

AN ABSTRACT OF THE THESIS OF

Winston Paul Smith for the degree of Doctor of Philosophy
in Wildlife Science presented on September 11, 1981
Title: Status and Habitat Use of Columbian White-tailed Deer in
Douglas County, Oregon.

Abstract approved: Bruce E. Coblentz
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A study conducted May 1978–December 1980 determined that the present geographic range of Columbian white-tailed deer, Odocoileus virginianus leucurus, (CWTD) in Douglas County, Oregon encompassed 1199 km². The area was predominately a Quercus woodland community, typical of the Interior Valley Zone of western Oregon. The CWTD distribution was not contiguous throughout its range; the highest densities occurred along the North Umpqua River between Glide and Wilbur. Ten habitats were described: grassland, grass-shrub, oak-savanna, open oak, closed oak, oak-conifer, oak-madrone, madrone, riparian and conifer.

CWTD exhibited a preference ($P < 0.05$) for grass-shrub, oak-savanna, open oak, closed oak, riparian and conifer habitats while selecting the remaining habitats less frequently ($P < 0.05$) than was expected from corresponding availabilities. Grassland use increased proportionally with biomass production of grasses and forbs during the spring and with mean monthly precipitation in the fall; CWTD utilized grasslands more frequently ($P < 0.05$) during the fall than in the spring. Fawns utilized woodland and brushland habitats more frequently ($P < 0.05$) than yearlings and adults; yearlings utilized grasslands more often ($P < 0.05$) and grass-

shrub habitats less frequently ($P < 0.05$) than adults. Adult males occurred less frequently ($P < 0.05$) in grass-shrub and more often ($P < 0.05$) in conifer habitats than adult females, particularly in the summer.

The population estimates for the 2745 ha study area were 628 and 740 CWTD representing an average density of 22.9 and 27.0 CWTD per km^2 , respectively. There existed a positive association ($P < 0.05$) between distribution and abundance of CWTD and the juxtaposition of suitable habitat to the North Umpqua River. A positive curvilinear relationship between CWTD density and percent woodland cover was observed; maximum densities occurred in areas supporting approximately 50% woodland cover. Fall herd composition estimates were 52 fawns and 30 bucks per 100 does. Secondary sex ratios departed from unity ($P < 0.05$) favoring males when summer rainfall was abnormally low.

Malnutrition and vehicle-inflicted injuries accounted for the largest proportion of known mortality. The ultimate cause of mortality among yearling and adult males and females was apparently associated with reproduction; these activities were more demanding ($P < 0.05$) on males. The median age at death for males (1.65) was less ($P < 0.05$) than that observed for females (2.15). Fawn survival and recruitment varied inversely with existing population densities and winter severity. Parasite loads were light and corresponded with observed seasonal differences in the physical condition of CWTD.

Convex polygon estimates of home range size for CWTD females and males averaged 21.1 ha and 32.8 ha, respectively. Elliptical home range estimates were invariably larger than corresponding convex polygon estimates and averaged 44.5 ha and 47.1 ha for females and males,

respectively. Home ranges were stable between years; however, males and females demonstrated significant shifts in center of activity among the seasons, behaviors observed to be associated with rutting and fawning activities, respectively.

CWTD and black-tailed deer demonstrated a local geographic and ecological segregation; there was a significant inverse correlation in the relative densities of the two species, and sympatric populations of black-tailed deer and CWTD differed ($P < 0.05$) in their frequency of occurrence among the ten habitats. Local geographic distributions and habitat-use patterns indicated that within preferred habitats, CWTD competitively excluded black-tailed deer.

Lowland riparian systems played a major role in CWTD ecology, representing an important environmental component in the life history of the species and serving as corridors of dispersal and recent geographic expansion.

Status and Habitat Use of Columbian White-tailed Deer
in Douglas County, Oregon

by

Winston Paul Smith

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed September 11, 1981

Commencement June 1982

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ACKNOWLEDGEMENTS

I would like to extend my sincere appreciation to a number of individuals and agencies; their cooperation, assistance, financial and logistic support, and invaluable advice and guidance represented a significant contribution to the overall success of this research endeavor.

The ranchers of Douglas County, particularly Ben Dawson, Jr., Bill Gilbreath, Clarence Gilkeson, Howard Henderlong, Richard and Julian Jones, Andy Kahn, Tom and T.J. Lindbloom, Darrell Marster and Frank Stay were very supportive and generous with their time and assistance.

I especially want to thank Wayne Mosher and Berl Oar, each of whom played a vital role in the initial organization of this project; without their help this study would have never become a reality.

The following persons assisted in the collection of field data and/or analysis: Brenda Albritton, Florence Chen, Holly Coe, Greg Kohn, Cindy Kranich, Joan Miller and Elaine Stewart. I would like to offer a special thanks to Holly Coe; her dedication and determination during the year that she assisted me in the field were an inspiration and responsible for my expecting and demanding more from myself. Ron Bartels and Larry Conn of the Oregon Department of Fish and Wildlife, the Oregon State Police and Douglas County Highway Department provided assistance in obtaining field data.

Dr. Bruce E. Coblenz, principal investigator and my major advisor during this study, provided valuable advice and suggestions

that ultimately improved the content of this thesis. Dr. Robert Anthony and Dr. W. Scott Overton were instrumental in my pursuing appropriate methods of analysis while Dr. Andrew Blaustein and Dr. Robert Storm served as committee members and provided additional constructive comments.

This study was supported by the American Petroleum Institute, the Douglas County Commissioners, the National Rifle Association's Grants-In-Aid Program, Oregon State University Agricultural Experiment Station, Oregon State University Computer Center, Roseburg Rod and Gun Club and the Wildlife Management Institute. The Oregon Cooperative Wildlife Research Unit and the Oregon Department of Fisheries and Wildlife provided logistic support.

Most importantly, I thank Jason, Jenny and Kathy for allowing me to pursue a life-long ambition. They experienced numerous inconveniences and sacrifices, suffered my frustrations and endured harassment, embarrassment and humiliation; all this for my personal edification. Their understanding, trust and encouragement during the past four years will always be remembered and appreciated.

Finally I thank Lisa Harris for typing preliminary drafts and the final copy of my thesis.

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STATUS AND HABITAT USE OF COLUMBIAN WHITE-TAILED DEER
IN DOUGLAS COUNTY, OREGON

INTRODUCTION

There are thirty recognized subspecies of white-tailed deer (Odocoileus virginianus) in North and Central America; eight subspecies of O. virginianus occur in South America (Halls 1978). The northern range includes all the southern Canadian provinces from Nova Scotia to British Columbia, and extends into the Northwest Territories (Halls 1978). White-tailed deer inhabit every state within the contiguous United States (with the possible exception of Utah), occur throughout Mexico (excluding Baja) and Central America, and extend as far south as 15° south latitude in South America (Halls 1978). In the United States, there are only three subspecies of white-tailed deer that occur west of the Rocky Mountains: the Coues' whitetail (O.v. couesi) which inhabits southern Arizona and southwestern New Mexico; the Idaho whitetail (O.v. ochrourus) which occurs in western Wyoming and Montana, most of Idaho, and portions of eastern Washington and Oregon; and the Columbian whitetail (O.v. leucurus), an inhabitant of portions of southwestern Washington, northwestern Oregon and southwestern Oregon.

The Columbian white-tailed deer, Odocoileus virginianus leucurus, was originally described by David Douglas in 1829. This taxonomic delineation was based on two co-types collected in western Oregon; one specimen was obtained from the region of the lower Columbia River and the second was collected in the Umpqua River valley in southwestern Oregon. Today, Columbian white-tailed deer

(CWTD) remain allopatric with the other western subspecies; the nearest geographic race (O.v. ochrourus) is approximately 300 km east of the eastern-most range of O.v. leucurus.

Historically, CWTD occurred throughout much of western Oregon and southwestern Washington (Fig. 1). Douglas (1829) reported that CWTD were common in the fertile prairies of the Cowlitz River and Multnomah River (Willamette River) within 100 miles of the Pacific Ocean. Apparently, CWTD preferred the oak woodlands and mixed prairies of the oak-savanna complex, a vegetative association that was characteristic of the interior river valley lowlands. Douglas (1914) reported CWTD throughout the central river bottomlands of western Oregon as far south as the Umpqua River valleys. Both Bailey (1936) and Crews (1939) concluded that CWTD originally exhibited a geographic range that extended south to Grants Pass, Oregon.

Prior to the settlement of Oregon and throughout most of the 19th century, the interior river valleys of western Oregon were largely uncultivated (Nash 1877, Douglas 1914). During this period, indians maintained an oak-savanna complex through fire management practices (Thilenius 1968). Extensive cultivation of western Oregon since early settlement has supplanted most of the native vegetative associations, leaving only patches of river bottomland associations adjacent to the largely agricultural lowlands (Thilenius 1968). Jewett (1914) and Bailey (1936) presented evidence that CWTD occurred in the Willamette Valley until late in the 19th century. Since then however, agricultural practices and curtailment of fires have altered the native habitat dramatically (Thilenius 1968); CWTD have sub-

sequently been extirpated from a large part of their historic range including the Willamette Valley. Today, the distribution of O.v. leucurus is limited to two remnant populations (Fig. 2); one is located along the lower Columbia River and the second population inhabits the interior valleys of Umpqua River in Douglas County, Oregon.

The limited distribution of CWTD and imminent threat to remaining habitat by encroaching agricultural and residential development prompted the U.S. Department of Interior to designate the Columbian white-tailed deer as an endangered species in 1968 (Gavin 1979). In 1972, the U.S. Fish and Wildlife Service purchased 2105 ha along the lower Columbia River and established the Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR). Interest in the status and ecological requirements of the refuge population prompted studies on habitat use by Suring and Vohs (1979) and population ecology by Gavin (1979).

In 1976, the Columbian White-tailed Deer Recovery Team (CWTDRT) outlined the objectives of a recovery plan to stop the decline of CWTD and maintain viable populations within the remaining suitable habitat; specific objectives included the restoration of the subspecies to a minimum population of 400 deer distributed among at least four viable subpopulations in secure habitat throughout their former range. Prior to 1978, efforts by the U.S. Fish and Wildlife Service resulted in the identification of at most three independent CWTD populations in the region of the lower Columbia River; the identification and securement of a fourth discontinuous population precludes any decisions

Figure 1. Historic range of Columbian white-tailed deer (Odocoileus virginianus leucurus) as determined from accounts by Douglas (1829, 1914), Jewett (1914), Bailey (1936) and Crews (1939).

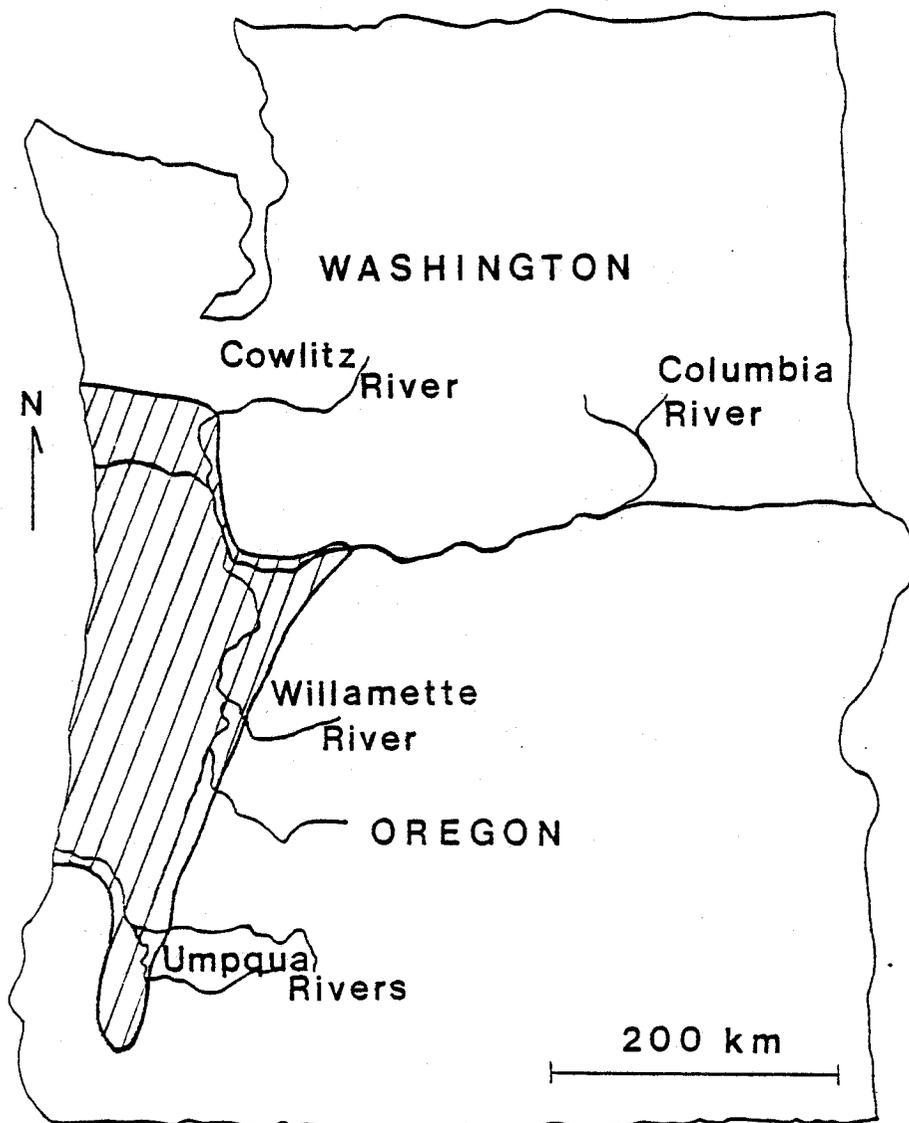


Figure 1.

Figure 2. Two geographic areas where remnant populations of Columbian white-tailed deer (Odocoileus virginianus leucurus) occur. The population along the North Umpqua River was the site of the study area.

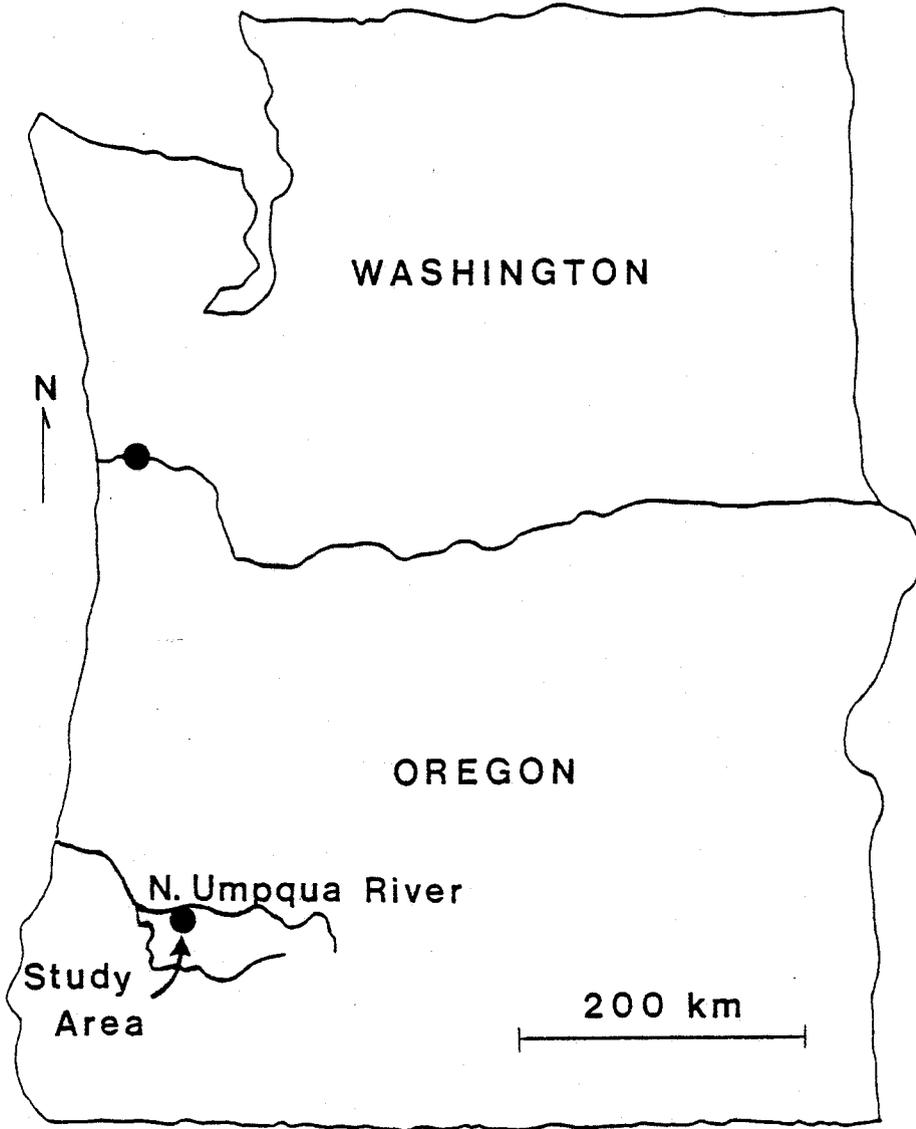


Figure 2.

regarding the removal of O.v. leucurus from the endangered species designation.

