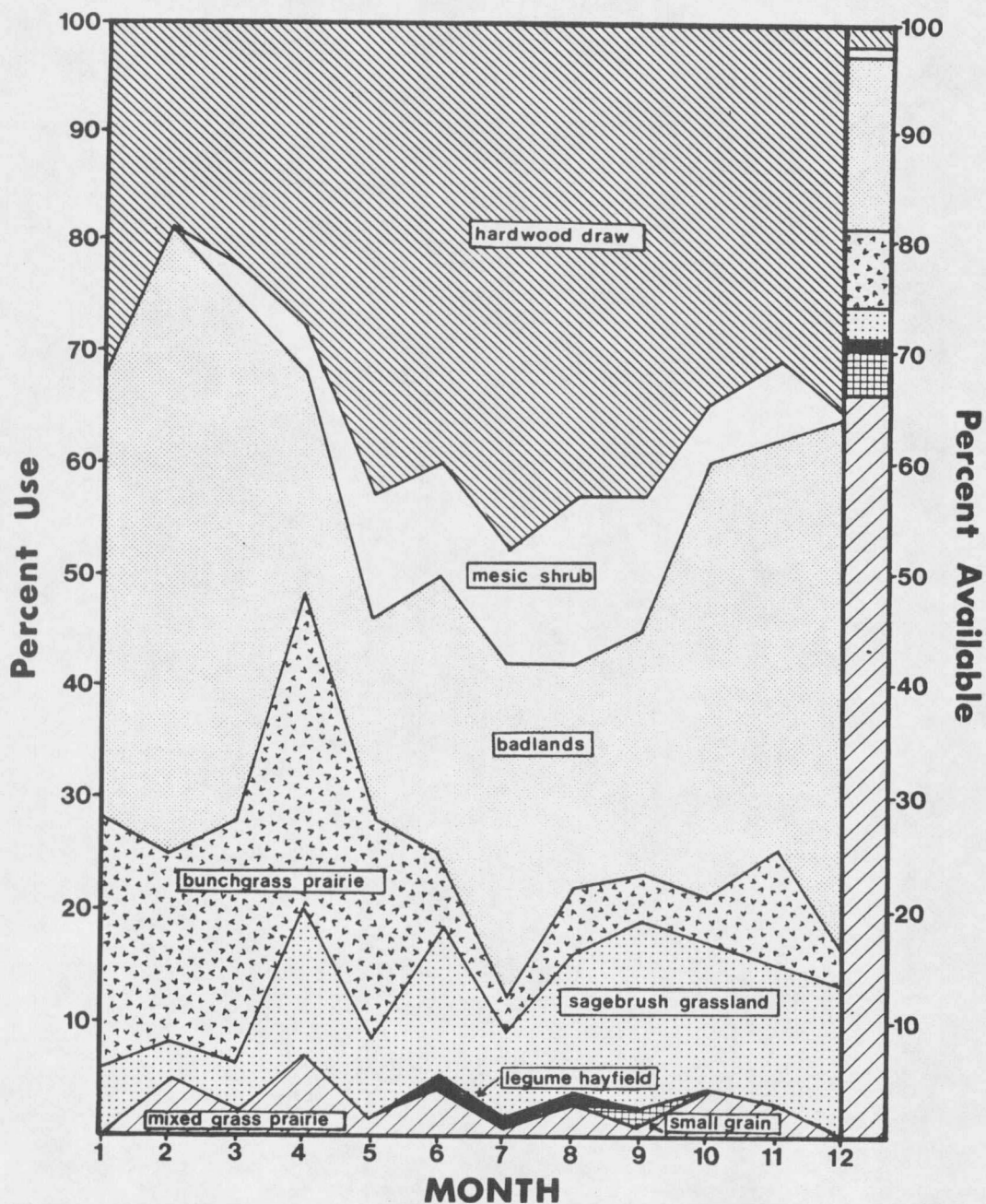


Figure 15. Monthly habitat use by radioed female mule deer on the Cherry creek area, 1983-1985, relative to cover type availability.

grainfield, and hayfield types were avoided ($P < 0.05$, Table 17). Badlands and hardwood draws were heavily used, accounting for 469 (73%) of 640 telemetry fixes during the period. Badlands were most important, accounting for 50% of all telemetry locations. Although hardwood draws were also important in winter, their use decreased compared to other seasons (Figure 15). Those used by deer were usually within the badlands or bunchgrass types, while those within or adjacent to other cover types often filled with drifted snow, making them unavailable.

Spring

During April and May, radioed deer selected sagebrush grassland, bunchgrass prairie, and hardwood draw types; used badland and mesic shrub types in proportion to their availability; and avoided mixed-grass prairie, grainfield, and hayfield types ($P < 0.05$, Table 17). The 3 selected types accounted for 184 (70%) of 262 telemetry locations.

April and May were months of transition from winter to summer habitat use patterns. Bunchgrass prairie was used more in spring than any other season (Table 17, Figure 15). With more bare ground, less litter (Table 1), and diverse topography, the bunchgrass prairie may have provided more early spring forage than the mixed-grass prairie. Use of the hardwood draw type increased as spring advanced.

Summer

Habitat use patterns of radioed deer remained nearly constant from June to September. Sagebrush grassland, badlands, mesic shrub, and hardwood draw cover types were selected; hayfield and bunchgrass prairie types were used in proportion to their availability; and mixed-grass prairie and grainfield types were avoided ($P < 0.05$, Table 17). Hardwood draws were most important, accounting for 280 (43%) of 645 radio locations.

Summer habitat use patterns indicated a preference by deer for more mesic cover types, which in turn represented habitat selection for foraging areas. In summer, badlands were used only when closely associated with hardwood draws or mesic shrub types. Badlands without inclusions of mesic types were virtually unused after mid-August. This contrasted with the winter use pattern, when hardwood draws were only used when associated with badlands.

Overall, use of legume hayfields in summer was in proportion to availability; however, all deer did not have access to such fields. Only 3 herd ranges overlapped alfalfa fields and those fields were highly preferred throughout the summer, based on an analysis utilizing spotlight observations ($P < 0.001$).

Autumn

During October and November, sagebrush grassland, badland, mesic shrub, and hardwood draw cover types were

selected by radioed mule deer; the bunchgrass prairie type was used in proportion to availability; and mixed-grass prairie, grainfield, and hayfield types were avoided ($P < 0.05$, Table 17). Badlands and hardwood draws were most important, accounting for 164 (71%) of 230 radio locations.

Habitat usage during October-November, 1983 and 1984, the time of the general deer season, was transitional between summer and winter patterns (Table 17, Figure 15). Disturbances associated with hunting season apparently had little if any effect, even in the years of heavy hunting pressure. In contrast, Swenson (1982) reported a shift in mule deer habitat use during the hunting season, to types that provided more security than those used either before or after the season, on another eastern Montana prairie.

The different response by deer on the 2 areas might have resulted from the greater interspersions of preferred cover types on Swenson's (1982) Box Elder Creek study area. On an annual basis, mule deer on Cherry Creek selectively used 5 cover types covering only 29% of the area while those on Box Elder Creek used 4 types covering 68% of the area (Swenson, unpubl. rpt., Mont. Dept. Fish and Game, 1978). On Cherry Creek, there were apparently no cover types that provided more security than those already being used.

Comparison of Survey and Radio-telemetry Data

Habitat use patterns based on survey data were similar to those based on telemetry data (Table 17), but significant ($P < 0.05$) observability biases, similar to those described by Gasaway et al. (1985), caused some differences between the 2 data sets. In 3 (10%) of 30 instances, sample sizes in the telemetry data were insufficient to demonstrate a significant use pattern, while survey data indicated significant selection. Only 2 cases of disagreement (1 data set indicating selection, and 1 indicating avoidance) occurred, and both involved use of the legume hayfield cover type (Table 17). Deer used legume hayfields during nocturnal and crepuscular periods, making both data sets biased.

Biases in habitat selection due to group size have also been demonstrated (Gasaway et al. 1985). However, there were no differences ($P > 0.05$) in the mean group size of deer located using radio telemetry or observed during aerial population surveys for any season during this study.

One potential source of bias in the assessment of habitat use based on both radio and survey data was the lack of information on nocturnal habitat use patterns. Dasmann and Taber (1956), Steigers (1981), and Vogel (1983) found deer were more likely to use open cover types after dark. On the Cherry Creek area however, observations during spotlight counts and incidental night-time

observations, indicated that crepuscular habitat use patterns reflected general trends during nocturnal periods.

Food Habits

The late summer diet appeared to be divided equally between forbs and shrubs (Table 18). Grasses constituted 2% of the total rumen volume and occurred in 29% of the rumens examined. Forbs comprised 47% of rumen volume and occurred in 86% of all rumens examined. The most prevalent forbs were yellow sweetclover and alfalfa. Shrubs made up 48% of the rumen volume and occurred in all samples. The two most abundant shrubs were snowberry and rubber rabbitbrush (Chrysothamnus nauseosus) (Table 18). Snowberry was the dominant shrub in the mesic shrub and hardwood draw cover types which were heavily used at this time (56% of all locations during August and September), indicating that those types were important foraging areas.

Autumn food habits (October and November) were transitional from a diet of succulent forage to one more fibrous. In October, grasses comprised 18% of the diet and by November only 3%. Snowberry dropped from 23% to 12% and shifted from predominantly green leaves to dry leaves and stems. In contrast, use of horizontal juniper (Juniperus horizontalis) and silver sagebrush increased over this period. The occurrence of rubber rabbitbrush, a preferred forage species (Mackie 1970, Eustace 1971, Dusek 1975), peaked during October and began to decline by November.

Table 18. Use of various plant taxa by mule deer on the Cherry Creek area, 1983-1984, based on analysis of 47 rumen samples. Data are recorded as frequency of occurrence / volume percentage within each period specified.

	Aug-Sep	Oct.	Nov.	Jan-Feb	Apr.
	(7) ¹	(10)	(22)	(5)	(3)
Monocots					
Grasses	29/1	80/18	64/3	60/2	100/29
Small Grains	14/1	10/1			
<u>Yucca glauca</u>		10/T ²	18/1	60/20	33/2
Total Monocots	29/2	80/19	86/4	100/22	100/31
Forbs					
<u>Chrysopsis villosa</u>			9/T		
<u>Medicago sativa</u>	14/13				67/T
<u>Melilotus officinalis</u>	57/28	20/7	5/2		
<u>Phlox hoodii</u>		20/3	27/1		
unid. Forbs	86/6	60/4	73/14	40/1	100/20
Total Forbs	86/47	60/14	73/17	40/1	100/20
Shrubs					
<u>Amelanchier alnifolia</u>	14/1	10/T			
<u>Arctostaphylos uva-ursi</u>			5/T	40/2	
<u>Artemisia cana</u>	14/1	80/14	82/21	80/15	100/26
<u>Artemisia tridentata</u>		10/T	5/T		33/T
<u>Atriplex nuttallii</u>			5/T		
<u>Chrysothamnus nauseosus</u>	57/9	70/19	77/16	60/7	
<u>Cornus stolonifera</u>			5/T		
<u>Fraxinus pennsylvanica</u>	14/T		14/2		33/T
<u>Juniperus horizontalis</u>	14/T	50/4	68/20	100/50	33/5
<u>Populus deltoides</u>	14/T		18/1	20/T	
<u>Prunus virginiana</u>	14/T		5/T	20/T	
<u>Rhus trilobata</u>	43/8	10/T	5/T		
<u>Rosa sp.</u>	71/3	70/1	18/T	20/1	33/T
<u>Salix sp.</u>	14/T		9/1	40/T	
<u>Shepardia argentea</u>	14/T	10/T	5/T		
<u>Symphoricarpos occidentalis</u>	86/24	90/23	91/12	60/1	33/2
unid. Shrubs	14/2		18/1		100/10
Total Shrubs	100/48	100/61	100/77	100/77	100/43

¹Sample size

²T= trace - less than 1/2 of 1%.

The winter diet shifted strongly to shrubs which constituted 77% of rumen volume and occurred in 100% of the 5 rumens sampled. Monocots made up nearly all of the remaining forage consumed, with soapweed (Yucca glauca) the only important species. Soapweed, silver sagebrush, rubber rabbitbrush, and horizontal juniper accounted for 92% of the total rumen volume during winter.

In spring (April), use of grasses was higher than other seasons. Forb use was comparable to autumn, greater than winter, and less than summer. Shrub use was comparable to late summer. Silver sagebrush was the single most important species, indicating peak utilization at a time when protein content and P:Ca ratios are also at their peak in this species (Eustace 1971).

There appeared to be some differences in the use of forage classes by mule deer during late autumn and winter, between 1975-1976 (Hamlin 1976) and 1983-1984. During low population densities, shrub utilization was slightly higher and use of monocots lower, similar to the findings of Nellis and Ross (1969). However, because sample sizes were small and Hamlin's (1976) data were based primarily on feeding site analysis, the differences were probably not biologically important. Silver sagebrush, rubber rabbitbrush, and horizontal juniper comprised the majority of the late autumn and winter diet during both periods (Hamlin 1976, Table 18).

Habitat Characteristics of Mule Deer RangesWinter

The availability of badlands appeared to be the single most important factor influencing mule deer distribution and habitat use during winter. The badland cover type dominated areas used as winter range, comprising an average of 44% of all 25 ha blocks occupied by deer from December through March.

The steep, rugged topography of badlands served to ameliorate environmental conditions by providing shelter from the wind, and more optimum snow depths. They also provided forage. Both feeding and bedding sites of deer were located predominantly on leeward slopes independent of slope aspect ($P < 0.05$, Figure 16); selection for warmer south-facing slopes did not occur ($P > 0.05$). Because wind was a constant factor in this environment, averaging 21 km/hr for 57 random measurements, minimum heat loss was apparently achieved by seeking shelter from the wind rather than slopes exposed to the sun. Kramer (1971) speculated that a similar lack of selection for southern exposures by deer reflected "... the small scale of land features", on his study area. This could also explain the phenomenon on the Cherry Creek area.

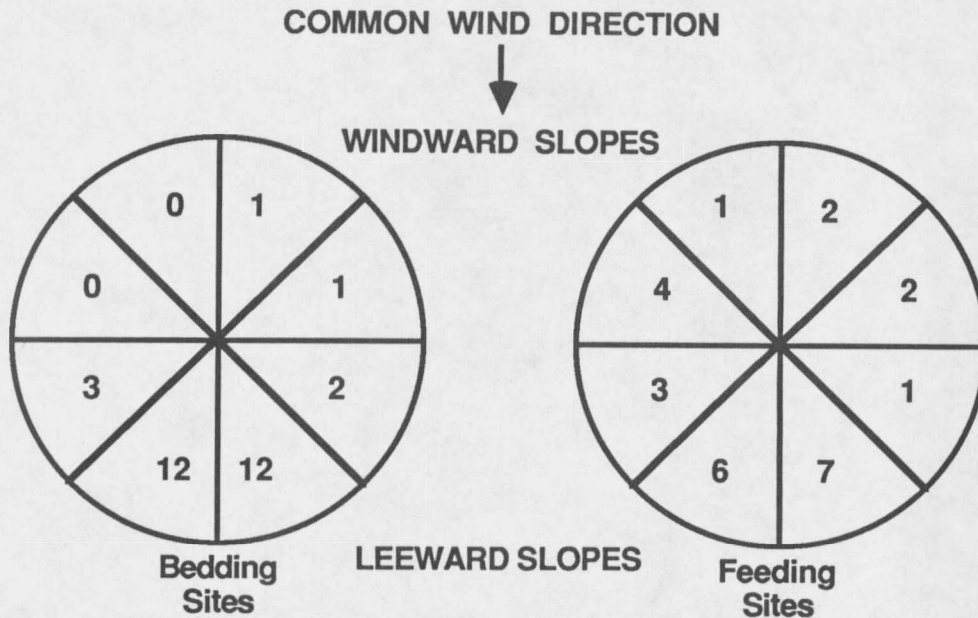


Figure 16. Number of mule deer groups observed during winter on the Cherry Creek study area using each slope aspect relative to a common wind direction.

