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WINTER HABITAT SELECTION BY THE SEXES OF WHITE-TAILED DEER

By
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Winter Habitat Selection by the Sexes of White-tailed Deer (102 pp.)

Director: Daniel H. Pletscher

Winter habitat selection by the sexes of white-tailed deer (*Odocoileus virginianus*) in west-central Montana was documented. Fifteen radio-collared deer were located throughout the winters of 1984-85 and 1985-86. Habitat characteristics were determined for each winter location from maps and aerial photos. Winter range characteristics were determined from 280 points randomly located inside the minimum convex polygon enclosing all winter radio-locations ("winter range sample"). The winter range sample was compared to a sample of 280 points randomly located across the area used throughout the year, and to winter deer locations. Locations of adult males and adult females were compared, and locations of each sex were compared to the winter range sample. Habitats available to the sexes were also quantified and compared. These analyses used Mann-Whitney U tests for ordinal variables and Bonferoni Z tests for nominal variables. Habitat along trails made by, or in the vicinity of, radio-collared deer was compared to a systematic sample by sign tests, and trails made by the sexes were compared by Mann-Whitney U tests. Browse was measured by twig counts along 26 trails. Browse in areas used by the sexes was compared by Mann-Whitney U tests.

The winter range was at lower elevation, steeper, had a more uniform canopy, and less logging than the surrounding area. On the winter range, deer selected steep, low elevation sites, favored north and northwest aspects, avoided south aspects, and preferred stands with greater canopy cover, larger trees, greater basal areas, and less logging. Males used an area adjacent to where most females concentrated. Females used more heavily browsed areas with lower elevations, steeper slopes, more logging, and fewer but larger trees, compared to males. These data support the hypothesis that males, being larger and more exhausted following the rut, avoid the heavily browsed areas used by females in winter. Segregation by white-tailed deer, however, does not appear as pronounced as in more polygynous species, in which sexual dimorphism is more highly developed.

Implications for management include retaining dense, mature conifer cover adjacent to, as well as within, traditional deer yards, to ensure availability of quality habitat for adult males, who appear to use the peripheries more than the cores of deer yards. Trapping, for either management or research, should be conducted around deer yards, as well as within them, whenever adult bucks are desired in the catch.

ACKNOWLEDGEMENTS

Successful research is usually a result of cooperative efforts by several parties; this thesis is no exception. As is often the case, the name on the cover reflects not so much who did all the work as who benefited from it. Perhaps the greatest contributor was my advisor, Dr. Daniel H. Pletscher. He gave an inordinate amount of time to the planning of the project, encouraged and helped throughout its implementation, then carefully and thoughtfully edited the many drafts of the thesis. Other members of my graduate committee, Drs. Les Marcum and Lee Metzgar, were involved in much the same way, to a somewhat lesser degree.

I am very much indebted to the staff of Lubrecht Experimental Forest. Forest Manager Hank Goetz was especially generous and helpful in allowing my use of the many facilities available at Lubrecht. Special thanks to Dave Zimmerman for competent help with frozen plumbing, uncooperative snowmobiles, and broken sleds. He also helped place and check traps during both winters.

The staff and students of the aptly named Montana Cooperative Wildlife Research Unit were quite helpful. Unit Leader Dr. Bart O'Gara generously lent both advice and equipment. He and Assistant Unit Leader Dr. Joe Ball both strengthened the thesis with their editing of drafts. Randy Matchett wrote the FORTRAN program

BONFER3.FOR, which was used to calculate the Bonferoni Z statistic.

My immediate predecessor on this project, Kevin Berner, located the winter range, established several of the trapsites, solved many of the access and logistic problems through trial and error, and passed on the knowledge of his experiences to me. Through his efforts, and those of the Director of the Mission Oriented Research Program, Dr. Bob Pfister, the need for this follow-up project was recognized, and funds were allocated.

Lisa Fairman helped check traps on a part-time basis. Miguel Guevara helped cruise timber during the summer of 1986. Dean Pearson helped compile data on timber and topography from maps.

Bob Henderson and John Firebaugh of the Montana Dept. of Fish, Wildlife & Parks provided traps, ear tags, and information on the deer harvested from the study area.

Al Christopherson, silviculturist for the Lolo National Forest, loaned maps and data for timber stands delineated by Fred Martin (Martin and Gerlach, 1982). Chuck Seeley, District Land Manager for Champion International Corp., allowed access to the company's files on land management measures and silvicultural treatments. Champion field personnel were uniformly friendly and helpful.

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INTRODUCTION

Management of federal lands for a variety of resources is required by law (e.g. Multiple Use, Sustained Yield Act, 16 U.S.C. 528-531). State lands, too, are often managed for a variety of uses. In 1981, the Montana State Legislature funded the Mission Oriented Research Program of the Montana Forest and Conservation Experiment Station specifically to provide information for improved multiple-resource production on second-growth forests in Montana (Pfister 1983). Such forests occur on both public and private lands.

The forest products industry is economically important in western Montana, employing over 7,200 workers, generating a payroll in excess of $200 million annually, and providing 44% of the economic base from 1981 to 1984 when estimated by the labor-income method (Anonymous 1987).

Logging is also ecologically important, affecting large areas of land in the region. There are approximately 3.8 million ha of commercial forest land in western Montana (Green and Van Hooser 1983:6). Approximately 407 million board feet Scribner were harvested from 9,600 ha annually between 1983 and 1986 on the 5 National Forests of western Montana (USDA Forest Service 1986a,b). Another 434 million board feet were harvested annually from State and private lands in western Montana (Montana Department of State Lands, 1973-1986). If the average number of board feet harvested per hectare is similar for State, private, and Forest Service lands, approximately 20,000 ha are logged annually in western Montana.

White-tailed deer (Odocoileus virginianus), which are common in the forests of western Montana, are a valuable and highly desirable wildlife species across North America (Langenau et al. 1984). Approximately 15,000 white-tailed deer are harvested annually in western Montana (Cada 1987), providing meat and recreation for thousands of people. Deer hunting also generates money for local economies through the sales of equipment, food, and services (Langenau et al. 1984). Nonconsumptive use of deer (e.g. searching for, and watching or photographing deer) is also quite common, and has been estimated to outweigh consumptive use (hunting) in both money spent and in number of participants by a margin of 3 to 1 in the midwestern United States (Horvarth 1974, Langenau 1979).

Timber management has profound influences, both positive and negative, on the quality of northern deer habitats. Logging in the northern Rockies can affect hiding cover, thermal cover, forage availability, and travel routes (Pengelly 1963, 1972; Keay and Peek 1980, Lyon and Jensen 1980, Mundinger 1982a,b; Peek 1984, Seeley 1985). Because logging is important in the northern

Rockies, and because it has important influences on deer habitat, coordination of deer and timber management is critical where production of both resources is desired.

Management for both timber and deer is often a goal of public land managers and private landowners. In developing management guidelines, Harris (1983:212) felt an "obvious need" was "information about specific nutritional and/or cover requirements during different seasons,...between the sexes, and at certain physiological stress periods." This study is an attempt to address this need.

Winter can be a period of stress for white-tailed deer in the northern portion of their range. Decreased quality and quantity of food, combined with increased energy drain due to less favorable weather result in deterioration of physiological condition and, in some cases, high mortality (Severinghaus and Cheatum 1956, Potvin et al. 1981, Matschke et al. 1984). Investigations across North America have established that during inclement weather, deer concentrate in sites that offer relief from deep, unstable snow, extreme cold, and wind (Verme 1965, Ozoga 1968, Moen 1968, Telfer 1970, Ozoga and Gysel 1972, Wetzel et al. 1975, Dickinson 1976, Drolet 1976, Mundinger 1981, 1982a, b). Differences in the quality of winter habitats have been linked to differences in physiological condition of deer (Seal et al. 1978);

where habitat does not provide adequate shelter from the elements, we can expect to find relatively lower reproductive success and survival. The relationship between logging and deer habitat, then, is especially critical on winter ranges.

Segregation of the sexes in winter has been observed in many ungulates (e.g. mule and black-tailed deer [Odocoileus hemionus] [Cowan 1956, Dasmann and Taber 1956, Miller 1974, Geist 1981], elk and red deer [Cervus elaphus] [Flook 1970, Geist 1981, Clutton-Brock et al. 1982], and bighorn sheep [Ovis canadensis] [Geist and Petocz 1977, Morgantini and Hudson 1981, Shank 1982]). Some authors have suggested that male white-tailed deer spend winter apart from females (Laramie and White 1966, Kelsall and Prescott 1971, McCullough 1979), while others have suggested that the sexes winter together (Geist and Bromley 1978). If the sexes do winter separately, maintenance or improvement of one local winter range for each distinct population may not be sufficient to maintain or improve local deer herds. Habitat improvement should logically be undertaken in areas where females winter, for example, when recruitment is limited by either poor physiological condition in adult females or high mortality of fawns during winter.

The Montana Department of Fish, Wildlife & Parks has recently identified "quality" management for trophy class bucks as an issue of current concern (Wildlife Division, MDFWP 1985). Antler development has been correlated with body condition of males during the preceding winter (Taber 1958), so improvement in trophy quality may be realized when food or shelter are improved in areas where males spend the winter.

This investigation focuses on habitat and forage selection by male and female white-tailed deer wintering on a second-growth forest in west-central Montana where a variety of silvicultural treatments are present. The areas used by the sexes are compared to each other and to habitat available in the area. The results are related to theories on the adaptive significance of sexual segregation, and the implications of the findings for management are discussed. Finally, recommendations are made for timber and land management on areas used by white-tailed deer during winter in western Montana.

STUDY AREA

The study area is located in west-central Montana, north of Potomac and west of Greenough. The eastern portion is on Lubrecht Experimental Forest, managed by the Montana Forest and Conservation Experiment Station, and the western portion is largely owned and managed by Champion International Corporation (Fig. 1).

The winter range was located by Berner (1985), who described the vegetation and topography of the Lubrecht

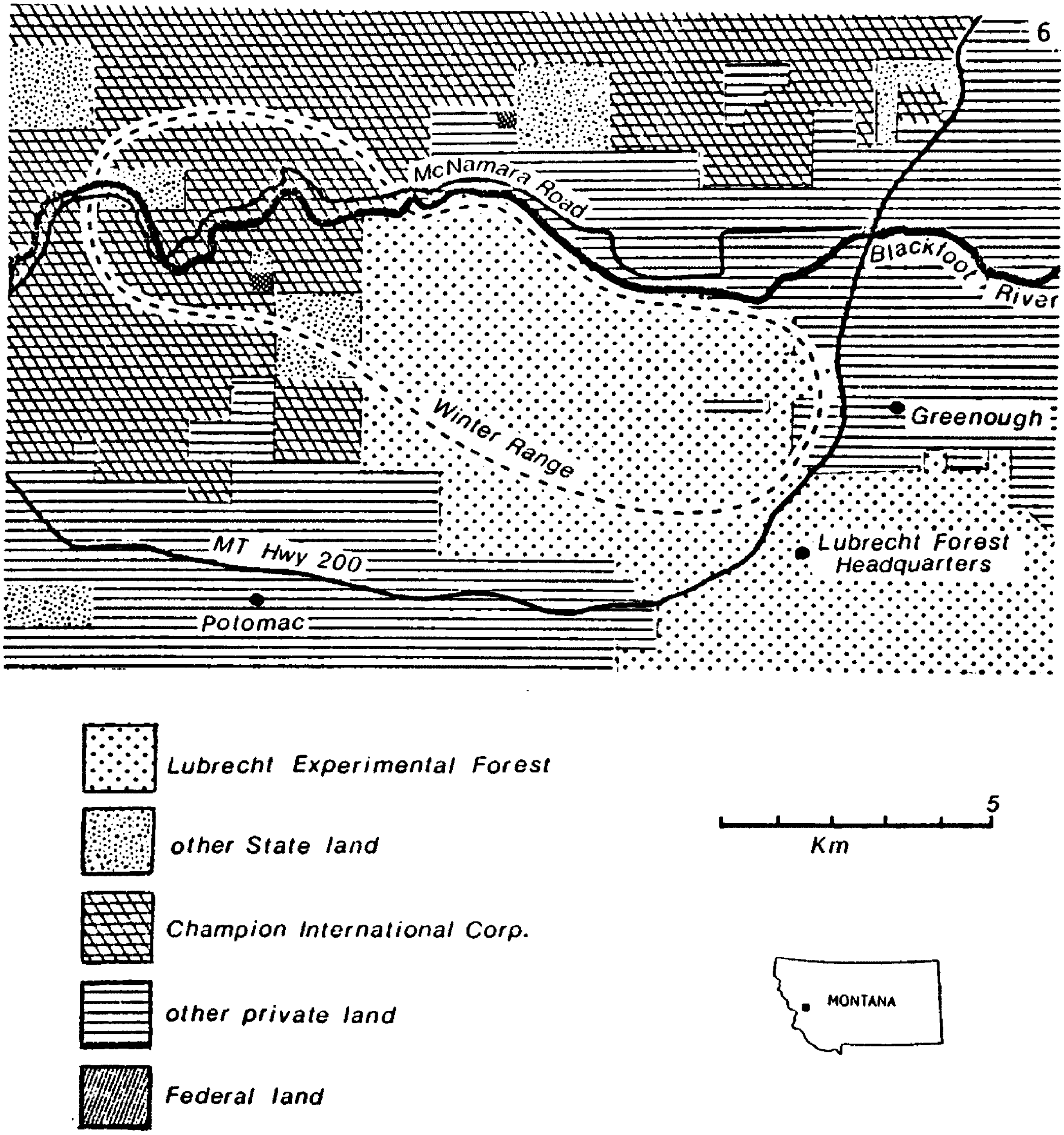


Figure 1. Location and land ownership of the study area.

Forest portion of the study area. The precise boundaries of the study area considered in this investigation were defined by the distribution and movement of deer trapped on Berner's study area.

Elevations vary from 1,070 m to 1,716 m. The topography is quite varied, ranging from flat benches to near-vertical slopes and cliffs. The study area is dissected by numerous draws and ephemeral drainages, which empty directly into the Blackfoot River. Rocks are typically conglomerates, mudstone, sandstone, and siltstone (Brenner 1964).

Most of the study area is timbered, though dry, unforested flats and slopes do occur. Forests are typically composed of Douglas-fir (Pseudotsuga menziesii) and western larch (Larix occidentalis) on moist north slopes, and Douglas-fir and ponderosa pine (Pinus ponderosa) on dry south slopes. (Plant names follow Scott and Wasser 1980).

Habitat types (Pfister et al. 1977) on part of the study area were mapped by Berner (1985). I expanded this map to the south and west during the summer of 1985 (Appendix I). The area is dominated by the Douglas-fir/common snowberry (Symphoricarpos albus) habitat type. Upper slopes are characterized by Douglas-fir/blue huckleberry (Vaccinium globulare), cold sites and frost pockets by Douglas-fir/dwarf huckleberry (V. caespitosum), and moist draws by Douglas-fir/northern twinflower (Linnaea borealis) habitat types. The steepest north slopes are typically in the Douglas-fir/mallow ninebark (Physocarpus malvaceous) habitat type. Dry flats and slopes are in either Douglas-fir/bunchgrass or ponderosa pine/bunchgrass habitat types, or nonforested bunchgrass types.

Precipitation at the Lubrecht Forest Headquarters (elevation 1,219 m) averages about 45 cm annually, with about 70% falling as snow. Average monthly snow depth for the period 1956-1982 peaked in February at about 39 cm, with mean depths over 60 cm occurring at about 5-year intervals. Temperatures vary between an average monthly low of -29 C in January to an average monthly high of 35 C in July (Steele 1983).

This area was logged by diameter limit cutting 50 to 100 years ago (Crabtree 1975), and is now considered second growth. Records of specific logging activities prior to 1900 are scanty, though it is known that logging camps were established in the area to supply timbers for the mining industry in Butte. Between 1904 and 1934, most trees greater than 36 cm dbh were cut (Crabtree 1975). Stand management files maintained by Champion International Corp. indicate that nearly all of the study area under their management has been logged by one or more partial or regeneration cuts since the mid 1960's. A much smaller percentage of the Lubrecht portion of the study area has received any stand treatment since the 1930's (Appendix II).

METHODS

Trapping

Deer were trapped during winter in single-gate Clover traps modified with the "Roper" double-looped wire trip mechanism described by Rongstad and McCabe (1984). All traps were placed at trapsites established by Berner (1985), or at sites within the winter range he documented. Each trap was prebaited for approximately one week with arboreal lichens (<u>Allectoria</u> spp.) and alfalfa hay.

Captured deer were tackled and restrained inside the trap. An assistant blindfolded the deer with a hood I designed from knit ski cap, which was secured with a Velcro™ fastener (Fig. 2). The deer were ear-tagged and aged. Body size and facial profile were used to distinguish fawns from older animals. The lower molars of adult deer were inspected with a flashlight to classify them as yearling, prime, or old. "Old" deer were defined as those with wear sufficient to eliminate the infundibulum on either cusp of the first molar (See Taber 1971:389). Collections of jawbones from Montana deer indicate that this occurs at about 6-1/2 years.