Surveys conducted by the CWTDRRT just prior to the completion of the 1976 recovery plan documented the occurrence of whitetails along the North Umpqua River in Douglas County; the status and ecology of this population however was unknown. The importance of maintaining a viable population in Douglas County soon became apparent to the recovery team; this population not only represented the crucial fourth subpopulation, it was the only CWTD population within the southern three-fourths of the historic range of CWTD. The members of the CWTDRRT and U.S. Fish and Wildlife personnel agreed that a stable CWTD population in Douglas County would increase the likelihood of CWTD ever reoccupying major portions of its native range.

During the winter of 1977-78 and the following spring, preliminary observations conducted by Oregon State University disclosed that the distribution of CWTD in Douglas County might be limited to private ranchlands; it was apparent that an impending conflict existed between increasing agricultural development and the availability of suitable CWTD habitat. In July of 1978 the U.S. Fish and Wildlife Service included the Douglas County population in the endangered species designation and immediately initiated efforts to protect and maintain a viable population. Upon the recommendation of the CWTDRRT and U.S. Fish and Wildlife Service, the Department of Fisheries and Wildlife, Oregon State University undertook a study that eventually would provide the ecological basis for the management

of the largest of the four CWTB populations.

This paper examines data recorded during a 27-month ecological study of CWTB in Douglas County, Oregon. It represents the culmination of an extensive and intense research effort to obtain fundamental life history information and determine the ecological requirements of the CWTB population that inhabits the Umpqua River interior valleys. Since virtually nothing was known about this population, we sought to document the present-day geographic distribution and estimate relative abundances within this portion of the CWTB native range. Of primary importance was defining critical habitat as well as determining its relative abundance, distribution and availability.

In addition to a gross description of the CWTB population, our general study plan outlined an intense research program to be conducted on a representative portion of the CWTB range. A study by Crews in 1939 and incidental observations recorded by Bill McCaleb (ODFW) during the 1950s and 1960s identified relatively high CWTB density areas and provided the basis for defining our study area. The objectives of our research effort focused on determining several population characteristics including total population size, density and dispersion, sex and age composition, proximate and ultimate mortality factors and recruitment. We also felt that it was important to examine daily and seasonal habitat use with respect to the availability of these various vegetative associations; this information would facilitate determining the relative importance of specific habitats through a calculation of relative preference indices.

Moreover, an extensive habitat sampling program would provide a quantitative characterization of the preferred vegetative associations. Finally, we thought that by monitoring the movements of marked individuals in the population we could arrive at some understanding of spatio-temporal activity patterns; examining seasonal home range dynamics with respect to phenology should provide some insight into why CWTD exhibited specific habitat preferences. An analysis of these data within the context of overall population trends, as determined from past and present-day geographic distributions and relative abundances, should provide an ecological foundation from which proper management recommendations can be formulated.

THE STUDY AREA

The study area is located in Douglas County in southwestern Oregon (Fig. 2), situated along the North Umpqua River between Winchester and Glide. It is comprised of portions of sections 11, 14, 20, 23, 29, 32, and 33 in T26S, R5W; portions of sections 7, 16, 17, 18, 19, 20, 21, and 30 in T26S, R4W; and sections 15, 21, 22, 25, 26, 27, and 28 of T26S, R5W, constituting 2745 hectares (Fig. 3).

The topography is typical of the Umpqua and Rogue interior valleys with numerous small mountains and rolling foothills producing a mosaic of small valleys and ridges. The elevation on the study area ranges from 135 meters above sea level along the North Umpqua River to 505 meters above sea level - a ridge crest which forms a portion of the southern boundary of the study area.

Temperatures along the interior Umpqua valley are moderate; the mean monthly maximum temperature was 20.2°C in August, and the mean monthly minimum was 4.9°C in January, the hottest and coldest months, respectively (United States Department of Commerce 1955-1980). The mean annual temperature (12.1°C) remains fairly consistent from year to year, however, annual precipitation may vary considerably (eg. 55.9 cm recorded in 1978 compared to 90.4 cm recorded in 1979). The mean annual precipitation 1955-1979 was 84.1 cm, with an average of 67.8 cm falling from October to March, producing wet winters and semi-drought summers. Snow cover is uncommon and rarely persists for more than a few days.

The natural vegetation of the area is classified as Quercus

Woodland community, and is typical of the Interior Valley Zone of western Oregon (Franklin and Dyrness 1973). The Quercus Woodland community represents a diverse array of vegetative associations, ranging from the sparsely stemmed stands of the oak-savannas with predominately grass understories, to the dense forests with well-developed mid-stories. Species composition of the oak woodland community may vary from pure Quercus types to communities with an abundance of other hardwood and conifer associates; particularly Arbutus menziesii, Acer macrophyllum, Pseudotsuga menziessi and Pinus ponderosa.

The oak woodlands are dominated by an overstory of Quercus garryana and Q. kelloggii, and generally occupy the more xeric sites. Quercus density decreases and the predominance of grass balds increases on increasingly xeric sites, particularly southern and southwestern slopes. The more mesic sites, generally northern exposures and/or higher elevations, are occupied by open stands of P. menziesii, P. ponderosa, and Libocedrus decurrens over a well-established Quercus canopy. The major shrub species are Rhus diversiloba, Holodiscus discolor, Corylus cornuta, and Rosa elganteria *(asterisk indicates introduced species). Dominant perennial grasses include Danthonia californica, Lolium perenne *, Festuca arundinacea *, and Holcus lanatus *. Bromus mollis *, Cynosurus echinatus *, and Taeniatherum asperum * represent the predominant annual grasses.

Black-tailed deer (Odocoileus hemionus columbianus) occur throughout most of the study area, but were generally observed in areas supporting low whitetail densities. Among the several potential

Figure 3. The study area situated along the North Umpqua River between Winchester and Glide, Douglas County, Oregon is outlined in black; the North Umpqua River represented the northern boundary.

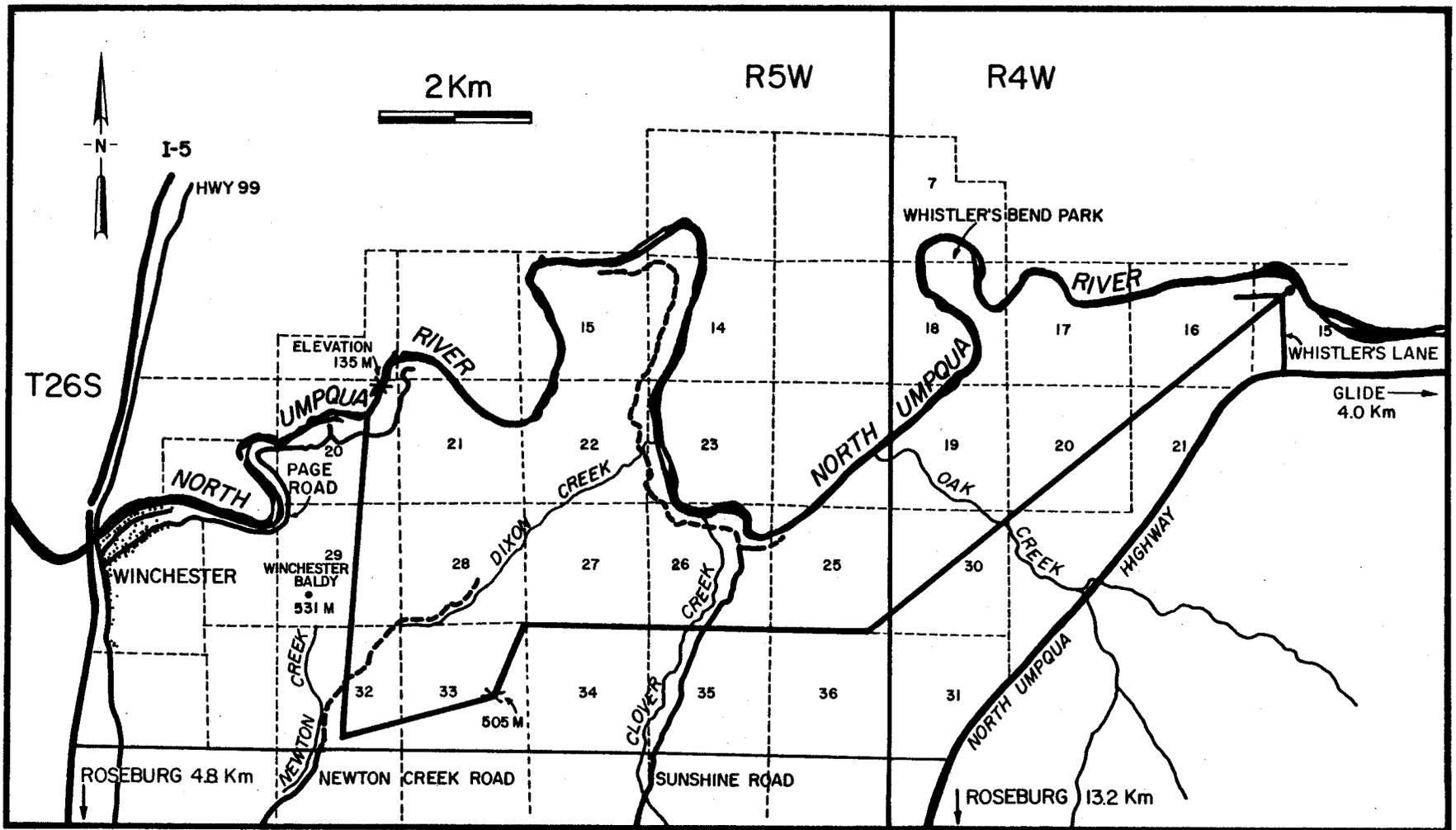


Figure 3.

predators occurring on the study area, red foxes (Vulpes vulpes) and stray domestic dogs (Canis familiaris) were encountered most frequently. Coyotes (Canis latrans) and bobcats (Felis rufus) were uncommon - owing to an intensive predator control program maintained by Douglas County.

The earliest detailed accounts of the interior Umpqua Valley were provided by David Douglas (1914). During his expedition in 1827, Douglas (1914) noted the predominance of oak woodlands throughout much of the low-lying interior Umpqua Valley, and emphasized that much of the area had been burned. Burning was a common practice of the indians, used to encourage deer to frequent certain feeding areas (Douglas 1914). With the arrival of white settlers, many of the prairies and grasslands which occupied extensive areas of the interior valleys became forests and woodlands, a consequence of less frequent fires (Nash 1882). Because of the abundance of native grasses, livestock production soon became the primary land use (Nash 1882). Increased livestock use and farmland development (i.e. clearing and/or burning) during the years that followed created new grasslands and savannas. By the 1920's, about 90% of the study areas was used for grazing with the remaining 10% under cultivation (Crews 1939). Today, the study area is in private ownership (except for Whistler's Bend County Park and 3 Bureau of Land Management (BLM) parcels totaling 81.5 ha.). Agricultural development and livestock production have intensified resulting in greater demands for improved pasture. Burning and clearing are still practiced over much of the study area - a consequence of which has been an 18.3% (183.7 ha.) reduction in available woodland cover since 1972.

MATERIALS AND METHODS

Field observations were conducted May-August 1978. Data were collected also during periods of observation conducted on week-end trips to the study area in September, October and November 1978, and in January, February and March 1979. Full time field studies resumed May 1979 and continued uninterrupted through August 1980. Vegetative data collected during the fall of 1980 and observations of marked deer during the period September-December 1980 were included also. Deer were observed through 9 X 36 binoculars and a 20X spotting scope.

Botanical and zoological nomenclature followed Hitchcock and Cronquist (1973) and Verts (1978) respectively. Arcsin and square root transformations were utilized with data expressed as percentages; the arcsin transformation was employed with data exhibiting a wide range of values, whereas the square root transformation was used with percentages between 0-20 or 80-100 (Steel and Torrie 1980:234). Yates' continuity correction was employed with frequency data when N was less than 50 (Sokal and Rohlf 1969:590). Unless otherwise noted, a probability level of less than 0.05 was accepted as indicating statistical significance.

Geographic Range

An estimate of the geographic range of the Douglas County CWTD population was obtained by plotting new locations on United States

Geological Survey topographical maps. Investigations, prompted by reports of CWTD in previously undocumented areas, provided additional distribution data. The investigations involved spotlighting those areas accessible by vehicle, traversing the area on horseback, or traversing the area on foot during the early morning and/or early evening hours. The geographic range was then calculated by connecting all the repeatable ($n \geq 2$) peripheral observations recorded on the topographic maps to form the smallest polygon that contained all the locations (Jennrich and Turner 1969). The area of the polygon served as an estimate of the total geographic area inhabited by the CWTD population, and was calculated according to the following equation

$$A = 1/2 \sum_{i=1}^n (x_i y_{i+1} - x_{i+1} y_i) \quad \text{Equation 1}$$

Equation 1 was multiplied by 0.49 to obtain the area of the geographic range in km^2 , as determined from the scale of the map and grid system.

Habitat Description

A general reconnaissance of the study area during the initial field season (May-August 1978) provided the basis for subdividing the Quercus Woodland community into 10 distinct habitats. Differences in species composition and structure (e.g. absence or presence of one of the three major vegetative strata) served as the primary criteria for delineating habitats. During the period June-August 1979, the habitats were sampled intensively, 14.2% (388.3 ha.) of the total study area. Whenever possible, data from 3 replicate areas of each habitat were collected. The number of plots per sample ($n=50$ for each

replicate) was derived from the precision of preliminary samples (Pieper 1978:9). A random-systematic sampling scheme was devised such that plots were located along a predefined transect that began at a randomly selected starting point. The distribution of plots (i.e. distance between plots) was adjusted among each of the samples so as to ensure that the entire habitat site would be included in the sampling procedure.

Herbaceous cover (% crown cover of grasses, forbs, and Rhus diversiloba during its first growing season) was estimated within a 2 X 5 dm plot (Daubenmire 1959). A cover class (derived from the estimated percentage of ground surface covered by vegetation) was assigned to each herbaceous species which occurred within the plot (Daubenmire 1959). Cover class estimates of litter and bare ground were also recorded. Percent frequency of occurrence and relative dominance (derived from % crown cover) of each species were calculated.

The line-intercept method was employed to estimate shrub crown cover (Canfield 1941). Intercept lines were incorporated within the general sampling scheme, extending from each plot site along the predefined transect. The intercept of each shrub species along a 20 meter intercept line was measured (to the nearest cm) with a metric tape. The total amount of intercept was summed for each line; cover and botanical composition were computed (Pieper 1978:81). The botanical composition served also as an index of relative dominance (as derived from % crown cover).

An estimate of canopy cover was obtained at each of the 50 plots within a sample with a forest densiometer (Lemmon 1956). The point-

centered quarter method (Cottam and Curtis 1956) was employed to obtain an estimate of tree density and relative dominance (as derived from basal area). The center of a plot served as the sampling point, and the distance (in cm) to the nearest tree in each of four quadrats was measured. In addition to the tree species, and its diameter at breast height (dbh), basal area and relative dominance were determined.

An obstruction-of-vision estimate was obtained at each of the 50 plots within a sample with a density board (Wight 1938). A reading was taken from a point 20 meters beyond the plot along the predefined transect, and the summed total was recorded. Also, the slope and aspect of each plot were determined.

Seasonal estimates of herbaceous cover and obstruction-to-vision were obtained in conjunction with phenological observations to provide a basis for evaluating white-tailed deer habitat preferences.

Collection of Habitat-Use Data

Habitat-use observations were conducted from horseback along a predefined transect (61.5 km), July 1979 - August 1980. The transect route was designed to include the habitats proportional to their occurrence on the study area. Starting times and locations differed systematically so as to collect data from each section of the transect for all obtainable time periods, and to minimize bias resulting from differences in individual patterns of behavior. Also, habitat-use data were collected during early morning and evening observation

periods, during spotlight censuses and while engaged in other activities (e.g., vegetation sampling) during the period May 1978 - August 1980. CWTD data were analyzed with multi-dimensional contingency tables in which the frequency of observations for each age and sex class were examined with respect to habitat, time of day, season and activity. Observations of seasonal habitat-use by black-tailed deer were recorded and compared to CWTD data. Chi-square goodness-of-fit tests (Sokal and Rohlf 1969:552) and Chi-square tests of independence (Sokal and Rohlf 1969:589) determined the statistical significance of observed departures from the expected, and provided the criteria for further analysis.

Additionally, seasonal spatial distributions of white-tailed deer and black-tailed deer throughout the study area were recorded on aerial photographs. Chi-square tests of independence (Sokal and Rohlf 1969:589) and the Runs Test (Siegel 1956:57) determined significant departures of the spatial distributions and sequence of observations from independence and randomness, respectively.

