



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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of

Doctor of Philosophy

in

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MONTANA STATE UNIVERSITY
Bozeman, Montana

April, 1987

D378
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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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ACKNOWLEDGEMENTS

The assistance of numerous people from Montana State University, Montana Department of Fish, Wildlife, and Parks, Bureau of Land Management, Livestock and Range Research Station, and many private landowners is gratefully acknowledged. R. J. Mackie directed and assisted in all phases of the project. G. L. Dusek, K. L. Hamlin, and D. F. Pac provided helpful suggestions during analysis and writing, K. L. Hamlin also allowed the use of his unpublished 1975-1980 data. H. E. Jorgensen assisted in vegetation sampling and calculations of winter severity. J. P. Weigand provided administrative support for the project and reviewed a draft of this thesis. C. S. Bittinger provided assistance in the use of statistical packages. R. L. Eng and H. D. Picton provided helpful editorial comments on the thesis. Individual contributions of D. A. Bricco, B. B. Compton, A. E. Darling, K. A. Kinden, N. S. Martin, L. L. Schweitzer, R. E. Short, and R. B. Staigmiller were also appreciated. Special thanks go to all the landowners of the area, especially Mr. and Mrs. L. B. Chapman, for permitting access to their lands, for their cooperation, friendship, and assistance. The study received financial support from the Montana Department of Fish, Wildlife, and Parks, Federal Aid Project W-120-R.

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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.