There was a curvilinear relationship between the shelter index and the unsheltered wind speed at sites used by deer (Figure 17). At low wind speeds, shelter indices for feeding deer were more variable than those of bedding deer, indicating that mule deer tolerated more severe conditions while feeding. Similar observations were reported by Staines (1976) for red deer (*Cervus elaphus*). There was no indication that decreasing air temperatures or temperatures adjusted for wind chill caused deer to seek shelter ($p > 0.05$). Over the temperature range observed

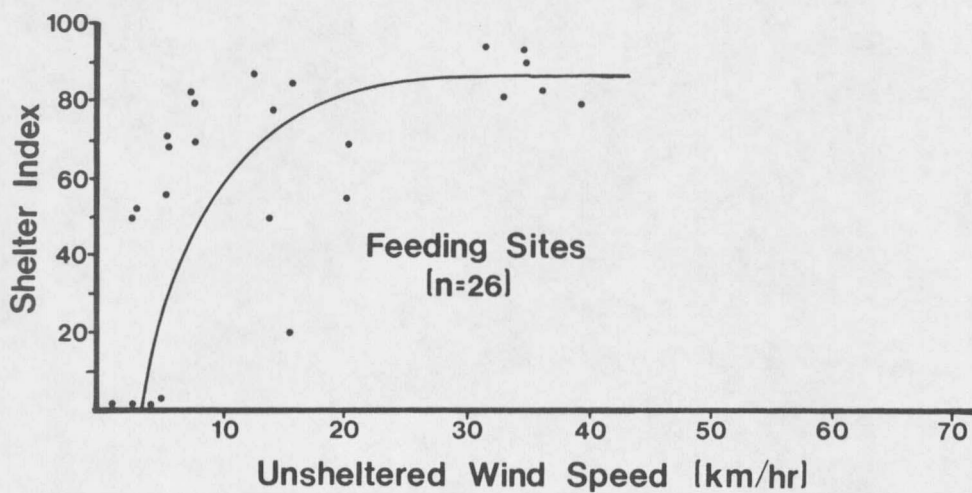
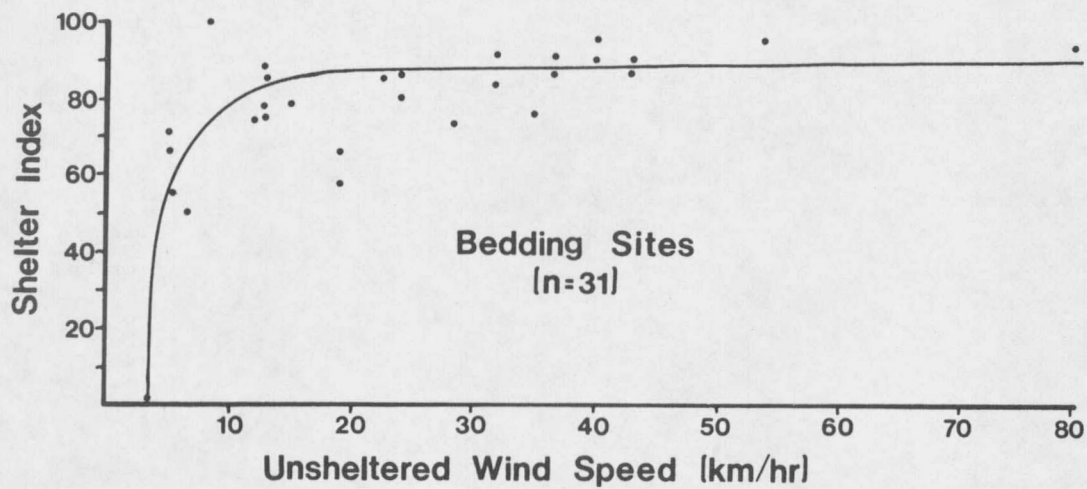


Figure 17. Relationship between the shelter index and unsheltered wind speed at bedding and feeding sites used by mule deer on the Cherry Creek study area during winter.

during this study (-24°C to 11°C) deer avoided windy sites at all wind speeds greater than 10 km/hr independent of temperature.

Large areas of badlands probably provided more favorable snow conditions. Drifted snow from the adjacent prairie accumulated around the periphery of badlands, while the diverse aspects and rugged terrain of badlands resulted in only small patches of drifted snow, interspersed with bare ground on wind blown and south-facing slopes. Badlands that attracted winter concentrations of mule deer were all larger than 3.7 km^2 . Martinka (1968), Dusek (1975), Severson (1981), and Swenson et al. (1983) have also documented the importance of rough terrain to minimize the effects of snow on wintering mule deer.

Badlands also provided the most favorable areas for foraging by mule deer during winter. All of the forage species eaten during winter could be found in or immediately adjacent to the badlands where their availability was only rarely limited by snow conditions.

Summer migrants, autumn migrants, and yearlong residents occupied significantly ($P < 0.05$) different habitats during winter. Summer migrants occurred in blocks with less hardwood draw and more sagebrush grassland and narrow mesic shrub type than either autumn migrants or yearlong residents. Autumn migrants occupied blocks with more edge of hardwood draws than either summer migrants or

yearlong residents (Table 19). Thus, autumn migrants and yearlong residents occupied more mesic winter ranges than summer migrants, but this apparently had no influence on winter habitat use patterns because of the over-riding importance of badlands.

Summer

The increased variability in habitat use and selection of cover types by deer from winter to summer, was accompanied by increased variability in the characteristics of specific ranges occupied. Although blocks occupied by all deer in summer were dominated by mixed-grass prairie and badlands (76% of each block), there were significant differences ($P < 0.05$) in characteristics of areas used by the three migration classes (Table 19).

Summer migrants moved to more mesic summer ranges containing less badlands and bunchgrass prairie, and more mixed-grass prairie, sagebrush grassland and mesic shrub types than their winter ranges (Table 19). These ranges also had less area in hardwood draws and more edge of the mesic shrub type than areas occupied by other migration types. This indicated that summer migrants occupied a relatively dry environment which included small patches of the mesic shrub type. These ranges apparently provided sufficient resources only through use of a variety of cover types.

Table 19. Comparison of habitat variables between seasons or migration classes for mule deer on the Cherry Creek study area, 1983-1985.

Comparison	For	No. of Blocks	Var. ¹	Difference & Direction
between migration classes	summer	310	A6	SM < AM < YR ²
			A8	SM < AM & YR
			E6	SM & AM < YR
			E8	SM < AM & YR
			A1	SM > AM & YR
			E7	SM > AM & YR
	winter	308	A8	SM < AM & YR
			A4	SM > AM & YR
			E7	SM > AM & YR
			E8	AM > SM & YR
between summer & winter	SM	224	A5	summer < winter
			A6	summer < winter
			A1	summer > winter
			A4	summer > winter
			A7	summer > winter
	AM	149	A4	summer > winter
			E5	summer < winter
	YR	235	no seasonal differences	

¹A=area, E=edge; 1=mixed-grass prairie, 2=small grain, 3=legume hayfield, 4=sagebrush grassland, 5=bunchgrass prairie, 6=badlands, 7=mesic shrub, 8=hardwood draw.

²SM=summer migrant, AM=autumn migrant, YR=yearlong resident

Legume hayfields were especially important to summer migrants as indicated by spotlight counts. The number of deer using alfalfa fields increased through the summer and peaked during early September (Figure 18) at 185 deer (4.3/ha) which was 88% of the deer counted within 2 km of these fields during the autumn aerial survey. The reduced use of fields during late summer, 1984 may have been caused by the lack of moisture and plant growth that year. Alfalfa growth in 1984 was so poor that only 3 of 7 fields were cut, whereas all were cut in 1983.

Autumn migrants occupied summer ranges that were intermediate to other deer, but most similar to yearlong residents. The only differences between ranges occupied by autumn migrants and yearlong residents were in the amount of area and edge of the badlands. Autumn migrants occupied summer ranges that differed from those of summer migrants in 5 habitat characteristics (Table 19). Their summer ranges contained more sagebrush grassland and less bunchgrass prairie edge than winter ranges. All of this suggested that autumn migrants compensated for reduced areas of badlands by using other cover types. In this sense, autumn migrants resembled summer migrants by using a variety of other cover types to adjust for deficiencies in summer habitat. It was only during late summer and autumn, when their needs could not be met on ranges occupied from December to mid-August, that they moved to alternate autumn

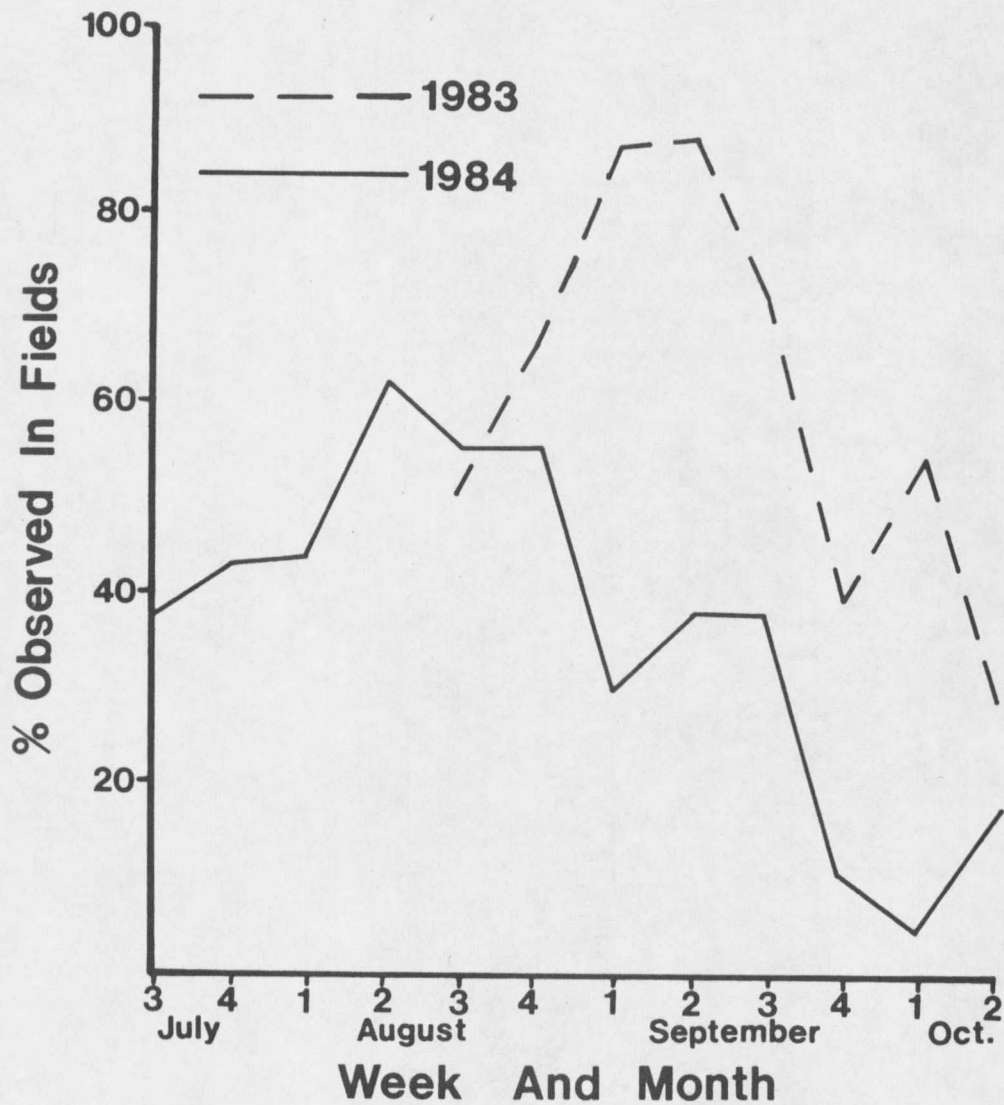


Figure 18. Alfalfa field use by mule and white-tailed deer on the Cherry Creek study area during July-October, 1983 and 1984. Data are the percent of the total number of deer counted in the drainage during the autumn survey which were observed during weekly spotlight counts.

ranges. It appeared that the autumn migration was in direct response to late summer forage dessication. If this was true, then autumn migrants may not migrate during exceptionally moist years, and yearlong residents might be forced to migrate during exceptionally dry years.

Yearlong residents occupied summer ranges that were the same as winter ranges (Table 19). These ranges were a complex of badlands and interspersed hardwood draws that apparently met both shelter and forage needs of mule deer.

Habitat, Dispersion, and Home Range Interactions

Both the size of individual home ranges and intensity of use may be indicative of the relative quality of a given area or unit of range for deer. Presumably, small home ranges result from close interspersion of all seasonal habitat requirements, while larger home ranges are associated with greater dispersion or scattered, patchy distribution of required resources. Likewise, areas receiving relatively intensive use (i.e. supporting relatively high densities of deer) seasonally, should be characterized by close interspersion of required habitat elements of sufficient abundance to meet the needs of many deer. These assumptions were used as the basis for interpreting the following analyses.

Winter

On the Cherry Creek area, small winter home ranges were characterized by blocks with greater amounts of badlands and hardwood draws, less mixed-grass prairie, and lower diversity than large home ranges ($P < 0.05$, Table 20). Deer apparently compensated for the lack of badlands and hardwood draws on their winter range by increasing their home range size and using a variety of other cover types as indicated by the increased diversity index within blocks occupied by deer with larger home ranges (Table 20).

Different habitat variables influenced how intensively a block would be used by the 3 migration classes (Table 20). The quantity of badlands was the only variable influencing how intensively a block was used by yearlong residents ($P < 0.05$, Table 20). If sites were sufficiently moist to provide succulent forage during summer, then the availability of badlands apparently became important in determining use through the remainder of the year.

Winter range blocks receiving high intensity use by summer migrants contained more badlands, less mixed-grass prairie, and had a lower diversity index than low intensity use areas ($P < 0.05$, Table 20). Autumn migrants exhibited more intense use of areas with more bunchgrass prairie and less mixed-grass prairie (Table 20). Thus, badland and/or bunchgrass prairie types were important components of winter range for all mule deer. These 2 types were most

Table 20. Comparison of habitat variables between high and low use areas, and large and small home ranges for mule deer on the Cherry Creek area, 1983-1985.

Comparison	For	No. of Blocks	Var. ¹	Difference & Direction
between large & small home ranges in winter	all	131	A1	large > small
			H	large > small
			A6	large < small
			A8	large < small
between high & low use areas in winter	SM	103	A6	low < high
			A1	low > high
			H	low > high
	AM	53	A5	low < high
			A1	low > high
between large & small home ranges in summer	all	149	A6	low < high
			A1	large > small
			A4	large > small
			A6	large < small
			A8	large < small
			E8	large < small
between high & low use areas in summer	SM	80	A4	low < high
			E8	low < high
	AM	65	A1	low > high
	YR	98	A6	low < high

¹A=area, E=edge H=diversity index; 1=mixed-grass prairie, 4=sagebrush grassland, 5=bunchgrass prairie, 6=badlands, 8=hardwood draw.

²SM=summer migrant, AM=autumn migrant, YR=yearlong resident

similar in plant species composition (Table 2) and land form. Apparently if an area of bunchgrass prairie type was large enough or interspersed within the badlands type, it also provided suitable winter habitat.

Summer

Differences in habitat characteristics ($P < 0.05$) of blocks occupied by deer with large and small summer home ranges further illustrated the importance of the badland-hardwood draw complex for summer as well as winter (Table 20). When badlands and hardwood draws were less abundant, deer used blocks with more sagebrush grassland and mixed-grass prairie and ranged over a larger area.

During summer, high use blocks for yearlong residents were associated with larger areas of badlands ($P < 0.03$). There was also a trend toward low intensity use blocks to have more mixed-grass prairie ($P < 0.10$). Autumn migrants demonstrated a similar pattern, with the amount of mixed-grass prairie decreasing ($P < 0.007$) and badlands increasing ($P < 0.10$) in high use blocks. Because the study area was dominated by badlands and mixed-grass prairie (83% of the area) both results reflected the importance of the badlands for summer range.