Capture, Handling and Marking

Deer were captured and marked throughout the entire study period. Several methods were employed to capture deer; including the remote injection of an immobilizing drug fired from a Cap-Chur gun (Palmer Chemical and Equipment Co., Inc., Douglasville, Georgia), and live-trapping with a three-sided drop-gate panel trap

(Oregon Department of Fish and Wildlife). Tranquilizing darts filled with a combination of ketamine hydrochloride¹ and xylazine hydrochloride², or nicotine salicylate, were fired at deer from a vehicle 10-40 m away. Selected drug dosages were 2.0 mg/kg, 2.5 mg/kg, and 5.5 mg/kg for xylazine hydrochloride, ketamine hydrochloride, and nicotine salicylate respectively. Also, during the period June 1979 - March 1980, six panel traps baited with a mixture of corn oats and barley, apples, and unprocessed molasses were set and checked daily. Fawns less than two weeks old were located by walking through grasslands, brushlands, and woodlands with the aid of a trained dog; and by observing the behavior of adult females (Downing and Mc Ginnes 1969). Once located, fawns were either immediately captured by hand, or with older fawns, pursued by the dog and restrained until capture was accomplished.

Captured deer were examined closely; sex, age, general physical condition, and a series of morphological measurements were recorded. Age determination in fawns followed criteria presented by Haugen and Speake (1958). External parasites were noted, and collected for identification. The rectal temperature of fawns along with the ambient temperature at examination time were recorded. All individuals were ear-tagged with numbered, color-coded Allflex livestock tags (Vet Brand, Inc., California). The color and placement of the tags allowed immediate sex and age determination, while the numbers facilitated the identification of specific individuals. Fawns cap-

¹Ketaset^R, Bristol Laboratories, Syracuse, NY 13201

²Rompun^R, Cutler Laboratories, Inc., Shawnee, KS 66201

tured during the 1979 and 1980 fawning seasons were fitted with motion-sensitive mortality transmitters (Model number LT24-2TS-HD-MS, Telemetry Systems, Inc., Wisconsin, 1978 catalog). A model RT20-A receiver and a model A-147-4 Cush Craft 4-element antennae (Telemetry Systems, Inc., Wisconsin, 1978 catalog) were employed to locate radio-collared fawns. Tranquilized deer were kept under constant surveillance until complete recovery was attained. All deer over 6 months of age were fitted with a white polyvinylchloride collar bearing large red luminous numerals of reflectant tape. The numerals were laminated with polyurethane and served to identify specific individuals.

Estimation of Population Size

The cohort of marked deer (i.e. yearlings and adults) was used as part of a capture-recapture ratio estimator (Schnabel, in Chapman and Overton 1966) of population size, in which observations subsequent to capture served as recaptures. Deer were observed while spotlighting (November 1979-January 1980) and during early morning censuses (November-December 1979 and August 1980) along a 10.5 km route through the intensive study portion of the study area. The starting point for each census within a censusing period differed in an attempt to minimize bias resulting from possible differences in individual patterns of behavior, whereas starting times within a censusing period remained consistent. During a census, the total number of marked and unmarked deer were recorded; the identity of each marked individual was noted. These data were compiled with other census data within a census period to provide a continuous total of

marked and unmarked deer for that period.

There are a number of assumptions inherent in capture-recapture methods for population estimation. Overton (1971:434) summarized these in the following statements:

1. There exists a well defined collection (population) of animals containing N individuals.
2. M of these individuals are marked, for example with a tag.
3. There exists a sample of n observations of animals from the population, containing x observations of marked animals.
4. The average probability \bar{p}_m of observing a marked animal is equal to the average^m probability \bar{p}_u of observing an unmarked animal. That is, $\bar{p}_m = \bar{p}_u$.

Although a large proportion of the census data was classified according to age and sex, the small number of marked individuals in some of these cohorts and the paucity of recaptures of these marked individuals precluded the use of the census data in a stratified population estimate. Therefore, an unstratified Schnabel population estimate was calculated for each census period (i.e. November, December, January and August) following the method and notation presented by Chapman and Overton (1966:173). To estimate population size, let

$$x = \sum_{i=1}^k x_i = \text{number of recaptures} \quad \text{Equation 2}$$

$$= \sum_{i=1}^k (n_i M_i) \quad \text{Equation 3}$$

where

x_i is the number of marked animals "captured" in the i^{th} day,
 n_i is the total numbered captured in the i^{th} day,
 M_i is the number of marked animals in the population in the i^{th} day

then

$$N = \lambda / x+1 \quad \text{Equation 4}$$

Confidence limits were computed for each population estimate following Chapman and Overton (1966:174, Table 1) for $x < 50$, where x approximates a Poisson distribution. When x was greater than 50, it was necessary to use the normal approximation to the Poisson to obtain the lower (\underline{x}) and upper (\bar{x}) limit (Overton 1971:435),

$$\underline{x} = (x+2) - 2 \sqrt{x+1} \quad \text{Equation 5}$$

$$\bar{x} = (x+2) + 2 \sqrt{x+1} \quad \text{Equation 6}$$

and solve the inequality for N :

$$P\{\underline{x} \leq \frac{\lambda}{N} \leq \bar{x} + 1 - \alpha\} \quad \text{Equation 7}$$

Tests for statistically significant differences in population estimates among census periods (months) or between census techniques (i.e. spotlighting versus early morning census) within a census period employed the following test statistic from Chapman and Overton (1966:175):

$$Z = \frac{x_0 - (x_0 + x_1) \frac{\lambda_0}{\lambda_0 + \lambda_1} \pm 1/2}{(x_0 + x_1) \left(\frac{\lambda_0}{\lambda_0 + \lambda_1} \right) \left(\frac{\lambda_1}{\lambda_0 + \lambda_1} \right)} \quad \text{Equation 8}$$

The Schnabel estimate provided an estimate of the total number of deer inhabiting the intensive study portion of the study area (Fig. 4), yet provided no direct means of obtaining a population density estimate from which the total population size of the entire study area could be derived.

Density estimates for the intensive study site were derived from the total area encompassed by the smallest polygon constructed

from the peripheral observations of the marked deer within this portion of the study area and from the area sampled during spotlight censuses as determined from aerial photographs and a series of measurements. These measurements incorporated effective identification distances (i.e. the maximum distance deer could be accurately identified), as determined from preliminary spotlight censuses and provided an estimate of the total area (ha) sampled during a census when multiplied times the length of the spotlight route.

Similar measurements were obtained within other portions of the study area and provided a means by which comparable density indices could be computed for the different habitat structure types. These relative density indices represent simply an expression of the total number of CWTB observed within a given habitat structure type divided by the total area sampled during the census. Assuming a correspondence between the density index and the Schnabel estimate obtained for the intensive study area, one could derive an estimate of total population size for the entire study area. A population density coefficient (D.C.) was obtained for each habitat structure type according to the following equation

$$D.C. = \frac{\text{relative density of habitat structure type}}{\text{relative density of intensive study area}} \quad \text{Equation 9}$$

The population estimate was calculated with the following expression

$$N_i = (D.C.)(\text{total area})(\text{density of intensive area}). \quad \text{Equation 10}$$

In order to insure comparable density indices, spotlight censuses were conducted throughout the study area simultaneously with the help of ODFW personnel and vehicles.

Figure 4. The intensive study portion of the study area. (See Figure 3 for relative location within entire study area)

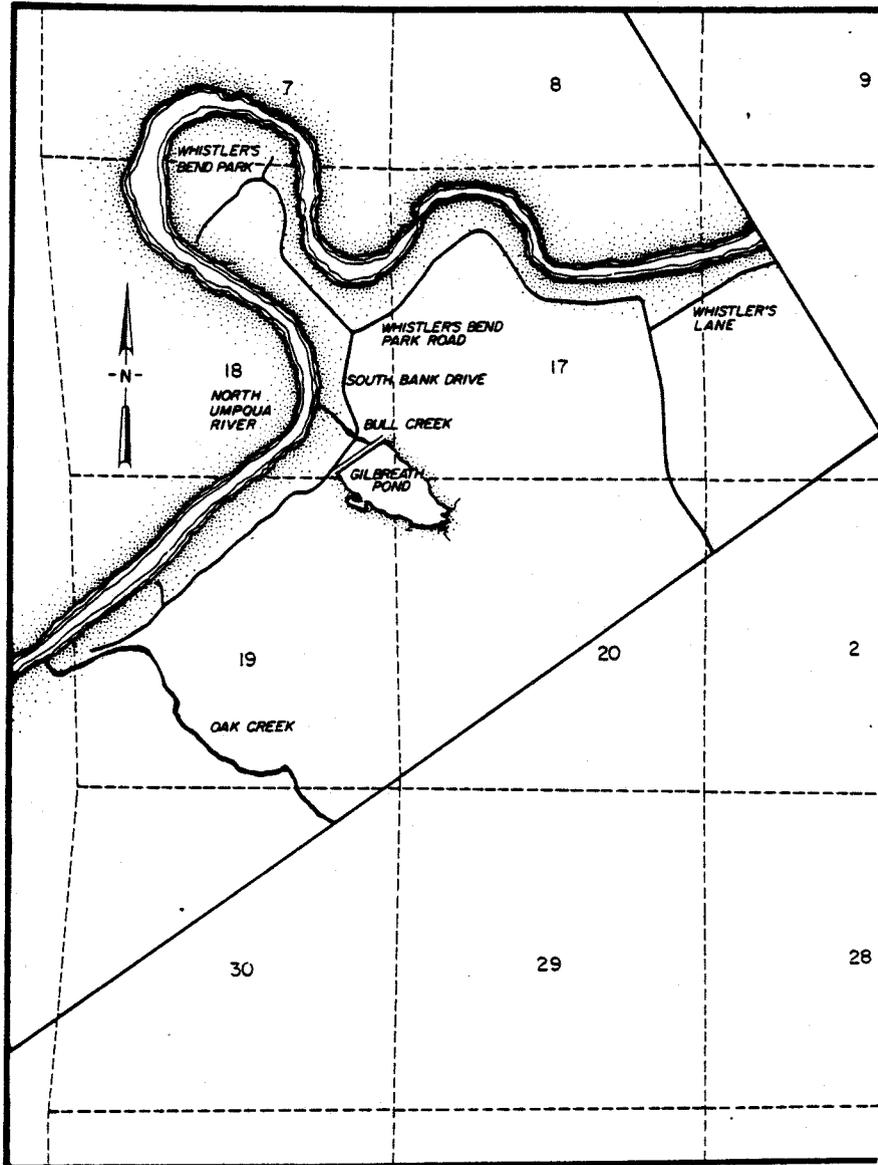


Figure 4.

Sex and Age Composition

The sex and age composition of the population was derived from observations recorded during spotlight, early-morning, and horseback censuses, June 1979-August 1980. Observations were classified according to the following sex and age classes: adult male, adult female, yearling male, yearling female, adult unknown, yearling unknown, fawn, or unknown. During the period December 1-May 1, adult and yearling females were combined into the single class does; adult and yearling males were classified as bucks whenever age was not discernible. Also, an antlerless deer category was used during the period February 1 - May 31 when males were generally indiscernible. June 1st was selected as the anniversary date; age delineations were as follows: fawn, birth-12 months; yearling, 12-24 months and adult, more than 24 months of age. Behavior, relative size, general body conformation, particularly the length and shape of the head, and the presence or absence of antlers served as criteria for classification (Gavin 1979). Adult and yearling males were discriminated on the basis of the number of tines; justification for which was provided by observations of known yearling males (n=33).

Collection of Mortality Data

The remains of dead deer were collected and examined throughout the study period. Road kills were obtained from ODFW, Oregon State Police (OSP), Douglas County Highway Department (DCHD), and as a result of reports from local ranchers and residents. Other mortalities were obtained through systematic searches conducted period-

ically, searches conducted within specific areas prompted by reports from local ranchers, observations of radio-collared fawns and through incidental observations (i.e. while engaged in other activities).

Once obtained, the sex, age, location, cause of death, and time of death were recorded. Also, whole weight and a series of morphological measurements were obtained for intact carcasses. Whenever possible, detailed necropsies were performed by veterinary pathologists. Generally however, field examinations were conducted; information regarding cause of death, physical anomalies and internal parasites were recorded. Often information concerning cause and time of death was provided by local ranchers. A physical condition index (PCI) derived from observed body fat deposits (Kistner et al. 1980) was obtained for recent intact mortalities. Whenever available, a rumen sample, fecal sample, skull and lower jaw, right kidney, right femur and external parasites were collected.

Fecal samples were preserved in polyvinyl alcohol (PVA) and formalin, and examined by a parasitologist at a later date. The PVA fecal samples were stained with a modified tri-chrome procedure (Markell and Voge 1965:292) while the formalin fecal samples were subjected to a formalin-ethylacetate concentration technique (Wheatley 1951). Fawn and yearling mortalities were aged according to tooth replacement (Severinghaus 1949). To age adults, a second premolar was extracted from each skull or lower jaw, sectioned with a microtome, decalcified with Cal-Ex II¹ and made into permanent

¹Cal-Ex II^R, Fisher Scientific Company, Fairlawn New Jersey 07410

stained slides with Paragon stain² (Crowe 1972). The slides were examined at 20-60 X with a binocular microscope and the number of cementum annuli were recorded.

Home Range Indices

Marked deer were observed from horseback, during early morning and spotlight censuses, and while engaged in other data collection, June 1978- December 1980. The location of each observation was plotted on 3.5 by 3.5 cm aerial photographs (scale: 1 cm = 120 m); date, time and activity (e.g., feeding, bedded) were recorded. Also, the age and sex of any deer associated with the marked individual were recorded. Consistent with previous studies of CWTD (Gavin 1979), sightings of marked individuals which occurred within 60 minutes of a previous observation were excluded in order to ensure independence of observations. Only location data from deer that were observed on at least 20 different occasions were included in the analysis. Adults and yearlings were included only if the total period during which observations were obtained for a certain individual exceeded four months. All locations were assigned X-Y coordinates derived from a master aerial photograph-grid system and employed in calculations of home range indices.

Home range estimates were obtained with two independent techniques. The first method involved drawing the smallest convex polygon that encompassed all of the capture points (excluding

²Paragon, Paragon C and C Co., Inc., 190 Willow Ave., Bronx, New York

inaccessible areas); the enclosed area served as an index of the animal's home range (Jennrich and Turner 1969:228). The capture points were ordered counterclockwise about their geometric center and the area of the polygon computed with the following equation

$$A = 1/2 \sum_{i=1}^n (x_i y_{i+1} - x_{i+1} y_i) \quad \text{Equation 11}$$

where (x_i, y_i) is the i th ordered capture point from a total of n points and $(x_{n+1}, y_{n+1}) = (x_1, y_1)$.

Home range indices were calculated also with a bivariate normal model described by Jennrich and Turner (1969), as modified by Koepl et al. (1975). This model, designed to evaluate non-circular as well as circular home ranges, portrays the area an animal occupies during its normal daily activities as a $(1-\alpha) \times 100$ confidence ellipse, and is computed with the determinant of the capture points covariance matrix. The area of the home range, as corrected for sample size and orientation of the ellipse (Koepl et al. 1975:85), is given by the statistic:

$$A_p = s_{xT} s_{yT} \frac{2(n-1) F_{\alpha(2, n-2)}}{(n-2)} \quad \text{Equation 12}$$

where s_{xT} and s_{yT} are transformed standard deviations of the major and minor axes of the ellipse, respectively, and the expression $\frac{2(n-1) F_{\alpha(2, n-2)}}{(n-2)}$ incorporates the F-statistic to adjust for sample size. The subscript p in the expression A_p represents the probability of inclusion for which the home range is being computed, such that, for $p = 0.95$, equation 12 represents a home range estimate which accounts for 95% of an animal's utilization of its habitat

(Jennrich and Turner 1969). Equations 11 and 12 were multiplied by 0.01486 to obtain the home range size in hectares, as determined by the scale of the grid system.

Elliptical home range models (Jennrich and Turner 1969, Koepl et al. 1975) require that the locational data approximate a bivariate normal distribution. In their model, Koepl et al. (1975) translated and rotated the locational data so that a measure of variability along the grid X or Y axis corresponded to a measure of variability along the major or minor axis of the ellipse, respectively, and so the center of activity was at coordinates (0,0) (Fig. 5). Additionally, if the difference of the mean X and mean Y from the coordinates is divided by the respective standard deviations (i.e. $X_T = (X - \bar{X}) / SD_X$, $Y_T = (Y - \bar{Y}) / SD_Y$), then a set of standardized and rotated coordinates (Z_1, Z_2) with zero mean and unit variance is defined. The sum of squares of these new coordinates follows approximately the theoretical Chi-square distribution with $k-1$ degrees of freedom, where k is the number of classes used in computing Chi-square (Moore and Stubblebine, in press).

A bivariate normal distribution can be viewed as representing a series of concentric contours of equal density (Fig. 6). That is, given n observations distributed among k contours one would expect n/k observations per contour. Given an expected number of observations per contour, the conformance of a set of bivariate locations to a bivariate normal distribution can be evaluated by determining the observed frequency distribution of locations among the contours and calculating the Chi-square statistic according to the following

equation (Sokal and Rohlf 1969:556)

$$\underline{\chi}^2 = \Sigma(f_i - \hat{f}_i)^2 / f_i \quad \text{Equation 13}$$

where f_i is the observed frequency distribution among the contours, and \hat{f}_i is the expected frequency distribution among the contours. This procedure is analagous to a Chi-square goodness of fit test for continuous univariate distributions; here the cells are replaced by contours.