Adult males and 2 adult females were fitted with radio collars. Standard Telonics collars of 5-cm wide

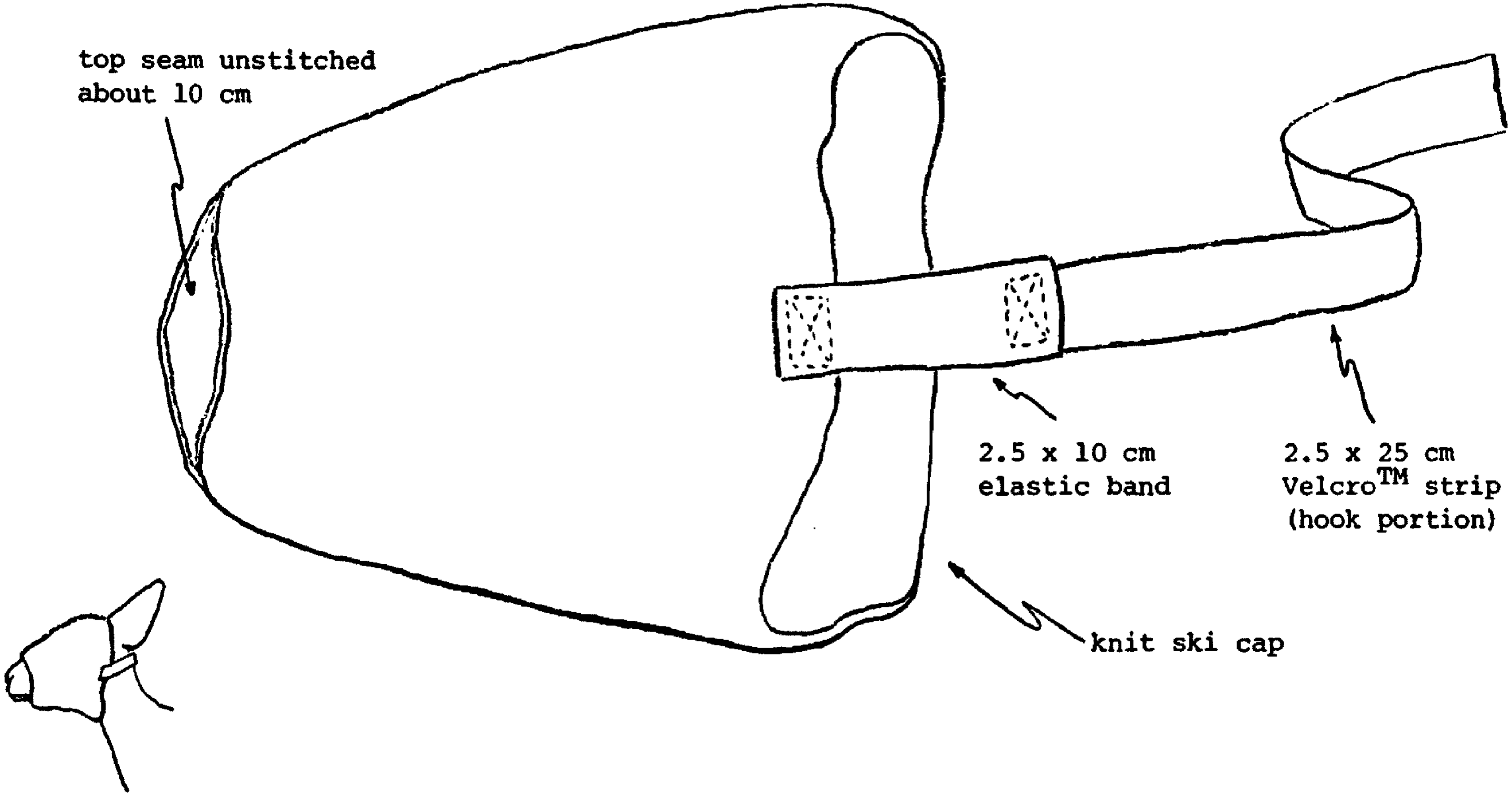


Figure 2. Hood used for blindfolding trapped deer. The hooks on the velco strip held firmly to the knit fabric, securing the hood in place.

machine belting were modified with a steel coil spring and a polyvinyl chloride sheath to accommodate neck-swelling in males (Fig. 3). Three adult female white-tailed deer radio-collared by Berner (1985) were available and used in this study. Six additional radio collars were placed on deer for this study. The objective was to collar as near to equal numbers of males and females as possible.

Radio Locations

Radio-collared deer were located by ground triangulation throughout the winters of 1984-85 and 1985-86. Bearings were obtained from various points along Montana Highway 200, McNamara Road (Fig. 1), and other logging roads. Snow depth, temperature, and wind speed were recorded at 4 locations along the route each day deer were located. Occasional locations were attempted after spring migrations and before fall migrations to allow estimation of the distance travelled between summer and winter ranges.

Winter locations were plotted on acetate overlays of a 1:24,000 scale topographic map. At least 3 bearings were required to define a location. Often such bearings did not meet at one point, but rather described a triangle or series of triangles. This lack of agreement among bearings is common in telemetry triangulation, and results from a number of factors. These include signal bounce, interference caused by mountainous terrain, animal

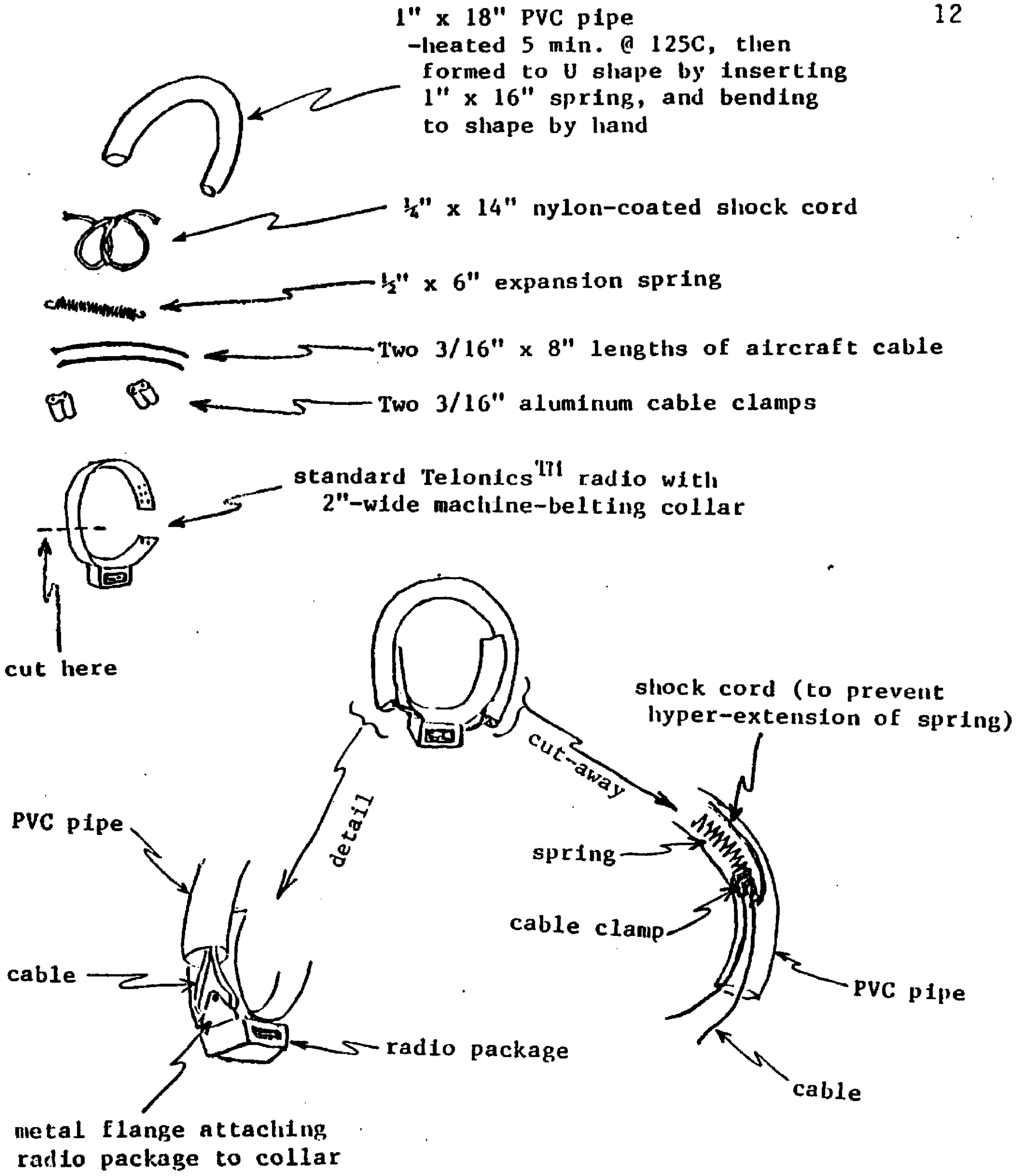


Figure 3. Expandable/retractable collar used on male deer to accomodate neck-swelling during the rut.

movement between fixes, and imprecision of the auditory signal produced by the telemetry receiver (i.e. wide angle over which signal strength was near-maximal). From any such group of bearings, a location was selected that was either the center of the smallest triangle, or at the intersection of 2 such triangles. The base and height of this "location triangle" (or the means of these dimensions if 2 triangles were used) were measured with a vernier caliper to the nearest 0.1 mm. The area of this triangle was used as an estimate of the precision of each location. Different maximum sizes for this location triangle were used for various analyses, depending on the level of precision desired. Selection of any such maximum excluded all locations from the analysis that did not meet the specified precision.

Elevation, to the nearest 3 m (10 ft), and aspect, to the nearest 45° category (e.g. N, NW, W, etc.), were determined for each location from a topographic map. Each location was assigned to a slope class (0-5, 5-25, 25-50, 50-100, >100%), calculated from the width of the interval between the 12.2-m (40-ft) contour lines immediately above and below each location. Habitat type at each location was determined from the habitat type map (Appendix I) and recorded.

All timber stands within the study area had been delineated from aerial photos, and several characteristics of each stand compiled (Martin and Gerlach 1982, Martin et al. 1983, Martin 1985). Characteristics recorded for each deer location included canopy pattern (uniform, mottled, partially broken, very broken, non-forested), % canopy cover (0-9, 10-24, 25-49, 50-69, 70-90, >90%) , mean tree height (<9 m, 9-18 m, 18-27 m, 27-37 m, >37 m), mean crown diameter (<1.8 m, 1.8-4.6 m, 4.7-7.3 m, 7.4-12.2 m, >12.2 m), topographic position (valley bottom, midslope drain, midslope, midslope ridge, major divide), and evidence of logging (logged, not logged). (The timber stand maps and their corresponding data sets were obtained from the head silviculturist of the Lolo National Forest, and from the office of the Mission Oriented Research Program). Logging history at each location was determined from a map of stand treatments, developed from logging records of Champion International Corp. and Lubrecht Experimental Forest (Appendix II).

The winter range was defined by the minimum convex polygon enclosing all radio-locations of deer in winter. Availability of topography, timber, logging treatments, and habitat types (as described for telemetry locations above) within this polygon was sampled at 280 randomly located points. This sample size was used to limit 90% of the errors of estimation to <5% (Mendenhall 1971:195). This random sample was compared to telemetry locations (with location triangles < 0.5 km^2) to identify habitat selection by deer on the winter range. Mann-Whitney U tests were used to compare ordinal variables (canopy pattern, canopy cover, tree height, crown size, elevation, and slope); Bonferoni Z tests were used to compare nominal variables (topographic position, aspect, evidence of recent logging, and logging treatments) (Neu et al. 1980). Habitat types were ordered from driest to most moist, following Pfister et al. (1977), and compared by a Mann-Whitney U test to determine whether deer used drier or moister habitats than randomly available. Habitat types were also grouped and compared by contingency table analyses to identify selection for and against specific habitat types. Logging treatment ages were compared by contingency table analyses, with treatment ages grouped by 10-year intervals, to identify treatment age classes used disproportionately. Selection coefficients ([Use - Available] / Available), which report the difference between observed and expected values as a proportion of the expected value, were calculated for aspects, habitat types, and logging treatments.

These analyses showed which features on the winter range were used disproportionately (either more or less than would be predicted on the basis of their availability). If deer select a winter range on the basis of the habitat available there, we would expect the most important features to be well represented. Comparisons of use to availability within this area may fail to identify these features as preferentially selected, even though they are highly preferred by the deer, simply because they are commonly available. Identification of the important features of the winter range, then, required additional analyses.

I compared the area used by deer during winter ("winter range") to the area used during the remainder of the year ("spring/summer/fall range"), in order to illustrate the differences between the 2 areas. These differences suggest why deer chose to spend winter where they did, while the differences between use and availability within the winter range illustrate how they used the area once on the winter range.

The spring/summer/fall range was defined as the area from which deer using the winter range migrated in fall. The precise boundaries of this area vary with each individual deer--much more so than do the boundaries of the winter range, since deer concentrate during winter, and individual winter ranges overlap extensively. It was assumed that uncollared deer migrated to the winter range from at least as far as the collared deer, and from all different directions. The boundary of the spring/summer/fall range, therefore, was defined by a circle centered at the center of mass (Black 1972) of the winter range, with a radius equal to the greatest distance any radio-collared deer was found from that center. The area inside the winter range polygon was included because deer (both collared and uncollared) were known to spend summer and fall there. The circle, then, enclosed habitats used throughout the year. Thus, it will be referred to as the "annual range".

The availability of habitats across the annual range was estimated from a sample of 280 randomly located points. Timber and topography were sampled from the aerial photo interpretation of Martin et al. (1983) and from USGS topographic maps, as described above for the telemetry locations. Availability across the annual range was compared to availability on the winter range by Mann-Whitney U tests (for ordinal variables) and Bonferoni Z tests (for nominal variables). Selection coefficients were calculated for aspects to show trends in use. Habitat types and logging treatments were not mapped for the entire annual range, so these variables were not used in this comparison.

Sexual differences.--Habitats used by, and selection patterns of, the sexes were compared by Kruskal-Wallis tests (Gibbons 1985) of female use vs. male use vs. availability across the winter range, for ordinal variables. The same set of comparisons (i.e. female use vs. male use, female use vs. availability, and male use vs. availability) was made by Bonferoni Z tests for nominal variables. Selection coefficients were calculated for aspects, habitat types, and logging treatments. More precise location data were used for these analyses (location triangles of less than 0.1 km^2), because this was an attempt to define more narrowly the sites used by discrete segments of the population.

Differences in habitat use between males and females may have resulted from differences in availability of habitats in the areas where the sexes wintered, or from differential use of habitats that were equally available to both sexes. Habitats available to each sex were estimated from random points inside 2 convex polygons: 1 enclosing all male locations and another enclosing all female locations. The same 280 random points used to estimate habitat availability across the entire winter range were used in this analysis. That subset of the 280 points that fell inside each of the 2 polygons was used to estimate habitat availability for each sex.

Habitats available to the sexes were compared to each other, and to availability across the winter range, using Kruskal-Wallis multiple comparisons (Gibbons 1985) for ordinal variables, and Bonferoni's Z tests for nominal variables.

Habitat use by each sex was compared separately to availability for each sex for features that differed in availability between the sexes ($P < 0.10$). Mann-Whitney U tests were used for ordinal variables, and Bonferoni's Z tests were used for nominal variables. Selection coefficients were calculated for aspects, habitat types, and logging treatments.

Locations of yearling males were not used in the analyses of sexual differences, because of the tendencies of this sex/age class to behave differently than adults of either sex (Nelson and Mech 1981, Marchinton and Hirth 1984).

Backtracking

Analyses based on telemetry locations, aerial photo interpretation, and map overlays can give a reasonable picture of home range location and habitat use, but many important variables are more accurately measured on the ground. Attributes such as browse production and use under the tree canopy cannot be measured on aerial photos, nor are they easily mapped. Individual deer trails in the snow were backtracked in order to more fully characterize winter habitat, as well as to test specific hypotheses concerning sexual segregation. Trees, topography, snow depth, browse availability, and browse use were measured along these trails.

On days with complete snow cover, an individual radio-collared deer was selected. The sex of the selected deer was alternated on successive attempts, to insure similar sample sizes. A receiver and hand-held "H" antenna were used to locate the deer by triangulation. I then approached the deer on foot, using the receiver as a guide, until I saw either the radio-collared deer or an uncollared deer whose sex was determined. That deer was backtracked, and habitat information was collected along its trail. A fresh track made by a deer of unknown sex was used if no deer were seen after 2 hours of searching. In these cases, the receiver consistently indicated that the radio-collared deer was nearby, so these data were interpreted as reflecting habitat use in areas inhabited by a deer of known sex. Tracks of adult deer accompanied by fawns were specifically avoided when selecting a fresh track after failing to locate a radio-collared male, to help guard against following a female's trail.