Summer migrants intensively used blocks having abundant sagebrush grasslands interspersed with hardwood draws. Hardwood draws were important to all deer on the

area, but because they were more scarce within the ranges of summer migrants, these deer tended to concentrate their activities around the few available areas of hardwood draws within their range.

Comparison to Habitat Use Patterns in Other Areas

The results of this study confirm the importance of resource distribution on movement patterns of mule deer as reported by Eberhart et al. (1984) and Severson and Carter (1978). They also support the conclusion of Severson and Carter (1978) that "rougher terrain and more extensive cover types apparently allowed . . . deer to fulfill requirements in smaller areas". On the Cherry Creek area, the interspersion of mesic hardwood draws and badlands appeared to provide all resources required by mule deer throughout the year and resulted in smaller home ranges. A combination of other cover types over a larger area was necessary to meet yearlong habitat requirements when adequate areas of interspersed badlands and hardwood draws were lacking.

The influence of badlands and bunchgrass prairie types on winter habitat use patterns has been discussed previously. Summer habitat use patterns seemed to be influenced by availability of high quality forage. In a dry environment such as this, it seems reasonable to assume that the availability of succulent forage would be quite limited, particularly in late summer and autumn. Other

studies (Martinka 1968, Mackie 1970, and Dusek 1975) have documented shifts in mule deer distribution during late summer, presumably to areas with more succulent forage. Late summer movements documented during this study probably reflected shifts to areas of better forage.

Although Severson (1981) believed that mule deer distribution in prairie environments centered around cover requirements, both cover and forage were important in determining the distribution of deer on the Cherry Creek area. Areas that provided only 1 component were not used. Interspersion of cover and forage, particularly in late summer, seemed essential for mule deer on the Cherry Creek area.

Other studies (Dusek 1975, Swenson, unpubl. rpt., Mont. Fish and Game, 1978, and Steigers 1981) have reported more use of grassland habitats by mule deer than was observed on the Cherry Creek area. However, a careful review of the data in those reports indicated that this difference was largely a reflection of the manner in which habitats were defined and mapped in the various studies. Although Dusek (1975) reported intensive use of a grassland vegetation type during both summer (63%) and winter (68%) in his northern Montana study area, this was not an indication of selection by mule deer because grasslands covered 62% of the study area. The preference of deer for slopes rather than bottoms or heads of coulees (Dusek

1975), indicated that deer used a grassland habitat more similar to the bunchgrass prairie of the Cherry Creek area.

Similarly, the grassland type of Swenson's (unpubl. rpt., Mont. Fish and Game, 1978) Box Elder Creek study area in eastern Montana, appeared to include both grassland types and some areas that closely resembled those mapped as badlands on the Cherry Creek area. Evaluation of deer distribution on Box Elder Creek indicated that mule deer avoided areas resembling mixed-grass prairie and used areas that resembled bunchgrass prairie and badlands of the Cherry Creek area.

A study on the prairie of South Dakota demonstrated that grasslands different from those on the Cherry Creek area were important habitats for mule deer (Steigers 1981). Vegetative descriptions at fawn bed sites indicated use of a prairie type by mule deer that was vegetatively and probably topographically different than either grassland type on the Cherry Creek area.

The avoidance of the mixed-grass prairie cover type by deer on the Cherry Creek area did not indicate avoidance of "grasslands", but rather, that needs for shelter and/or forage were not met in that type. Habitats that support mule deer in prairie environments can be very limited in their distribution and abundance. Any that provide cover and forage throughout the year, are probably suitable mule deer habitat regardless of what plant species dominate.

HABITAT RELATIONSHIPS AND POPULATION REGULATION

Mule deer seemed to occur in several semi-isolated subpopulations across the Cherry Creek study area. They used traditional herd ranges and limited their movements to the same general area used by other members of their social group. Differences in movement patterns, and habitats occupied by 3 such subpopulations which exhibited extremes in long-term fawn:adult ratios during spring (which were assumed to reflect recruitment rates into the adult population), provided insight to some of the factors influencing the nature and process of population regulation in prairie environments.

The 2 subpopulations having the highest average fawn recruitment rates, occupied areas with different cover type composition (Table 21). Area 1 was dominated by mixed-grass prairie, badlands, and sagebrush grasslands with only a few scattered areas of the mesic shrub and hardwood draw cover types (Table 21). Four (29%) of 14 marked females were yearlong residents on the winter range, while the remainder migrated to alternate summer ranges. The lack of hardwood draw and mesic shrub cover types and the summer migration, indicated that this environment was relatively dry. However, area 1 included 5 alfalfa fields scattered through the summer range. These fields

Table 21. Cover type composition (%) of areas occupied by subpopulations of mule deer on the Cherry Creek study area with extremes in spring fawn recruitment rates during 1976-1986.

	Area 1	Area 2	Area 3
Population Characteristics			
Area size (km ²)	49	27	20
Adults observed	254	196	28
Fawns observed	118	94	10
Mean annual density	0.84	1.19	0.21
Fawns:100 Adults	47	48	36
Habitat Characteristics			
Mixed-grass prairie	55	31	42
Small grain	T ¹	2	0
Legume hayfield	1	0	0
Sagebrush grassland	10	0	4
Bunchgrass prairie	1	31	6
Badlands	32	28	48
Mesic shrub	1	1	0
Hardwood draw	T	7	0

¹T=less than 0.5%

apparently provided high quality forage in late summer and early autumn for deer that moved to them as indicated by the intensive use they received. Because of the summer migration, those deer which remained on the winter range could disperse throughout the few available mesic sites at a greatly reduced density. Thus, most deer inhabiting area 1 had high quality forage (alfalfa) available to them through the summer, even though they inhabited a rather xeric environment.

The subpopulation inhabiting area 2 relied almost exclusively on native cover types for forage. Nine of 10 marked females were yearlong residents and 1 was a summer migrant. Yearlong residents had some of the smallest summer home ranges of any deer, and the home ranges of individuals inhabiting this area were smaller than most other deer, including yearlong residents in other subpopulation units ($P < 0.05$). The abundance of hardwood draws, the small home ranges, and yearlong residency all indicated that this was a very mesic environment. Though habitats in areas 1 and 2 were quite different, both provided deer with mesic cover types through the use of native or agricultural types.

The subpopulation inhabiting area 3 had the lowest overall fawn recruitment rate. The fact that it was dominated by badlands and mixed-grass prairie, with no areas of the mesic shrubs or hardwood draws (Table 21),

indicated that area 3 was one of the driest deer ranges on the study area. Habitats providing suitable late summer and autumn feeding sites were apparently very limited on area 3. Although no deer were marked in this area, surveys during late summer and early autumn indicated that many of these deer fed along roadsides where vegetation received additional moisture via runoff from the pavement, and remained green longer than surrounding rangeland. Although roadside vegetation quality was sufficient to attract deer, it apparently was not sufficiently abundant and/or enduring to positively affect reproductive success.

The summer season can have a significant impact on the reproductive success of mule deer which occupy hot, dry environments (Julander et al. 1961, Anthony 1976, Pederson and Harper 1978). Body fat reserves are at a minimum in female mule deer at the time of birth and early lactation (Anderson et al. 1972). Their fat reserves increase during late summer and autumn as fawns become self-sufficient, and peak during the breeding season (Anderson et al. 1972). In many arid environments, the time of maximum moisture stress for plants corresponds to the time when females need to build fat reserves. Condition of adult females during the breeding season influences reproductive success during the following year (Verme 1969). Forage quality and quantity also influence the growth rate of fawns which in turn influences overwinter survival by affecting

thermoregulatory capabilities (Moen 1966).

Based on the previous discussion, fawn production and recruitment on the Cherry Creek area appeared to be closely related to the relative availability of mesic habitats and the quality of forage during late summer and early autumn. Most of the vegetation on the area became desiccated by mid-August when the legume hayfield, mesic shrub, and hardwood draw cover types provided the only significant amounts of green vegetation and thus were the major foraging areas. However, the quantity and quality of forage was probably not equal in all portions of these cover types. Prairie environments are characterized by extremely variable annual and seasonal climates which result in variation in the availability of food and cover (Mackie 1983). The Cherry Creek study area was no exception: average annual precipitation ranged from 14-42 cm during 1975-1985. A high degree of variation was also evident between and within cover types across the study area. Variability in forage quality was also likely to be expressed on a finer scale that would not be readily apparent to human observers, but which would be apparent to deer and utilized through selective foraging behavior within favorable microsites.

Interrelationships between environmental characteristics, behavioral responses, and population dynamics indicated that mule deer made subtle adaptations

to both short and long-term environmental variation. This suggested an hypothesis on population regulation which might apply in similar prairie environments. I hypothesize that there are only 3 general types of habitats based on the resources which they provide: nonhabitats that support no deer, maintenance habitats that provide for the survival of adults, and reproductive habitats that provide for both adult survival and successful reproduction. Deer density, relative to the availability of each of these habitats, should be in a constant state of flux because of variation in annual and seasonal weather patterns, and population size. A continually variable resource base should in turn, be expressed through variation in population dynamics.

Either reproductive or maintenance habitats could potentially limit population size. However, the limited nature of mesic habitats, and the relatively low natural mortality rates of adults on Cherry Creek, and other areas (Caughley 1970, McCullough 1979, Hanks 1981, and Skogland 1985), suggests that adult survival would remain relatively unaffected in the absence of hunting. Under these conditions, variation in population dynamics would most likely be expressed in terms of variable rates of initial fawn production, or fawn recruitment into the adult segment of the population.

This hypothesis could explain the pattern of population growth and fawn recruitment on the study area

during 1975-1986. At low population levels and limited harvests of 1975-1980, the population grew steadily at 30%/year which indicated that environmental variation had little if any affect on the rate of population growth. The population was relatively large in 1982-1983 but above average precipitation and near normal temperatures provided sufficient habitat quality to insure high fawn recruitment rates. Three consecutive dry years (1983-1985) presumably reduced the relative availability of reproductive habitat, even though the number of adults declined, causing continued reductions in fawn production and recruitment.

Traditional theories on natural regulation of ungulate populations have developed around the concept of forage quantity, quality, and availability (Klein 1965, 1968, Caughley 1976, Peek 1980, Caughley 1981, and Skogland 1985), particularly on the winter range (Carpenter and Wallmo 1981), though summer range can also be limiting (Taber and Dasmann 1958, Pederson and Harper 1978). Caughley (1981) conceptualized the process as an interactive plant-herbivore system where herbivores increase at a rate influenced by the availability of forage, and forage plants increase at a rate influenced by the population density of herbivores. Alternative theories on population regulation have been proposed implicating predation (Haber 1980, Peek 1980), availability of suitable home ranges (Gavin et al. 1984), territoriality (Ozoga et

al. 1982), or the interactions of many factors (McCullough 1979).

It appeared that the number of females on the Cherry Creek area might have been naturally regulated by a combination of forage interactions and availability of suitable home ranges if the population had not been reduced through harvest. Forage availability influenced population dynamics but not in the interactive way proposed by Caughley (1981). With the exception of rubber rabbitbrush, there was little evidence to suggest that the availability of preferred forage species was limited by increased population size. In that sense, deer did not influence, nor were they limited by the quantity of available forage as proposed by Klein (1968). Forage quality, particularly in late summer and early autumn, has the potential to influence reproductive success (Verme 1969) and may have ultimately determined the relative availability of "reproductive habitat" in this study. However, native forage quality was probably dependent on plant growth as influenced by site and climatic conditions and not by the size of the mule deer population. If the population had continued to grow, then limited availability of new home range sites (Gavin et al. 1984) in suitable maintenance and reproductive habitats might have limited further population growth through the dispersal of young.

COMPARATIVE ECOLOGY AND RELATIONSHIPS OF
WHITE-TAILED DEER TO MULE DEER.

Population Characteristics and Dynamics

Population Size

Historically, white-tailed deer were only locally abundant in some areas along major river drainages in eastern Montana. Prior to 1941, they had disappeared from much of their range in this region (Allen 1971). They apparently began expanding their range into upland habitats of eastern Montana during the 1940's and 1950's. The first observations of white-tailed deer on the Medicine Lake National Wildlife Refuge in northeastern Montana, were made in 1943 (Cook 1945). A report from a long-time resident (L. B. Chapman, pers. comm.), indicated that they first appeared on the study area in 1954.

An estimated 170 white-tailed deer occurred on the study area when surveys were first conducted in the winter and spring of 1975-1976 (Table 22). Subsequent estimates suggest that spring populations gradually declined to around 100 deer in 1979, increased to a maximum of 335 in 1983, and declined to approximately 75 animals in 1986. Early winter (December-January) population estimates followed a similar pattern except for 1977-1978. Autumn

Table 22. White-tailed deer population estimates on the Cherry Creek study area from December 1975 to April 1986.

DATE	TOTAL	ADULTS	FAWNS	FEMALES	MALES
Dec. 75	170	105	65	87	18
Apr. 76	170	105	65	87	18
Dec. 76	128	80	48	66	14
Mar. 77	128	80	48	66	14
Jan. 78	160	95	65		
Mar. 78	116	89	27		
Jan. 79	100	57	43		
Jan. 80	165	82	83	71	11
Sep. 82	429	256	173	186	70
Dec. 82	351	239	112	181	58
Mar. 83	335	230	105	174	56
Jul. 83	585	315	270	210	105
Oct. 83	335	252	83	176	76
Dec. 83	312	235	77	160	75
Apr. 84	303	233	70	159	74
Jul. 84	484	303	181	194	109
Oct. 84	326	232	94	174	58
Dec. 84	120	96	24	70	26
Mar. 85	107	91	16	66	25
Jul. 85	175	107	68	74	33
Sep. 85	120	105	15	73	32
Dec. 85	64	51	13	35	16
Apr. 86	75	60	15	41	19

population size, first estimated in 1982, decreased from 429 in 1982 to 335 in 1983, remained essentially stable at 326 in 1984, and declined sharply to 120 animals by 1985. Summer population estimates, available only for 1983-1985, declined steadily from 585 to 175. Overall, the estimates indicated that white-tailed deer numbers fluctuated widely, from 64 to 585 during the study.

During the spring of 1976, there were nearly as many white-tailed deer on the area as mule deer (93 white-tailed deer:100 mule deer). At peak populations of both species in 1983, the ratio was 31:100. Although populations of both species subsequently declined, white-tailed deer decreased more rapidly such that by 1986 the ratio had dropped to 17:100.

Productivity

Data on productivity of marked white-tailed deer on the area (Table 23) were inadequate to determine age-specific rates, but the general pattern of older females being most productive (Verme 1969) was evident. All but 1 (a 2-year-old at breeding) of 12 mature females tested were pregnant (Table 23).

The fawn:doe ratios calculated for marked females during 1983 and 1984 averaged 43 fawns:100 females. This was slightly below the 54 and 47 fawns:100 females observed during autumn surveys in 1983 and 1984, respectively. Marked deer averaged 1.14 fawns/producing female (n=16) by

Table 23. Age specific pregnancy rates, autumn fawn recruitment rates (% success and fawns:producing female), and projected fawns:100 total females in autumn for marked female white-tailed deer on the Cherry Creek study area, 1983-1985. Sample sizes are recorded in parentheses.

Age at fawning	% Pregnant	% Rearing > 1 fawn	Fawns: female	Fawns: 100 females
2-3	75 (4)	40 (5)	1.00	40
4-7	100 (4)	61 (18)	1.09	66
8+	100 (4)	43 (7)	1.33	57

autumn, whereas all females observed during autumn aerial surveys averaged 1.29 fawns/producing female (n=29). Fawn-at-heel ratios during July decreased from 1.80 in 1976 and 1982, to 1.24 and 1.30 in 1983 and 1984, respectively.

Mortality

Fawn mortality rates decreased from July to April (Table 24). Monthly mortality rates averaged 30% from July to September, 18% from October to November, and 3% from December to April. Mortality rates were higher during summer and autumn for white-tailed deer (mean 65% and 32%, respectively) than for mule deer (mean 41%, and 21%, respectively) but overwinter mortality was much lower for

Table 24. Finite seasonal mortality rates (percent) for white-tailed deer on the Cherry Creek area during 1982-1986.