To determine the observed frequency distribution, a numerical value must be computed for each contour according to the following equation (Moore and Stubblebine, in press)

$$C_i = -2 n(1-i/k) \quad \text{Equation 14}$$

where C_i is the i th contour, and k is the total number of contours. The contour values represent intervals within which the standardized and rotated locational data are distributed. The segregation of the locational data among the respective contour intervals was accomplished through the mathematical evaluation of Z_1 and Z_2 according to the expression $(Z_1^2 + Z_2^2)$. The observed frequency is obtained then by comparing the resolved sum of squares expression for each coordinate pair (Z_1, Z_2) to the respective contour values, and tabulating the number of coordinate pairs that fall within each contour interval.

Enumeration of contours for a specific test can be somewhat arbitrary. To remain consistent when evaluating numerous sets of locational data however, I have specified two criteria for determining the number of contours:

Figure 5. Orientation of ellipse with respect to fixed grid X and Y axes. Line segments \overline{ab} and \overline{cd} represent major and minor axes of ellipse, respectively. θ designates angle through which coordinate pairs are rotated, and (\bar{X}, \bar{Y}) denotes the center of activity.

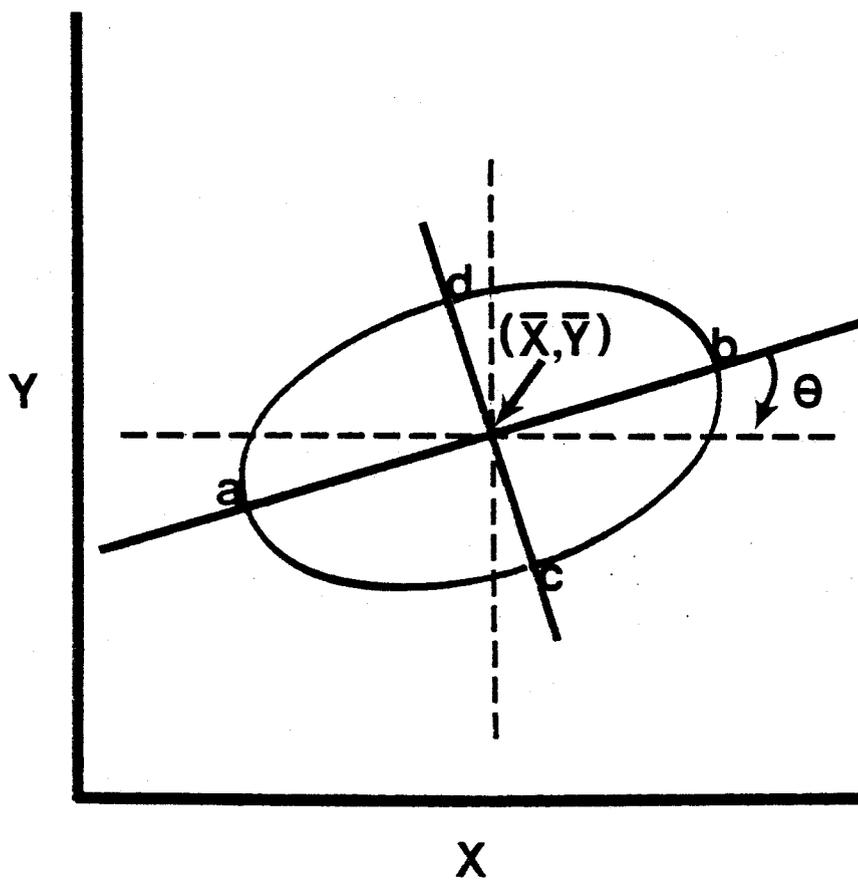


Figure 5.

Figure 6. Bivariate normal distribution as represented by a series of concentric contours of equal density.

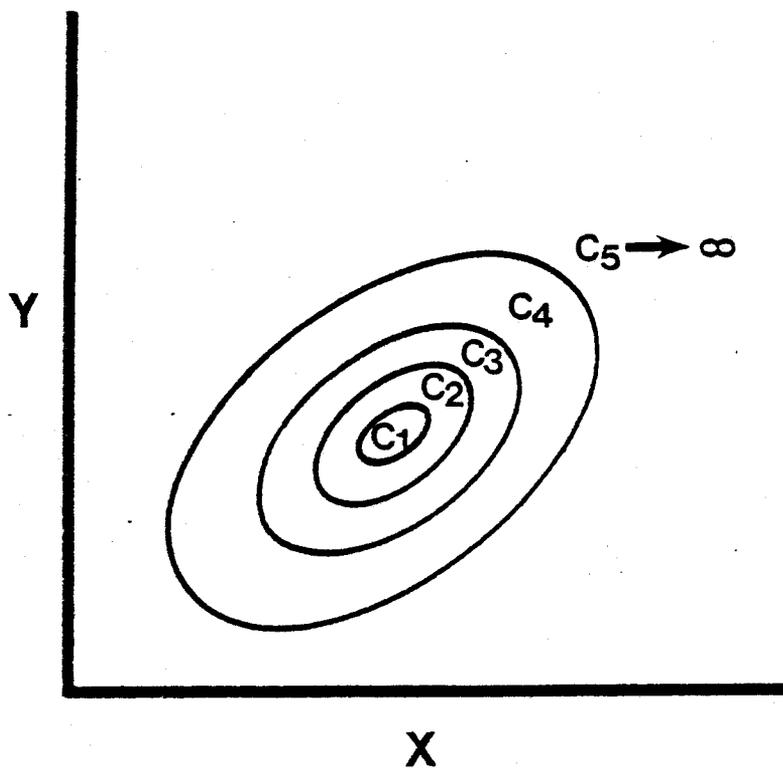


Figure 6.

(1) A minimum of five observations per cell

(2) The number of contours equals the greatest integer

that can be obtained from $n/5$ observations.

The first criterion follows the general rule for establishing classes when employing the Chi-square goodness of fit test for continuous distributions (Steel and Torrie 1980:474). The second criterion maximizes the degrees of freedom ($d.f. = k-1$) and consequently increases the sensitivity of the test, i.e. provides a smaller tabular critical Chi-square value.

A Fortran IV program designed to test the conformance of locational data to bivariate normality according to the foregoing procedure is presented in Appendix A.

The Chi-square goodness of fit test is not conclusive, as it is not as sensitive to departures from bivariate symmetry (Moore and Stubblebine, in press). For this reason a test for skewness (G_1) (Sokal and Rohlf 1969:113) was employed in instances when a significant departure from normality did not occur with the Chi-square test. If Z_1 and Z_2 are jointly distributed, then Z_1 and Z_2 are each normally distributed (Neter and Wasserman 1974:395), conformance of which can be further substantiated with the univariate test for skewness.

RESULTS AND DISCUSSION

GEOGRAPHIC RANGE

The present geographic range of the CWTD population in Douglas County extends from Oldham Creek - 8.0 km northeast of Oakland, south to Cow Creek - 4.8 km southwest of Riddle. The southeastern-most observations were along Morgan Creek - 1.5 km north of its intersection with the South Umpqua River, whereas the northwest boundary extends to the town of Umpqua. The eastern and western boundaries were Fall Creek - 0.5 km south of Little River, and Hawkins Lake (BLM), respectively, encompassing a total of 1199 km² (463 mi²) (Fig. 7). The whitetail distribution is not contiguous throughout its geographic range, owing to the interspersed small mountains and associated coniferous forests. The highest whitetail densities were observed in the region between Glide and Winchester, north of Buckhorn Road and south of the North Umpqua River (Fig. 8) in which Quercus woodland predominated.

Crews (1939) reported the distribution of "Oregon white-tailed deer" (O.v. leucurus) was limited to a small area northeast of Roseburg, within this same high density region (Fig. 8), and encompassed approximately 79 km². Observations recorded during the 1960s, and intensive spotlight counts conducted in 1970 indicated that the old White-tailed Deer Refuge supported the highest densities of CWTD (William McCaleb ODFW, unpublished data). This area described by Crews (1939) and McCaleb (personal communication) apparently represented the recent center of dispersal for the Douglas County herd.

Figure 7. Geographic distribution of Columbian white-tailed deer
(Odocoileus virginianus leucurus) in Douglas County, Oregon,
1978-1980.

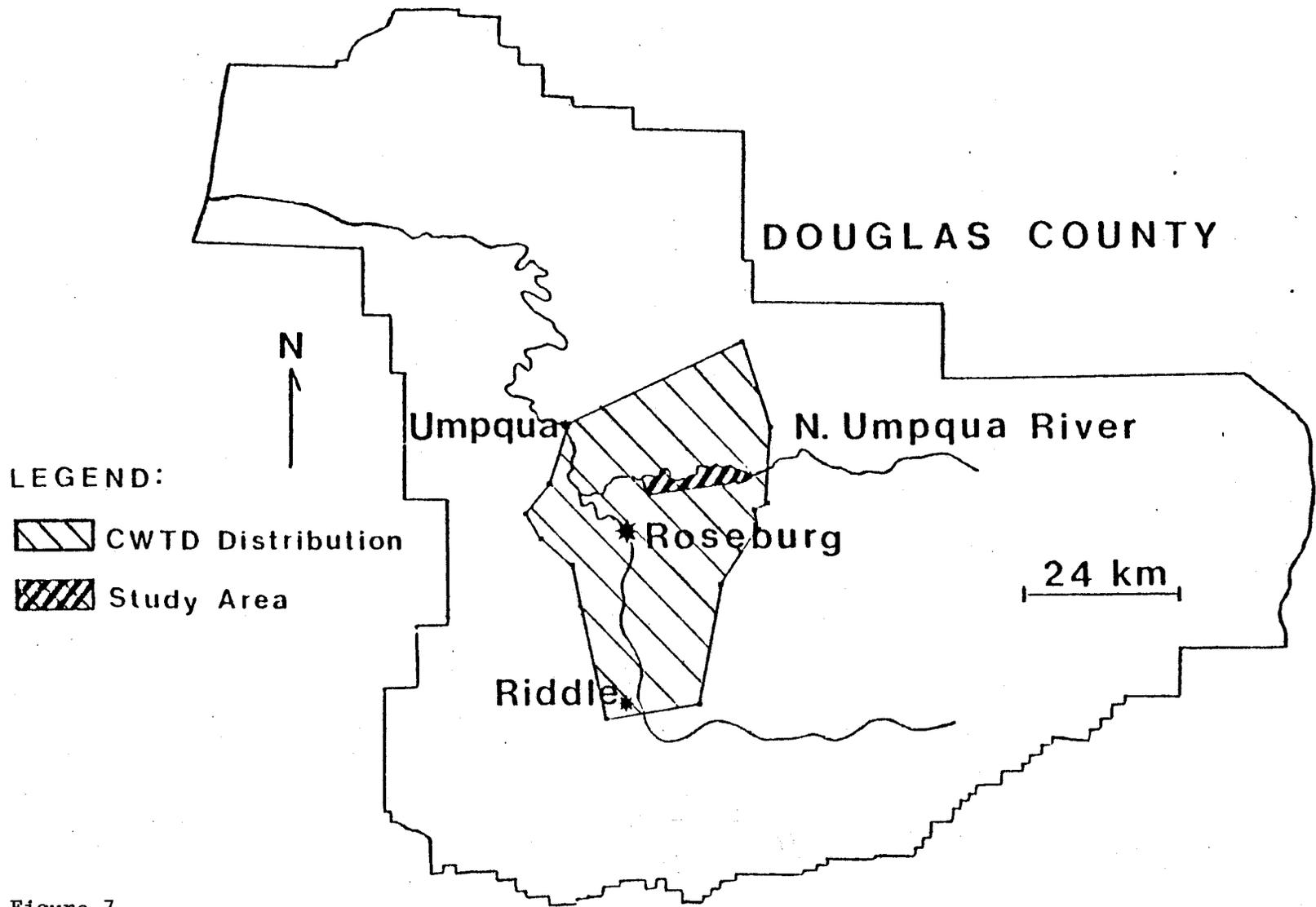


Figure 7.

Figure 8. Location of Columbian white-tailed deer (Odocoileus virginianus leucurus) high-density region within the current geographic distribution in Douglas County, Oregon.

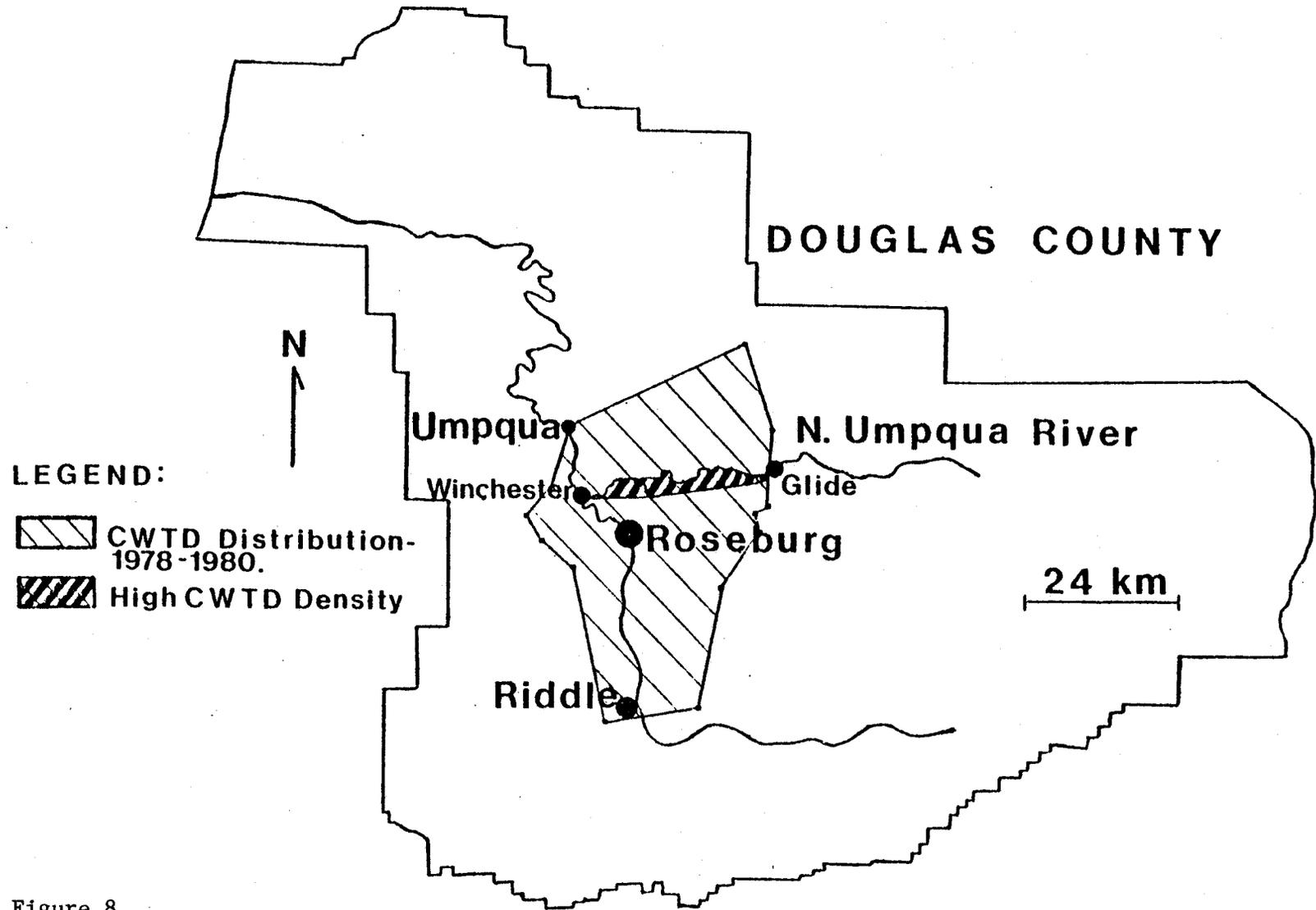


Figure 8.

The historical range of Columbian whitetails (Fig. 1) included the present geographic distribution in Douglas County. From the time just prior to the settlement of western Oregon until 1939, the distribution of CWTD was reduced to incorporate only a very small portion of its native range in Douglas County, apparently a result of intensive hunting and development practices during that period (Nash 1882; Crews 1939).

During the period of the White-tailed Deer Refuge, 1928-1952, CWTD were protected from hunting. A change in ODFW policy in 1952 dissolved the refuge and exposed CWTD to hunting pressure. Annual spotlight censuses conducted by ODFW since 1952 (unpublished data) have documented subsequent increases in whitetail distribution. Since 1939, it appears a 15 - fold increase in geographic range has occurred. Today, CWTD inhabit approximately 25% of their historical range in Douglas County.