Temperature, elevation, and snow depth under the forest canopy and in a nearby forest opening were measured at the beginning of each trail. The track was then followed opposite to the direction the deer was moving when it made the track. This avoided further harassment of the deer, and allowed collection of data along feeding and normal travel routes, rather than along escape routes. As the track was followed, the number of shrubs and twigs of each species within a horizontal distance of 0.6 m and a vertical distance of 1.5 m of the trail was recorded. This zone (1.2 x 1.5 m) was used to approximate the reach of a browsing adult deer. Shrub species were identified using winter field characteristics described by Morris et al. (1962). Unbrowsed, recently browsed, and older browsed twigs within the 1.2 x 1.5 m zone along the trail were counted. The twig-count method was found by Shafer (1963) to be an efficient, precise, and statistically tractable method for estimating browse production. Twig counts were not converted to weight estimates for this study, however. The number of shrubs within distinct patches of a single species were tallied, rather than recording each shrub separately, to expedite counting. Within each patch, twigs were counted by groups of five. Occasionally, patches were recounted to check the precision of the method. Variables calculated from the twig counts were: 1) availability of twigs prior to recent browsing (unbrowsed plus newly browsed twigs/pace), 2) absolute amount browsed recently (newly browsed twigs/pace), 3) percent of available twigs browsed recently (newly browsed twigs/unbrowsed and newly browsed twigs X 100), and 4) the ratio of browsed to unbrowsed twigs (new and old browsed twigs/unbrowsed twigs). Browse statistics were computed for each plant species individually, for all species combined, and for species grouped by quality class (poor, fair, or good). This quality ranking was based on published literature (e.g. Morris et al. 1962, Kufeld et al. 1973), personal observation, and the advice of Dr. Earl Willard, University of Montana professor of Range Management, who has spent considerable time in the study area.

Topography and trees were systematically sampled at points spaced at 100-pace intervals along the trail. Slope was measured with a clinometer to the nearest percent, aspect was measured with a compass to the nearest degree, snow depth was measured with a tape measure to the nearest 2.5 cm (1 in), and overstory canopy closure was visually estimated to the nearest 10%. Trees within a variable-radius plot were selected with a Cruiser's Crutch™ basal area angle gage. The species and diameter at breast height (dbh) to the nearest 2.5 mm (0.1 in) were recorded for each tree sampled. From these data, I calculated basal area (ft^2/ac), stem density (stems/ac), and mean dbh following Husch et al. (1972). I also calculated stem density by diameter class (saplings: 0.3-12.7 cm, poles: 12.7-22.9 cm, sawtrees: 22.9-45.7 cm, mature trees: >45.7 cm) to facilitate discussion of tree size distributions. Each of these variables was calculated for individual species, for live evergreens combined, and for all species combined. Species composition was further quantified by calculation of the percentage of stems (per unit area) of each species and of live evergreens. English units were converted to metric equivalents for reporting results after statistical analyses were completed.

Trails made by deer of known sex were followed until they were not distinguishable from trails made by other deer of unknown sex. Trails made by deer of unknown sex were followed until a fresh track was no longer apparent, or until shortly after sunset.

Estimates of timber and topography available on the winter range were calculated from a sample of 130 systematically located points. These points were located at 0.5 km intervals along parallel north-south transects spaced 1 km apart. At each such point, aspect and slope were measured, and timber was cruised, as described above. Snow depth was not measured, because this sampling was done during the summer. Browse use was measured only along trails, and not along the systematic sample.

Individual points along a given trail were not independent of one another, as were the points in the systematic sample. Therefore, comparing all points along the trails to all points in the systematic sample would be comparing unlike data sets. Rather, each trail was designated as a sample unit to be compared to the systematic sample. Mean values for ordinal variables (i.e. slope, elevation, overstory canopy closure, percentage of trees of each species, mean dbh, stem density [for individual size classes and for all trees], and basal area) were calculated for each trail. These means were compared to corresponding means for the systematic sample by (nonparametric) sign tests. Aspects were grouped by 90° categories (N, E, S, W, or flat if slope < 5%), and the percentage of points in each category was calculated for each trail and for the systematic sample. The percentages for trails were compared to the percentages for the systematic sample by sign tests. Selection coefficients, based on grand means for all trails, were calculated to illustrate trends in selection by deer for aspects and tree size classes.

Sexual differences.--Areas used by the sexes were compared by Mann-Whitney U tests of sample means along male trails to sample means along female trails. Variables used in these comparisons included elevation, slope, aspect, snow depth, browse availability and use measures, canopy closure, percent species composition, dbh and basal area (for individual tree species, combined live evergreens, and all tree species combined), and stem density (by species group and size class).

Differences noted between male and female trails, as in telemetry locations, may have resulted from differences in what was available to each sex, or from differences in selection patterns. Estimates of availability for each sex were derived from the systematic sample used to estimate availability across the entire winter range. Two polygons were constructed: one around all male trails, and another around all female trails. Those points along the systematic transects inside each of these polygons were used to estimate availability for each sex, hereafter referred to as the male and female availability samples. Mann-Whitney U tests were used to compare the male and female availability samples.

Selection patterns of the sexes were documented by comparing means for male and female trails to means for total availability by sign tests. The tests were repeated for variables that differed in availability to the sexes (following the results of the male and female availability sample comparisons). In such cases, means for the male and female trails were compared to means for the corresponding (male and female) availability samples.

Selection coefficients were also calculated for each of the above comparisons to illustrate patterns in use of aspects and tree size classes.

In discussing results, the term "preferred" refers to cases in which deer use of a feature was significantly ($P < 0.10$) greater than availability of that feature, and "avoided" refers to the opposite. As discussed below, "avoidance" may occur as a result of either active avoidance by an animal, or from moderate use of an abundant feature. The modifiers "somewhat" or "tended" will be used when selection coefficients indicate trends in deer use not shown to be statistically significant at the 0.10 level.

RESULTS

Radio Locations

Twenty-five deer were trapped between 15 December 1984 and 13 February 1985 and between 4 January 1986 and 2 February 1986 (Table 1). Locations of 5 radio-collared females were used in the analyses. Because of collar loss and hunting season mortality, 10 different males (including 2 yearlings) were collared with 4 different expandable collars.

I plotted and measured 490 winter locations for these 15 deer; 465 locations had location triangles of < 0.5 km^2, and 407 had location triangles of < 0.1 km^2 (173 for females, 211 for adult males, and 23 for yearling males).

The convex polygon enclosing all 490 winter locations encompassed 4100 ha. The greatest distance a radio collared deer was found from the winter range center was 18 km, covered by a 4-year-old male. This distance resulted in a defined annual range of approximately 101,800 ha (Fig. 4).

Winter Range vs. Annual Range.--Topography and timber on the winter range differed from that of the annual range in several respects (Table 2). The winter range was at lower elevation, steeper, and had proportionally greater representation of valley bottoms. The winter range was more uniformly timbered, had greater canopy cover, and had less evidence of recent logging. Tree heights and crown

Table 1. Deer captured during the winters of 1984-85 and 1985-86 on Lubrecht Experimental Forest, Montana; and deer radio-collared by Berner (1985) used in this study.

Year			Ear Tags		Radio Collar		Number of
Date	Sex	Age[1]	Right	Left	Color[2]	Freq.	Locations
1984							
12/26	F	Y	14033	14034			
12/29	F	P	14040	14039	RYBu	150.261	59
12/29	F	F	14048	14047			
1985							
1/3	M	P	14020	14021	W	150.440	13
1/9	M	P	14024	14022			
1/9	M	P	14045	14046	RW	150.240	15
1/11	F	P	14023	14043			
1/15	M	P	14030	14029	O	150.300	14
1/15	F	Y		14031			
1/16	M	P	A11797	A11798	G	150.420	47
1/16	F	P	A11799	A11800			
1/17	F	P	14023	14043			R[3]
1/18	F	P	A11795				
2/11	?	F	A11794	A11793			
2/13	F	O	A11777	A11776	YG	150.320	7
1986							
1/4	M	Y	117890	117891	O	150.300	16
1/5	M	Y	117886	117887	RW	150.240	11
1/6	?	F					
1/7	F	?					
1/7	F	P	117885	117884			
1/7	F	P	117883	117882			
1/8	F	P	117881				
1/9	M	P	117880	117879	BkW	150.440	54
1/25	M	P	A11797	A11798	O	150.300	R[3]
1/25	M	P		117878	G	150.420	40
1/31	F	?					
2/2	M	P			RW	150.240	31
Collared by Berner:							
1983							
7/13	F	?	14005		R	150.340	69
8/23	F	P	14011		W	150.280	50
1984							
1/3	F	P	14019		Bu	150.390	64

[1] F=fawn, Y=yearling, P=prime adult, O=old adult

[2] Bu=blue, Bk=black, G=green, O=orange, R=red, W=white, Y=yellow

[3] Recapture

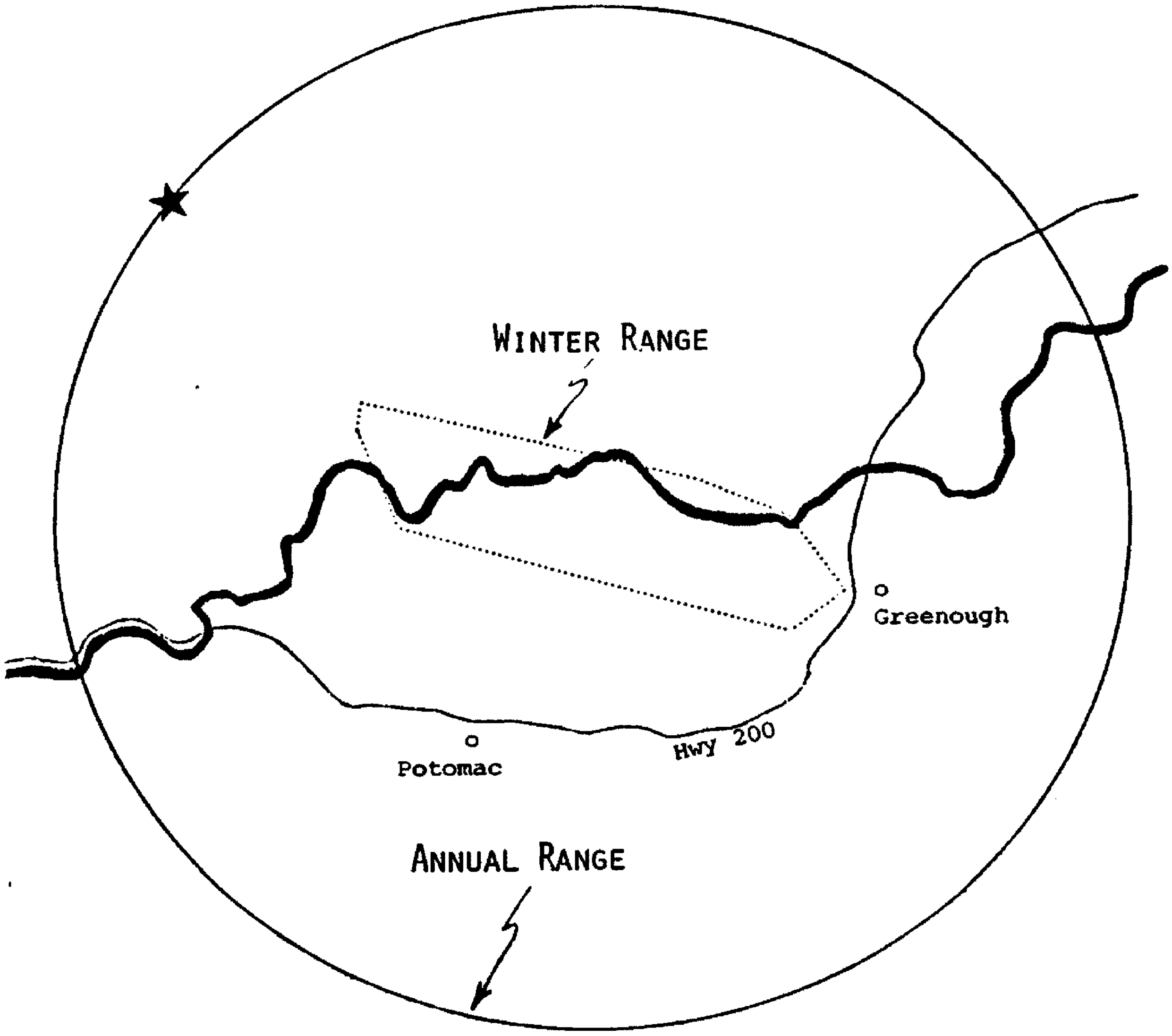


Figure 4. Relative sizes of winter range and annual range.

Table 2. Selection for topography and timber by white-tailed deer in winter, as indicated by telemetry and random points.

	Availability[1]			Statistical Comparisons[2]	
Variable Type FEATURE Value	Annual Range (A)	Winter Range (W)	Deer Use[1] (D)	W vs. A	D vs. W
Ordinal Variables					
ELEVATION (m)	1170	1115	1116	A>W***	W>D***
SLOPE (%)	5-25	5-25	5-25	W>A***	D>W***
CANOPY PATTERN[3]	VB	U	U	W>A*	
CANOPY COVER(%)	>80	>80	>80		W>D***
TREE HEIGHT (m)	18-27	18-27	18-27		D>W***
CROWN DIAM.(m)	5-7	5-7	5-7		D>W***
Nominal Variables					
TOPOGRAPHIC POSITION					
Valley Bottom	4	9	8	W>A*	
Midslope Drain	2	1	1		
Midslope	93	90	91		
ASPECT					
South	13	10	3		W>D*
Southwest	12	8	5		
West	10	5	5		
Northwest	9	12	21		D>W*
North	15	23	34		D>W**
Northeast	21	26	22		
East	10	10	7		
Southeast	10	7	4		
LOGGING EVIDENCE					
Nonforested	14	13	7		W>D**
Unlogged	55	78	88	W>A***	D>W***
Logged	31	9	5	A>W***	W>D*

[1] Modal value for ordinal variables, % in each category for nominal variables.

[2] Mann-Whitney U tests for ordinal variables, Bonferoni's Z tests for nominal variables. * = P < 0.10, ** = P < 0.05, *** = P < 0.01.

[3] U = Uniform, M = Mottled, PB = Partially Broken, VB = Very Broken, NF = Nonforested. Greater value indicates more uniform canopy pattern.

sizes were similar in the 2 areas. North aspects tended to be more common and south aspects tended to be less common on the winter range (Fig. 5).

Habitat Selection on the Winter Range.--Once on the winter range, deer selected for low elevations, steep slopes, north and northwest aspects, and selected against south aspects (Table 2, Fig. 5). No selection was detected for topographic positions, but deer selected for moister habitats than were randomly available. Relatively dry habitat types (esp. nonforested bunchgrass types) were avoided by deer, while moister habitats were used variously (Table 3). The Douglas-fir/common snowberry habitat type was especially preferred. Deer selected areas with taller trees, larger crowns, and less logging. Forested stands showing no evidence of logging were preferred (Table 2). Only active cuts and "unlogged" second growth stands (cuts >50 years old) were used somewhat more than they were available, while cuts between 1 and 30 years old were used less than they were available (Table 4). Both canopy reduction and regeneration cuts were used somewhat less than they were available. The lack of statistical significance in the examination of logging methods may have resulted from positive selection for active cuts, but avoidance of older cuts.

Sexual Differences.--Males appeared to use the east end of the study area, separate from the females, who used

WINTER RANGE VS. ANNUAL RANGE

DEER LOCATIONS VS. WINTER RANGE

MALE USE VS. FEMALE USE

MALE AVAILABILITY VS. FEMALE AVAILABILITY

FEMALE USE VS. TOTAL AVAILABILITY

MALE USE VS. TOTAL AVAILABILITY

FEMALE USE VS. FEMALE AVAILABILITY

MALE USE VS. MALE AVAILABILITY

Figure 5. Selection coefficients ((Use-Availability)/ Availability) for aspects, as indicated by telemetry locations and random points. For comparisons of males to females, coefficients calculated by: (male-female)/ female.

Table 3. Selection for habitat types (Pfister et al. 1977) by deer on the winter range, as indicated by telemetry locations and random points (Bonferoni Z tests). Habitat types are listed from driest to most moist.

Common Name	Abbreviation	% Avail. on the Winter Range (W)	% Deer Use (D)	Selection Coefficients ([D-W]/W)	W vs. D[1]
Nonforested	NF	13	3	-0.77	W>D***
Ponderosa Pine Series	PIPO	3	1	-0.67	
Douglas-fir/Bunchgrass[2]	PSME/BUNCH	4	1	0.00	
Douglas-fir/Pinegrass	PSME/CARU	4	5	-0.25	
Douglas-fir/Common Snowberry	PSME/SYAL	46	60	0.30	D>W**
Douglas-fir/Mallow Ninebark	PSME/PHMA	13	9	-0.30	
Douglas-fir/Dwarf Huckleberry	PSME/VACA	6	9	0.50	
Douglas-fir/Blue Huckleberry	PSME/VAGL	3	1	-0.67	
Douglas-fir/Northern Twinflower	PSME/LIBO	9	11	0.22	

[1] ** = $P < 0.01$ *** = $P < 0.001$

[2] includes Pfister et al.'s (1977) PSME/FEID, PSME/FESC, and PSME/AGSP

Table 4. Selection for logging treatments by white-tailed deer in winter, as indicated by telemetry locations and random points.