Season	Total Adult	Fawn	Adult Female	Adult Male
10/82-12/82	7	35	3	17
12/82-04/83	2	6	4	3
04/83-04/84	26	74	24	30
04/83-10/83	26	69 ¹	16	28
10/83-12/83	7	7	9	1
12/83-04/84	1	9	1	1
04/84-04/85	75	91	66	77
04/84-10/84	9	48	10	47
10/84-12/84	71	74	60	55
12/84-04/85	5	33	6	4
04/85-04/86	63	81	53	52
04/85-10/85	2	78	1	3
10/85-12/85	53	13	52	50
12/85-04/86	0	0	0	0
Mean				
Annual	55	82	48	53
Apr.-Sep.	10	65	9	26
Oct.-Nov.	35	32	31	31
Dec.-Apr.	2	12	3	2

¹Rates for fawns are calculated from July-September

white-tailed deer (12% vs. 43%), resulting in a somewhat higher annual mortality rate for white-tailed deer (82%) as compared to mule deer (70%).

Numbers of adult males and females significantly declined from spring through summer, when an average of about 9% of the females and 26% of the males were lost from

the population. Records of marked deer suggested that this resulted largely from dispersal of yearlings (Table 25); 2 of 5 neckbanded females and all 4 neckbanded yearling males dispersed.

Table 25. Number of marked white-tailed deer females lost from the Cherry Creek study area population during 1983-1985, by cause, season, and age class. C=cripple loss, E=emigration, H=harvest, I=illegal kill, U=undetermined.

FEMALE LOSSES					
Age Class	Number Alive	Total	Autumn	Winter	Summer
0	4	1	0	1U	0
1	5	2	0	0	2E
2	9	2	2H	0	0
3	12	1	1I	0	0
4	9	3	3H	0	0
5	9	2	1C 1H	0	0
6	10	1	1I	0	0
7	8	1	1C	0	0
8+	15	7	2C 1I 4H	0	0
Total	81	20	17	1	2

Some natural mortality was documented during summer. The only marked adult male on the area died of epizootic hemorrhagic disease (EHD) during September 1984. EHD was also the suspected cause of death for 5 deer observed during the October 1984 aerial survey. Overall, only 1 of 25 marked deer died, indicating that the effect of EHD on the population was probably minimal. EHD outbreaks on and around the Cherry Creek area during the summers of 1976, 1977, and 1978 (Walcheck 1978) may have contributed to the declining white-tailed deer population (Table 22) during those years. About 33% of all white-tailed deer on the Yellowstone River died as a result of EHD in 1977 (Swenson 1979).

Most adult mortality during 1982-1986 occurred during hunting season. Autumn mortality rates averaged 31% for both adult females and adult males (Table 24). Hunting was indicated as the primary cause of mortality among marked females, accounting for 16 (80%) of 20 documented deaths during autumn (Table 25). Another marked female was killed illegally, prior to the hunting season. Of the 17 marked white-tailed deer killed, 3 were shot illegally and 4 were found dead as a result of wounds. Crippling losses and illegal kills accounted for a much larger portion (41%) of the total white-tailed deer dying during autumn than mule

deer (15%). Mortality rates for adults were lower during winter than other seasons, averaging only 3% for females and 2% for males.

Distribution

White-tailed deer, like mule deer, occurred in scattered aggregations across the study area, though the dispersion of white-tailed deer was even more restricted. From 1975 to 1986, white-tailed deer were observed in only 19% of the blocks on the study area during all seasons, 7% of the blocks during spring, 4% during summer, 8% during autumn, and 11% during winter. Their distribution remained essentially the same throughout the study ($P < 0.001$), though some shifts in relative concentration areas occurred.

White-tailed deer densities were much lower than those observed for mule deer because of the lower numbers and more scattered distribution across the area. Winter density peaked at $0.63/\text{km}^2$ in December 1982 as compared to a peak of 2.3 mule deer/ km^2 . Local white-tailed deer densities were quite variable across the area, reaching up to $5/\text{km}^2$ which was comparable to the lower range of local mule deer densities.

The restricted dispersion of both species promoted significant ($P < 0.05$) interspecific overlap (Figure 19). During the entire study, 54% of the 25 ha blocks on the area were never occupied by either species. The greatest overlap occurred during winter when 7% of the blocks were

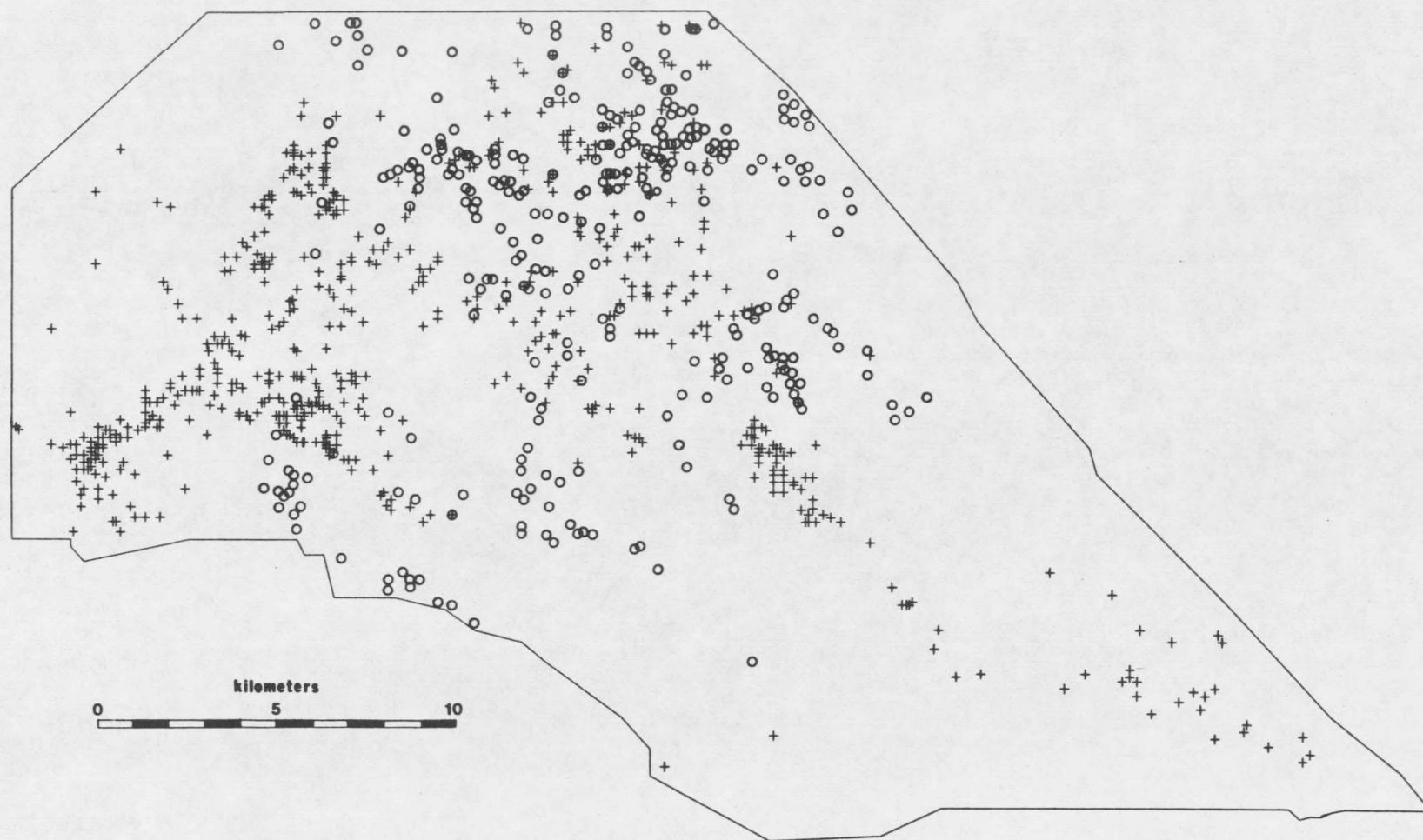


Figure 19. Winter distribution of mule deer (+) and white-tailed deer (o) on the Cherry Creek study area from 1975 through 1985.

occupied by both species, with the least in summer (1%); overlap during spring (4%) and autumn (4%) was intermediate (Table 26). Blocks occupied by white-tailed deer that were also occupied by mule deer, were more common than blocks occupied by mule deer that were also occupied by white-tailed deer (Table 26).

Table 26. Percent of 2,713, 25 hectare blocks on the Cherry Creek study area occupied exclusively by mule deer (MD), exclusively by white-tailed deer (WT), both species (MW), and neither species (NO) from 1975 to 1986. Also, the percent of the area occupied by mule deer that also contained white-tailed deer (MMW) and the percent of the area occupied by white-tailed deer that also contained mule deer (WMW).

Season	MD	WT	MW	NO	MMW	WMW
Spring	11	3	4	82	25	51
Summer	9	3	1	87	7	19
Autumn	16	4	4	76	20	52
Winter	12	4	7	77	36	61

Interpretation of range overlap (Table 26) was complicated by 2 factors. First, 6 (40%) of 15 radioed white-tailed deer which occupied the study area in winter, moved off the area in spring, reflecting general movements and distribution of the population. Thus, the number of

blocks occupied by both species was representative of interspecific overlap on the survey area, but not between the populations except during winter. This resulted from the selection of the area as a mule deer study area. The second factor complicating the interpretation, was that the summer data were based on only 1 survey flight while more flights were completed during autumn (8), winter (9), and spring (9), providing more opportunity to observe overlap during these seasons.

Age and Sex Composition

Fawn:doe ratios averaged 66:100 (range 21-134:100) in autumn and 64:100 (range 34-117:100) in winter during 1975-1986 (Table 27). Percentage of fawns in the population averaged 30% (range 12-44%), 34% (range 20-43%), and 30% (range 15-43%) during autumn, winter, and spring, respectively. Buck:doe ratios were high in autumn averaging 57:100 (range 33-92:100) and dropped to 31:100 (range 15-47:100) after the hunting season. The herd composition of white-tailed deer was comparable to that of mule deer during all seasons except autumn, when the buck:doe ratio was greater for white-tailed deer ($P < 0.02$).

Herd composition estimates for white-tailed deer were less precise than those for mule deer. Replicate surveys from late August to mid-October, 1983 and 1984, resulted in coefficients of variation for fawn:doe ratios of 13 and

Table 27. White-tailed deer buck:doe:fawn ratios and percent bucks, does, and fawns during autumn, winter, and spring on the Cherry Creek study area during 1975-1986.

Year	AUTUMN			WINTER			SPRING					
	Ratio buck:doe:fawn	Percent buck doe fawn		Ratio buck:doe:fawn	Percent buck doe fawn		Ratio buck:doe:fawn	Percent buck doe fawn				
1975-76 ¹	64:100:50	26	41	33	21:100:75	11	51	38	21:100:75	11	51	38
1976-77 ¹	74:100:44	34	46	20	21:100:73	11	52	37	21:100:73	11	52	37
1977-78 ¹	59:100:68	26	44	30	-- --- --	--	--	40	-- --- --	--	--	23
1978-79 ¹	-- --- --	--	--	--	-- --- --	--	--	43	-- --- --	--	--	--
1979-80 ¹	92:100:52	32	34	34	15:100:117	7	43	50	-- --- --	--	--	--
1980-81 ²	72:100:134	23	33	44	-- --- --	--	--	--	-- --- --	--	--	42
1981-82 ²	52:100:95	21	41	38	-- --- --	--	--	--	-- --- --	--	--	43
1982-83	38:100:93	16	44	40	32:100:62	16	52	32	32:100:60	17	52	31
1983-84	43:100:47	23	52	25	47:100:48	24	51	25	47:100:44	24	53	23
1984-85	33:100:54	18	53	29	37:100:34	22	58	20	38:100:24	23	62	15
1985-86	44:100:21	27	61	12	46:100:37	25	55	20	46:100:37	25	55	20

¹Data from Hamlin, 1976-1980.

²Unpub. data, Mont. Dept. Fish, Wildl., and Parks, Fed. Aid Proj. W-130-R.

17%, respectively, and for buck:doe ratios of 22 and 26%, respectively. The greater variability in estimates for white-tailed deer relative to those of mule deer probably reflected both the much smaller total sample sizes and the fact the surveys were designed to count mule deer.

The age structure of the female segment of the population during 1983 and 1984 was pyramidal (Table 28). Females 2-years or younger comprised 52% of the total female population, 3-7-year-olds 33%, and 8-year-olds and older 15%, which was similar to mule deer. Also like mule deer, male white-tailed deer, 4-years of age or older, were very rare and comprised an estimated 2% of the male population and less than 1% of the total population (Table 28). Fawns comprised 55%, and males 1-3 years old comprised 43% of the total male population during 1983 and 1984.

Group Size

As with mule deer, average group size was not correlated with population size. Therefore, group composition was evaluated by combining all data from 1975 to 1986.

The average number of white-tailed deer per group generally increased from June to February and declined from February to May for groups containing any adult females,

Table 28. Percentage of white-tailed deer estimated for each age class on the Cherry Creek study area during spring 1983 and 1984. Number of males recorded in age class 4 represents all males 4 and older.

Age Class	Females	Males
0	19	55
1	18	19
2	15	14
3	11	10
4	5	2
5	7	
6	6	
7	4	
8+	15	
Total Deer	211	109

mature males, or yearling males (Figure 20). Males typically occurred in larger groups than females. There was less sexual segregation and group size was larger during November as compared to October or December (Table 29, Figure 20). This indicated that neither species experienced a temporary breakup of doe groups during the rut as reported by Hawkins and Klimstra (1970) and Gavin et al. (1984).

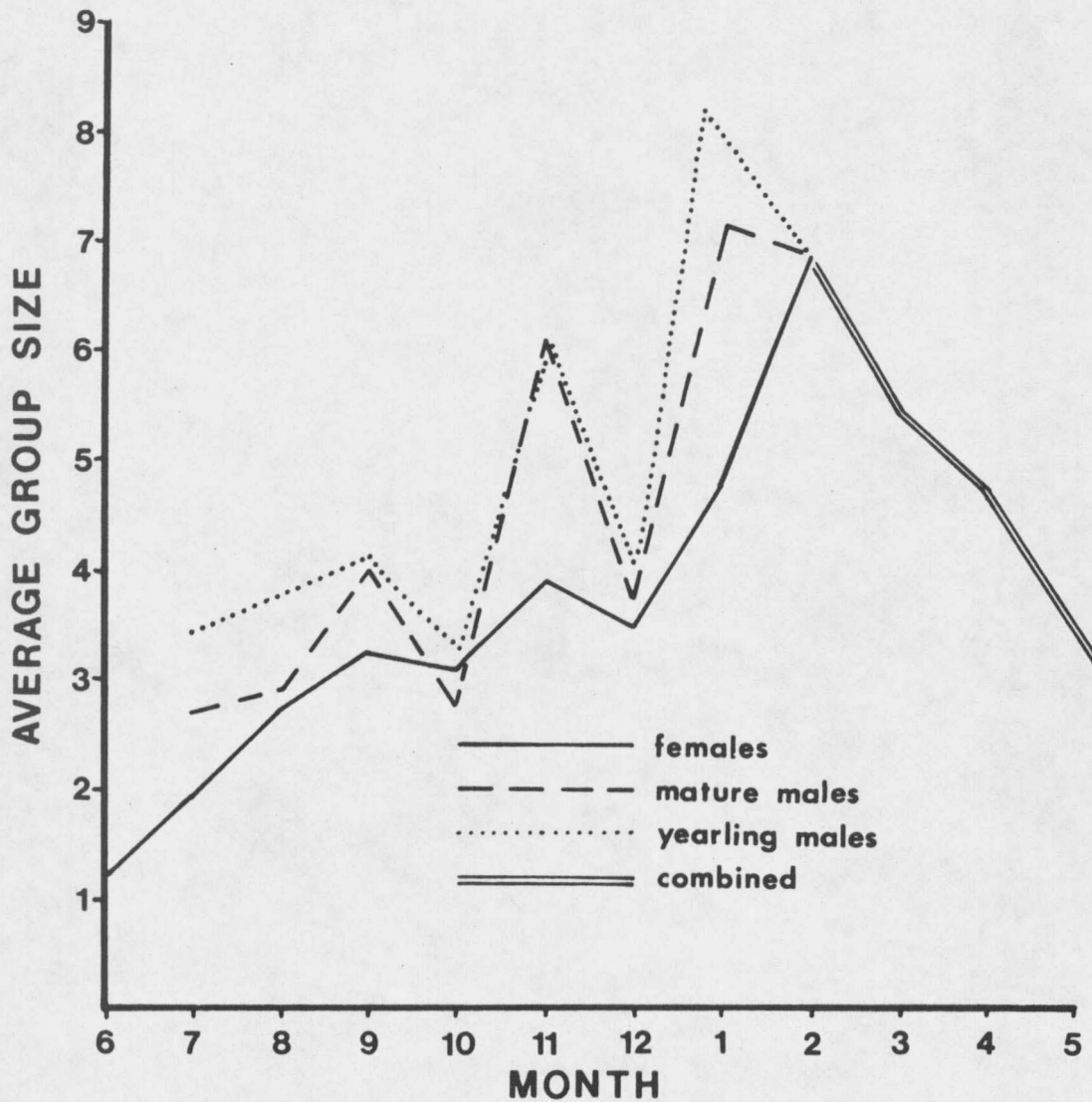


Figure 20. Average total group size of white-tailed deer groups on the Cherry Creek study area that contained adult females, yearling males, and mature males during 1975-1985. Sexes were combined from February through May.