A close look at the distribution of CWTD within Douglas County, particularly the peripheral locations, provides some insight into the pattern of recent dispersal. It is probably not coincidental that 4 of the 6 reported geographic boundaries represent riparian lowlands. Further examination reveals that the areas within the geographic range in which the CWTD distribution is discontinuous are characterized by small mountains and a paucity of riparian lowlands. Furthermore, the expansion of geographic range in recent years, as suggested from ODFW spotlight trend counts, was associated with riparian zones or immediately adjacent lowland areas. These observations indicate that CWTD have relied heavily on riparian zones

as avenues for dispersal and suggest that further geographic expansion depends upon the distribution and availability of these riparian avenues and the juxtaposition to suitable habitat.

HABITAT DESCRIPTION

A general reconnaissance of the study area during the initial field season provided the basis for delineating ten distinct habitats. Generally, the habitats were segregated according to species composition and/or structural characteristics of the vegetative associations. A comprehensive description of each habitat was accomplished through an extensive vegetative sampling program. The species composition of the respective vegetative strata for each of the habitats on the study area is presented in Appendix B; frequency of occurrence, percent cover and relative dominance of each plant species within the respective stratum are included.

Grassland. The grassland habitat typically represented areas supporting primarily herbaceous vegetation with very few (if any) trees and a sparse shrub component. These areas included some natural prairies and grass balds but were predominately pasturelands. Preliminary observations revealed discernible differences between pasturelands and grasslands that were not recently exposed to livestock use, and justified a stratified sampling scheme with separate descriptions of "livestock" and "without livestock" grassland habitat. Grasslands represented 922 ha or 33.6% of the total study area.

Grasslands supporting livestock exhibited a fairly uniform spatial distribution of herbaceous vegetation; the mean percent herbaceous cover was 81.1% ($s_{\bar{x}} = 1.48$). The mean obstruction-to-vision value was 20.5 ($s_{\bar{x}} = 0.04$, maximum value = 21) and reflected

the general scarcity of tall herbaceous vegetation. The most dominant herbaceous species (in order of their relative dominance) were hedgehog dogtail (Cynosurus echinatus), medusahead (Taeniatherum asperum) and soft brome (Bromus mollis) comprising 51% of the total herbaceous cover. California oatgrass (Danthonia californica) was the only common native grass, occurring in 37% of the plots and representing an average of 5.7% herbaceous cover. Many of the pasturelands were subjected to periodic controlled burning and seeded to sub-clover (Trifolium subterraneum), perennial ryegrass (Lolium perenne) and tall fescue (Festuca arundinacea).

Grassland areas without livestock averaged 78.1% ($s_{\bar{x}} = 1.69$) herbaceous cover; the mean index of obstruction was 19.6 ($s_{\bar{x}} = 0.12$) and reflected a somewhat greater vertical density as compared to livestock grasslands. Dominant herbaceous species included soft brome, hedgehog dogtail, perennial ryegrass, medusahead, California oatgrass and foxtail fescue (F. megalura). Native grasses included California oatgrass, pine bluegrass (Poa scabrella), Sandberg's bluegrass (P. sandbergii) and blue wildrye (Elymus glaucus). Grasslands without livestock were typically free of disturbance and fires; occasionally, certain portions experienced mowing late in the growing season to reduce potential fire hazard.

Oak-savanna. Savannas are open woodlands consisting of scattered trees and shrubs in an otherwise grass-covered region (Dasmann 1959). Typically, savannas occur as natural boundaries between forest and grasslands, regions where local differences in soil or microclimate favor an interspersed vegetation (Dasmann 1959). In western

Oregon, those regions exhibiting a natural interspersed of oak woodland and grassland were historically maintained by Indians through fire management practices. Oak-savannas accounted for 13.2% (362 ha) of the total study area.

Oak-savanna habitat represented oak-woodland/grassland complexes with an average tree density of 95.6 stems per hectare ($s_{\bar{x}} = 20.6$). Oregon white oak (Quercus garryana) comprised 95.4% of the existing basal area while California black oak (Q. kelloggii) and Oregon ash (Fraxinus latifolia) accounted for 4.2% and 0.4% of the total basal area, respectively. The mean DBH per stem was 32.9 cm ($s_{\bar{x}} = 0.87$) and mean percent canopy cover was 25.5% ($s_{\bar{x}} = 2.94$). The average shrub cover was 5.9% ($s_{\bar{x}} = 1.33$); poison oak (Rhus diversiloba) and wild rose (Rosa elganteria) were the predominant shrub species. Mean percent herbaceous cover was 76.8% ($s_{\bar{x}} = 2.32$); dominant grasses and forbs included medusahead, hedgehog dogtail, California oatgrass, poison oak (new-growth), soft brome, perennial ryegrass and pale flax (Linum angustifolium). The mean index of obstruction was 18.4 ($s_{\bar{x}} = 0.46$).

Grass-shrub. The grass-shrub habitat comprised 4.4% (121 ha) of the total study area. Generally, these areas supported very few trees and exhibited a dense shrub component; the mean percent shrub cover was 34.4% ($s_{\bar{x}} = 1.76$). By far the dominant shrub species was poison oak, occurring in 98.7% of the sampling points and representing 96.2% of the shrub cover. Wild rose and wild lilac (Ceanothus integerrimus) accounted for 3.7% and 0.1% of the shrub cover. Mean percent herbaceous cover was 73.1% ($s_{\bar{x}} = 1.77$) and the average index of

obstruction was 10.1 ($s_{\bar{x}} = 0.67$). New-growth poison oak accounted for 36.8% of the herbaceous ground cover; additional dominant herbs included hedgehog dogtail, tall fescue, timber oatgrass (D. intermedia) and medusahead.

Open oak. Open oak habitat occupied 17.1% (469 ha) of the study area and represented relatively uniform-aged oak woodlands with a well-developed overstory and herbaceous understory; the shrub layer was sparse and often non-existent. The mean percent canopy cover and herbaceous cover were 69.6% ($s_{\bar{x}} = 2.21$) and 71.3% ($s_{\bar{x}} = 2.38$), respectively; shrub cover averaged 6.1% ($s_{\bar{x}} = 0.72$). The average tree density was 665.0 stems per acre ($s_{\bar{x}} = 62.0$) while the mean DBH per stem was 22.1 cm ($s_{\bar{x}} = 0.59$). Oregon white oak and California black oak were the dominant tree species and accounted for 77.4% and 17.6% of the existing basal area. Poison oak and wild rose averaged 3.7% and 2.3% ground cover, respectively, and accounted for 61% and 38% of the shrub cover. Dominant grasses and forbs included hedgehog dogtail, California oatgrass, perennial ryegrass, new-growth poison oak, Geranium spp., soft brome, California hedgeparsley (Caucalis microcarpa), tall fescue and least hop-clover (T. dubium). The average index of obstruction was 14.2 ($s_{\bar{x}} = 0.61$).

Closed oak. Closed oak habitat represented even-aged oak woodlands with three well-developed vegetative strata; these areas occupied 8.7% (239 ha) of the study area. The overstory was relatively dense with essentially a continuous canopy. The mean tree density was 1266 stems per hectare ($s_{\bar{x}} = 118$) while the average percent canopy cover was 90.3% ($s_{\bar{x}} = 1.53$). Oregon white oak and California black oak accounted for 69% and 25% of the existing basal area, respectively;

the mean DBH was 21.2 cm ($s_{\bar{x}} = 0.66$). The shrub layer averaged 47.6% ($s_{\bar{x}} = 3.34$) ground cover; poison oak and wild rose occurred with a frequency of 0.72 and 0.52 and represented 72% and 20% of the total shrub cover, respectively. Dominant herbaceous species included new-growth poison oak, orchard-grass (Dactylis glomerata), hedgehog dogtail, velvet-grass (Holcus lanatus), tall fescue and blue wild-rye; mean percent herbaceous cover was 58.4% ($s_{\bar{x}} = 2.25$).

Oak-conifer. Oak-conifer habitat represented dense mixed oak-conifer stands averaging 1364 stems per hectare ($s_{\bar{x}} = 136$), and occupied 11.3% (310 ha) of the study area. The mean DBH per stem was 21.5 cm ($s_{\bar{x}} = 0.78$) and the average canopy cover was 89.7%. Douglas-fir (Pseudotsuga menziesii), Oregon white oak and madrone (Arbutus menziesii) were the dominant tree species comprising 40.2%, 28.9% and 18.3% of the existing basal area, respectively. Mean percent shrub cover was 21.2% ($s_{\bar{x}} = 3.20$); poison oak, young madrone trees and wild rose were the dominant components of the mid-story. Herbaceous cover averaged 30.5% ($s_{\bar{x}} = 2.99$); dominant grasses and forbs included new-growth poison oak, sword-fern (Polystichum munitum) and hedgehog dogtail. The mean index of obstruction was 5.15 ($s_{\bar{x}} = 0.68$), indicative of the dense multi-strata structure of the habitat.

Oak-madrone. On more xeric sites, many woodlands were co-dominant stands of Oregon white oak and madrone; this vegetative association occupied 6.1% (167 ha) of the study area. Oak-madrone woodlands averaged 78.4% ($s_{\bar{x}} = 2.04$) canopy cover and had a mean density of 1283 stems per hectare ($s_{\bar{x}} = 81.2$). Oregon white oak and madrone

comprised 44% and 32% of the existing basal area; the mean DBH per stem was 15.7 cm ($s_{\bar{x}} = 0.46$). The shrub layer averaged 31.7% ($s_{\bar{x}} = 2.44$) ground cover; poison oak predominated accounting for 90% of the total shrub cover. Mean percent herbaceous cover was 46.5% ($s_{\bar{x}} = 2.59$); dominant grasses and forbs included new-growth poison oak, hedgehog dogtail, tall fescue, blue wild-rye, California oatgrass and California hedge-parsley. The mean index of obstruction was 7.32 ($s_{\bar{x}} = 0.59$) reflecting a relatively dense multi-strata vegetative association.

Madrone. Fourteen percent (38.5 ha) of the study area was occupied by essentially monotypic stands of madrone. Madrone habitat represented dense multi-layered woodlands averaging 3762 stems per hectare; the mean index of obstruction was 3.04 ($s_{\bar{x}} = 0.43$). The average DBH per stem was 10.3 cm ($s_{\bar{x}} = 0.25$) and mean percent canopy cover was 79.3% ($s_{\bar{x}} = 2.52$). The shrub stratum was predominantly poison oak, occurring with a frequency of 0.71 and accounting for 98% of the shrub cover; total shrub cover averaged 28.4% ($s_{\bar{x}} = 2.76$). The understory averaged 25% herbaceous cover; dominant grasses and forbs included tall fescue, new-growth poison oak, hedgehog dogtail and iris (*Iris tenax*).

Riparian. Portions of the study area that were otherwise a part of the terrestrial environment experienced periodic seasonal flooding. These areas together with other poorly-drained sites exhibited vegetative associations that were best characterized as riparian communities and comprised 3.1% (85 ha) of the total study area. Some of the riparian sites were without an overstory (eg. seeps, ephemeral

streams), but typically riparian habitat represented relatively dense woodlands exhibiting three vegetative strata. The average tree density was 622 stems per hectare ($s_{\bar{x}} = 80.2$) while the mean DBH per stem was 28.1 cm ($s_{\bar{x}} = 0.72$). Within woodland sites, the canopy was essentially continuous; the overall mean percent canopy cover was 81.5% ($s_{\bar{x}} = 2.21$). Oregon white oak and Oregon ash were the dominant tree species and accounted for 70.0% and 28.5% of the existing basal area; California black oak and red alder (Alnus rubra) were also fairly common on a number of sites. The mean percent shrub cover was 4.63% ($s_{\bar{x}} = 0.81$); dominant shrub species included wild rose, Oregon viburnum (Viburnum ellipticum) and poison oak. Owing to low-reaching tree canopies and a relatively tall dense understory, the mean index of obstruction was 10.9 ($s_{\bar{x}} = 0.63$). The average herbaceous cover was 69.1% ($s_{\bar{x}} = 1.95$); the dominant herbaceous species were common rush (Juncus effusus), tall fescue, velvet-grass, hedgehog dogtail and sedges (Carex spp.) including dense sedge (C. densa).

Conifer. Mixed conifer stands occupied the northern slopes at higher elevations and represented 1.1% (30.1 ha) of the study area. Typically, the coniferous forests exhibited a continuous canopy with a relatively sparse shrub layer and intermittent understory. The average canopy cover was 92.3% ($s_{\bar{x}} = 1.26$) while mean percent shrub and herbaceous cover were 5.83% ($s_{\bar{x}} = 1.36$) and 21.4% ($s_{\bar{x}} = 2.49$), respectively. The average tree density was 541 stems per hectare ($s_{\bar{x}} = 50.5$) while mean DBH per stem was 41.8 cm ($s_{\bar{x}} = 1.00$). Douglas-fir was the dominant tree species and comprised 91% of the existing

basal area. Dominant shrub species included hazelnut (Corylus cornuta), wild rose and poison oak while hedgehog dogtail, sword-fern, lady-fern (Athyrium filix-femina) and velvet-grass were among the dominant herbaceous species. The mean index of obstruction was 12.0 ($s_{\bar{x}} = 0.84$).

Comparison of vegetative and structural characteristics. Mean basal area per hectare differed among the habitats (Appendix C). Coniferous forests had a substantially greater standing basal area per hectare (74.25 m^2) than the remaining woodland habitats; oak-conifer, closed oak and riparian habitats averaged 49.53, 44.68 and 38.57 m^2 per hectare, respectively. Kruskal-Wallis one-way analysis of variance ranks tests (Steel and Torrie 1980:542) revealed that each of the vegetative and structural habitat parameters differed significantly among the habitats (Table 1). Subsequent to each analysis of variance ranks test, a Dunn's multiple comparison test (Daniel 1978:212) was employed to determine which habitats were significantly different with respect to each specific parameter.

The oak-savanna habitat exhibited significantly less percent canopy cover and tree density than the remaining woodland habitats (Table 1). Open oak, riparian and conifer habitats exhibited similar percent canopy cover and tree densities, but displayed significantly fewer stems per hectare than closed oak, oak-conifer and oak-madrone habitats; madrone exhibited the densest tree stands. Grass-shrub and closed oak habitats exhibited the densest shrub layer; oak-madrone and madrone habitats displayed similar percent shrub cover while oak-conifer stands exhibited significantly less shrub cover.

Table 1. Tree density, mean diameter at breast height, obstruction to vision index, and mean % cover of the tree, shrub and herbaceous vegetative strata for each of the habitats on the study area. (Within rows, values that share common letters are not significantly different, $P > 0.05$)

	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
Canopy % Cover	-	-	-	25.5a	69.9b	90.3b	89.7b	78.0b	79.3b	81.5b	92.3b
Tree Density (stems/ha)	-	-	-	95.6a	665.b	1266c	1364c	1283c	3762d	622.b	541.b
DBH (cm)	-	-	-	32.9bc	22.1acb	21.2abc	21.3abc	15.7ab	10.3a	28.1abc	41.8c
Shrub % Cover	-	-	34.4d	5.9a	6.1a	47.6d	21.2b	31.7c	28.4c	4.63a	5.83a
Herbaceous % Cover	81.1b	78.1bc	73.1bc ab	76.8bc	71.3bc	58.4bcd	30.5ad	46.5acd	25.0a	69.1bc	21.4a
Obstruction Index	20.5e	9.6e	10.1cd	18.4de	14.2cde	9.30abc	5.15ab	7.32abc	3.04a	10.9cd	12.0de

Oak-savanna, open oak, riparian and conifer habitats all had a shrub cover of 6.1% or less.

A significant inverse correlation ($r = 0.74$) existed between percent canopy cover and percent herbaceous cover among the habitats. Generally, grassland, grass-shrub and the more open woodland habitats exhibited similar understories whereas conifer, madrone and oak-conifer habitats displayed significantly less herbaceous cover. Also, a significant inverse correlation existed between the index of obstruction and corresponding shrub cover ($r = 0.71$) and canopy cover ($r = 0.78$) estimates. Typically, grassland, grass-shrub and open woodlands exhibited significantly less vertical vegetative density while madrone, oak-conifer, oak-madrone and closed oak afforded the greatest obstruction-to-vision.

Phenology and seasonal variation. In western Oregon, herbaceous growth begins in the fall with the onset of the rainy season (Sharrow 1979). The increase in biomass production of forbs and grasses is gradual through mid-March after which a dramatic increase occurs (Fig. 9). Generally, grasses and forbs on the study area continued vegetative growth throughout May, at which time maturity and seed production occurred. Correspondingly, biomass production drops off dramatically in late May and early June (Fig. 9). Annual bromes, for example, germinated in the fall, experienced a short growth burst in the spring and produced seed by the end of May (see also Harris and Goebel 1976). Perennials however, remained vegetative throughout their first growing season and exhibited longer growing seasons than annuals in subsequent years. Tall fescue grew con-

tinually through the winter and during one year remained green throughout the summer (see also Rampton 1945). Sanders (1965) observed that seed production in both tall fescue and perennial ryegrass did not occur until July 30 - August 8.