FEATURE Value	% Avail. on the Winter Range (W)	% Deer Use (D)	D vs. W (Z tests[1])	Selection Coefficients ([D-W]/W)
AGE OF FIRST CUT				
Active	3	4		0.33
1-10 Years	8	3	W>D*	-0.63
11-30 Years	19	9		-0.53
>50 Years	76	83		0.09
AGE OF LAST CUT				
Active	3	4		0.33
1-10 Years	18	10	W>D**	-0.44
11-30 Years	4	2		-0.50
>50 Years	76	83		0.09
FIRST CUT METHOD				
Unlogged	76	83	D>W**	0.09
Salvage	1	1		0.00
Canopy Reduction[2]	14	9		-0.36
Regeneration Cut[3]	9	7		-0.22
LAST CUT METHOD				
Unlogged	76	83	D>W**	0.09
Salvage	1	1		0.00
Canopy Reduction[2]	11	8		-0.27
Regeneration Cut[3]	12	8		-0.33

[1] * = $P < 0.10$, ** = $P < 0.05$.

[2] Thinning, Tree Selection, or Overstory Removal cuts.

[3] Shelterwood or Seedtree cuts.

the west end more extensively (Fig. 6).

Use of topography differed between the sexes in several respects (Table 5). Elevations were similarly available to the sexes, but females preferred lower elevations than randomly available, while males did not. Consequently, females used lower elevations than did males (Table 5). Females used steeper sites than did males, although slopes were similarly available to the sexes. Both sexes used steeper sites than were randomly available.

Both sexes preferred north aspects and avoided south aspects (Table 5, Fig. 5). Males used northeast aspects more and west aspects less than did females. West aspects, however, were less available to males than females. Northeast aspects were preferred by males, but avoided by females.

Habitat types, which reflect many abiotic factors of a site, were also differentially used by the sexes (Tables 6 and 7). Females used the Douglas-fir/ninebark habitat type more than did males. The steep north-facing slopes on which this habitat type was found, however, were more common in the areas used by females. Males used Douglas-fir/dwarf huckleberry and Douglas-fir/northern twinflower habitat types significantly more than did females (Table 6). Males tended to prefer these habitat types, both of which were found in relatively cold but moist pockets,

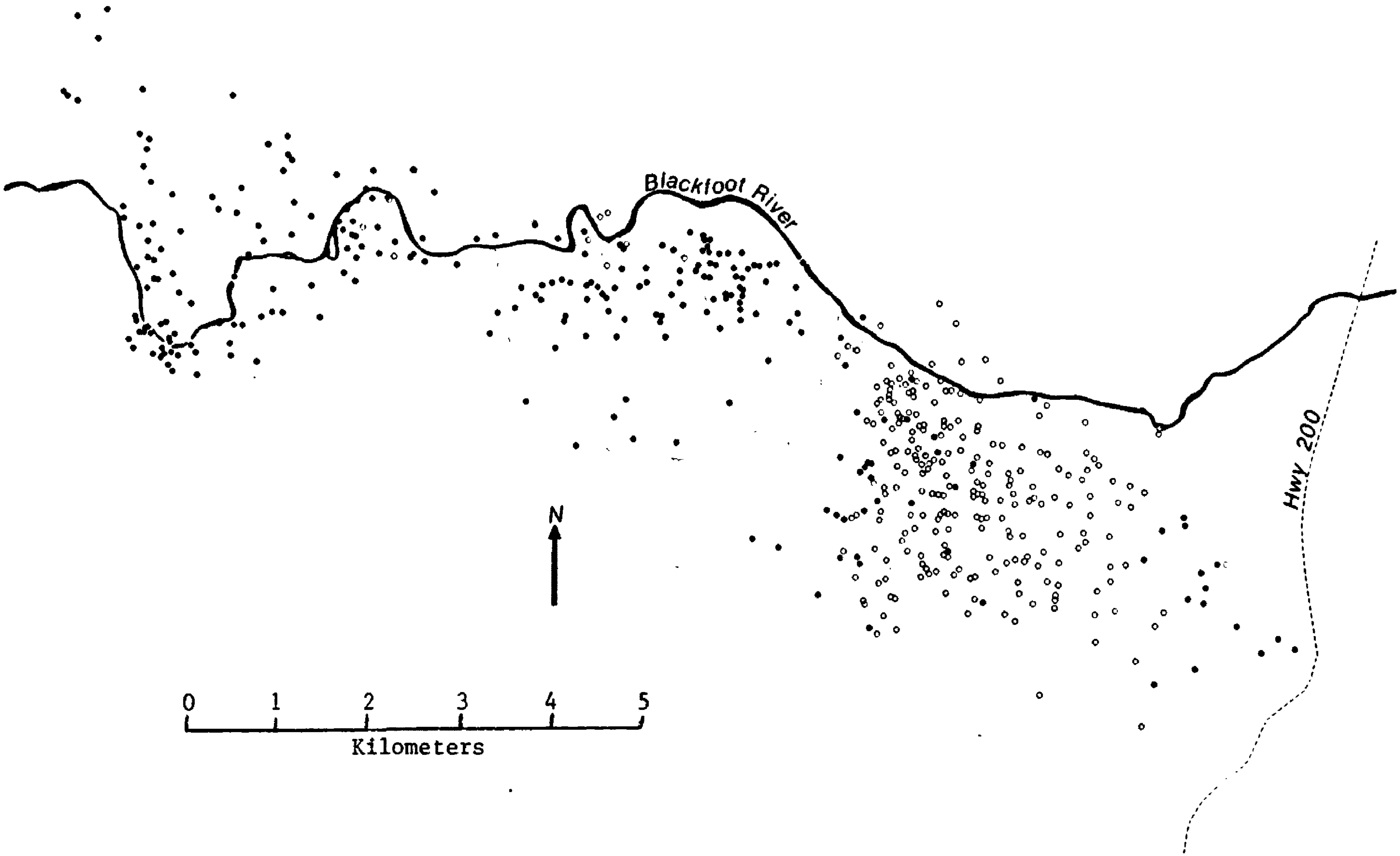


Figure 6. Distribution of telemetry locations of male and female white-tailed deer during the winters of 1984-85 and 1985-86 (● = female, o = male).

Table 5. Selection by male (M) and female (F) white-tailed deer for topography, as indicated by telemetry locations and random points.

Variable Type	Data[1]					Statistical Comparisons[2]					
	Deer Use		Availability			FU	FU	MU	FA	FU	MU
FEATURE	Female	Male	Female	Male	Total	vs.	vs.	vs.	vs.	vs.	vs.
Value	(FU)	(MU)	(FA)	(MA)	(TA)	MU	TA	TA	MA	FA	MA
Ordinal											
ELEVATION	1097	1222	1116	1116	1116	M>F**	A>F**				
SLOPE	25-50	5-25	5-25	5-25	5-25	F>M**	F>A**	M>A**			
MOISTURE[3]	-	-	-	-	-	M>F*		M>A**			
Nominal											
ASPECT											
South	5	1	9	6	10			A>M***			
Southwest	8	2	7	2	8			A>M*	F>M*		
West	8	2	5	1	5	F>M*			F>M**		
Northwest	20	21	13	16	12		F>A*	M>A*			
North	35	32	23	25	23		F>A*			U>A**	
Northeast	14	30	26	32	26	M>F***	A>F*			A>U***	
East	5	10	10	13	10						
Southeast	6	1	8	5	7	F>M**		A>M***			
TOPOGRAPHIC POSITION											
Valley Bottom	7	9	9	5	9						
Drain	1	2	1	2	1						
Midslope	93	92	90	93	90						

[1] Modes given for ordinal variables, % in each category for nominals.

[2] Kruskal-Wallis multiple comparisons for ordinal variables, Bonferoni Z test for nominal variables (* = P < 0.10, ** = P < 0.05, *** = P < 0.01).

[3] As indicated by ordered habitat types (see table 3 for order).

Table 6. Selection for habitat types by male (M) and female (F) white-tailed deer in winter, as indicated by telemetry locations and random points (Bonferoni Z tests). See Table 3 for common names of abbreviated habitat types. Habitat types are listed from driest (NF) to most moist (PSME/LIBO).

	% Composition					Statistical Comparisons[1]					
	Deer Use (U)		Availability (A)								
Habitat Type	Female (FU)	Male (MU)	Female (FA)	Male (MA)	Total (TA)	FU vs. MU	FU vs. TA	MU vs. TA	FA vs. MA	FU vs FA[2]	MU vs. MA[2]
NF	3	3	10	12	13		A>F***	A>M***			
PIPO	0	1	3	2	3		A>F*				
PSME/BUNCH	5	3	3	4	4						
PSME/CARU	3	1	5	2	4						
PSME/SYAL	60	59	45	58	46		F>A**	M>A*			
PSME/PHMA	19	1	14	2	13	F>M***		A>M***	F>M***		
PSME/VACA	5	14	7	3	6	M>F**					
PSME/VAGL	1	0	4	3	3			A>M**			
PSME/LIBO	4	19	9	15	9	M>F***		M>A**			

[1] * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$

[2] Results of FU vs.FA and MU vs. MA reported only for habitat types not equally available to males and females.

Table 7. Selection coefficients ((Use - Availability) / Availability) for habitat types, as indicated by telemetry locations of male and female deer. For comparisons of males vs. females, coefficients calculated by: (male - female) / female.

	Male Use vs. Female Use	Male Avail. vs. Female Avail.	Female Use vs. Total Avail.	Female Use vs. Female Avail.	Male Use vs. Total Avail.	Male Use vs. Male Avail.
NF	0.00	0.20	-0.77	-0.70	-0.77	-0.75
PIPO	1.00	-0.33	-1.00	-1.00	-0.67	-0.67
PSME/BUNCH	-0.40	0.33	0.25	-0.67	-0.25	-0.25
PSME/CARU	-0.66	-0.66	-0.25	-0.40	-0.75	-0.50
PSME/SYAL	-0.02	0.29	0.30	0.33	0.28	0.02
PSME/PHMA	-0.95	-0.85	0.46	0.36	-0.92	-0.50
PSME/VACA	1.80	-0.57	-0.17	-0.29	1.33	3.67
PSME/VAGL	-1.00	-0.25	-0.67	-0.75	-1.00	-1.00
PSME/LIBO	3.75	0.67	-0.56	-0.56	1.11	0.27

while females tended to avoid them (Table 7). The driest sites, which were nonforested, were avoided by both sexes. The Douglas-fir/common snowberry habitat type, which was the most commonly available habitat type, was preferred by both sexes. The high-elevation Douglas-fir/blue huckleberry habitat type was used little by either sex, with the avoidance by males significant.

No differences between the sexes were found for canopy pattern or canopy coverage. Trees in the stands used by males, however, were shorter and had smaller crowns than trees in stands randomly available, and smaller crowns than did stands used by females (Table 8).

Nonforested sites were avoided, and forested but unlogged sites were preferred by both sexes (Table 8). Selection for logged sites was somewhat negative, and intermediate between selection for unlogged sites and against nonforested sites (Table 9). Recently logged sites, and especially regeneration cuts between 1 and 30 years old, however, were more available to females than to males. Selection tended to be negative for such cuts, and positive or near zero for stands unlogged since the 1930's (Tables 8 and 9). Active cuts were somewhat preferred by females, but not by males (Table 9). Stands in which the canopy had been reduced by thinning, tree selection, or overstory removal during the first entry were equally available to the sexes, but avoided only by males.

Table 8. Selection by male (M) and female (F) white-tailed deer for forest stand characteristics, as indicated by telemetry and random points.

	Data^{1}					Statistical Comparisons^{2}					
Variable Type	Deer Use (U)		Availability (A)			FU	TA	TA	FA	FU	MU
FEATURE	Female	Male	Female	Male	Total	vs.	vs.	vs.	vs.	vs.	vs.
Value	(FU)	(MU)	(FA)	(MA)	(TA)	MU	FU	MU	MA	FA^{3}	MA^{3}
Ordinal											
CANOPY											
Pattern^{4}	U	PB	U	U	U						
Cover(%)	>80	>80	>80	>80	>80						
TREE											
Height(m)	18-27	18-27	18-27	18-27	18-27			A>M**			
Diameter(m)	5-7	5-7	5-7	5-7	5-7	F>M**		A>M**			
CUT AGE											
First Cut(yr)	>50	>50	>50	>50	>50	M>F**		M>A**	M>F**		M>A**
Last Cut(yr)	>50	>50	>50	>50	>50	M>F**		M>A**	M>F**		M>A**
Nominal											
LOGGING											
Nonforested	7	4	10	13	13		A>F*	A>M***			
Unlogged	87	93	80	85	78		F>A**	M>A**			
Logged	6	4	9	2	9			A>M**	F>M***		
1ST CUT AGE											
Active	6	2	3	3	3						
1-10 Yrs	5	2	8	2	8			A>M**	F>M***		
11-30 Yrs	15	2	15	2	14	F>M***		A>M***	F>M***		
> 50 Yrs	74	94	74	92	75	M>F***		M>A***	M>F***		
LAST CUT AGE											
Active	6	2	3	3	3						
1-10 Yrs	18	2	18	2	18	F>M***		A>M***	F>M***		
11-30 Yrs	2	2	4	1	4						
> 50 Yrs	74	94	74	92	75	M>F***		M>A***	M>F***		

(Continued)

Table 8 (Cont.)

	Data[1]					Statistical Comparisons[2]					
Variable Type	Deer Use		Availability			FU	FU	MU	FA	FU	MU
FEATURE	Female	Male	Female	Male	Total	vs.	vs.	vs.	vs.	vs.	vs.
Value	(FU)	(MU)	(FA)	(MA)	(TA)	MU	TA	TA	MA	FA[3]	MA[3]
Nominal											
1ST CUT METHOD											
Unlogged	74	94	74	92	75	M>F***		M>A***	M>F***		
Can.Red.[5]	16	6	14	8	14	F>M**		A>M***			
Regen.[6]	9	0	10	0	9	F>M***		A>M***	F>M***		
LAST CUT METHOD											
Unlogged	74	94	74	92	75	M>F***		M>A***	M>F***		
Can.Red.[5]	13	6	12	8	11						
Regen.[6]	13	0	13	0	12	F>M***		A>M***	F>M***		

[1] Modal values for ordinal variables, % composition for nominal variables.

[2] Kruskal-Wallis multiple comparisons for ordinal variables, Bonferoni's Z test for nominal variables (* = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$).

[3] Results of FU vs. FA and MU vs. MA reported only for variables for which Female Availability and Male Availability were not equal.

[4] U = Uniform, M = Mottled, PB = Partially Broken, VB = Very Broken, NF = Nonforested. Greater value indicates more uniform canopy pattern.

[5] Canopy Reduction Cuts = thinning, tree selection, or overstory removal cuts.

[6] Regeneration Cuts = shelterwood or seedtree cuts.

Table 9. Selection coefficients ((Use - Availability) / Availability) for logging treatments used by the sexes, as determined from telemetry locations and random points For comparisons of males to females, coefficients calculated by: (male - female) / fem

	Male Use vs. Female Use	Male Avail. vs. Female Avail.	Female Use vs. Total Avail.	Female Use vs. Female Avail.	Male Use vs. Total Avail.	Male vs Male A
LOGGING EVIDENCE						
Nonforested	-0.43	0.30	-0.46	-0.30	-0.69	-0.
Logged	-0.33	-0.78	-0.33	-0.33	-0.56	1.
Unlogged	0.07	0.06	0.12	0.09	0.19	0.
1ST CUT AGE						
Active	-0.66	0.00	1.00	1.00	-0.33	-0.33
1-10 Years	-0.60	-0.75	-0.38	-0.38	-0.75	0.00
11-30 Years	-0.87	-0.87	0.07	0.00	-0.86	0.00
> 50 Years	0.27	0.24	-0.01	0.00	0.25	0.02
LAST CUT AGE						
Active	-0.66	0.00	1.00	1.00	-0.33	-0.33
1-10 Years	-0.89	-0.89	0.00	0.00	-0.89	0.00
11-30 Years	0.00	-0.75	-0.50	-0.50	-0.50	1.00
> 50 Years	0.27	0.24	-0.01	0.00	0.25	0.02
1ST CUT METHOD						
Unlogged	0.27	0.24	-0.01	0.00	0.25	0.02
Canopy Red.	-0.63	-0.43	0.14	0.14	-0.57	-0.38
Regen. Cut	-1.00	-1.00	0.00	-0.10	-1.00	0.00
LAST CUT METHOD						
Unlogged	0.27	0.24	-0.01	0.00	0.25	0.02
Canopy Red.	-0.57	-0.33	0.18	0.08	-0.45	-0.25
Regen. Cut	-1.00	-1.00	0.08	0.00	-1.00	0.00

Females used such stands in proportion to their availability, and more than did males.

In summary, then, the sexes appeared to spend winter spatially segregated. The areas occupied by females had been logged more recently, and the remaining trees were larger than those in areas used by males. This perhaps resulted from thinnings or seedtree and shelterwood regeneration cuts, in which relatively large trees were left after the cut.

Females used steeper slopes at lower elevations than did males, though these features were equally available to the sexes. Males appeared to prefer moist sites, while females did not.

Backtracking

All Trails vs. Winter Range.--I collected data along 31 deer trails. Browse data from 26 trails (13 of each sex) and forest stand data from 22 trails (11 of each sex) were used in the analyses.