Table 29. Group composition of white-tailed deer on the Cherry Creek study area during July-January, 1976-1986. Data are percentage all females, mature males, and yearling males which occurred in each category.

	MONTH						
	7	8	9	10	11	12	1
FEMALES							
Alone	38	13	8	7	4	7	1
In groups/no fawns	28	27	23	25	29	16	9
Alone with fawns	16	19	20	14	4	10	11
In female/fawn groups	4	25	22	42	25	39	62
With mature males	2	2	7	2	30	11	5
With yearling males	9	12	12	9	2	12	5
In mixed groups	3	2	8	1	6	5	7
Number observed	180	371	396	294	110	379	250
MATURE MALES							
Alone	10	14	13	13	0	18	10
Mature male groups	38	27	23	38	0	11	0
With females	10	11	16	7	91	43	30
With yearling males	25	25	16	35	0	13	15
In mixed groups	17	23	32	7	9	15	45
Number observed	40	44	83	40	11	62	20
YEARLING MALES							
Alone	2	16	9	22	0	19	0
Yearling male groups	17	30	21	18	0	0	0
With females	37	32	31	29	50	49	53
With mature males	33	16	12	27	0	15	20
In mixed groups	11	6	27	4	50	17	27
Number observed	46	99	110	45	2	53	15

The courtship behavior of male white-tailed deer is more aggressive than that of mule deer (Geist 1981, Marchinton and Hirth 1984) and may result in a temporary breakup of the doe social group. Although aggressive chases of does by bucks were observed among white-tailed deer, the more common pattern was for mature bucks to tend groups of does which resulted in the increased group size during November. This pattern of tending doe groups is apparently common in more open habitats (Marchinton and Hirth 1984). Average female group size from June to January was larger for mule deer than for white-tailed deer ($P < 0.02$).

The social organization of white-tailed deer (Table 29) generally resembled that for mule deer (Table 9) on the study area, though sexual segregation seemed to be more nearly complete in white-tailed deer. Over 62% of all female white-tailed deer associated with other females, with fawns, or were alone (Table 29) from July to January as compared to 49% for mule deer. While most mature male white-tailed deer were associated with females during the rut (43-91%), fewer (10-30%) were observed with females during other seasons. Most yearling males of both species occurred with females, mature males, or in mixed groups (54-100%).

Condition Indices

Dressed weights of fawns averaged 21.6 and 24.0 kg for females and males, respectively. Weights of yearling females averaged 34.8 kg (range 29.5-37.7 kg) and those of mature females averaged 40.2 kg (range 34.0-49.9 kg). Weights of yearling and mature males averaged 41.4 kg (range 34.0-45.4 kg) and 59.0 kg (range 48.0-70.3 kg), respectively. There were no differences between weights of mule and white-tailed deer of the same age when comparing within years ($P > 0.05$). Antler main beam length and diameter of yearling males averaged 17.0 cm (range 3.5-31 cm) and 1.44 cm (range 0.7-2.0 cm), respectively; averages for mature males were 36.4 cm (range 31-46 cm) and 2.61 cm (range 1.9-3.2 cm), respectively. Antlers of yearling mule deer were slightly larger than those of yearling white-tailed deer, but antlers of mature males of both species were comparable in size.

Although sample sizes were small, trends in white-tailed deer physical condition mirrored those of mule deer. Weights of all deer were generally lower in 1983 and 1984, and antlers of yearling males were smaller in 1984 as compared to other years (Table 30). Decreased fawn-at-heel ratios in 1983 and 1984 also indicated poorer condition because neonatal fawn production is influenced by physical condition (Verme 1969).

Table 30. Dressed weights (kg), antler beam lengths and diameters (cm, measured 2.5 cm above the bur) of hunter killed white-tailed deer from the Cherry Creek study area. Sample size is recorded in parentheses.

YEAR	FAWNS		ADULT FEMALES		ADULT MALES					
			Age (years)		Age (Years)					
			1.5	2+	1.5		2+			
	Fem. Wt.	Male Wt.	Wt.	Wt.	Wt.	Beam length	Beam diam.	Wt.	Beam length	diam.
1975	21(4)	24(5)	35(2)	44(4)	49(3)	----	1.9(6)	63(6)	----	2.6(12)
1982	--	--	--	--	45(1)	20.2(3)	1.6(3)	61(1)	33.5(1)	2.5(1)
1983	--	--	--	41(4)	40(2)	23.0(3)	1.8(3)	57(4)	36.8(5)	2.4(5)
1984	24(1)	--	34(5)	38(11)	36(5)	12.2(5)	1.2(5)	56(6)	36.8(8)	2.5(8)
1985	--	--	38(1)	43(2)	41(2)	15.3(2)	2.0(1)	59(9)	36.0(10)	2.9(8)
Mean	21.6	24.0	34.8	40.2	41.1	17.0	1.44	59.0	36.4	2.61

Factors Influencing Population Dynamics

Several factors including EHD, severe winter weather, variable fawn production or survival, and dispersal probably influenced population trends during the study. However, because of the absence of detailed data from 1976 through 1981, assessment of the relative importance of these factors was only speculative.

As noted earlier, outbreaks of EHD in the vicinity of the study area could have caused or contributed to the apparent decline in spring population size from 1976 to 1977. Overwinter mortality of approximately 28% occurred from January to March, 1978 which coincided with the wettest and coldest winter weather during the past 11 years (Figure 11). Though the winter of 1978-1979 was even more severe, and may have affected overwinter survival, population estimates were not available to evaluate its effects. Increases in fawn recruitment rates and possibly lowered mortality rates among adult females probably contributed to population growth from 1980 through 1983. Substantial declines in the number of adult males and females observed during summer, 1983-1985, were probably caused by dispersal of yearlings, and may have also occurred in earlier years.

Trends during 1982-1986 were influenced primarily by 2 factors: 1) increased harvests reflecting more liberal hunting regulations (Table 12) designed to control deer

numbers, and 2) decreased fawn production and survival.

Increased harvest rates appeared to be the overriding factor. During 1983, antlerless deer tags (6.2 tags/100 km²) were valid for either species and harvest rates were relatively low (Table 31). During 1984, more liberal permit quotas (24.7 tags/100 km² for antlerless white-tailed deer + 27.7 tags/100 km² for antlerless deer of either species with each hunter allowed up to 5 permits) resulted in nearly a 6-fold increase in the rate of harvest. During 1985, unlimited numbers of permits were available, but only 1/hunter was allowed. Although this restriction resulted in a decreased harvest rate compared to 1984, the harvest rate in 1985 was still 5-times greater than that recorded in 1983 (Table 31).

Table 31. Harvest rates for adult male and female, mule and white-tailed deer on the Cherry Creek study area, 1982-1985. Data are percentage of the preseason population which disappeared from the study area during the hunting season.

Year	Mule Deer		White-tailed Deer	
	Females	Males	Females	Males
1982	1	62	3	17
1983	9	59	9	1
1984	37	65	60	55
1985	27	48	48	50

It is widely believed that white-tailed deer are less vulnerable to hunters than mule deer in areas where the species are sympatric (Kramer 1972). This may have been true for males, but apparently was not the case for females on the Cherry Creek area. During 1982 and 1983 when hunting permits were good for either species, females of both species experienced similar rates of harvest, while male harvest rates were higher for mule deer than for white-tailed deer (Table 31). During 1984 and 1985 liberal regulations designed to encourage the harvest of antlerless white-tailed deer, increased the rate of harvest for both males and females.

Several factors including use of open habitat, predictable escape behavior, accessibility, and hunter incentive, appeared to promote high rates of harvest for white-tailed deer. Heavy hunting pressure caused many white-tailed deer to shift from use of hardwood draws to more open habitats where they could watch for approaching hunters as described by Sparrowe and Springer (1970). Although this made them harder to approach, it also made them easier to find. When deer observed hunters, they normally ran to the nearest cover where hunters could then plan an approach with the highest likelihood of success. Deer could be pursued in this manner for several kilometers until they ultimately were shot or escaped.

During 1984, each hunter could purchase up to 6 permits which seemed to give hunters more incentive to shoot both species of deer. Access was also very good. The willingness of private landowners to grant free access to their land and the gentle terrain which made it possible to drive within 500 m of any point on 99% of the study area, along with a limited amount of escape cover, also contributed to the increased harvest rates. The same factors which contributed to an increased harvest of white-tailed deer on the Cherry Creek area also increased harvests in Wisconsin. During an experimental deer hunt within an enclosure in central Wisconsin, hunters shot the entire population of 544 white-tailed deer in 44 days (Creed and Kubisiak 1973).

No significant correlations were found between any of the climate indices described for mule deer, and white-tailed deer fawn:doe ratios in autumn and winter, or percent fawns in spring ($P > 0.08$). Relationships between natural mortality rates and population density or hunting mortality could not be evaluated because natural mortality rates were only available for 3 years. Productivity and mortality rates varied considerably over the study period, but no statistically reliable models could be developed with the available data. However, this is not meant to suggest that there were no factors which affected white-tailed deer. The drought of 1983-1985, for example, may

have influenced physical condition and rates of fawn production and survival in a manner similar to that observed in the mule deer population.

Home Range and Movements

Radio-equipped, female white-tailed deer (n=16) were located an average of once every 8 days. Neckbanded deer were located much less frequently and were usually found when they accompanied radioed deer. A total of 1,979 locations was obtained for 34 marked females, providing detailed data for 24 females, which suggested that white-tailed deer on the area utilized several different movement patterns.

Eleven (46%) of 24 females occupied yearlong home ranges consisting of variable numbers of subareas within each overall range, similar to that found by Sparrowe and Springer (1970) and Eberhardt et al. (1984). Eight others (33%) moved an average of 6.1 km (range 3.6-9.6 km) between separate ranges used from December to August, and alternate ranges used in late summer and autumn. All autumn ranges were near grain fields. The remaining 5 (15%) females moved between 2 or more distinct ranges at various times of the year. One moved between 2 ranges separated by 13 km; the northernmost occupied in spring, the southern during summer, and either during autumn and winter. Another occupied 3 distinct ranges, 1 from August-November, a winter range from December-April, and an intermediate

fawning range from May-July. Distance from late summer range to fawning range was 4.5 km, from late summer to winter range, 13.2 km, and from fawning range to winter range, 8.7 km. The other 3 females used 1 range in spring and autumn and another in summer and winter.

Individual deer were originally assigned to 1 of 3 movement categories similar to those used for mule deer. However, an analysis of monthly average activity radii (AARs) using 2-4 points/animal/month and testing for differences due to collar type (radio or neckband), migration class, and months, showed a significant difference only among months ($P < 0.05$). Apparently, there were no discrete movement patterns used by segments of the white-tailed deer population; rather each deer was apparently responding to the unique distribution of resources within her home range. A plot of monthly average activity radius for all female white-tailed deer (Figure 21) revealed rather large AARs throughout the year except during the fawning season in June and July. More importantly, monthly AARs varied greatly among individual deer.

In contrast to mule deer, seasonal AARs of white-tailed deer were significantly smaller in summer than winter (Table 32). Females exhibited individual patterns

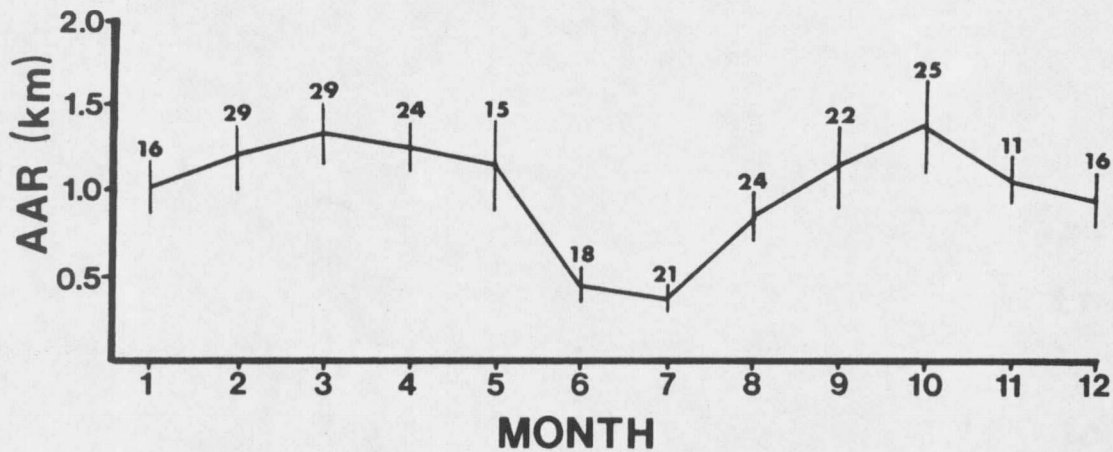


Figure 21. Monthly average activity radius ($\text{km} \pm \text{SE}$) for female white-tailed deer on the Cherry Creek area, 1983-1985. Number of deer months is recorded above each point.

of movement which ranged from relatively small seasonal and annual home ranges to large shifts within the home range throughout the year.

Home ranges of white-tailed deer on the Cherry Creek area were generally larger than most of those reported in the literature (Table 33). Overall, winter home ranges on the Cherry Creek area (6.3 km^2) were most similar to those in eastern South Dakota (4.6 km^2 , Sparrowe and Springer 1970), and southern New Brunswick (3.3 km^2 , Drolet 1976). Summer home ranges on the Cherry Creek area (3.3 km^2) were most similar to those in eastern South Dakota (2.6 km^2 , Sparrowe and Springer 1970), southern New Brunswick (2.2 km^2 , Drolet 1976), New York (2.2 km^2 , Tierson et al. 1985),

Table 32. Estimates of average activity radius (AAR) and polygon home range size for female white-tailed deer on the Cherry Creek study area, 1983-1985.

Season	No.	No. pts/deer		AAR (km)			Polygon (km ²)		
	Deer	X	Range	X	SE	Range	X	SE	Range
Annual	16	39	17-65	1.18	0.11	0.49-1.85	9.98	2.04	2.35-24.42
Summer	19	15	10-19	0.92	0.09	0.35-1.49	3.26	0.56	0.42-8.81
Winter	17	15	10-24	1.19	0.10	0.46-1.73	6.34	1.06	1.12-13.70

Table 33. Estimates of white-tailed deer home range size from this study and from the literature. Estimates were reported for adult females unless the study found no differences because of age or sex in which case all deer were used.