Most of the shrub species first displayed signs of new-growth during mid-April. Poison oak, for example, displayed the first signs of growth on April 13 during 1979; the first discernible leaves were observed on April 18. During 1980, corresponding phenological events occurred on April 15 and April 22, respectively. By the middle of May, most shrubs were completely leafed-out and oak trees initiated new-growth. Some tree species including Oregon ash, big-leaf maple (Acer macrophyllum) and red alder began leafing out as early as late April. Generally, the woodland canopies were fully erupted by the first part of June.

Throughout the year, a number of seasonal changes in vegetation and habitat structure occurred. The most apparent was a decrease in canopy cover. Except for madrone and conifer stands, a substantial reduction in percent canopy cover was observed through autumn and winter. A Kruskal-Wallis one-way analysis of variance ranks test (Steel and Torrie 1980:542) revealed that significant changes in herbaceous cover occurred through the seasons among all of the habitats (Table 2). Generally, herbaceous cover was significantly greater in spring and summer (Dunn's multiple comparison test, Daniel 1978:212). The major exception occurred within coniferous forests; herbaceous cover was significantly greater in fall, winter and early spring (Table 2). This is not surprising as

Figure 9. Seasonal dry matter production (kg/hectare/day) of an improved pasture in western Oregon. (taken from Sharrow 1979)

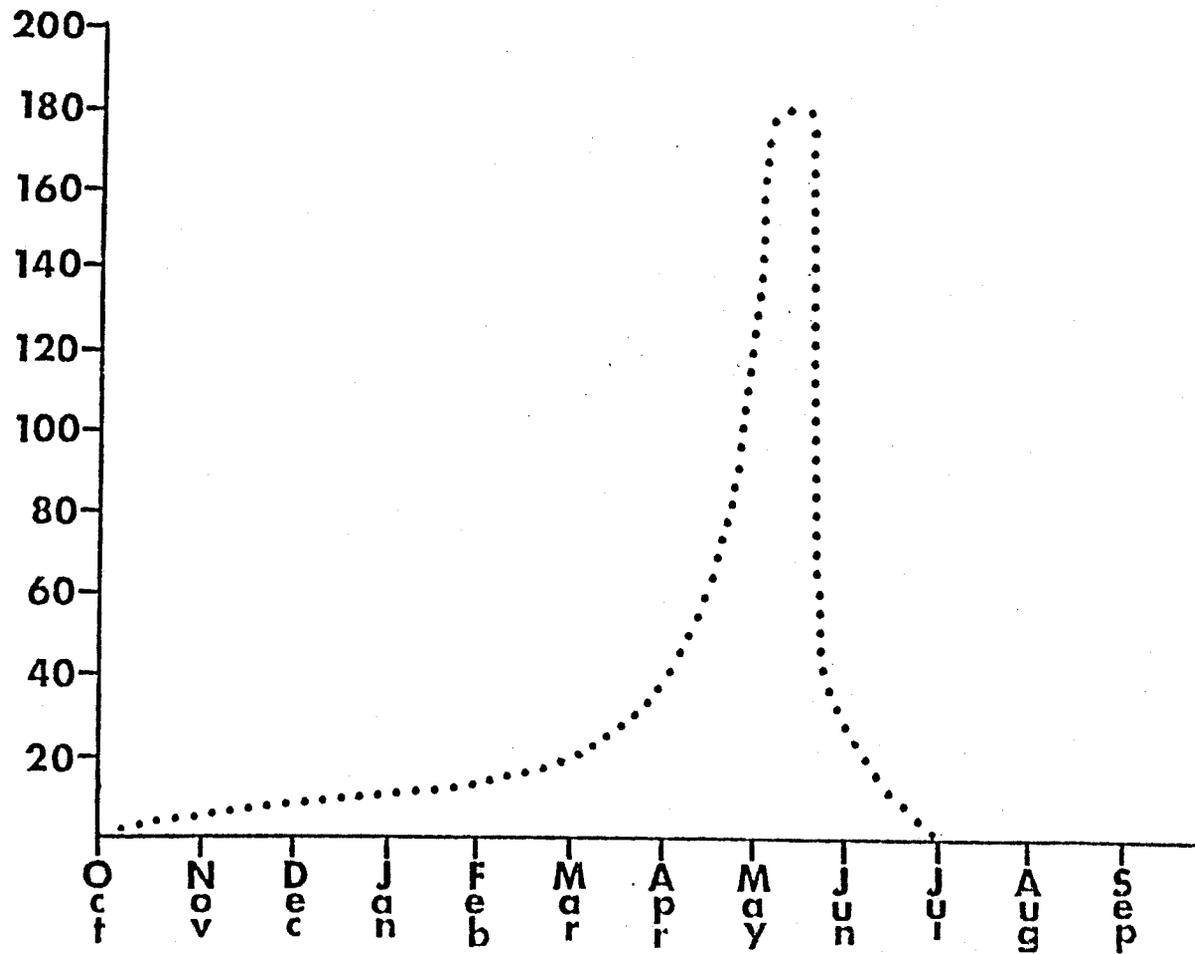


Figure 9.

the difference in herbaceous growth under a year-round canopy will generally reflect changes in precipitation rather than sunlight. A similar phenomenon was observed in madrone habitat where the greatest herbaceous cover was recorded in winter and early spring.

Concomitant changes in vegetation density were observed (Table 2). A Kruskal-Wallis analysis of variance test (Steel and Torrie 1980:542) disclosed that significant changes in obstruction-to-vision occurred in all the habitats except oak-savanna, open oak, oak-conifer and riparian habitats. Riparian and oak-conifer habitats consistently exhibited the densest vegetative structure. Seasonal differences in obstruction-to-vision were apparently associated with changes in herbaceous vertical density and percent shrub cover; both grassland types displayed changes through the season and the greatest disparity in obstruction-to-vision occurred within the closed oak and grass-shrub habitats, two vegetative associations that exhibited well-developed shrub strata (Appendix B).

The spatial distribution (frequency of occurrence) and abundance (percent crown cover) of the shrub and herbaceous species among the habitats are presented in Appendix D and Appendix E, respectively.

Table 2. Seasonal comparisons of mean percent herbaceous cover and mean obstruction-to-vision among the habitats on the study area. (Within columns, values that share common letters are not significantly different, $P > 0.05$)

	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
Herbaceous % Cover											
Summer	70.4 b	75.4 a	57.7 a	75.2 a	64.5 a	65.5 a	33.0 ab	53.2 a	25.0 ab	66.1 a	24.6 a
Fall	80.4 a	81.4 ab	63.0 b	-	41.4 b	41.4 b	26.8 a	40.4 b	17.6 b	46.4 b	39.9 b
Winter	80.1 a	78.1 a	50.0 a	66.5 b	33.0 b	36.5 b	36.9 b	35.2 b	28.2 a	40.9 b	38.2 b
Spring	78.8 ab	84.6 b	51.5 a	65.2 b	60.2 a	58.3 a	34.1 ab	55.2 a	28.6 a	58.6 a	39.2 b
Obstruction Index											
Summer	20.5 ac	19.5 ac	12.6 ab	18.4 a	15.0 a	9.3 a	6.9 a	5.0 a	3.0 a	6.8 a	15.1 ab
Fall	20.2 c	19.0 a	7.4 ac	-	15.9 a	7.1 a	5.7 a	3.5 a	2.0 a	4.3 a	14.8 b
Winter	20.9 a	20.0 c	14.5 b	19.7 a	17.7 a	15.4 b	7.6 a	7.8 b	4.3 b	7.1 a	17.5 a
Spring	19.6 b	17.3 b	5.2 c	19.3 a	15.1 a	4.2 c	5.5 a	8.1 b	2.8 a	5.7 a	14.0 ab

HABITAT USE

During the period May 1978–December 1980, 12077 CWTB observations were recorded; habitat, date, time of day, group size, age, sex and activity were noted. Each individual represented a single observation of habitat-use; the total number of individuals observed within a specific habitat during the period of study provided an estimate of proportionate use. The total area of each habitat on the study area was determined using a Bryant Grid (Bryant 1943) and a compensating polar planimeter (Mosby 1971) with a series of aerial photographs. The proportion of the total study area represented by a specific habitat provided an estimate of habitat availability.

Annual Habitat Use. Generally, the frequency of use among the ten habitats differed significantly from that commensurate with the corresponding availability of the habitats (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552)(Fig. 10). The z statistic was employed to compute individual confidence intervals (99.5%) for the proportion of occurrence in each habitat; the z statistic is a normal approximation for variables that follow a normal distribution (Neu et al. 1974). Collectively, the individual intervals represented a 95% family confidence interval that facilitated simultaneous comparisons of the proportion of occurrence in each habitat with the corresponding availability (Neu et al. 1974). If the expected frequency of occurrence (as determined from the availability of the habitat) was greater than the computed interval then the habitat was utilized significantly less than would be expected; if the expected

Figure 10. The proportion of Columbian white-tailed deer occurring among the ten habitats May 1978-December 1980 and the relative abundance of the habitats represented on the study area in Douglas County, Oregon.

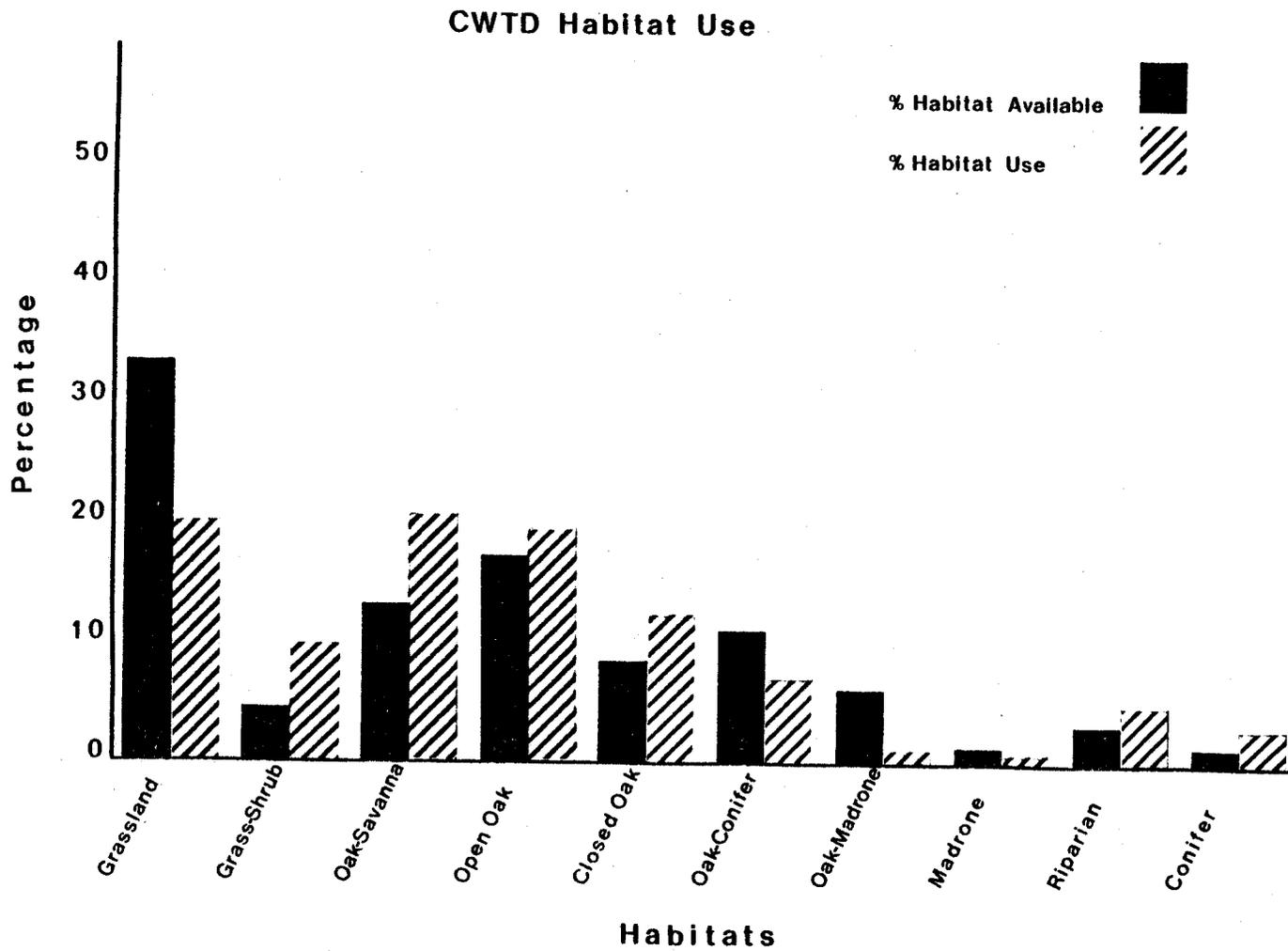


Figure 10.

use was less than the computed interval, the habitat experienced significantly greater use. Accordingly, grass-shrub, oak-savanna, open oak, closed oak, riparian and conifer habitats received significantly greater use and were apparently preferred by CWTD (Table 3). Conversely, grassland, oak-conifer, oak-madrone and madrone habitats were utilized significantly less than would be expected from their availability (Table 3).

Seasonal Habitat Use. Analysis of the monthly frequency distribution of occurrence among the ten habitats revealed apparent trends in CWTD habitat use that corresponded with seasonal climatic and phenological patterns (Fig. 11). During early spring and fall, CWTD generally increased their use of habitats that supported a well-developed herbaceous layer; grassland, grass-shrub, oak-savanna and open oak habitats each supported herbaceous understories that averaged more than 70% ground cover (Appendix B) and experienced a marked increase in use by CWTD during spring and fall (Fig. 11). Late March to early April typically marks the beginning of the spring growing season and western Oregon experiences an exponential increase in herbaceous biomass production through mid-May (Sharrow 1979). Examination of monthly foraging activity revealed that CWTD exhibited temporal grazing patterns (i.e. grasses and forbs) that were consistent with seasonal trends in habitat-use (Fig. 12); percent grazing increased from January through April and from August through November.

The relationship between frequency of habitat use and phenology was most apparent among grassland habitats; CWTD exhibited a significantly greater frequency of grassland habitat use (comparison of

Table 3. Occurrence of Columbian white-tailed deer among the ten habitats represented on the study area, Douglas County, Oregon, during the period May 1978-December 1980. (notations from Neu et al. 1974)

Habitat	Total Area (ha)	Proportion Of Total Area ^a (p_{i0})	Number Of CWTD Observed	Proportion Observed In Each Habitat (\bar{p}_i)	95% Family Confidence Interval ^b
GRASSLAND	922	0.336	2443	0.202	$0.192 \leq p_i \leq 0.212$
GRASS-SHRUB	121	0.044	1206	0.100	$0.091 \leq p_i \leq 0.107$
OAK-SAVANNA	362	0.132	2520	0.209	$0.199 \leq p_i \leq 0.219$
OPEN OAK	469	0.171	2385	0.198	$0.188 \leq p_i \leq 0.208$
CLOSED OAK	239	0.087	1484	0.123	$0.115 \leq p_i \leq 0.131$
OAK-CONIFER	310	0.113	860	0.071	$0.064 \leq p_i \leq 0.078$
OAK-MADRONE	167	0.061	125	0.010	$0.007 \leq p_i \leq 0.013$
MADRONE	39	0.014	93	0.008	$0.006 \leq p_i \leq 0.010$
RIPARIAN	85	0.031	599	0.050	$0.044 \leq p_i \leq 0.056$
CONIFER	30	0.011	362	0.030	$0.026 \leq p_i \leq 0.034$
TOTAL	2744		12077		

^aProportions of total area represent expected Columbian white-tailed deer observations in corresponding habitat.

^bIndividual habitat proportion estimates represent 99.5% confidence intervals.

Figure 11. Monthly frequency distribution of Columbian white-tailed deer observations among the ten habitats represented on the study area in Douglas County, Oregon during the period May 1978-December 1980.