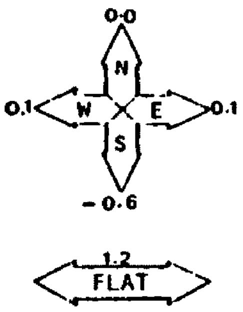
Deer trails were at lower elevations, and on similar slopes, as compared to sites randomly available (Table 10). Deer avoided south aspects. Flat areas were underrepresented on a significant majority of trails (Table 10), but a few trails were entirely (or nearly so) on flat ground. Thus trails had a greater average percent of flat sites than did the systematic sample (Table 10, Fig. 7).

Canopy closures along deer trails did not differ

Table 10. Availability of topography and trees along systematic transects, and selection for these features as measured along deer trails (sign tests).

Feature Feature	Mean for Systematic Transects	Mean for Deer Trails	Syst.Trans (ST) vs. Deer Trails(DT)[1]
Slope (%)	29	30	
Elevation (m)	1280	1219	ST>DT***
Aspect (%)			
South	14.1	5.7	ST>DT***
West	15.7	16.5	
North	39.7	39.2	
East	25.6	27.7	
Flat	4.9	10.9	ST>DT**
Canopy (%)	49	46	
DBH (cm)			
Larch	30	31	
Ponderosa Pine	32	38	
Douglas-fir	26	25	
Live Evergreens	28	27	
All Species	28	26	DT>ST**
Basal Area (m^2/ha)			
Larch	4.8	5.5	
Ponderosa Pine	5.0	5.8	ST>DT**
Douglas-fir	14.5	21.5	DT>ST**
Live Evergreens	18.6	27.2	DT>ST***
All Species	24.6	33.5	DT>ST***
Species Composition (%)			
Larch	24	13	
Ponderosa Pine	16	21	ST>DT**
Douglas-fir	58	63	DT>ST**
Live Evergreens	61	82	DT>ST***
Stems/ha			
Larch	206	186	
Ponderosa Pine	140	97	ST>DT***
Douglas-fir	498	731	DT>ST**
Live Evergreens	523	819	
All Species	862	1039	DT>ST**

[1] * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$



ALL TRAILS VS. TOTAL AVAILABILITY

MALE TRAILS VS. FEMALE TRAILS

MALE AVAILABILITY VS. FEMALE AVAILABILITY

FEMALE TRAILS VS. TOTAL AVAILABILITY

MALE TRAILS VS. TOTAL AVAILABILITY

FEMALE TRAILS VS. FEMALE AVAILABILITY

MALE TRAILS VS. MALE AVAILABILITY

Figure 7. Selection coefficients ((Use-Availability)/Availability) for aspects, as indicated by deer trails and systematic transects. For comparisons of males to females, coefficients calculated by: (male-female)/female.

significantly from canopy closures generally available. Deer did exhibit selection preferences for several other forest stand characteristics, however (Table 10). Tree diameters averaged significantly larger, and basal areas were greater along trails than in the systematic sample. A greater percentage of the trees along trails were evergreen, especially Douglas-fir, though a smaller percentage were ponderosa pine. In general, deer favored larger trees (Table 11). Avoidance of smaller larches and ponderosa pines was statistically significant, as was preference for sawtrees of all species combined. Deer did somewhat prefer sites with more evergreen saplings than average. These areas were, perhaps, favored as feeding sites, because areas in the sapling stage of succession would also likely support many shrubs.

Sexual Differences.--Sixteen of the 31 trails were located after attempting to find a radio-collared female, and 15 of the trails were located after attempting to find a radio-collared male. Five of the trails were made by positively-identified females; 4 were made by positively-identified males. In all other cases, trails were assumed to reflect habitat use in an area inhabited by a deer the sex of the target deer.

Trails of males and females were at similar elevations, in spite of the females' selection for lower elevations, and the males' proportionate use of

Table 11. Tree size distribution along systematic transects, and selection for tree size classes as measured along deer trails.

Size Class Species	Mean for Systematic Transects (ST)	Mean for Deer Trails (DT)	ST vs. DT (Sign Tests)[1]	Selection Coefficients ((DT-ST)/ST)
Western Larch				
Saplings/ha	106	91	ST>DT**	-0.14
Poles/ha	64	52	ST>DT**	-0.19
Sawtrees/ha	34	39		0.15
Mature trees/ha	2	4		1.00
Ponderosa Pine				
Saplings/ha	56	12	ST>DT***	-0.79
Poles/ha	44	38	ST>DT***	-0.14
Sawtrees/ha	36	40	ST>DT**	0.11
Mature trees/ha	4	7		0.75
Douglas-fir				
Saplings/ha	194	311		0.60
Poles/ha	184	259	DT>ST**	0.41
Sawtrees/ha	113	149		0.32
Mature trees/ha	7	12		0.71
Live Evergreens				
Saplings/ha	154	333		1.16
Poles/ha	215	277	DT>ST**	0.29
Sawtrees/ha	145	191		0.32
Mature trees/ha	10	19		0.90
All Species				
Saplings/ha	367	432		0.18
Poles/ha	299	351		0.17
Sawtrees/ha	184	232	DT>ST**	0.26
Mature trees/ha	12	23		0.29

[1] * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$

elevations (Table 12). Steeper slopes were more available to females than to males, but neither sex showed a preference for steeper or gentler slopes than available, and use of slopes by the sexes was statistically similar (Table 12). Both sexes avoided south aspects, and used north and east aspects proportionately. Males used west aspects somewhat more than did females, although they were less available to males. Flat sites were somewhat more available to males, but females tended to prefer them while males did not (Table 12, Fig. 7). Snow depths appeared similar along male and female trails.

The sexes did not differ in their use of canopy closures, which were similarly available to males and females (Table 13). Species composition (Table 13) did not differ in areas available to the sexes, except that ponderosa pine was more available to males than to females. Species composition, however, was similar along male and female trails for all tree species (and groups of species, i.e. evergreens and all species combined). Both sexes selected for a greater percentage of evergreens than was available.

Females used areas with relatively large evergreens, and selected sites within that area that supported trees of larger than average dbh. Males used areas with smaller trees, but did select for sites within that area supporting larger than average evergreens (Table 13).

Table 12. Selection by male (M) and female (F) white-tailed deer for snow depth and topography, as measured along deer trails and systematic samples (Mann-Whitney U and sign tests).

	Group Means					Statistical Comparisons[1]					
	Deer Trails		Availability (A)			Mann-Whitney		Sign Tests			
Feature	Female (FU)	Male (MU)	Female (FA)	Male (MA)	Total (TA)	FU vs. MU	FA vs. MA	TA vs. FU	TA vs. MU	FU vs. FA[2]	MU vs. MA[2]
Snow Depth(cm)	19	23	-	-	-						
Elevation(m)	1184	1242	1285	1283	1280			A>F***			
Slope(%)	35	25	33	19	28		F>M***				
Aspect(%)											
South	0	11	16	7	14			A>F*	A>M***		
West	11	22	21	7	16		F>M*				
North	47	31	40	36	40						
East	26	30	21	39	26						
Flat	16	6	1	11	5						

[1] * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$

[2] Results of FU vs. FA and MU vs. MA reported only for variables for which Female Availability and Male Availability were not equal.

Table 13. Selection by male (M) and female (F) white-tailed deer for forest stand characteristics, as measured along deer trails and systematic samples.

	Group Means					Statistical Comparisons[1]					
	Deer Trails(U)		Availability (A)			Mann-Whitney		Sign Tests			
Feature Species	Female Trails (FU)	Male Trails (MU)	Female Areas (FA)	Male Areas (MA)	Total Avail (TA)	FU vs. MU	FA vs. MA	TA vs. FU	TA vs. MU	FU vs. FA[2]	MU vs. MA[2]
Canopy (%)	40	52	48	54	49						
DBH (cm)											
Larch	35	28	32	24	30						
Ponderosa Pine	38	37	36	28	32		F>M*				
Douglas-Fir	27	23	27	25	26						
Live Evergreens	29	24	29	25	28	F>M**	F>M*				U>A*
All Species	29	24	29	25	28	F>M**		F>A*			
Stems/ha											
Larch	163	208	227	154	206			A>F*			
Ponderosa Pine	65	129	83	241	241		M>F***	A>F***	A>M*	A>U**	A>U*
Douglas-Fir	548	914	528	430	498	M>F**			M>A***		
Live Evergreens	607	1031	478	590	523	M>F**			M>A***		
All Species	785	1293	852	852	862	M>F**					
Basal Area(m^2/ha)											
Larch	6	5	5	4	5						
Ponderosa Pine	5	7	4	7	5		M>F***				
Douglas-Fir	20	24	16	14	15				M>A*		
Live Evergreens	25	30	19	20	19				M>A***		
All Species	31	36	25	26	25			F>A*	M>A***		
Spp. Composition(%)											
Larch	13	14	17	14	24						
Ponderosa Pine	22	19	17	33	16		M>F***				
Douglas-Fir	60	66	54	41	58						
Live Evergreens	83	81	65	71	61			F>A*	M>A*		

[1] * = P < 0.10, ** = P < 0.05, *** = P < 0.01

[2] Results of FU vs. FA and MU vs. MA reported only for variables for which Female Availability and Male Availability were not equal.

The size distributions of trees in sites available to, and used by, the sexes differed by species, though some trends were apparent (Tables 14 and 15). Sites used by males tended to have more saplings than did sites used by females (this tendency was significant for ponderosa pine and combined live evergreens). Sites used by males also had more poles (significant for Douglas-fir, live evergreens, and all species combined), slightly more sawtrees (significant for all species combined), and fewer mature trees (significant for larch, live evergreens, and all species combined).

Saplings of all species except ponderosa pine were somewhat less abundant in the areas available to males (ponderosa pine saplings were significantly more abundant in the area available to males). Pole-trees of all species except larch were somewhat more abundant in areas available to males (significant for ponderosa pine and live evergreens). Sawtrees were similarly available to the sexes, except for ponderosa pine sawtrees, which were significantly more abundant in the area available to males. Mature trees of all species except ponderosa pine were more abundant in the area available to females (significant for larch and Douglas-fir).

With respect to selection patterns displayed by the sexes, males tended to prefer smaller size classes of trees then did females. Avoidance of larch and ponderosa

Table 14. Selection for size classes of timber male (M) and female (F) white-tailed deer, as measured along deer trails and systematic transects.

	Group Means					Statistical Comparisons[1]					
	Deer Trails(U)		Availability (A)			Mann-Whitney		Sign Tests			
Species Size Class	Female Trails (FU)	Male Trails (MU)	Female Areas (FA)	Male Areas (MA)	Total Avail (TA)	FU vs. MU	FA vs. MA	TA vs. FU	TA vs. MU	FU vs. FA[2]	MU vs. MA[2]
Western Larch											
Saplings/ha	73	108	121	71	106			A>F*			
Poles/ha	52	53	67	49	64			A>F*			
Sawtrees/ha	32	46	36	34	34						
Mature Trees/ha	7	0	2	0	2	F>M***	F>M**		A>M*		A>U*
Ponderosa Pine											
Saplings/ha	0	23	26	110	56	M>F*	M>F*	A>F***		A>U**	A>U*
Poles/ha	24	52	28	71	44		M>F**	A>F*	A>M*	A>U*	A>U*
Sawtrees/ha	33	47	26	54	36		M>F***				A>U**
Mature Trees/ha	8	6	3	5	4						
Douglas-fir											
Saplings/ha	219	404	218	117	194						
Poles/ha	184	334	173	206	184	M>F**			M>A*		
Sawtrees/ha	129	169	128	103	113						
Mature Trees/ha	17	7	9	4	7		F>M*				
Live Evergreens											
Saplings/ha	219	447	129	163	154	M>F*					
Poles/ha	200	353	189	262	215	M>F***	M>F*		M>A*		U>A*
Sawtrees/ha	164	218	149	156	145				M>A*		
Mature Trees/ha	24	14	11	9	10	F>M**		F>A***			
All Species											
Saplings/ha	292	571	376	307	367						
Poles/ha	263	442	271	341	299	M>F**			M>A*		
Sawtrees/ha	199	266	190	195	184	M>F*			M>A*		
Mature Trees/ha	32	14	14	9	12	F>M***		F>A***			

[1] * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$

[2] Results of FU vs. FA and MU vs. MA reported only for variables for which Female Availability and Male Availability were not equal.

Table 15. Selection coefficients ((Use - Availability) / Availability) for tree size classes used by the sexes. For comparisons of males to females, coefficients calculated by: (male - female) / female.

Comparison Species	Saplings per ha	Poles per ha	Sawtrees per ha	Mature Trees per ha
Male Use vs. Female Use				
Larch	0.45	0.02	0.44	-1.00
Ponderosa Pine	****	1.17	0.42	-0.25
Douglas-fir	0.84	0.82	0.31	-0.59
Live Evergreens	1.04	0.77	0.33	-0.42
All Species	0.96	0.68	0.34	-0.56
Male Avail. vs. Female Avail.				
Larch	-0.41	-0.27	-0.06	-1.00
Ponderosa Pine	3.23	1.54	1.08	0.67
Douglas-fir	-0.46	0.19	-0.19	-0.56
Live Evergreens	0.26	0.39	0.05	-0.18
All Species	-0.18	0.26	0.03	-0.36
Female Use vs. Total Avail.				
Larch	-0.31	-0.19	-0.05	2.50
Ponderosa Pine	-1.00	-0.45	-0.08	1.00
Douglas-fir	0.13	0.00	0.14	1.43
Live Evergreens	0.42	-0.07	0.13	1.40
All Species	-0.20	-0.12	0.08	1.67
Female Use vs. Female Avail.				
Larch	-0.40	-0.22	-0.11	2.50
Ponderosa Pine	-1.00	-0.14	0.27	1.67
Douglas-fir	0.00	0.64	0.01	0.89
Live Evergreens	0.70	0.06	0.10	1.18
All Species	-0.22	-0.03	0.05	1.29
Male Use vs. Total Avail.				
Larch	0.02	-0.17	0.35	-1.00
Ponderosa Pine	-0.59	0.18	0.31	0.50
Douglas-fir	1.08	0.82	0.50	0.00
Live Evergreens	1.90	0.64	0.50	0.40
All Species	0.55	0.48	0.44	0.17
Male Use vs. Male Avail.				
Larch	0.52	0.08	0.35	0.00
Ponderosa Pine	-0.79	-0.27	-0.13	0.20
Douglas-fir	2.45	0.62	0.64	0.75
Live Evergreens	1.74	0.35	0.40	0.56
All Species	0.86	0.30	0.36	0.56

**** = positive infinity

pine saplings was significant for females, but not for males (Table 14). Males also showed a somewhat greater preference for Douglas-fir and evergreen saplings than did females (Table 15).

Females tended to avoid pole stands (significant for larch and ponderosa pine). Males also tended to avoid larch and ponderosa pine pole stands, but preferred Douglas-fir pole stands.

Males tended to prefer sawtrees of any species (significant for evergreens and all species combined), while females tended to avoid larch and ponderosa pine sawtrees and somewhat preferred only Douglas-fir sawtrees.

Both sexes tended to prefer mature trees, but females showed comparatively stronger preference for mature trees of each species (significant for live evergreens and all species combined). Males showed only weak preferences for mature evergreens, and a significant avoidance of mature larches.

When all tree species and sizes were lumped, males were found to use sites with more stems per hectare than females (Table 13). This apparently was due to the males' use of sites with more poles and sawtrees than either generally available, or than used by females. Females, on the other hand, selected for sites with more mature trees than either generally available, or than used by males.

Basal area, which is dependant on both the number and size of the trees present, did not differ significantly between male and female trails for any of the tree species or species combinations tested. Males did select for sites with greater basal areas of Douglas-fir, combined live evergreens, and all species combined than was generally available. Females also selected for sites with greater basal areas of all species combined than was generally available. Basal area of ponderosa pine was greater in the area available to males than in the area available to females, but neither sex showed selection for sites with greater or less pine basal area than was available to them, and use did not differ between the sexes.

Browse data from 26 trails (13 of each sex) were used in the analyses. Of 25 species of shrubs encountered along these trails, 11 were classed as "poor", 10 as "fair", and 4 as "good" quality forage (Table 16).

The areas used by the sexes appeared to differ with respect to browse availability and use in several ways (Table 17). Twigs of several shrubs were more abundant in areas used by females. Dogwood was the only species which was more abundant in areas used by males. There were also more shrubs of all species combined in areas used by females. The areas used by females, however, had higher densities of browsed twigs for all quality classes, indicating that more deer had been using the area. A

Table 16. Browse species encountered along deer trails, with quality classifications. Nomenclature follows Scott and Wasser (1980).