HABITAT	POLYGON HR (KM ²)			SOURCE
STUDY AREA	Ann.	Sum.	Win.	
Prairie-Agriculture				
E. Montana	9.98	3.26	6.34	This study
E. South Dakota		2.59	4.60	Sparrowe & Springer 1970
Conifer forest				
SE. Montana		3.84	0.80	Dusek 1980
NW. Montana		0.71	0.21	Leach 1982, Mundinger 1978
Mixed forests				
NW. Minnesota		0.84	0.18	Nelson & Mech 1981, 1984
S. New Brunswick		2.20	3.30	Drolet 1976
New York		2.21	1.32	Tierson et al. 1985
Riparian conifers				
S. Washington	0.19			Gavin et al. 1984
Riparian hardwoods				
Central Iowa	1.47		1.10	Gladfelter 1978
Prairie-brushland				
S. Texas	0.59			Michael 1965

and southeastern Montana (3.8 km^2 , Dusek 1980). Most other home range estimates for white-tailed deer were smaller (Table 33).

Despite the small sample of marked deer, a relatively high incidence of dispersal was indicated for yearlings on the study area. During 1983 and 1984 when marked deer were available and the population was at a peak, 1 definite and 5 probable dispersals were documented. All 4 males marked as fawns, "disappeared" as yearlings from the area in June, suggesting dispersal. Two (40%) of 5 females collared as fawns dispersed. One, neckbanded in January 1984 and observed regularly with a radioed female until September 30, 1984, was found dead (an apparent roadkill) on May 6, 1985, 51 km southeast of her last known location. The other, tagged as a fawn in January 1983, disappeared on March 10, 1983, and was subsequently relocated 4 times between January 22 and October 20, 1984 on an apparently new home range, 12 km southwest of her natal range.

These apparent dispersal patterns and rates were generally consistent with those reported for white-tailed deer in other areas. Although dispersal in yearling males typically peaks in autumn, at the start of the males first breeding season, it may occur at any time after deer leave the winter range (Nelson and Mech 1984, Kammermyer and Marchinton 1976, and Hawkins et al. 1971). Dispersal rates reported for males have ranged from 80% (Hawkins et

al. 1971) to 33% (Gladfelter 1978), and those for females have ranged from none (Nelson and Mech 1984) to 24% (Gladfelter 1978).

There were no dispersals recorded over 37 deer years for mature females 2-years or older. Within the study area, mature females used the same general areas for fawning each year, but exhibited much less fidelity to other seasonal ranges. Six (40%) of 15 marked females observed for 2-3 years used different seasonal ranges in 2 consecutive years.

White-tailed deer had significantly larger ($P < 0.05$) home ranges than mule deer both seasonally and annually. Movement patterns of white-tailed deer were much more variable than those of mule deer. This suggested that white-tailed deer did not establish and use traditional home ranges as did mule deer; instead they continually shifted between areas used intensively for a few days to a few weeks as reported for mule deer in south-central Washington (Eberhardt et al. 1984). Mule deer occupied winter ranges in the high elevation badlands and all migrants moved down to summer ranges following a nearby drainage. These movements tended to increase separation and maintain integrity between herd ranges. In contrast, white-tailed deer exhibited no consistent pattern within the population. Movements of individual white-tailed deer tended to interweave individual home ranges across the

entire area. For example, one female moved north 13 km each spring to an area that served as winter range for 5 other radioed females who were generally abandoning the area at that time. This interweaving of herd ranges and the apparent increased propensity for dispersal among females, suggest that white-tailed deer on this area may have greater potential than mule deer for pioneering new habitats and replacing local populations that might be reduced by various causes.

Habitat Selection

On an annual basis, radio-collared white-tailed deer selected mesic shrub and hardwood draws; avoided mixed grass prairie, sagebrush grassland, and badlands; and used small grain, legume hayfield, and bunchgrass prairie cover types in proportion to their availability (Figure 22, Table 34). Hardwood draws were the most heavily utilized cover type overall, accounting for 392 (61%) of 641 telemetry locations. Habitat selection based on deer observed during aerial surveys indicated that small grain, legume hayfield, sagebrush grassland, bunchgrass prairie, mesic shrub, and hardwood draw types were selected, and badlands and mixed grass prairie types were avoided (Table 34).

During winter (December-March), radioed deer selected only hardwood draws, (Table 34) which accounted for 130 (60%) of 216 radio locations during winter. Survey data also indicated that deer selected hardwood draw, as well as

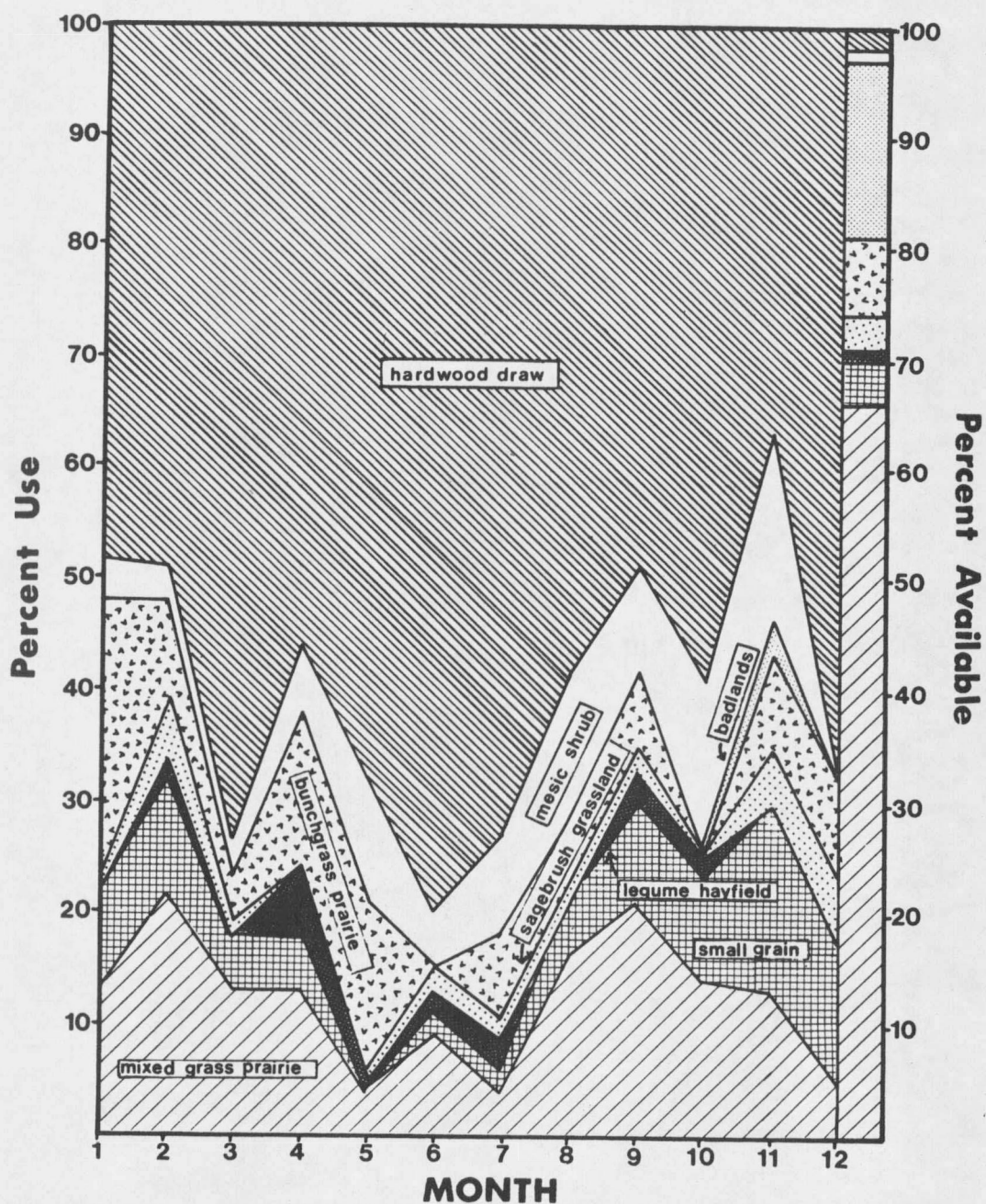


Figure 22. Monthly habitat use by radioed female white-tailed deer on the Cherry Creek area, 1983-1985, relative to cover type availability.

Table 34. Habitat use of white-tailed deer on the Cherry Creek study area based on radio locations (1983-1985) and deer observed during aerial surveys (1975-1986). Data are percentage of observations occurring in each cover type and a selection coefficient indicating avoidance (A), selection (S), and use in proportion to availability (U). Blanks indicate insufficient data available for test.

	Annual		Spring		Summer		Autumn		Winter	
Cover Type	Radio Survey		Radio Survey		Radio Survey		Radio Survey		Radio Survey	
Mixed-grass prairie	12 A	16 A*	8 A	16 A	9 A	11 A	16 A	13 A*	16 A	17 A*
Small grain	7 U	12 S*	3 U	18 S*	3 U	2 A	12 S	16 S*	8 U	5 S*
Legume hayfield	2 U	2 S	4	2 S	2	13 S*	2	5 S*	1	0 U
Sagebrush grassland	2 A	5 S*	0	6 U*	2 U	12 S	2 U	8 S*	3 U	4 U
Bunchgrass prairie	8 U	10 S*	15 U	13 S*	4 U	0 A*	5 U	3 A*	9 U	11 S*
Badlands	0 A	7 A*	0 A	5 A*	0 A	0 A	1 A	1 A	1 A	11 A
Mesic shrub	8 S	6 S	8 S	5 S	9 S	23 S*	14 S	16 S*	2 U	2 U
Hardwood draw	61 S	42 S*	62 S	35 S*	71 S	39 S*	48 S	38 S*	60 S	50 S*
Total Observations	641	3021	112	986	180	187	133	664	216	1184

*Indicates significant ($P < 0.05$) differences between the use frequencies of each type.

small grain and bunchgrass prairie types (Table 34). Both data sets indicated that deer avoided mixed-grass prairie and badland cover types.

Radio-equipped deer selected both hardwood draw and mesic shrub types during spring (April-May), when they accounted for 79 (70%) of 112 radio locations (Table 34). Although insufficient radio locations were available to test for selection of bunchgrass prairie and legume hayfields, both received greater use in spring than any other season. Survey data demonstrated that deer selected these 2 types, as well as small grain, sagebrush grassland, mesic shrub, and hardwood draw types. Both data sets indicated avoidance of mixed-grass prairie and badland types.

Habitat selection and avoidance patterns of radioed deer in summer (June-August) were similar to spring, with mesic shrub and hardwood draw cover types selected and mixed-grass prairie and badlands cover types avoided (Table 34). Use of hardwood draws was greatest in June during the peak of fawning. Survey data indicated that legume hayfield and sagebrush grassland types were also selected, and bunchgrass prairie and small grain types were avoided: both data sets indicated avoidance of mixed-grass prairie and badland types (Table 34).

During autumn (September-November), radioed white-tailed deer selected the hardwood draw, mesic shrub, and

small grain cover types, and avoided mixed-grass prairie and badlands (Table 34). Survey data also indicated selection of legume hayfield and sagebrush grassland types, and avoidance of the bunchgrass prairie type. The most significant shift in habitat use throughout the year occurred in autumn when some deer moved into harvested grain fields to feed on waste grain. Use of the small grain type resulted in significant shifts in home range centers and increased home range size (Figure 21).

There were no differences in average group size of deer observed during aerial surveys as compared to radio located groups during any season ($P > 0.05$). However, there were differences in the observability of deer among cover types and in the distribution of radio-equipped deer in the population (Table 34). In spite of these potential sources of bias, results from aerial survey data were remarkably similar to telemetry data. The data sets disagreed only on the annual use of the sagebrush grassland cover type which could be attributed to uneven distribution of radios within the population. Sagebrush grasslands were important to white-tailed deer occupying the south-central portion of the study area where there were no radioed deer. In 9 (29%) of 31 remaining cases, the increased number of deer observed during aerial surveys increased sample sizes sufficiently to show significant selection or avoidance where radio data did not.

Food Habits

Data on food habits of white-tailed deer were limited to autumn, when rumens of hunter-killed deer were sampled. However, these data supported, and helped to explain, habitat use patterns during autumn. Cereal grains and snowberry were the 2 most abundant items in the autumn diet, which corresponded with high levels of use in the small grain, mesic shrub, and hardwood draw cover types, the principal sources of these forages.

Autumn diets in 1975 were dominated by browse while diets in 1983 and 1984 were dominated by cereal grains and included more grasses and forbs (Table 35). Some of those differences could have been caused by the locations where samples were collected. For example, the only 2 samples containing yellow sweetclover, which accounted for 15% of the diet in October, were obtained from deer shot near the only 2 sweetclover fields on the area.

Habitat, Dispersion, and Home Range Interactions

White-tailed deer occupied 25 ha blocks during summer that were not different ($P > 0.05$) than blocks on which they occurred in winter (Table 36). This was identical to the relationship for yearlong resident mule deer and provided additional evidence that white-tailed deer had no consistent seasonal migration patterns on the area. Large home ranges and extensive movements allowed deer to select

Table 35. Use of various plant taxa by white-tailed deer on the Cherry Creek study area based on analysis of 25 rumen samples. Data are recorded as frequency of occurrence / percent of diet within each period specified.

Species	1975 ¹		1983-1984	
	Oct.	Nov.	Oct.	Nov.
	(7) ²	(3)	(6)	(9)
Monocots				
Grasses	14/T ³	33/1	83/7	56/2
Cereal grains	42/24	33/9	83/35	89/45
<u>Yucca glauca</u>				11/3
Total Monocots	48/24	33/10	100/42	100/50
Forbs				
<u>Medicago sativa</u>	14/T		17/2	33/4
<u>Melilotus officinalis</u>			33/15	
Other Forbs	42/1	67/T	83/11	89/7
Total Forbs	42/1	67/T	100/28	89/11
Shrubs				
<u>Artemisia cana</u>	14/1			44/T
<u>Chrysothamnus nauseosus</u>	28/3		33/1	22/T
<u>Symphoricarpos occidentalis</u>	100/66	100/87	100/28	78/35
Other Shrubs	14/8	67/4		33/2
Total Shrubs	100/78	100/91	100/29	100/38

¹1975 data from Hamlin (1976)

²Number of rumens examined

³T= trace - less than 1/2 of 1%

Table 36. Comparison of habitat variables for white-tailed deer on the Cherry Creek study area, 1983-1985.

Comparison	For	No. of Blocks	Var. ¹	Difference & Direction
between summer & winter	all	209		no seasonal differences
between high & low use areas	summer	72	H	low < high
			A3	low < high
	winter	66	H	low < high
between large & small home ranges	summer	105	A1	large > small
			A2	large > small
			E7	large > small
			A3	large < small
			E3	large < small
			E5	large < small
			A8	large < small
	winter	129	A1	large > small
			A2	large > small
			E7	large > small
			E6	large < small
			A8	large < small

¹A=area, E=edge H=Diversity; 1=mixed-grass prairie, 2=small grain, 3=legume hayfield, 5=bunchgrass prairie, 6=badlands, 7=mesic shrub, 8=hardwood draw.

preferred cover types during summer and winter that were widely scattered within the same general area occupied yearlong.

Differences ($P < 0.05$) in diversity, and the amount of area and edge of cover types between 25 ha blocks occupied by deer with large vs. small home ranges and, between those used at high (3 or more observations/block) and low (1 observation/block) intensities, revealed that several habitat characteristics influenced occupancy of an area by white-tailed deer (Table 36). Blocks with higher diversity were used more intensively during both summer and winter (Table 36). This contrasted with the effects of habitat diversity on mule deer during winter (Table 20), and might suggest that white-tailed deer needed a diversity of cover types to provide for their needs throughout the year; whereas the annual needs of mule deer could be met solely by badlands and hardwood draws. Small grain, legume hayfield, bunchgrass prairie, mesic shrub, and hardwood draw cover types were all important at some time to the survival of white-tailed deer in this area.

The amount of area in legume hayfields was the only other variable influencing intensity of use in summer. Blocks with more area in legume hayfield were used more frequently than other blocks (Table 36).