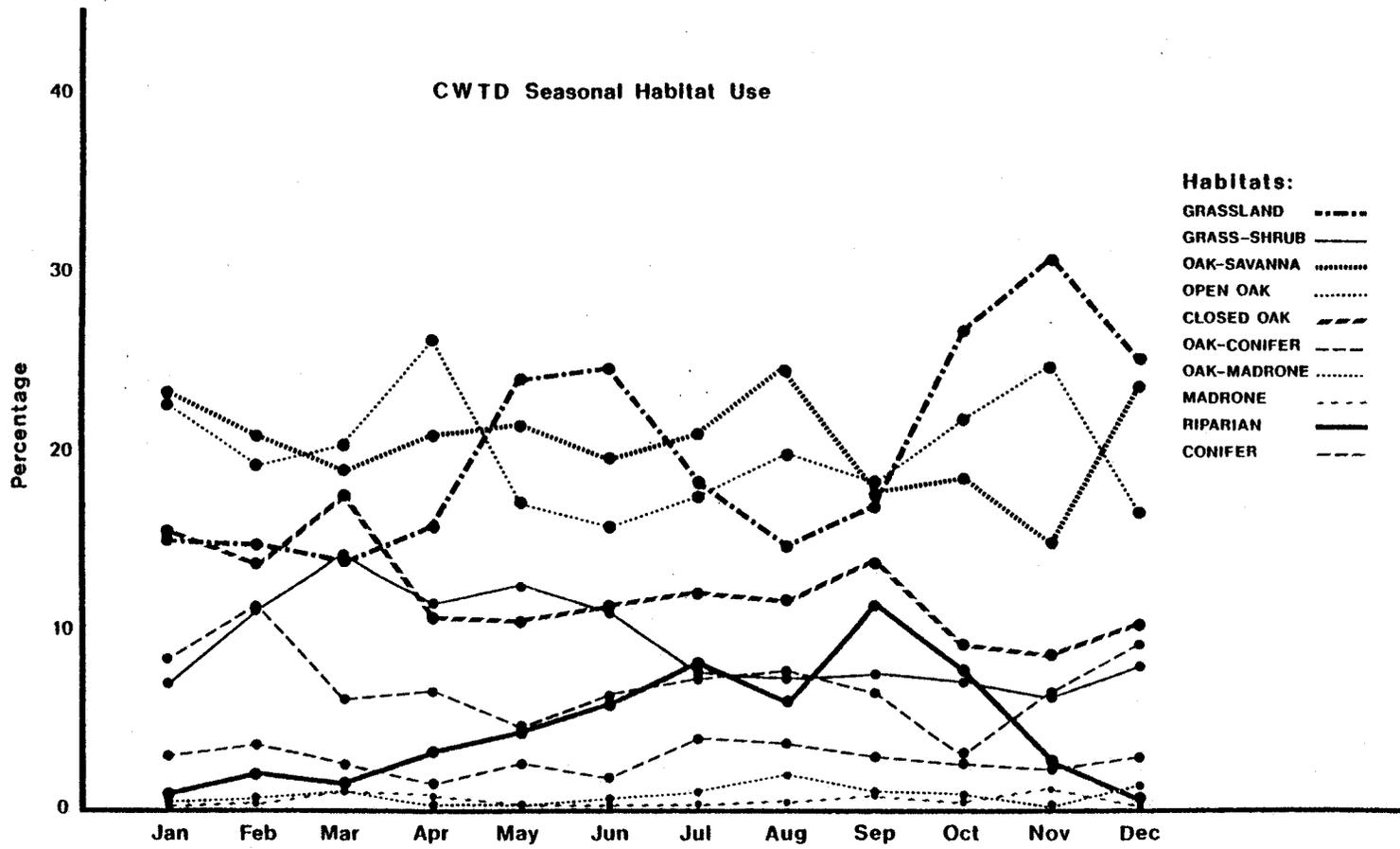


Figure 11.

proportions in independent samples, Snedecor and Cochran 1980:124) during late spring and early autumn (Table 4). Indeed, the bimodal pattern of grassland use closely paralleled two important phenological events: spring growth and maturity of herbaceous vegetation and the fall green-up (Fig. 13). As biomass production of grasses and forbs (kg/ha/day) increased through April and May, the frequency of grassland habitat use increased proportionally. Also, the frequency of grazing in grassland habitats during spring (0.30) was significantly greater (comparison of proportions in independent samples) than that observed during the winter (0.24). As forbs and grasses matured in late May and early June, biomass production, nutrient content and palatability decreased dramatically (Hulbert 1955, Harris and Goebel 1976, Sharrow 1979); correspondingly, CWT use of grassland habitats (Fig. 13) decreased significantly (comparison of proportions in independent samples).

A significant increase in grassland habitat use in the fall (Table 4 and Fig. 13) was accompanied by a significant increase in the frequency of grazing among grasslands from 27.1% in the summer to 38.8% during autumn (comparison of proportions in independent samples, Snedecor and Cochran 1980:124). Early fall marked the beginning of the rainy season and as mean monthly precipitation (cm) increased from August through November, grassland habitat use increased proportionally. Both the frequency of occurrence and frequency of grazing in grasslands were highest during autumn and suggests a strong reliance upon herbaceous forage during this period. Although grass and forb biomass production is comparably low during this

Table 4. Seasonal occurrence of Columbian white-tailed deer among the ten habitats represented on the study area¹, Douglas County, Oregon, during the period May 1978–December 1980. (notations from Neu et al. 1974; F.C.I. = family confidence interval)

HABITAT	P_{i_0}	WINTER (Jan-Mar)		SPRING (Apr-Jun)		SUMMER (Jul-Sep)		AUTUMN (Oct-Dec)	
		\bar{p}_i	95% F.C.I.						
GRASSLAND	0.336	0.147a	0.128–0.166	0.224b	0.205–0.242	0.169a	0.150–0.188	0.277c	0.250–0.304
GRASS-SHRUB	0.044	0.117a	0.100–0.134	0.118a	0.104–0.132	0.078b	0.064–0.092	0.074b	0.058–0.090
OAK-SAVANNA	0.132	0.208a	0.186–0.230	0.207a	0.189–0.225	0.221a	0.200–0.242	0.194a	0.170–0.218
OPEN OAK	0.171	0.207a	0.185–0.229	0.191a	0.174–0.208	0.189a	0.169–0.209	0.211a	0.186–0.236
CLOSED OAK	0.087	0.159a	0.139–0.179	0.112b	0.198–0.126	0.124b	0.107–0.141	0.097a	0.079–0.115
OAK-CONIFER	0.113	0.087a	0.072–0.102	0.062b	0.052–0.072	0.076ab	0.063–0.089	0.062b	0.047–0.077
OAK-MADRONE	0.061	0.012ab	0.006–0.018	0.006a	0.003–0.009	0.016b	0.010–0.022	0.010ab	0.004–0.016
MADRONE	0.014	0.012a	0.006–0.018	0.005a	0.002–0.008	0.007a	0.003–0.011	0.008a	0.003–0.013
RIPARIAN	0.031	0.019a	0.012–0.026	0.052b	0.042–0.062	0.080c	0.066–0.094	0.041b	0.029–0.053
CONIFER	0.011	0.033ab	0.023–0.043	0.022a	0.016–0.028	0.040b	0.030–0.050	0.028ab	0.018–0.038

¹Proportions within a specific row that share common letters are not significantly different ($p \geq 0.05$).

Figure 12. Monthly proportion of observations in which Columbian white-tailed deer were observed foraging on grasses and forbs on the study area in Douglas County, Oregon during the period May 1978-December 1980.

CWTD Utilization of Grasses and Forbs: 1978-80

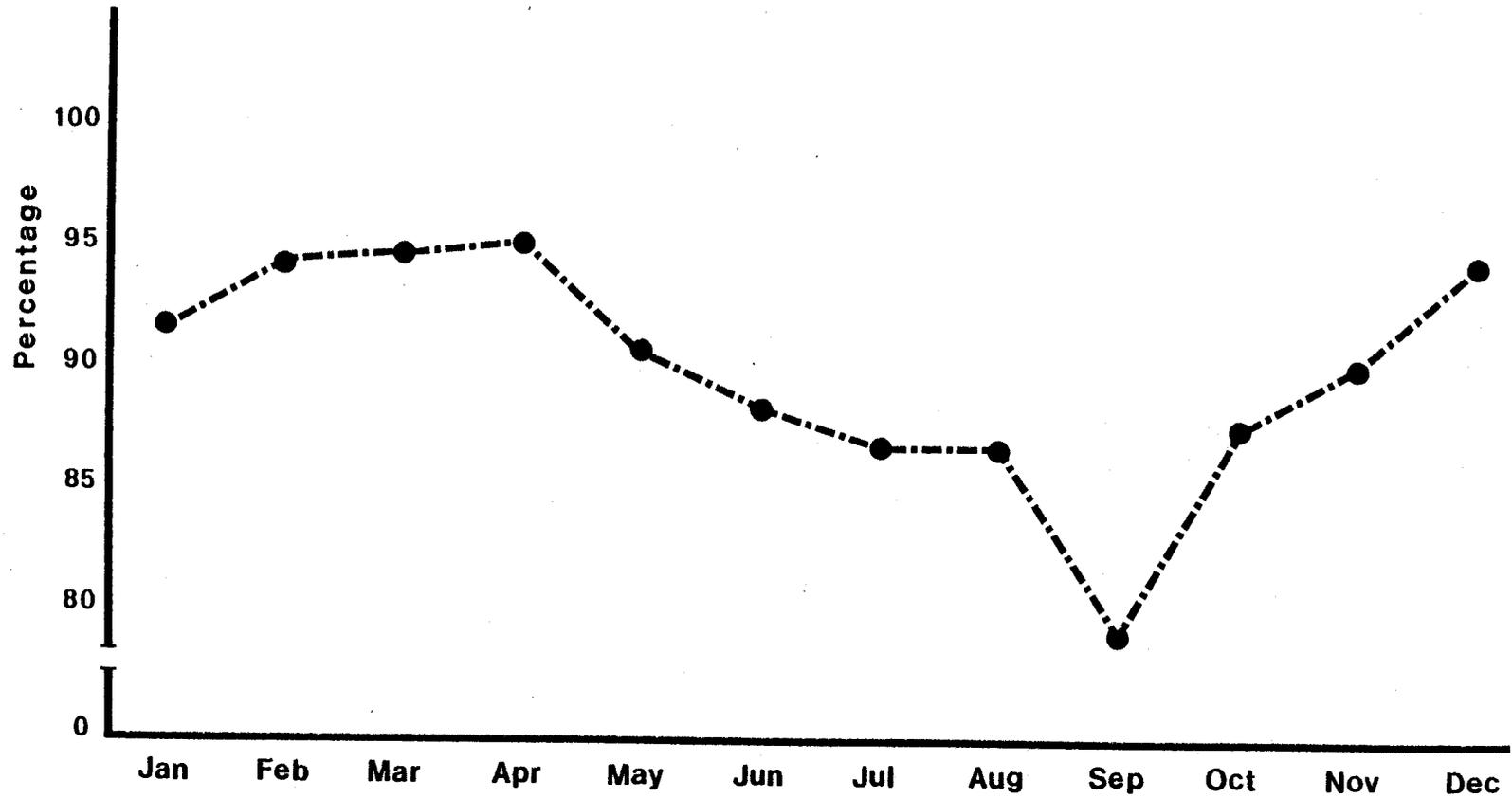


Figure 12.

Figure 13. Monthly frequency distribution of grassland habitat use by Columbian white-tailed deer on the study area in Douglas County, Oregon during the period May 1978-December 1980. Biomass production of grasses and forbs (kg/ha/day) in western Oregon (Sharrow 1979) and mean monthly precipitation (cm) on the study area (U.S. Department of Commerce) during 1979-1980.

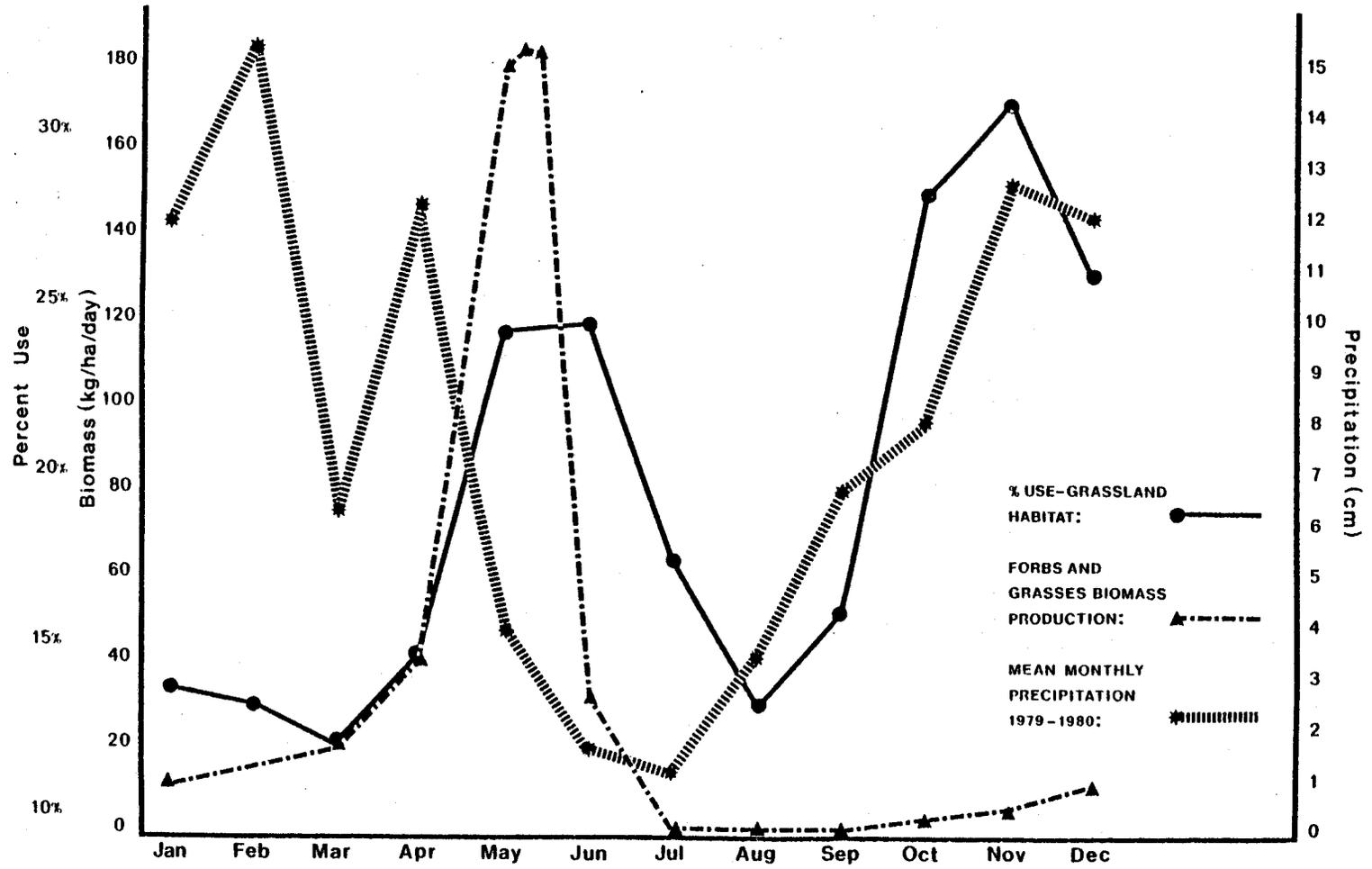


Figure 13.

period, fall herbaceous new-growth represents the most palatable and nutritious forage available (Steve Sharrow, personal communication). During the spring, young trees and shrubs are flourishing and produce palatable and nutritious new-growth. The dependence upon herbaceous forage during spring is seemingly not as crucial; CWTD exhibited use of grasslands significantly less during spring than autumn and significantly increased their use of grass-shrub and closed oak habitats (Table 4)(comparison of proportions in independent samples, Snedecor and Cochran 1980:124). A concomitant increase in the frequency of browsing was also observed during spring.

CWTD exhibited monthly habitat use patterns that closely conformed to specific seasonal climatic trends (Fig. 11). Generally, the frequency of use among woodland habitats varied with temperature and in some instances precipitation; habitat selection was apparently associated with reducing thermal stress, or other biological needs (e.g. water, palatable forage) during corresponding periods of environmental stress. The most apparent climatic trend occurred among riparian habitats (Fig. 11): there was a significant positive correlation ($r = 0.86$) between ambient temperature and the frequency of riparian habitat use and a significant inverse correlation ($r = 0.79$) between mean monthly precipitation and the occurrence of CWTD within riparian habitats. The response by CWTD to changes in ambient temperature and precipitation represented a significant increase in the use of riparian habitats (comparison of proportions in independent samples, Snedecor and Cochran 1980:124) during late spring and summer (Table 4).

A similar pattern of use occurred among conifer, oak-conifer and oak-madrone habitats. CWTD utilized conifer and oak-conifer habitats most frequently during summer and winter (Fig. 11), periods when CWTD were exposed to the greatest temperature extremes (U.S. Department of Commerce 1955-1980). Analysis of diel frequency distributions among the habitats (see Daily Habitat Use) disclosed that CWTD more frequently utilized conifer and oak-conifer habitats during the hottest and coldest times of the day during summer and winter, respectively. Intensive observations conducted during and following a snow storm indicated that CWTD preferred conifer, oak-conifer and oak-madrone habitats for thermal cover. Oak-madrone apparently provided good thermal cover during the summer as well; CWTD significantly increased their use of oak-madrone habitats during this period (comparison of proportions in independent samples, Snedecor and Cochran 1980:124).