Quality Class Common Name	Scientific Name
Poor Quality	
Sitka alder	*Alnus sinuata*
Common pipsissewa	*Chimaphila umbellata*
Mallow ninebark	*Physocarpus malvaceus*
Red raspberry	*Rubus idaeus*
Western thimbleberry	*Rubus parviflorus*
Scouler willow	*Salix scouleriana*
Birchleaf spirea	*Spirea betulifolia*
Indiancurrant coralberry	*Symphoricarpos orbiculatus*
Blue huckleberry	*Vaccinium globulare*
Rock clematis	*Clematis columbiana*
Quaking aspen	*Populus tremuloides*
Fair Quality	
Bearberry manzanita	*Arctostaphylos uva-ursi*
Big sagebrush	*Artemisia tridentata*
Creeping barberry	*Berberis repens*
Snowbrush ceanothus	*Ceanothus velutinus*
Rose	*Rosa* spp.
Gooseberry	*Ribes* spp.
Russet buffaloeberry	*Sheperdia canadensis*
Common snowberry	*Symphoricarpos albus*
Lewis mockorange	*Philadelphus lewisii*
Good Quality	
Rocky Mountain maple	*Acer glabrum*
Saskatoon serviceberry	*Amelanchier alnifolia*
Red-osier dogwood	*Cornus stolonifera*
Common chokecherry	*Prunus virginiana*

Table 17. Means for browse availability and use measures, calculated from counts of twigs along trails in areas used by male and female deer. Significantly different pairs are enclosed in parentheses (Mann-Whitney U tests, * = P < 0.10, ** = P < 0.05).

Variable:	Avail. Twigs		Shrub Density		Amt.Browsed		% Recently Browsed		Total % Browsed	
Calculation[1]:	U+N/Km		Shrubs/Km		N/Km		(N/U+N)x100		(N+O/N+O+U)x100	
Species Sex:	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Sitka alder	0	32	0	1	0	0	0	1	1	15
Prince's pine	0	1	0	1	0	0	0	9	0	17
Ninebark	(2122	60)**	(105	5)**	17	2	(1	21)*	34	58
Red raspberry	0	0	0	0	0	0	0	0	0	0
Thimbleberry	(3	0)**	(1	0)**	1	0	24	0	68	0
Scouler willow	41	36	2	3	7	0	0	1	19	23
White spirea[2]	603	1891	124	236	10	20	2	1	9	10
Coralberry	8	1	1	1	1	0	11	29	40	90
Huckleberry	32	717	6	103	2	12	24	1	44	21
Rock clematis	(2	0)*	(0.3	0)*	0	0	7	0	7	0
Quaking aspen	0	0	0	0	0	0	0	0	0	0
Big sagebrush	0	4	0	1	0	0	0	4	0	48
Kinnikinnick	0	7	0	1	0	0	0	4	0	12
Mahonia	1	5	1	2	0	2	17	13	17	29
Ceanothus	9	0	5	0	7	0	72	0	95	0
Rose	(56	28)*	40	17	14	3	(22	40)**	(86	92)**
Gooseberry	40	75	9	12	16	9	44	36	84	67
Buffaloeberry	14	34	1	1	1	2	19	21	75	68
Snowberry[2]	4707	2687	631	617	4	0	0	0	1	2
Mockorange	59	0	1	0	1	0	2	0	15	0
Mountain maple	16	33	4	3	5	4	33	47	84	69
Serviceberry	(91	54)*	(23	15)*	(34	14)*	42	34	88	85
Dogwood	(0	10)*	(0	0.4)*	0	2	0	23	0	60
Chokecherry	8	0	3	0	(5	0)**	(62	0)**	95	97
Poor Quality	2208	847	161	114	28	15	6	10	30	37
Fair Quality	179	156	64	35	(41	17)*	27	29	68	74
Good Quality	115	97	31	18	(43	20)*	(37	28)**	87	85
All Species	2505	1102	(250	169)*	(115	53)*	11	11	43	43

[1] N=newly browsed twigs, O=older browsed twigs, U=unbrowsed twigs, Km=Kilometer

[2] Twigs of these 2 abundant and widespread species were counted only on the first 8 trails. Therefore, they are not included in calculations for quality classes and all species.

greater percentage of the good quality twigs had been browsed recently in the female areas, while a greater percentage of the available ninebark and rose twigs (both fair quality species) had been eaten recently in the male areas. It appeared, then, that the forage available in the areas used by the sexes was qualitatively similar, but that it was more available and more heavily browsed in the areas used by females.

DISCUSSION

Habitat Selection by White-tailed Deer

This investigation identifies specific habitat features used greater than, less than, and in proportion to their availability. Proportionate use of a habitat feature implies that the feature was prevalent enough to "comfortably" meet an animal's need for that particular feature, given the conditions during which the data were collected. That is, the animal did not need to purposely seek out (select for) or avoid (select against) that feature. Significant departure from proportionate use implies that the amount or arrangement of a given habitat feature was not optimum, and the animal adjusted its use of the area accordingly. Use of a feature significantly less than availability of that feature, however, may result from either active avoidance of the feature, or from availability in excess of an animal's moderate use. Thus a feature which is required by an animal, at small to moderate levels, may appear to be avoided when in fact it is not.

Weather is an obvious condition affecting deer habitat use during winter (Verme 1968, Ozoga and Gysel 1972, Drolet 1976, Peek 1984). Snow depth was somewhat shallower than normal during both winters of this study, while temperature was lower than normal during the first winter, but closer to normal during the second winter (Fig. 8). Habitat selection patterns are assumed to reflect this.

Topography.--The winter range was at a lower elevation than the surrounding terrain, with a significantly greater representation of valley bottoms (Table 2). Deer use on the winter range was further concentrated at the lower elevations (Tables 2 and 10). I observed deer and deer tracks along many of the highest ridges in the study area during winter, but found the greatest concentrations at mid- to lower elevations. Snow depth and, perhaps, the abundant browse along the river made lower elevations favorable for deer in winter. Many other studies of white-tailed deer winter ranges in the northern Rocky Mountains have found the greatest concentrations of deer along creek bottoms and mid-slopes (e.g. Niels et al. 1955, Pengelly 1961, 1963; Martinka 1968, Keay and Peek 1980, Mundinger 1982a, b; Slott 1980, Freedman 1983, Nelson et al. 1984, Berner 1985). A few studies, however,

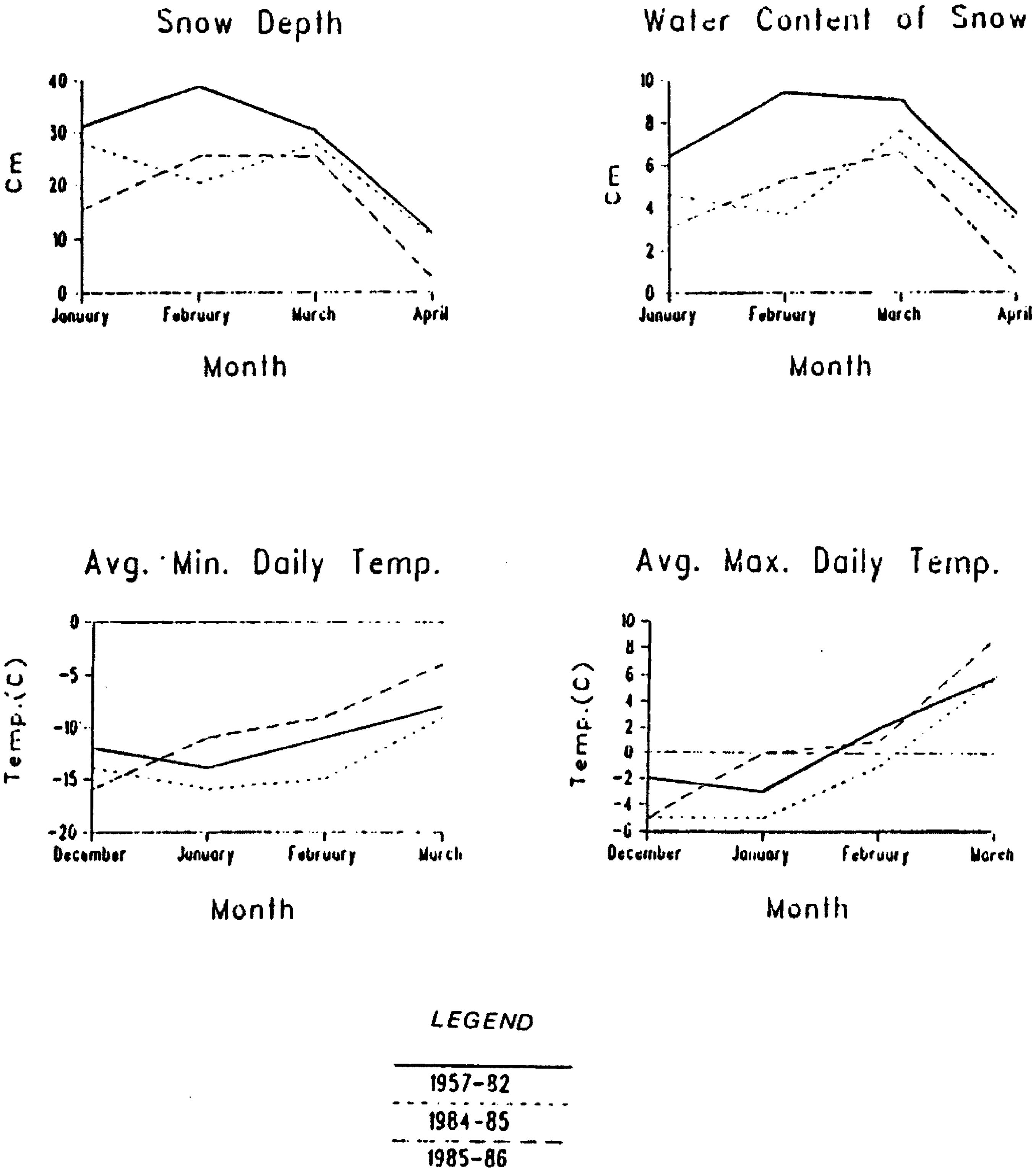


Figure 8. Snow and Temperature patterns during the study period, compared to the 1957-1982 averages.

have documented deer concentrating well up on the slopes, possibly above temperature inversions (Dickinson 1976, Seeley 1985).

This winter range was steeper than the surrounding terrain (Table 2). Telemetry results indicated that deer further selected for slopes that were steeper than the average available on the winter range (Table 2). Backtracking results indicated that flat sites were used occasionally, but avoided most of the time (Table 10, Fig. 7). Steep slopes probably offered deer superior hiding cover and potential escape cover. Much of the timber had been harvested in the west portion of the study area (Appendix II), except on very steep slopes where access and erosion are potential problems. Some of the perceived selection for steep sites, then, may instead have resulted from selection for tree cover. Most studies of whitetail winter ranges have found that deer use flat or gently rolling terrain (e.g. Telfer 1970, Pengelly 1961, Potvin et al. 1981, Seeley 1985). Some workers, however, have noted the use of steep slopes (e.g. Dickinson 1976, Seeley 1985). Berner (1985) found that deer in this area avoided flat areas, and used other slopes in proportion to their availability. Such behavior would result in the use of steeper slopes than randomly available, as observed in this study.

This winter range faces predominantly north and northeast, with relatively few southern exposures. Deer used the northern exposures preferentially, and avoided the less common southern slopes (Tables 2 and 10, Figures 5 and 7). Most winter ranges reported in the literature are on south-facing slopes, with associated east and west aspects (e.g. Hosley and Ziebarth 1935, Niels et al. 1955, Pengelly 1961, 1963, Dickinson 1976, Boer 1978, Keay and Peek 1980, Owens 1981, Slott 1980). Others have reported winter concentrations on various aspects, including north (e.g. Jahnke 1977, Nelson et al. 1984, Seeley 1985). Berner (1985) found northeast slopes preferentially selected by deer in this area.

Although my results indicate that southern exposures were avoided, I often observed deer on the south slopes in the west end of the study area. These slopes were dominated by large, scattered ponderosa pines. The combination of an open canopy and southern exposure often resulted in relatively shallow snow after a few days of sunshine. Apparently, however, the north slopes provided more important habitat during most of the winter.

The sizes of white-tailed deer winter ranges reported in the literature vary from 28 ha (Pengelly 1961) to 28,000 ha (Boer 1978). Factors influencing this variation include deer population size, habitat quality, weather, and technique used to define winter range boundaries.

Tree Characteristics.--White-tailed deer use a wide variety of tree species during winter over their vast North American distribution. Douglas-fir forests, with components of mature ponderosa pine and western larch, were selected on this particular range (Table 10). Most winter ranges in the northern Rocky Mountains are found in forests of evergreen conifers. A few studies in the region have found that whitetails also use deciduous forests of western larch, cottonwood (Populus spp.), and quaking aspen (P. tremuloides) (Pengelly 1961, Allen 1968, Martinka 1968). Similarly, a wide variety of tree species, primarily evergreen conifers, are used as winter cover by deer in the midwestern and northeastern United States.

Evergreen species appear to be preferred for winter cover because of their ability to intercept snow, improve support characteristics of snow, reduce wind speeds, and maintain stable temperatures under the forest canopy (Ozoga 1968). The use of deciduous forests, perhaps, reflects either feeding sites or a lack of evergreen cover in the area.

Sites with evergreens were preferred by deer in this study, but ponderosa pine appeared to be avoided. Deer trails had significantly fewer stems per ha (in all size classes except mature), lower basal areas, and lower percentages of ponderosa pine than did the systematic sample (Table 11). Deer may have avoided ponderosa pine stands because such stands in the study area usually had low canopy coverage and very few shrubs in their understories. The open canopies would allow accumulation of deep snow following winter storms, and the lack of shrubs, due to dry summer conditions, would make them poor sites for feeding. Their southern exposures, however, resulted in rapid melting of snow, so snow was often shallow or missing under these stands, especially late in the winter following several sunny days. Under such conditions, deer did use ponderosa pine stands, and, as my results indicate, especially those with large, mature trees. Dried bunchgrasses and forbs were probably taken as food at this time. A possible bias against encountering ponderosa pine along trails existed because backtracking was done only on days with complete snow cover, when use of ponderosa pine stands was low. No backtracking was done when snow was gone from the south slopes, when deer were probably using them the most, because the deer could not be tracked across such areas. Deer use of ponderosa pine stands, however, was low during periods of complete snow cover.

Canopy cover in the stands used by deer in this study ranged from zero to 100% . Radio locations indicated that canopies > 80% were used over 40% of the time. Approximately 80% of the points along trails had canopies spread fairly uniformly between 30 and 70%. Most studies of whitetail winter ranges indicate that as weather becomes more severe, stands with denser canopies are used. Winter ranges in the northern Rockies with canopies greater than 50% have been reported by Owens (1981), Nelson et al. (1984), and Seeley (1985). Berner (1985) found that deer on this winter range preferred forest stands with canopy closures greater than 80%.

The winter range was more uniformly timbered than the annual range, however over 55% of the canopies at radio locations were considered "partially broken " or "very broken". Broken or patchy canopy patterns appear to be a common characteristic of winter ranges (Pengelly 1961, Drolet 1976, Nelson and Mech 1981, Mundinger 1982b). This arrangement is perhaps best because it offers deer areas of dense thermal cover in close proximity to forest openings, where food is usually more abundant. This same characteristic (i.e. dense cover in close proximity to open feeding areas) is also found where deer winter near ridgetops or near riparian areas. Near ridgetops, deer use open south slopes for feeding and loafing, and densely timbered north slopes for thermal cover in inclement weather (Dickinson 1976). A patchy canopy pattern may result in a relatively low overall canopy closure--perhaps around 50%, as found along trails in this study. Often these trails followed the edges of dense timber stands. Low canopy cover on one side of the trail, and high cover on the other side often resulted in a recorded canopy cover of near 50%. It is important to note that a canopy of 50% caused by clumping of trees is much more suitable on a deer winter range than a canopy of 50% achieved by thinning, which produces a more uniform, but less thermally favorable, stand. Also, timber in strips is more useful to deer than isolated islands of timber, because the strips can serve as travel corridors between feeding sites, while deer must cross open areas, which may be covered by deep snow, to reach isolated islands of timber (Krefting and Phillips 1970, Telfer 1974, Boer 1978).

Other characteristics of forest stands, beyond canopy closure, are important in determining the value of a stand as winter deer habitat. For example, the trees in the stand must be large enough to provide thermal cover. Deer on this winter range selected for trees that were larger than average with respect to height and crown diameter (Table 2). Both characteristics indicate older than average stands. Many other studies have indicated that mature stands are the most commonly used in winter (e.g. Niels et al. 1955, Pengelly 1963, Verme 1965, Wetzel et al. 1975, Drolet 1976, Mundinger 1981, 1982a, b; Owens 1981, Freedman 1983, Nelson et al. 1984, Seeley 1985). Berner (1985) found stands with residual old growth to be preferentially selected on this winter range. Larger trees likely provide better winter habitat for deer because they are more effective than smaller trees at intercepting snow (Kirchhoff and Schoen 1987) and reducing wind, and generally have greater forage production in their understories.

I found that deer selected stands with more evergreen poles per ha and more sawtrees per ha of all species than available (Table 11). Dense pole stands were probably used for thermal and hiding cover, though their ability to intercept snow was probably inferior to that of older stands. While backtracking, I often observed that deer had fed on arboreal lichens (Allectoria spp.) growing on the many small, low branches in these stands. Stands of sawtrees (i.e. dbh between 23 and 46 cm) were probably the major source of thermal cover during the winters studied in this area.