During summer, deer with smaller home ranges used 25 ha blocks with increased area of hardwood draws, increased

area and interspersions of legume hayfields, increased interspersions of bunchgrass prairie, and decreased area of mixed-grass prairie, small grain, and mesic shrub cover types (Table 36). Use of grain fields increased home range size because grain fields were generally larger than hayfields and surrounded by mixed-grass prairie and associated mesic shrub or sagebrush grassland types in the adjacent drainages. Because these areas had less hardwood draw cover than many of the areas associated with legume hayfields, deer had to travel farther between feeding and bedding areas. The effect of cover interspersions on movements of white-tailed deer has also been documented by Carlsen and Farnes (1957), who found that deer ranged more widely in open prairie-deciduous forest habitats than in more dense coniferous forests. Apparently, larger home ranges are also required to effectively use areas with widely scattered cover patches.

Increased area in small grain, mesic shrub, and mixed-grass prairie cover types increased deer movements and home range sizes in winter also (Table 36). The inclusion of hardwood draws interspersed among badlands resulted in decreased home range size, even though white-tailed deer were rarely observed in the badlands type (Table 34).

Comparison to Habitat Use Patterns in Other Areas

During mild winters with little snow cover, deer moved widely, utilizing a variety of cover types. However,

during more severe weather they used hardwood draws interspersed among small areas of badlands, apparently for the increased shelter that they provided. Rongstad and Tester (1969) reported a similar shelter seeking response, with use of cedar lowlands increasing when snow depths exceeded 25 cm.

Badlands could minimize snow accumulation for white-tailed deer in the same way as they did for mule deer. By using hardwood draws or other cover types within the badlands, white-tailed deer could benefit from more the favorable environmental conditions provided by the badlands, while restricting their movements to drainage bottoms or other areas of more gentle terrain which they seem to prefer (Hudson et al. 1976, Swenson et al. 1983).

The importance of winter ranges which provided suitable shelter, was illustrated by the movements of 4 females during February-March 1983. During February 1983, warm weather melted the snow cover, causing all 4 deer to move 6-8 km, to areas of mixed-grass prairie and grain fields used during spring and autumn. A snowstorm which deposited 10 cm of snow on the area on March 6, caused them all to return to their normal winter range which contained badlands interspersed with hardwood draws.

Others (Allen 1968, Martinka 1968, and Zwank et al. 1979) have also observed a preference by white-tailed deer for overhead tree cover during winter, presumably to

maintain a more favorable energy balance. However, Moen (1966) and Kramer (1971) reported that white-tailed deer used open prairie rather than adjacent tree cover because it provided better forage even though deer were more exposed to environmental extremes.

White-tailed deer on the Cherry Creek area seemed to utilize both strategies as winter conditions changed. Deer were more mobile under conditions of light snow cover, feeding in open agricultural fields and bedding in adjacent drainages. When snow depths increased and temperatures dropped, they moved to more protected areas and utilized native forages, adopting an energy conservation strategy, similar to the pattern reported by Drolet (1976).

A strategy of energy conservation might not work for white-tailed deer on the Cherry Creek area without some use of agriculture during the year. Deer voluntarily restrict forage intake and utilize stored fat reserves over winter, even when provided with unlimited supplies of high quality forage (Thompson et al. 1973). The use of waste grain during autumn and legume hayfields throughout the year might provide the needed energy reserves for overwinter survival. The importance of agricultural crops on the Cherry Creek area was indicated by habitat use patterns and the fact that all tagged white-tailed deer used agricultural crops, whereas only 24 (25%) of 96 marked female mule deer utilized agricultural crops.

During the remainder of the year, habitat use patterns centered around the availability of forage and cover as described by Suring and Vohs (1979). Availability of cover appeared most critical during June, at the peak of fawning, when use of hardwood draws peaked. During the rest of the spring-autumn period, use of small grain, legume hayfield, bunchgrass prairie, and mesic shrub cover types apparently provided necessary forage. In early spring the bunchgrass prairie, small grain, and legume hayfield types provided succulent green forage while the shrubs in the mesic shrub type were still dormant. In contrast, shrubs provided green forage, and waste grain provided a high energy forage during autumn.

Interspecific Interactions in Habitat Use

Mule and white-tailed deer had different habitat preferences which limited range overlap, to areas that met the habitat needs of both species. White-tailed deer primarily utilized areas with more mixed-grass prairie and agricultural crops, mule deer largely used areas with more badlands, while both species utilized areas of hardwood draws (Table 37). A model of general habitat needs in relation to interspecific distribution is presented in Figure 23. Mule deer required winter ranges with terrain that provided suitable shelter, and summer habitat with mesic sites that provided adequate summer and autumn

Table 37. Average composition (%) of 25 hectare habitat blocks occupied by mule deer (MD), white-tailed deer (WTD), and jointly by both species (MW) on the Cherry Creek study area during summer and winter, 1975-1985.

Percent of:	Summer			Winter		
	MD	MW	WTD	MD	MW	WTD
Mixed-grass prairie	38	48	51	25	37	43
Small grains	T ¹	2	3	T	T	8
Legume hayfields	T	3	4	0	T	2
Badlands	39	21	16	54	37	19
Hardwood draws	6	6	6	5	10	8
Other	16	20	20	16	15	20

¹T=Trace - less than 1/2 of 1%

forage. White-tailed deer required overhead tree cover in proximity to agricultural fields and areas that do not accumulate snow during winter. When overhead cover was scattered within rough terrain and remained sufficiently moist throughout the summer, and these areas were in proximity to agricultural crops, the 2 species ranges overlapped.

The lack of association between these 2 species seemed to be caused by the lack of familial ties as suggested by Kramer (1973) rather than intrinsic interspecific avoidance mechanisms. This conclusion was

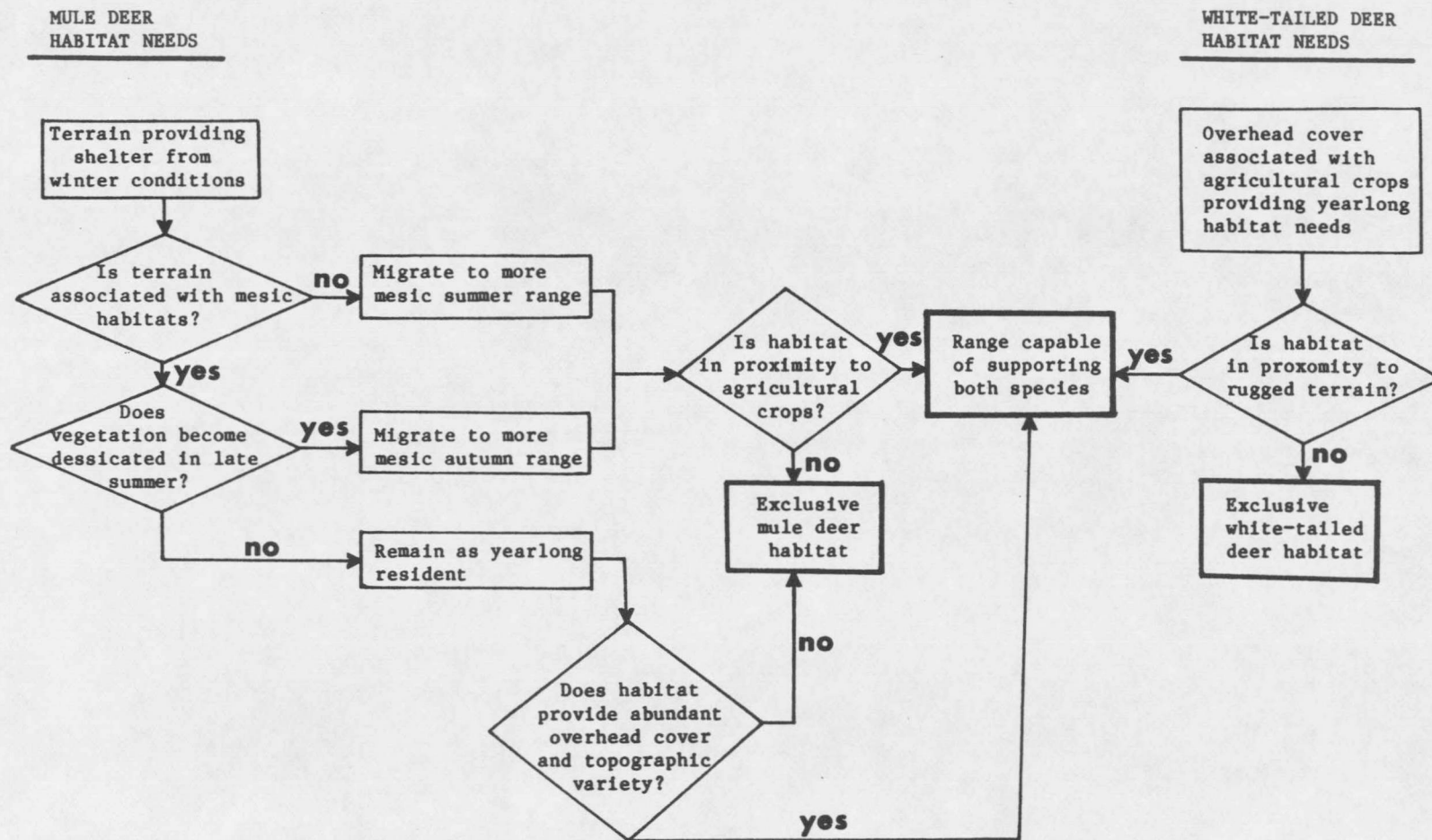


Figure 23. Habitat characteristics which influence distribution and range overlap of mule and white-tailed deer on the Cherry Creek study area.

supported by measurements of association between radio-equipped deer in 2 areas where the species home ranges overlapped. In both areas, the mean distance between apparently unrelated mule deer was not significantly different than the mean distance between mule deer and white-tailed deer ($P > 0.50$).

Because of the differences in habitat use between the 2 species, it would be unlikely that any permanent changes in relative abundance could occur in the absence of major habitat or environmental changes. This conclusion was also supported by Wiggers and Beasom (1986) who suggested that reductions in mule deer abundance in Texas resulted from habitat changes rather than interspecific interactions.

COMPARATIVE ECOLOGY AND RELATIONSHIPS OF PRONGHORN
ANTELOPE TO MULE DEER

Population Trends

Pronghorn antelope on the Cherry Creek area ranged well beyond the study area boundaries. Consequently, the number of pronghorns observed during aerial surveys (Table 38) varied greatly between seasons and years depending on their distribution. During 1982-1986, pronghorn numbers did not appear to fluctuate as widely as those of mule deer. Highest numbers were typically observed during autumn, when counts ranged from 289 in 1983 to 469 in 1984. Counts during winter and spring were most variable because pronghorns wintered along the periphery of the study area. Pronghorns were more likely to be within the survey area

Table 38. Aerial survey counts of pronghorn antelope on the Cherry Creek study area during autumn, winter, and spring, 1982-1986.

Year	Autumn	Winter	Spring
1982-83	320	123	157
1983-84	289	188	327
1984-85	469	338	187
1985-86	354	69	137

during mild winters, or when spring surveys were flown in April, than during winters with normal to severe conditions or when spring surveys were completed in March.

Males comprised 13%, 24%, 29%, and 27% of the autumn counts from 1982 through 1985, respectively. Counts of fawns were not made because adult females and fawns are difficult to distinguish after August (Bayless 1969).

Habitat Use

Although no pronghorns were marked, patterns of habitat use based on observations made during aerial surveys (Table 39) were believed to be indicative of seasonal preferences on the study area. Amstrup and Burnham (1978) reported no apparent biases in habitat use between radio-equipped and unmarked pronghorns. Grasslands provided the most important habitats for pronghorns. The mixed-grass prairie cover type was selected from spring through autumn and was avoided during winter. The bunchgrass prairie type was selected in all seasons but summer. These 2 grassland types accounted for 3071 (90%) of 3421 pronghorn observations. Among other cover types, only legume hayfields and sagebrush grasslands were selected, both during autumn, while all others were either avoided or used in proportion to their availability ($P < 0.05$).

Table 39. Habitat use by pronghorn antelope on the Cherry Creek study area, 1982-1985. Data are percent of total observations occurring in each cover type and selection coefficient (SC) indicating whether the type was avoided (-), selected (+), or used in proportion to its availability (0).

Cover Type	Spring		Summer		Autumn		Winter	
	%	SC	%	SC	%	SC	%	SC
Mixed-grass prairie	73	+	82	+	71	+	54	-
Small grain	3	0	5	0	2	0	0	-
Legume hayfield	0	-	3	0	4	+	0	-
Sagebrush grassland	5	0	1	-	6	+	3	0
Bunchgrass prairie	18	+	8	0	14	+	43	+
Badlands	1	-	0	-	1	-	0	-
Mesic shrub	0	-	1	0	2	0	0	-
Hardwood draw	0	-	0	-	0	-	0	-
No. Observed	878		245		1477		821	

The importance of grasslands to pronghorns on the area is consistent with findings elsewhere. Sixty-eight percent of all pronghorns in North America occur in grassland habitats (Yoakum 1978) and 56% occur on wheatgrass (Agropyron spp.) dominated prairies (Sundstrom et al. 1973). Grasslands were the only native cover types on the Cherry Creek area that provided open terrain with vegetation < 38 cm tall which pronghorns prefer (Yoakum

1978). The winter shift from mixed-grass to bunchgrass prairie (Table 39) was probably influenced by topographic relief in the bunchgrass prairie type which provided sheltered sites (Bruns 1977) that were not as available in the mixed-grass prairie.

The mesic shrub cover type was only used in proportion to its availability during summer and autumn, and was avoided from winter through spring. However, snowberry, the dominant plant species of the type, is an important autumn food for pronghorns in Montana (Couey 1946, Cole 1956).

Avoidance of badlands and hardwood draws probably resulted from the rugged terrain and height of the vegetation, respectively. Pronghorns avoid rugged terrain and vegetation > 76 cm (Sundstrom et al. 1973, Yoakum 1978).

Sagebrush grasslands were selected only in autumn, when silver sagebrush is an important item in the pronghorn diet (Cole 1956, Cole and Wilkins 1958). The presence of Wyoming big sagebrush (Artemisia tridentata wyomingensis) and/or silver sagebrush is characteristic of optimum pronghorn habitat, and areas dominated by these species have consistently high fawn production (Sundstrom et al. 1973). However, heights of silver sagebrush plants in the sagebrush grassland cover type were generally taller than 38-46 cm, heights preferred by pronghorns, and the percent

sagebrush coverage in the mixed-grass prairie and bunchgrass prairie were much lower than the 5-20% considered optimum for pronghorns (Sundstrom et al. 1973, Yoakum 1978). These data, plus the fact that many of the pronghorns leave the study area during winter, a time when the presence of sagebrush is especially important (Bayless 1969), suggest that the study area itself was incomplete or suboptimal yearlong pronghorn habitat.

Increased use of legume hayfields through summer and autumn was consistent with the findings of Cole (1956). Mesic feeding sites appeared to be as important to pronghorns in summer and autumn as they were to deer. In western Kansas, alfalfa was important in the pronghorn's diet only during spring and autumn when succulent native forbs were not available (Sexson et al. 1981).

The pattern of increased use of the small grain cover type from spring to summer, decreased use in autumn, and avoidance during winter, differed somewhat from other studies reporting peak use from autumn to spring (Cole and Wilkins 1958, Sexson et al. 1981). However, grain fields may not be as important when alfalfa fields are available (Cole 1956), as they were on the Cherry Creek area.

Habitat Overlap with Mule Deer

Pronghorns and mule deer had relatively distinct habitat patterns and needs on the area. Hardwood draws and badlands were selected by mule deer and avoided by

pronghorns. Conversely, pronghorns selected mixed-grass prairies that mule deer avoided (Table 39). Both species selected only the legume hayfield, sagebrush grassland, and bunchgrass prairie types during autumn, and the bunchgrass prairie type during winter.

Range overlap between pronghorns and mule deer occurred in blocks with more of the legume hayfield, sagebrush grassland, and bunchgrass prairie cover types, and intermediate amounts of other types compared to blocks occupied exclusively by either species (Table 40). Sagebrush grasslands provided foraging areas for pronghorns and feeding and bedding areas for mule deer, legume hayfields were used as feeding areas by both species, and the bunchgrass prairies provided shelter from environmental extremes for both species. This may account for the overlap in blocks with increased area in these types.

Interspecific competition appeared insignificant between pronghorns and mule deer on this area. Although food habits were not compared, habitat use patterns indicated that alfalfa, silver sagebrush, and snowberry were important food items for both species. However, use of alfalfa was greatest during the growing season, allowing regrowth to at least partially replenish the supply. Use of snowberry by both species appeared greatest during autumn, prior to leaf drop so that the supply of snowberry was depleted by leaf drop rather than joint use. Both

observations indicated little opportunity for interspecific forage competition. Range use competition was limited by broad differences in habitat use patterns.

Table 40. Average composition (%) of 25 hectare blocks occupied by pronghorn antelope (ANT), mule deer (MD), and jointly by both species (AMD) on the Cherry Creek study area, annually and during autumn, 1982-1985.

Percent of:	Annual			Autumn		
	ANT	AMD	MD	ANT	AMD	MD
Mixed-grass prairie	73	51	41	72	51	49
Small grains	2	1	T ¹	1	1	1
Legume hayfields	T	1	T	T	1	1
Sagebrush grassland	4	7	4	4	7	5
Bunchgrass prairie	7	10	9	7	9	7
Badlands	11	26	40	13	25	31
Mesic shrub	2	1	1	2	2	2
Hardwood draws	1	3	4	1	4	4

¹T=Trace - less than 1/2 of 1%

MANAGEMENT IMPLICATIONS

The most consistent population estimates resulted from the use of both a Lincoln index and mortality rates of marked deer. Long-term population data also helped to increase the precision of seasonal population estimates. Estimates based on any single source of data were not adequate for estimating population size throughout the study. Management programs designed to monitor population trends should be based on more than 1 source of data.

Different rates of harvest are required each year if the management goal is to maintain relatively stable populations in highly variable environments such as the Cherry Creek area. Natural mortality rates of adults averaged 8% during 1982-1986 and were additive to harvest mortality. An allowable harvest rate for most years would be equal to the recruitment rate of yearlings into the adult population (estimated as the percent of the spring population which consisted of fawns) minus 8% natural mortality. Harvest rates below this level should allow the population to increase and harvest rates above this level should cause the population to decline. If natural mortality rates changed, harvest rates should be adjusted accordingly.

Effective management in this type of environment may require annual changes in hunting seasons and harvest

quotas. The time lag between the peak population size and the peak harvest rate was influenced by the fact that managers were required to set season regulations 10 months prior to the hunting season. More flexibility in the process of setting seasons and permit quotas could help reduce the population fluctuations which have occurred in past years.

Deer of both species were extremely vulnerable to hunters. The restricted distribution of suitable habitat predictably concentrated deer into relatively small portions of the study area. In addition, almost the entire study area could be accessed from a vehicle. Regulations designed to limit the use of vehicles by hunters may help to reduce the vulnerability of deer in this environment.

Several indicators of physical condition collected during the hunting season including dressed weights, antler diameter and length, diastema length, and kidney fat deposits all reflected changes in physical condition which influenced spring fawn recruitment rates. Diastema measurements seemed to be the most sensitive indicator of physical condition and was 1 of the easiest to collect. Diastema measurements may provide a rapid means of assessing the physiological condition of deer shot by hunters.

Because mule deer used traditional herd ranges, had low female dispersal rates, and high adult male mortality

rates, intensive and selective shooting could be used to control local populations and thereby reduce crop depredation. This was not the case for white-tailed deer which exhibited high dispersal rates and inconsistent patterns of seasonal home range use from year to year. Control of white-tailed deer causing crop damage in prairie habitats would require more regular, intense harvests in problem areas. White-tailed deer were susceptible to heavy harvests under intensive hunting pressure directed exclusively at that species.

Patterns of habitat preference were adequately documented by complete coverage aerial surveys. If determination of habitat preferences were the only data required, they could be obtained without going to the expense of radio telemetry studies. Two factors contributed to the ease of determining habitat use. Deer were concentrated locally because of habitat preferences. Also, because vegetation was deciduous and provided sparse overhead cover, there were few places where deer could hide. Aerial surveys should provide adequate habitat use information in similar open habitats.

Habitat complexes were important to deer. Only the badlands-hardwood draw complex met the annual habitat needs of mule deer. A variety of other cover types were required to meet their annual needs when this complex was lacking. There was no single cover type complex that provided white-

tailed deer with suitable habitat on an annual basis. Increased habitat diversity was utilized by this species. Small areas of agricultural crops, particularly legume hayfields, interspersed with hiding cover, helped to improve habitat quality for mule deer and seemed almost essential for white-tailed deer. The maintenance of preferred cover type complexes in good condition is essential to the survival of deer in this environment. Planting of forage crops such as alfalfa or yellow sweetclover in areas where high quality late summer forage is limited or lacking might help to increase the number of deer in some areas. Conversely, elimination of hardwood draws and agricultural crops might help control local deer populations.

The presence of white-tailed deer apparently had little impact on the mule deer population during this study. Interspecific overlap was greatest on wintering areas but overwinter mortality rates suggested that winter habitat had little potential for limiting population size. Each species had distinct habitat preferences which limited overlap to areas where their preferred habitats overlapped. Where this occurred, there was no evidence to indicate that either species had a competitive advantage. As a given habitat filled with deer, the population with the highest rate of increase would eventually dominate the area.

Because of the differences in habitat use between the 2 species, it seems unlikely that any permanent changes in relative abundance could occur in the absence of major habitat or environmental changes. Habitat modifications have the potential to change the relationships between the 2 species. Mule deer exhibited a traditional pattern of distribution and movement, whereas white-tailed deer patterns were much more flexible. Therefore, white-tailed deer should be more adaptable to change and more quickly adjust to either favorable or detrimental habitat changes.

The presence of pronghorn antelope had no discernable effect on the mule deer population. The presence of cattle apparently had little effect in most instances because of the opportunity for habitat partitioning provided by the rough terrain which mule deer preferred. However, overlap between cattle and mule deer may increase in areas where there is less rough terrain and therefore less opportunity for refined habitat partitioning. Under these conditions the presence of cattle might have a negative impact on deer. Increased cattle stocking rates or changes in the class or species being grazed may also decrease the opportunities for habitat partitioning and therefore, negatively impact the mule deer population.

People management may be one of the biggest challenges for wildlife management in this area. This study has documented some of the biological relationships which might

be used to meet management objectives. However, the opportunity to implement management plans could be limited by a lack of public support. Maintenance of a reliable data base on the biological attributes of mule deer populations and communicating this information to all concerned parties may eventually provide wildlife biologists with more options in the management of those populations through increased support from a better informed public.

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APPENDIX

Table 41. Observability estimates (No. deer observed / population estimate present x 100) of mule and white-tailed deer on the Cherry Creek study area during aerial survey flights.

SEASON	MULE DEER	WHITE-TAILED DEER
Summer		
July 1983	47	50
Autumn		
October 1983	51	53
October 1984	57	47
September 1985	54	31
Early winter		
January 1984	65	54
December 1984	68	50
December 1985	86	50
Late winter		
March 1983	65	39
April 1984	58	67
March 1985	58	57
April 1986	59	65

Table 42. Plant species composition in the six native cover types on the Cherry Creek study area based on an estimated ubiquity index (frequency x constancy x 100). Cover types are: 1 mixed-grass prairie, 2 sagebrush-grassland, 3 bunchgrass prairie, 4 badlands, 5 mesic shrubs, 6 hardwood draws.

SPECIES	COVER TYPE					
	1	2	3	4	5	6
GRASSES & SEDGES						
<u>Agropyron caninum</u>		5			22	36
<u>A. cristatum</u>		T			T	
<u>A. dasytachyum</u>	2	5	T	2		
<u>A. repens</u>		T			1	T
<u>A. smithii</u>	97	78	1	T	41	5
<u>A. spicatum</u>		1	64	39		
<u>Andropogon scoparius</u>			T	T		
<u>Aristida longiseta</u>			T	T		
<u>Bouteloua gracilis</u>	19	4	30	T		
<u>Bromus ciliatus</u>		T			1	1
<u>B. inermis</u>						T
<u>B. tectorum</u>	T	3				1
<u>Calamagrostis montanensis</u>	1	1	3	T	T	
<u>Calamovilfa longifolia</u>		T	3	4	T	
<u>Carex filifolia</u>	4		76	2		
<u>C. species</u>					T	
<u>Distichlis stricta</u>	1	T				
<u>Elymus canadensis</u>					1	15

Table 42. Continued:

<u>Equisetum laevigatum</u>						T
<u>Koeleria cristata</u>	14	4	31	1	T	
<u>Muhlenbergia cuspidata</u>		T	3	T		
<u>M. richardsonis</u>					1	T
<u>Oryzopsis hymenoides</u>				T		
<u>Poa pratensis</u>	T	10			72	37
<u>P. sandbergii</u>	25	4	7			
<u>P. trivalis</u>						T
<u>Sitanion hystrix</u>		T				
<u>Stipa comata</u>	86	39	54	2	T	
<u>S. viridula</u>	13	27	T		7	T

TREES AND SHRUBS

<u>Amelanchier alnifolia</u>						2
<u>Artemisia cana</u>	1	57	2	1	1	T
<u>A. tridentata</u>				T		
<u>Atriplex nuttallii</u>	T	T	T	2		
<u>Chrysothamnus nauseosus</u>				2		
<u>Crataegus succulenta</u>						T
<u>Elaeagnus commutata</u>				T		
<u>Eurotia lanata</u>	T	T	2	2		
<u>Fraxinus pennsylvanica</u>						15
<u>Juniperus communis</u>				T		
<u>J. horizontalis</u>			T	6	T	T
<u>J. scopulorum</u>						T

Table 42. Continued:

<u>Populus tremuloides</u>						T
<u>Prunus virginiana</u>			T	T		32
<u>Rhus trilobata</u>			1			1
<u>Ribes aureum</u>					1	1
<u>R. setosum</u>					T	3
<u>Rosa arkansana</u>	1	T	1	2		
<u>R. nutkana</u>		T			22	10
<u>Shepardia argentea</u>					T	T
<u>Symphoricarpos occidentalis</u>		9		2	97	48
<u>Yucca glauca</u>				T		

FORBS

<u>Achillea millefolium</u>	1	5			15	8
<u>Agoseris glauca</u>					1	
<u>Allium textile</u>	T	T	1	T	T	T
<u>Apocynum androsaemifolium</u>					T	
<u>Arctium minus</u>						5
<u>Artemisia campestris</u>			T	T		
<u>A. frigida</u>	30	15	48	3	T	T
<u>A. ludoviciana</u>		T	T		27	1
<u>Aster falcatus</u>		T		T	5	1
<u>Astragalus miser</u>			T	1		
<u>A. missouriensis</u>			T	T		
<u>A. pectinatus</u>				1		
<u>A. purshii</u>			1	T		

Table 42. Continued:

<u>A. spatulatus</u>			1	1		
<u>Calochortus</u> species			T	T		
<u>Calylophus serrulata</u>	T		T	T		
<u>Camelina microcarpa</u>		T			T	
<u>Campanula rotundifolia</u>						T
<u>Chenopodium fremontii</u>						1
<u>C. leptophyllum</u>			T	T		
<u>C. murale</u>						T
<u>Chrysopsis villosa</u>			1	2		
<u>Cirsium flodmanii</u>					8	1
<u>C. undulatum</u>	T		1			
<u>Clematis ligusticifolia</u>					T	1
<u>Collomia linearis</u>	T	T	T	T	1	T
<u>Comandra umbellata</u>		T	4	9		
<u>Convolvulus arvensis</u>					T	
<u>Coryphantha vivipara</u>	T					
<u>Cryptantha bradburyana</u>				T		
<u>Descurainia sophia</u>		1				T
<u>Draba</u> species					T	T
<u>Echinacea pallida</u>	T		1	T		T
<u>Erigeron strigosus</u>		T	T			
<u>E. flavum</u>			T	3		
<u>E. pauciflorum</u>			2	5		
<u>Erysimum asperum</u>			T			
<u>E. cheiranthoides</u>						1

Table 42. Continued:

<u>E. inconspicuum</u>	T			T		
<u>Euphorbia glyptosperma</u>	T	T				
<u>Gaillardia aristata</u>	T					
<u>Galium boreale</u>		T			8	32
<u>G. triflorum</u>					T	T
<u>Gaura coccinea</u>	1	1	2	1		
<u>Glycyrrhiza lepidota</u>				T	5	
<u>Grindelia squarrosa</u>				T		
<u>Geum aleppicum</u>					T	T
<u>Gutierrezia sarothrae</u>	T	1	6	33		
<u>Hedeoma hispida</u>	T	T				T
<u>Helianthus maximiliani</u>					1	
<u>Heracleum lanatum</u>						T
<u>Hymenopapus filifolius</u>				6		
<u>Hymenoxys acaulis</u>	T			T		
<u>Lactuca pulchella</u>	T	1		T	1	1
<u>Lappula redowskii</u>		T			1	25
<u>Lepidium densiflorum</u>	1	1	1	T		
<u>Lesquerella alpina</u>		T	1	2		T
<u>L. ludoviciana</u>		1				
<u>Liatris punctata</u>		T	1	1	5	1
<u>Linum perenne</u>	T	T	T	1	T	
<u>L. rigidum</u>	T	T	T	1		
<u>Lithospermum incisum</u>				T		
<u>Lupinus species</u>			T			

Table 42. Continued:

<u>Lygodesmia juncea</u>	1	1	3	T		
<u>Machaeranthera grindelioides</u>			T	3		
<u>Melilotus officinalis</u>	T	T	T		1	2
<u>Mentzelia decapetala</u>				T		
<u>Monarda fistulosa</u>					1	3
<u>Musineon divaricatum</u>			T			
<u>Myosotis sylvatica</u>						T
<u>Nepeta cataria</u>						2
<u>Opuntia species</u>	T	T	T			
<u>Orthocarpus luteus</u>	T					
<u>Oxytropis besseyi</u>				T		
<u>O. lagopus</u>				4		
<u>Paronychia sessiliflora</u>			T			
<u>Parthenocissus vitacea</u>					T	T
<u>Penstemon albidus</u>	T	T	3	T		
<u>P. nitidus</u>				1		
<u>Petalostemon candidum</u>		T	3	1	T	
<u>P. purpureum</u>			1	T		
<u>Phlox hoodii</u>	1		37	7		
<u>P. alyssifolia</u>				2		
<u>Plantago patagonica</u>	T	4	3		T	
<u>Potentilla arguta</u>	T		T			
<u>Psoralea esculenta</u>	T	T	T			
<u>Ratibida columnifera</u>		T			1	
<u>Rhus radicans</u>					8	1

Table 42. Continued:

<u>Rorippa islandica</u>		T				T
<u>Sanicula marilandica</u>						T
<u>Senecio canus</u>			1	3		
<u>S. species</u>						T
<u>Smilacina stellata</u>					2	10
<u>Solidago mollis</u>					5	
<u>S. missouriensis</u>	T		T	2	T	1
<u>Sphaeralcea coccinea</u>	20	5	2	1	T	
<u>Taraxacum officinale</u>	16	24	T		6	49
<u>Thalictrum occidentale</u>					T	4
<u>Thermopsis rhombifolia</u>		T	T	3		
<u>Thlaspi arvense</u>						T
<u>Tragopogon dubius</u>	5	4	1		1	1
<u>Trifolium species</u>					T	
Unknown composite	T	1	T	T	T	T
Unknown forb A	T		T			
Unknown forb B		T				
Unknown forb C			T			
Unknown forb D				T		
Unknown forb E						T
Unknown legume A	T	T			T	T
Unknown legume B	T					
Unknown legume C		T				
Unknown legume D			T			
Unknown legume E					1	

Table 42. Continued:

Unknown legume F			T	1		
<u>Vicia americana</u>	6	11			2	1
<u>Viola canadensis</u>					1	7
<u>V. nuttallii</u>		T	T			1
Total number of species	53	67	74	78	64	70

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