Dense stands seem to be the most commonly used for winter habitat by white-tailed deer. Stem density on the winter range averaged 862 stems per ha for all tree species combined. The average stem densities along trails were similar to this (Table 10). Owens (1981) reported 886 to 1223 stems per ha on winter ranges in northwestern Idaho, while Ozoga (1968) reported that the best winter deer yards in upper Michigan had greater than 2350 stems per ha. Other authors have made reference to "dense" stands as preferred winter habitat, especially during severe weather (e.g. Hosley and Ziebarth 1935, Telfer 1970). More dense stands probably would be used by deer during severe winters in this area.

Dense stands of larger than average trees produce greater than average basal areas. The average basal area of stands available on the study area was 25 m^2/ha. Deer trails averaged 33 m^2/ha, and had significantly greater basal areas than the average available (Table 10). This is somewhat below the average of about 45 m^2/ha basal area on high quality winter range in upper Michigan 'Ozoga 1968). Seeley (1985), working in western Montana, found winter deer use in stands ranging from zero to 90 m^2/ha basal area, with greater deer use at higher basal areas.

Habitat types are site classifications which are based on the vegetation present, but reflect many of the abiotic factors affecting the site (Pfister et al. 1977). My analyses showed that Douglas-fir/common snowberry was a preferred habitat type (Table 3). Pfister et al. (1977) stated that this habitat type is usually found on "moderately warm slopes and benches". Berner (1985) also found the Douglas-fir/common snowberry habitat type preferred by deer in this area during winter, and other habitat types used in proportion to their availability. Keay and Peek (1980) found that whitetails in east-central Idaho preferred unburned Douglas-fir/ninebark habitat types, which were used proportionately in this study.

Habitat types available in the Idaho study area differed from those available in this study area, however. Seeley (1985:ix) concluded that deer preferred the most moist habitat types available on winter ranges in west central Montana. I found that deer did use more moist habitats than randomly available, but feel that this was more a result of the deer's avoidance of dry, nonforested types rather than a preference for moist types.

Sexual Segregation in Ungulates

Winter segregation between the sexes has been observed in a number of ungulate species. Several theories have been advanced to explain sexual segregation in ungulates during winter. Following is a brief summary of these hypotheses:

1) Predator avoidance. Culling predators might learn to recognize and preferentially select the exhausted post-rut males from a group of both sexes. Males, therefore, should either avoid areas used by females or shed their "signs of maleness" (antlers) shortly after the breeding season (Geist and Bromley 1978).

2) Agonistic behavior reduction. Energy expenditure is reduced, and therefore chances for winter survival increased, if sexual segregation results in a lower frequency and intensity of sexual and agonistic behavior (Morgantini and Hudson 1981).

3) Sexual dimorphism. Different body sizes,

functions, (i.e. reproductive activities) or organs (i.e. sexual and secondary sexual organs) result in segregation due to differences in:

a) foraging abilities in deep snow (Telfer and Kelsall 1982),

b) shelter requirements (Watson and Staines 1978, Staines et al. 1982, Clutton-Brock et al. 1982:249)

c) qualitative nutrient requirements (Watson and Staines 1978, Staines et al. 1982, Clutton-Brock et al. 1982:247-249),

d) quantitative food requirements (Staines et al. 1982, Clutton-Brock et al. 1982:247-249).

4) Intraspecific competition reduction. Segregation increases survival of offspring and potential mothers of future offspring, and/or it increases survival of individual males, because competition for limited resources is reduced (Geist and Petocz 1977, Watson and Staines 1978, McCullough 1979, Clutton-Brock et al. 1982, Staines 1982, Telfer and Kelsall 1984).

Geist and Bromley's (1978) hypothesis (theory 1, above) predicts that species in which males shed their antlers soon after the breeding season (such as white-tailed deer) will winter in herds of mixed sex. This would allow males to mimic females, and thus reduce the chances of predators recognizing them as males, which are often in poor physical condition following the rut. If adult males are consistently in worse physical condition than other deer during winter, however, they would be consistently selected by predators from any group in which they occurred, regardless of whether they carried antlers.

The avoidance of female winter yards observed in this study could be hypothesized as a means for adult males to avoid being tested against females and young in confrontations with predators. Geist and Bromley's hypothesis, however, predicts that males which leave the areas used by females should retain their antlers and join into "fraternal" groups. Whitetails do not retain their antlers through the winter. The bucks may join into fraternal groups during winter, but studies of social grouping by the sexes during winter are conspicuously lacking from the literature on white-tailed deer.

It appears that whitetail bucks may take advantage of both female mimicry and sexual segregation as means of reducing predation during winter. The stands of comparatively smaller trees favored by males could provide superior hiding cover, especially from predators relying on visual cues. Male use of areas with relatively low deer density, as compared to the areas used by females, might further help them avoid predation if predators concentrated their efforts in those areas where the greatest number of deer were found.

Despite these theoretical advantages, however, males which have segregated from females would likely be relatively vulnerable to predators. First, they would not have the network of trails made by, and available to, the females. Second, the smaller trees in these areas would intercept less snow and would thus make locomotion (escape) more difficult. The poor physical condition of males, combined with the deep snow through which they would have to flee, would likely lead to rapid exhaustion and increased vulnerability. Predators might even learn through experience that deer wintering in the areas frequented by males were easier to catch than those in the deer yards, where females and young were found. This could result in relatively higher rates of predation on males that segregated.

Predation studies have consistently found that adult males are over-represented in wolf kills (Mech and Frenzel 1971, Kolenosky 1972, Hoskinson and Mech 1976, Mech and Karns 1977, Nelson and Mech 1981, 1986). Whether the predation rate for adult males would be higher if males integrated with females is an open question. Clearly, however, segregation does expose males to serious risks with respect to predators; risks they would not face if they did not segregate. Reduction of predation alone, then, appears to be an inadequate explanation for sexual segregation.

Morgantini and Hudson (1981) maintained that segregation of the sexes during non-breeding periods was adaptive because it reduced the amount of energy spent on sexually oriented agonistic behavior (theory 2). They believed, though did not demonstrate, that such behaviors would be more common among males if (non-estrous) females were present than if no females were present. Thus it would be in the best interest of individual males to avoid areas used by females. The advantages of segregation under this system would be eliminated by the evolution of males which did not respond to the presence of non-estrous females by increasing their aggression toward conspecifics outside of breeding seasons. Testicular atrophy following the breeding season (reviewed by Verme and Ullrey 1984) could be one physiological mechanism maintaining such a behavior pattern. Observations by Geist and Petocz (1977), Hirth (1977), McCullough (1979), and myself suggest that adult males are peaceful toward conspecifics on those occasions when they are found among females and young during nonbreeding periods. This hypothesis, then, seems unlikely as an explanation for sexual segregation.

Several authors have concluded that segregation results from a simple preference by males to avoid females and young except during the rut (e.g. Watson and Staines 1978, Shank 1982, Staines et al. 1982, Ordway and Krausman

1986). Such behavioral mechanisms may well exist, and serve to maintain segregation. They probably would not, however, be retained unless the individuals displaying such behaviors gained some reproductive or survival benefit(s). The benefits, then, not the behaviors, would be the underlying cause for segregation.

Telfer and Kelsall (1984) noted that white-tailed deer exhibited a moderate degree of sexual dimorphism relative to other ungulates. This dimorphism, they felt, would confer a slight advantage to males in deep snow, and would allow them to use areas inaccessible to females (theory 3a). The authors concluded, however, that whitetails showed a much greater degree of adaptation to snow in their behavior (i.e. trail making, feeding on food above the snow, and migrating to areas of favorable snow conditions), rather than in their morphology. Segregation by the males to areas of lower deer density (outside the regular deer yard), but with deeper snow, would negate many of the benefits conferred by the behavioral traits associated with whitetails in winter. Even a deer larger than its conspecifics would be benefitted by remaining in the company of other deer, from the standpoint of "snow-coping" if, as the authors suggest, behavioral adaptations are the whitetail's major means of coping with snow. It is doubtful that dimorphism for snow-coping predated segregation. It does seem clear, however, that natural selection would favor larger deer among those that consistently wintered in areas with deep snow and relatively low deer densities.

Staines et al. (1982) and Watson and Staines (1978) suggested that male red deer in Scotland used areas with more heather (Calluna vulgaris) because they required the greater thermal cover offered there (theory 3b). Adult males are usually the sex/age class in the poorest condition going into winter because of the rigors of the rutting season. Their larger size, and thus lower surface-to-volume ratios, however, should make them more thermally efficient than females and able to endure cold with less thermal cover. The smaller trees found in the areas where male white-tailed deer wintered in the present study would have provided poorer thermal cover than the larger trees in the areas occupied by females (Ozoga 1969, Kirchoff and Schoen 1987). The bucks apparently, however, made up for this deficit at least partially by selecting areas with greater than average densities of larger than average trees (Table 8).

Several authors have suggested that males and females have different nutrient requirements during winter, and therefore segregate to areas where their respective needs are best met (theory 3c). Staines et al. (1982) observed that male red deer in Scotland ate proportionally more heather and less grass than did females during winter.

They noted, however, that while heather was less abundant in the areas used by females, it was of higher nutritional value and sufficiently available in the female areas to adequately support the stags. Shank (1982) found differences in the winter diets of male and female bighorn sheep in Alberta. He attributed these differences solely to differences in the plant communities where the sexes wintered, and not to differences in food preference.

No differences in food preferences were evident in my study. There were differences in the availability of several browse species in the areas used by the sexes (Table 17), but the ratio of browsed to unbrowsed twigs, which can be used as an indicator of the preference for each species, differed only for rose, which was more heavily browsed in male areas. Segregation clearly could not have occurred on the basis of this preference, however, because rose shrubs were equally available, and rose twigs were more available, in female areas.

Males of many ungulate species are larger than females. Males must, therefore, either eat more food than females, or process the food they do eat more efficiently. Several authors have proposed that males can consume the quantity of food they require most efficiently by avoiding areas that are heavily grazed by the large number of females that concentrate during the winter (theory 3d). Where females concentrate in the best-quality sites, males must either use sites of lower quality or integrate and compete with the females. Male ungulates have been observed in habitats offering lower quality food during winter by Watson and Staines (1978), McCullough (1979), Staines et al. (1982), and Clutton-Brock et al. (1982). The ability of males to subsist on these low quality/high volume diets is reportedly improved by the proportionately larger rumens in males (McCullough 1979, Staines et al. 1982). Bighorn sheep rams, however, used a higher quality range than did females and juveniles in Alberta (Shank 1982). It is probable that the range used by the ewes in Shank's study was in poorer condition simply because it had been subjected to heavy grazing by generations of female and young sheep, which outnumbered the adult rams. Spatial segregation by rams in this case would certainly benefit them from a nutritional standpoint. Thus Shank's observations are consistent with the hypothesis that males segregate to maximize their food intake.

I found that the areas used by male white-tailed deer had fewer available twigs of several species, and fewer shrubs, than did areas used by females. There did not, however, appear to be differences between the areas with respect to the quality of food available (Table 17). The greater quantity of browsed twigs in the female areas suggests that more deer were using these areas. Data were not collected on deer densities in the male and female areas, but observations made during fieldwork strongly supported this hypothesis. My data, then, are compatible with the hypothesis that males use areas with lower availability of quality forage, but also with lower deer densities and less competition for food.

Intraspecific competition for food during winter is common among ungulates in temperate and colder climates (Clutton-Brock et al. 1982, Taber et al. 1982, Matschke et al. 1984). Several authors have suggested that this competition is reduced by sexual segregation (theory 4). Most authors have interpreted the segregations they observed as females using the highest quality areas, and males using other, lower quality areas. Some of these authors felt that the primary value of segregation was in favoring the offspring of males that did not compete with females and young during winter (Geist and Petocz 1977, Watson and Staines 1978). Such a system would only benefit males that had actually bred with the females they were avoiding. Furthermore, the benefits in increased offspring survival would have to be greater than the costs of segregation, if such segregation reduced an individual male's chances for breeding in the future. Costs would include a typically lower quality diet, decreased ability to detect predators (if groups of males were smaller than groups of females), and decreased ability to evade predators (if less escape cover in the form of trails through the snow, cliffs, etc., was available).

Others have proposed that segregation of males to areas of lower deer densities favors these males directly, because they are able to avoid competition with females and maximize their own food intake (Clutton-Brock et al. 1982, Staines et al. 1982). Segregation on this basis would be a result of different nutritional requirements of animals with differences in anatomy (which have evolved primarily to optimize breeding success in each sex [Clutton-Brock et al. 1982]). Under this hypothesis, the evolution of larger body size in males (i.e. sexual dimorphism) would have resulted from competition for breeding privileges, and would have preceded segregation. Competition reduction demanded by that dimorphism would be only a secondary cause of segregation--a means to an end (the end being maximizing food intake). Segregation, in turn, would have resulted in the selection for proportionally larger rumens in males, to enable them to cope with the typically low quality diets upon which they frequently would have to subsist. This hypothesis, which is extensively developed by Clutton-Brock et al. (1982), is thus only an extension of theory 3d. My data, as discussed above, are compatible with this theory.

<u>Sexual segregation in white-tailed deer</u>.--I found that males used an area contiguous with, but centered several km to the east of, where most females wintered. The area

used by the males was less steep than the area used by females. Females avoided high elevations, while males did not. Less logging had occurred in the area used by males, and the trees were somewhat smaller. The males apparently made up for the smaller trees by selecting sites with high densities of larger than average trees. There were fewer shrubs available in the areas used by males. The shrubs that were available to males, however, were less browsed than those available to females, suggesting that deer densities were higher in the areas used by females. Observation of deer and deer tracks during 2 winters indicated that the latter suggestion was correct. Deer densities were not quantified, however.

Some females (with young) did use the area used by males. All trapping was done within the area which later became designated "available to males" (Fig. 6). Females were trapped in this area (Table 1), but the ratio of adult males to adult females was nearly 1:1, much higher than expected, especially for a hunted population. The ratio of adult males to females and young trapped by Berner (1985) in this area during the winter of 1983-84 was 3:1. Females radio-collared in this area tended to leave it, joining many other deer in the area to the west. Males tended to stay in the areas where they were trapped for the remainder of the winter, then disperse in spring. These observations support the hypothesis that this area was used disproportionately by adult males.

Laramie and White (1964) reported that adult bucks in New Hampshire were most commonly found at the periphery of winter deer yards, rather than within them (with the females and young). McCullough (1979) also found that males were usually separate from females and young during winter in Michigan. He felt, however, that this tendency may not have been fully expressed within the enclosure of the George Reserve, where he worked.

The use of peripheral areas by adult bucks would explain why Mattfeld et al. (1974) found this sex/age class less vulnerable to box trapping in winter than in spring and summer. Winter trapping effort is usually concentrated in deer yards, where overall deer density is greatest, but the proportion of adult males would be relatively low. After spring dispersal, this relationship would no longer exist, and the sex ratio of trapped deer would be expected to shift, with adult males more evenly represented in the catch. This is exactly what Mattfeld et al. (1974) found.

Use of deer yard peripheries by adult males would also explain the greater vulnerability of adult bucks to predation, as compared to either females or yearling males (Mech and Frenzel 1971, Kolenosky 1972, Hoskinson and Mech 1976, Mech and Karns 1977, Nelson and Mech 1981, 1986). The observation that most wolf kills occur outside deer wintering areas (Kolenosky 1972, Fritts and Mech 1981, Nelson and Mech 1981) is also consistent with this finding.

Further studies to confirm or refute this relationship between the sexes are recommended. An examination of winter trapping records could be of help. If adult males use areas of low deer density during winter, there should be a significant negative correlation between trap nights per deer captured and proportion of adult males captured at individual trap sites. Unfortunately, data on individual traps were not maintained during this study, so such correlations cannot be attempted with my data.

A graphic display of the ratio of males:females caught at individual sites, plotted on a map of the area trapped might also be enlightening. Such a display might well show the geographic distribution of males and females during the study period.

The information needed for these analyses could be obtained from existing records, or from future investigations designed to answer other questions but dependent on a sample of trapped deer. A relatively large sample of deer would probably be necessary, but intensive deer trapping programs have been conducted in many places, and adequate data probably exist.

Differences between white-tailed deer and other ungulates.--Sexual segregation in elk, red deer, and bighorn sheep, which has been well documented in the literature, appears to take the form of what Selander (1966) termed "macrogeographic allopatry". That is, the sexes use areas separated from one another by unoccupied areas. The segregation of white-tailed deer, however, appears to be closer to "microgeographic allopatry", in which the sexes use adjacent areas of either similar or different habitat. The underlying causes of sexual segregation offer an explanation for this difference.

From the preceding discussion, it appears that intraspecific competition is reduced by sexual segregation, as males are better able to maximize forage intake by avoiding areas heavily used by females. The greater demands for food by males results from their larger body size, which has been selected for to help them gain dominance, and thus breeding privileges. Such sexual dimorphism is favored in species with polygamous breeding systems (Selander 1966), and especially in those species in which 1 or a few males do most of the breeding. If sexual segregation results from sexual dimorphism, macrogeographic allopatry should be more common in harem-breeding species, while microgeographic allopatry or sympatry should be more common in species forming smaller groups or pair-bonds during the breeding season.

Implications of Microgeographic Allopatry in Deer.--The observation that male white-tailed deer winter in areas adjacent to areas in which females winter has important ramifications. When a substantial catch of adult bucks is desired during winter, for either research or management purposes, trapping effort should be extended well beyond the area in which the greatest number of deer concentrate.

Habitat improvements in the areas surrounding traditional deer yards may result in an improvement of the physical condition of adult bucks where microgeographic allopatry occurs. Certainly both consumptive and nonconsumptive users would value an increased opportunity to see large, healthy bucks.

Management of White-tailed Deer Winter Ranges

Many studies, including this one, have shown that white-tailed deer in the northern Rocky Mountains usually spend winter in dense, mature conifer stands located at relatively low elevations. These stands typically border rivers, streams, lakes, meadows, or agricultural fields (Pengelly 1961, Peek 1984). Such stands intercept snow, reduce wind, and moderate temperatures (Ozoga 1968). Shrubs are often lacking in the understory of these stands, likely due, in most cases, to the combined effects of advanced plant succession and overbrowsing by high densities of deer (Pengelly 1961, Freedman 1983). Small opening, riparian areas, and the edges of mature stands often provide forage, as they represent ecotones between mature forests and areas of either earlier successional stage or greater water availability. Within the mature stands, arboreal lichens often serve as food (Mundinger 1981). Studies across North America have repeatedly demonstrated that during winter, little use is made of forage located far from cover (Krull 1964, Krefting and Phillips 1970, Wetzel et al. 1975, Drolet 1978, Lyon and Jensen, 1980).

Logging on deer winter ranges is likely to continue, especially where the land is privately owned and managed, considering the accessibility and high timber volumes of these stands. With proper planning, however, moderate timber harvest need not severely impact the quality of the deer habitat in most areas. Several factors which should be considered when planning for logging on winter ranges are discussed below.

The most obvious consideration is the need to retain dense, mature timber (for thermal cover) adjacent to regenerating stands in the shrub stage of succession (for feeding). The thermal cover should be adequate to protect deer during the most severe winters encountered in a given area, not merely adequate for an average winter. The arrangement of cuts should provide a high ratio of edge to area cut, and the edges should be immediately adjacent to thermal cover. There should be a continuous supply of such edges over time, rather than relatively short periods of abundant browse followed by decades of little browse. New feeding edges, therefore, may need to be produced as others outgrow the shrub stage of regeneration. Riparian areas should be considered permanent feeding sites, and the forest stands bordering them protected from large-scale timber harvests. Travel corridors, in the form of dense, mature stands to intercept snow, should be provided to allow deer to move among the stand treatments present in the area. If the stand(s) bordering the riparian area are left intact, they could well serve as effective travel corridors.

Rapid regeneration following logging should be encouraged through appropriate harvesting methods and site preparation. Shrub growth, however, is desirable on a winter range, and should not be eliminated. In any regeneration, evergreen conifers should be favored. Western larch is a poor choice for deer winter ranges because its deciduous nature renders it less effective in intercepting snow, retaining heat, and slowing winds.

Road construction should be kept to a minimum, to retain as much habitat security as possible for the deer. These roads should be closed to the public during winter wherever possible, to minimize harassment. (One effective way to prevent vehicular traffic on logging roads after logging operations have ceased for the season is to block roads with one or more large logs). Firearms and dogs are both potential sources of harassment and mortality, and should be restricted on the winter range.

Where public use can be restricted, cutting should probably be done during mid-winter, at or slightly after the average date of peak snow depth (determined from local weather records). This would make tops, limbs, and arboreal lichens ("tree moss") available to deer as food, and would temporarily reduce snow depths, improving access for the deer. Deer feeding in such situations, however, are vulnerable to harassment and poaching, so cutting might best be undertaken at other times of the year where this may be a problem.

On south slopes, deer browsing the crop-tree regeneration can be a problem (Niels et al. 1955). These areas should not be harvested until abundant browse is established elsewhere nearby (e.g. on the facing north slope).

Where an improvement in the size or condition (i.e. trophy quality) of adult bucks is desired, the quality of habitat both inside and outside traditional deer yards should be assessed. The nutritional status of females is critical in determining the size of the antlers of their male offspring (Geist 1986) and should not be overlooked. Full development of trophy potential in adult bucks cannot be expected, however, where adequate winter range exists only in isolated islands, which are fully utilized by the female segment of the population. Where the habitat adjacent to deer yards is only marginal, bucks of only marginal quality can be expected. The management considerations discussed above could benefit adult bucks if applied to an area larger than just the area of greatest winter deer concentrations.

The white-tailed deer is an important and highly valued resident of North America's forests. With reasonable planning, forest managers can ensure that large, healthy whitetails will remain a commonly encountered resident of Montana.

APPENDIX I. Habitat types on the study area (map expanded from Berner 1985). See table 3 for common names of habitat types.

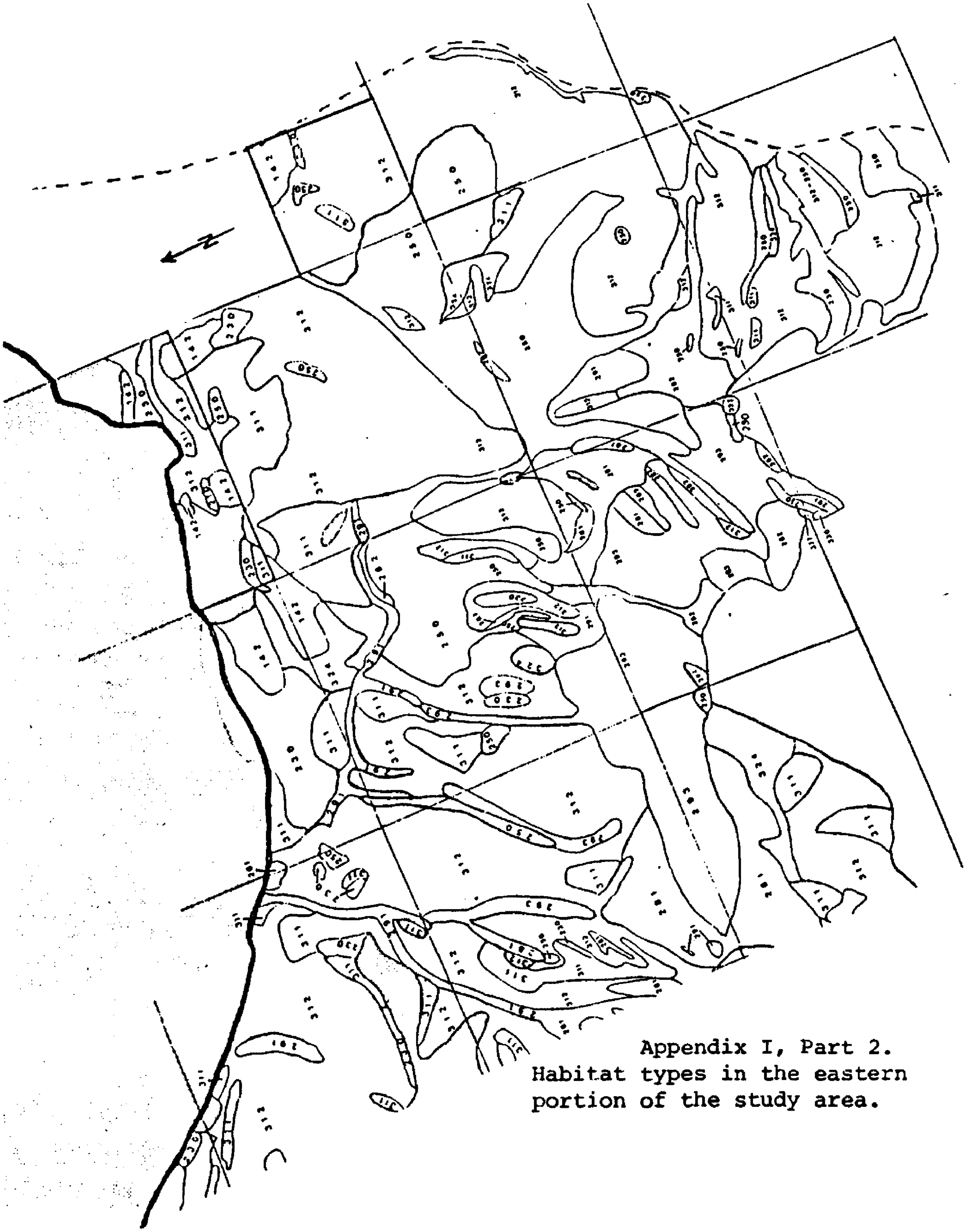
Key to habitat types (from Pfister et al. 1977)

No.	Habitat type
130	PIPO/AGSP
142	PIPO/FEID,FESC
171	PIPO/SYAL,SYAL
199	PIPO/CAGE[1]
210	PSME/AGSP
220	PSME/FEID
230	PSME/FESC
250	PSME/VACA
261	PSME/PHMA,PHMA
262	PSME/PHMA,CARU
281	PSME/VAGL,VAGL
291	PSME/LIBO,SYAL
293	PSME/LIBO,VAGL
299	PSME/CAGE,CAGE[1]
311	PSME/SYAL,AGSP
312	PSME/SYAL,CARU
322	PSME/CARU,ARUV
324	PSME/CARU,PIPO
324	PSME/CARU,PIPO

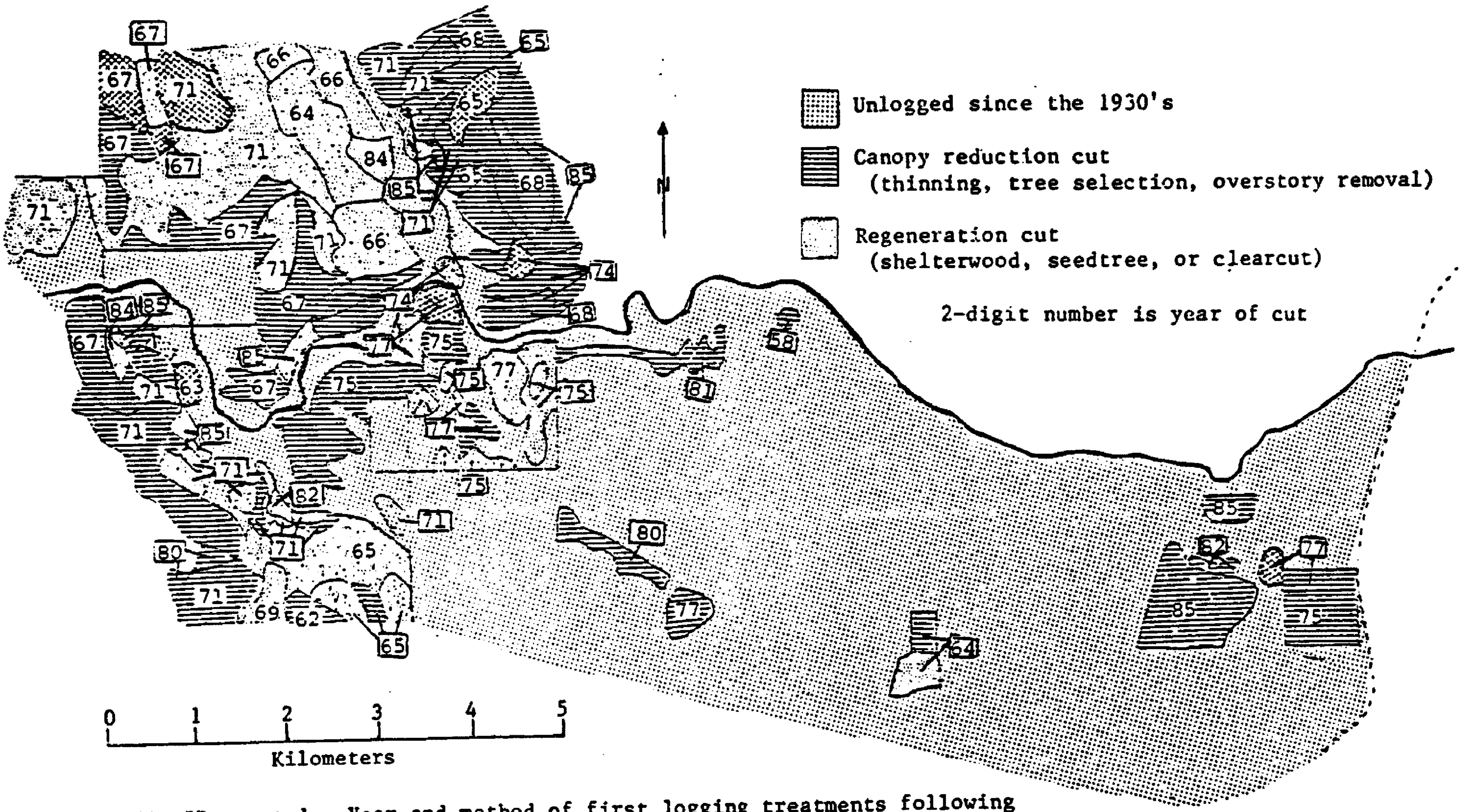
Nonforested areas shaded.

[1] Community type proposed by Berner (1985).

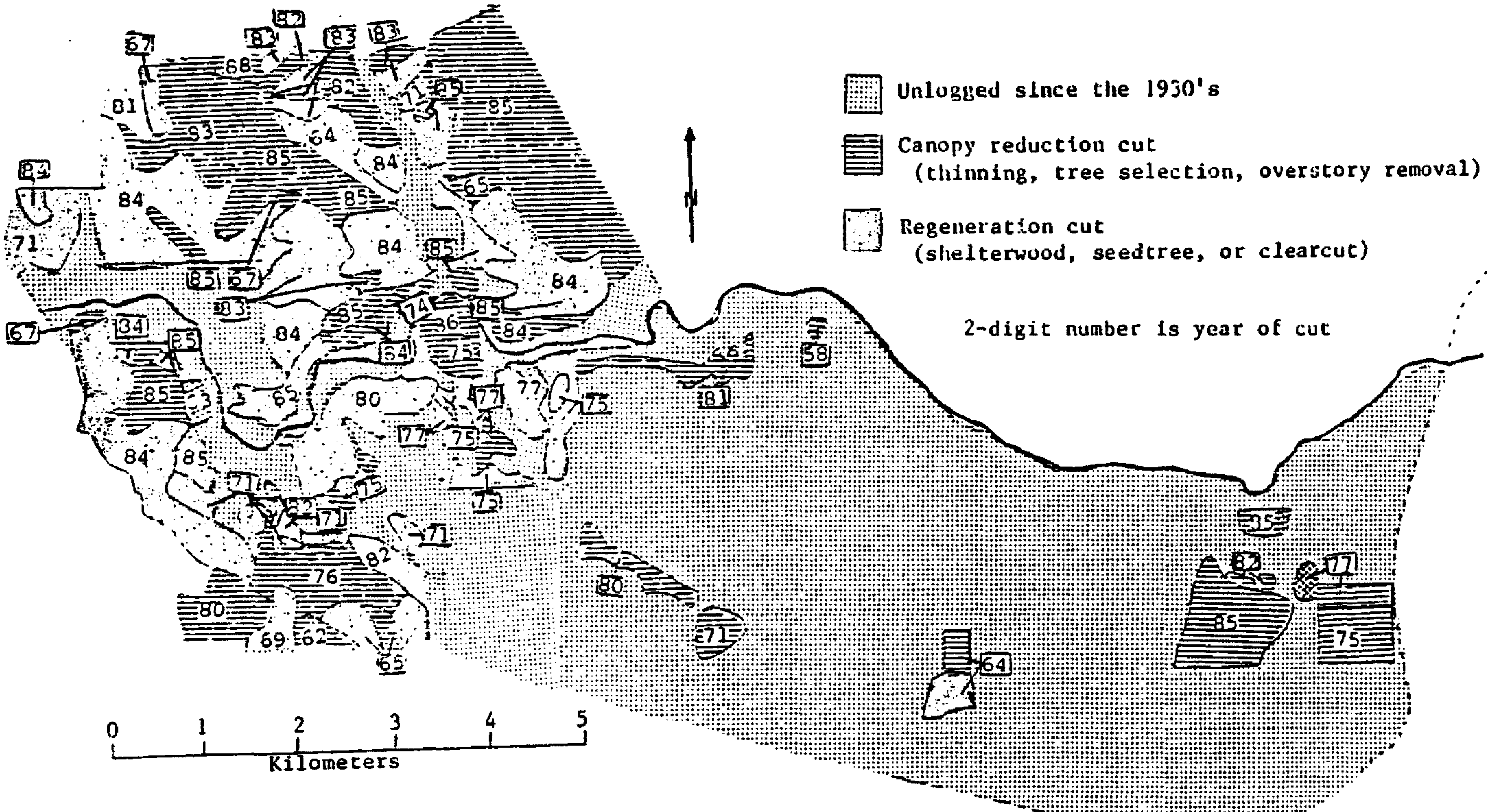
Appendix I, Part 1.
Habitat types in the western portion of the study area.



Appendix I, Part 2. Habitat types in the eastern portion of the study area.



Appendix II, part 1. Year and method of first logging treatments following logging between 1880 and 1936.



Appendix II, part 2. Year and method of last logging treatments.

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