Daily Habitat Use. Examination of the daily frequency distribution of CWTD among the ten habitats for six four-hour activity periods indicated distinct diel patterns of habitat use (Table 5). During late evening (21:00-24:00) and early morning (01:00-04:00) periods, CWTD favored grassland, grass-shrub, oak-savanna and open oak habitats (Table 5). This pattern remained fairly consistent throughout the year except during late fall and winter when there was an increase in use among woodland habitats. During mid-morning (09:00-12:00) and on through late afternoon (13:00-16:00) CWTD increased their frequency of use of woodland habitats while significantly decreasing their use of grasslands (comparison of proportions in

Table 5. Seasonal frequency of Columbian white-tailed deer habitat use for six 4-hour activity periods May 1978-December 1980, Douglas County, Oregon. (Within a column, values represent the proportion of observations occurring in the habitats)

Habitats	01:00-04:00	05:00-08:00	09:00-12:00	13:00-16:00	17:00-20:00	21:00-24:00
WINTER (Jan-Mar)						
GRASSLAND	0.147	0.060	0.021	0.073	0.338	0.550
GRASS-SHRUB	0.117	0.138	0.113	0.105	0.088	0.050
OAK-SAVANNA	0.208	0.198	0.129	0.184	0.263	0.125
OPEN OAK	0.207	0.235	0.173	0.216	0.159	0.275
CLOSED OAK	0.159	0.195	0.182	0.182	0.071	0
OAK-CONIFER	0.087	0.104	0.101	0.115	0.034	0
OAK-MADRONE	0.012	0.003	0.009	0.024	0.015	0
MADRONE	0.012	0.004	0.011	0.028	0.010	0
RIPARIAN	0.019	0.011	0.018	0.036	0.015	0
CONIFER	0.033	0.050	0.034	0.038	0.007	0
SPRING (Apr-Jun)						
GRASSLAND	0.221	0.218	0.061	0.042	0.237	0.510
GRASS-SHRUB	0.118	0.140	0.108	0.069	0.119	0.059
OAK-SAVANNA	0.208	0.238	0.161	0.141	0.210	0.161
OPEN OAK	0.192	0.196	0.175	0.239	0.187	0.161
CLOSED OAK	0.112	0.097	0.204	0.180	0.112	0.040
OAK-CONIFER	0.062	0.060	0.185	0.088	0.033	0.005
OAK-MADRONE	0.006	0.008	0.005	0.005	0.004	0
MADRONE	0.005	0.005	0.003	0.005	0.008	0.007
RIPARIAN	0.052	0.016	0.082	0.167	0.081	0.037
CONIFER	0.022	0.022	0.016	0.064	0.010	0.020
SUMMER (Jul-Sep)						
GRASSLAND	0.167	0.156	0.034	0.008	0.227	0.323
GRASS-SHRUB	0.007	0.105	0.081	0.048	0.053	0.032
OAK-SAVANNA	0.221	0.279	0.105	0.053	0.132	0.340
OPEN OAK	0.190	0.190	0.152	0.156	0.258	0.148
CLOSED OAK	0.125	0.109	0.265	0.138	0.120	0.040
OAK-CONIFER	0.077	0.071	0.136	0.109	0.057	0.032
OAK-MADRONE	0.015	0.011	0.037	0.013	0.012	0
MADRONE	0.007	0.003	0.018	0.021	0.002	0.004
RIPARIAN	0.080	0.023	0.097	0.207	0.118	0.072
CONIFER	0.040	0.053	0.073	0.021	0.020	0.008

Table 5 continued.

Habitats	01:00-04:00	05:00-08:00	09:00-12:00	13:00-16:00	17:00-20:00	21:00-24:00
	AUTUMN (Oct-Dec)					
GRASSLAND	0.277	0.145	0.103	0.170	0.488	0.456
GRASS-SHRUB	0.074	0.080	0.187	0.019	0.051	0.041
OAK-SAVANNA	0.194	0.170	0.142	0.245	0.216	0.187
OPEN OAK	0.211	0.281	0.241	0.209	0.146	0.176
CLOSED OAK	0.097	0.152	0.088	0.151	0.042	0.031
OAK-CONIFER	0.062	0.088	0.148	0.055	0.016	0.005
OAK-MADRONE	0.010	0.012	0.012	0.022	0.002	0
MADRONE	0.008	0.002	0.027	0.014	0.002	0
RIPARIAN	0.040	0.034	0.033	0.069	0.016	0.104
CONIFER	0.028	0.035	0.018	0.047	0.023	0

independent samples, Snedecor and Cochran 1980:124), especially in late spring and summer. As early evening approached (17:00-20:00), the occurrence of CWTB among grassland, grass-shrub and oak-savanna habitats increased, particularly during autumn and winter.

CWTB primarily used grassland and oak-savanna habitats during twilight hours and periods of darkness. An average of 89% and 83% of the observations recorded in grassland and oak-savanna habitats, respectively, occurred during the periods 01:00-08:00 and 17:00-24:00 (except during summer when the period 17:00-20:00 was excluded), a significant departure from random utilization (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552). CWTB utilized oak-savanna habitats significantly more frequently during daylight hours ($\bar{X} = 0.17$) as compared to grasslands ($\bar{X} = 0.11$) (comparison of proportions in independent samples, Snedecor and Cochran 1980:124); oak-savanna habitats afforded significantly more escape cover than grasslands (Appendix C) (Wilcoxon Mann-Whitney two sample test, Steel and Torrie 1980:542) and suggested a significant association between diel habitat selection and the presence of escape cover. Indeed, 84% (10112/12077) of the CWTB habitat-use observations occurred within 25 meters of escape cover. The most apparent seasonal influence on daily patterns of grassland and oak-savanna habitat use were associated with changes in daylight-darkness regimes (Table 5); for example, CWTB utilized grassland habitats within the 17:00-20:00 activity period significantly more often during winter (0.34) as compared to summer (0.11) (comparison of proportions in independent samples).

Diel patterns of habitat use among woodland habitats suggest that there were additional environmental variables influencing habitat selection; the most apparent association was between daily temperature regimes and what appeared to be selection of thermal cover (Table 5). During late spring and summer, CWTD significantly increased the frequency of use of riparian habitats during the time period 13:00-16:00 (comparison of proportions in independent samples, Snedecor and Cochran 1980:124), the hottest time of the day (Table 5). Similar patterns of habitat selection during mid-day occurred among closed oak, oak-conifer, conifer, oak madrone and madrone habitats during late spring and summer (Table 5). Correspondingly, a significant decrease in the use of habitats affording less thermal cover (i.e. grassland, oak-savanna) occurred during these periods (comparison of proportions in independent samples).

Conifer, oak conifer and closed oak habitats seemingly afforded good thermal cover during colder periods also. The frequency of use among these habitats differed significantly with respect to time of day (comparison of proportions in independent samples, Snedecor and Cochran 1980:124); 71%, 75% and 70% of the observations recorded during winter among oak-conifer, conifer and closed oak habitats, respectively, occurred during the period 21:00-08:00, typically the coldest part of the day. Open oak habitats received relatively consistent daily use and were generally preferred throughout the year (Tables 4 and 5). Open oak habitats were comparably large contiguous woodland stands and supported a moderately dense canopy and a well-developed herbaceous layer, characteristics that apparently

afforded good escape and thermal cover throughout the day and provided palatable forage year-round.

Habitat Use Among Age Classes. There were apparent differences in CWTD habitat use among age classes (Fig. 14). Generally, fawns utilized woodland and brushland habitats more often and occurred among grasslands less frequently than yearlings and adults. Fawn utilization of grassland and oak-savanna habitats was significantly less than adults and yearlings (comparison of proportions in independent samples, Snedecor and Cochran 1980:124) however, fawn utilization of madrone habitats was significantly greater than yearlings and adults (comparison of proportions in independent samples). Yearlings and adults differed significantly in the frequency of occurrence among grassland and grass-shrub habitats (comparison of proportions in independent samples); yearlings utilized grasslands more frequently than adults while occurring in grass-shrub habitats significantly less (Fig. 14).

Generally, CWTD fawns exhibited a preference for grass-shrub, open oak, closed oak, madrone and riparian habitats while avoiding grassland and oak-madrone habitats; oak-savanna, oak-conifer and conifer habitats were utilized proportionally (Table 6). Analysis of seasonal habitat use patterns revealed that fawns exhibited a significantly greater preference for grass-shrub and open oak habitats during late spring and summer (Table 7) while closed oak habitats received significantly greater use during winter (Table 7) (comparison of proportions in independent samples, Snedecor and Cochran 1980:124). Grassland habitats were utilized least frequently.

Figure 14. Proportion of Columbian white-tailed deer fawns, yearlings and adults occurring among the ten habitats represented on the study area in Douglas County, Oregon during the period May 1978-December 1980 (within a specific habitat values that share common letters are not significantly different, $P>0.05$).

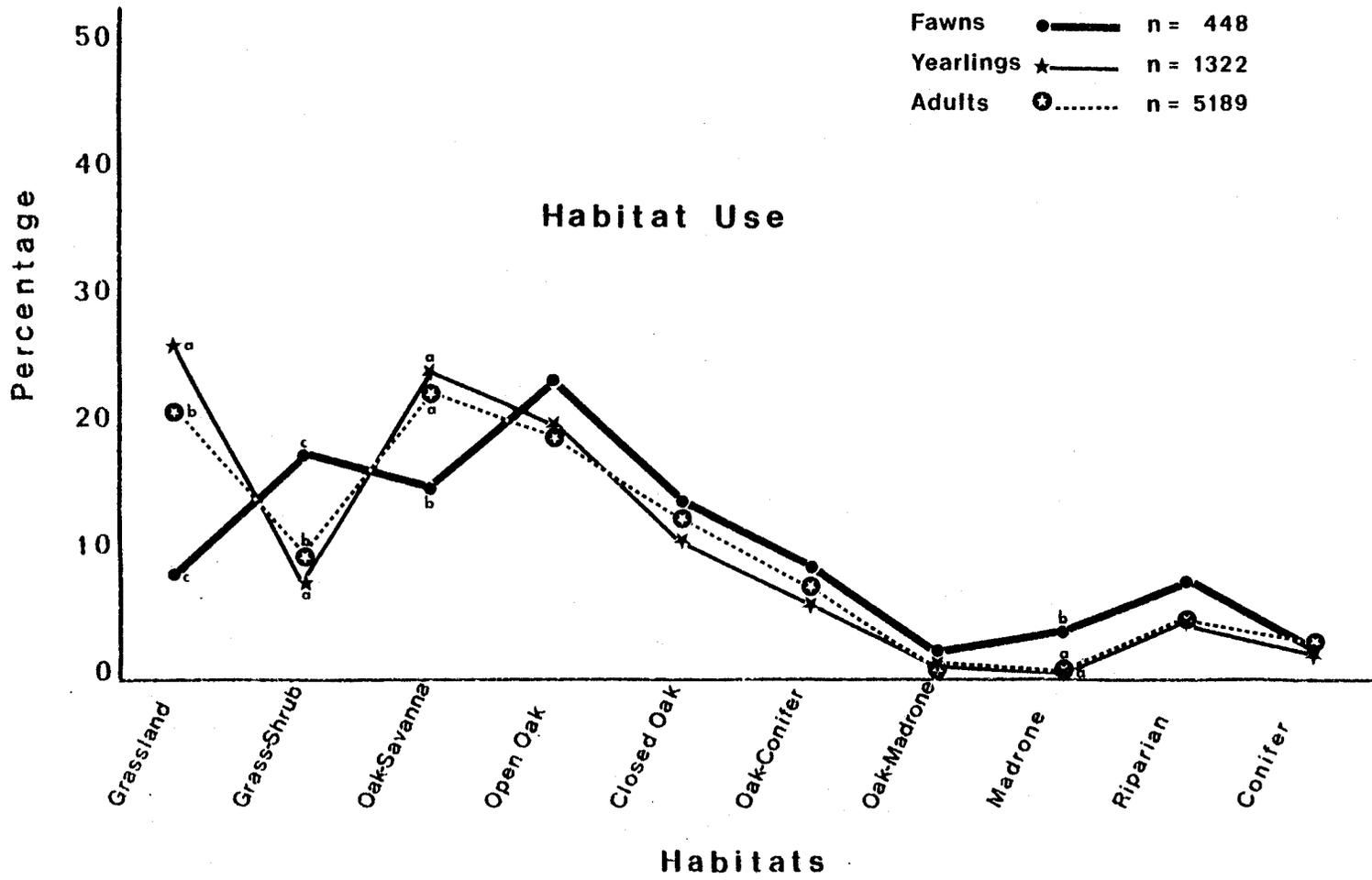


Figure 14.

Table 6. Occurrence of Columbian white-tailed deer fawns, yearlings and adults among the ten habitats represented on the study area in Douglas County, Oregon during the period May 1978-December 1980. (notations from Neu et al. 1974)

Habitat	Proportion Of Total Area ^a (p_{i0})	Proportion Observed In Each Habitat (\bar{p}_i)	95% Family Confidence Intervals ^b
FAWNS (n = 448)			
GRASSLAND	0.336	0.076	$0.041 \leq p_i \leq 0.111$
GRASS-SHRUB	0.044	0.170	$0.120 \leq p_i \leq 0.220$
OAK-SAVANNA	0.132	0.147	$0.100 \leq p_i \leq 0.194$
OPEN OAK	0.171	0.225	$0.172 \leq p_i \leq 0.280$
CLOSED OAK	0.087	0.136	$0.090 \leq p_i \leq 0.182$
OAK-CONIFER	0.113	0.085	$0.048 \leq p_i \leq 0.122$
OAK-MADRONE	0.061	0.020	$0.002 \leq p_i \leq 0.039$
MADRONE	0.014	0.038	$0.015 \leq p_i \leq 0.063$
RIPARIAN	0.031	0.078	$0.042 \leq p_i \leq 0.114$
CONIFER	0.011	0.025	$0.004 \leq p_i \leq 0.046$
YEARLINGS (n = 1322)			
GRASSLAND	0.336	0.258	$0.224 \leq p_i \leq 0.292$
GRASS-SHRUB	0.044	0.071	$0.051 \leq p_i \leq 0.091$
OAK-SAVANNA	0.132	0.234	$0.214 \leq p_i \leq 0.254$
OPEN OAK	0.171	0.191	$0.161 \leq p_i \leq 0.221$
CLOSED OAK	0.087	0.105	$0.081 \leq p_i \leq 0.129$
OAK-CONIFER	0.113	0.057	$0.039 \leq p_i \leq 0.075$
OAK-MADRONE	0.061	0.010	$0.002 \leq p_i \leq 0.018$
MADRONE	0.014	0.004	$0.000 \leq p_i \leq 0.008$
RIPARIAN	0.031	0.046	$0.032 \leq p_i \leq 0.062$
CONIFER	0.011	0.024	$0.012 \leq p_i \leq 0.036$

^aProportions of total area represent expected Columbian white-tailed deer observations in corresponding habitat.

^bIndividual habitat proportion estimates represent 99.5% confidence intervals.

Table 6 continued.

Habitat	Proportion Of Total Area ^a (p_{i0})	Proportion Observed In Each Habitat (\bar{p}_i)	95% Family Confidence Intervals ^b
ADULTS (n = 9189)			
GRASSLAND	0.336	0.213	$0.197 \leq p_i \leq 0.229$
GRASS-SHRUB	0.044	0.094	$0.083 \leq p_i \leq 0.105$
OAK-SAVANNA	0.132	0.220	$0.204 \leq p_i \leq 0.236$
OPEN OAK	0.171	0.187	$0.172 \leq p_i \leq 0.202$
CLOSED OAK	0.087	0.124	$0.111 \leq p_i \leq 0.137$
OAK-CONIFER	0.113	0.073	$0.063 \leq p_i \leq 0.083$
OAK MADRONE	0.061	0.009	$0.005 \leq p_i \leq 0.013$
MADRONE	0.014	0.006	$0.003 \leq p_i \leq 0.009$
RIPARIAN	0.031	0.045	$0.037 \leq p_i \leq 0.053$
CONIFER	0.011	0.029	$0.022 \leq p_i \leq 0.036$

^aProportions of total area represent expected Columbian white-tailed deer observations in corresponding habitat.

^bIndividual habitat proportion estimates represent 99.5% confidence intervals.

Table 7. Seasonal frequency distribution of Columbian white-tailed deer fawns among the ten habitats on the study area in Douglas County, Oregon during the period May 1978-December 1980.

HABITAT	WINTER	SPRING	SUMMER	FALL
GRASSLAND	0.075	0.089	0.036	0.098
GRASS-SHRUB	0.155	0.223	0.193	0.109
OAK-SAVANNA	0.161	0.143	0.096	0.174
OPEN OAK	0.205	0.250	0.241	0.217
CLOSED OAK	0.199	0.116	0.084	0.098
OAK-CONIFER	0.075	0.098	0.096	0.076
OAK-MADRONE	0.006	0.027	0.012	0.043
MADRONE	0.056	0.009	0.044	0.033
RIPARIAN	0.043	0.036	0.169	0.109
CONIFER	0.025	0.009	0.024	0.043

during the summer while riparian habitats experienced a significant increase in use during this period (Table 7) (comparison of proportions in independent samples). Similar shifts in frequency of use occurred among oak-conifer habitats during late spring and summer (Table 7) and among madrone habitats during winter and summer (Table 7).

Seasonal patterns of habitat use among CWTD fawns were apparently associated with a need for escape and thermal cover. Young fawns are vulnerable to intense predation pressure and thermal stress, particularly during late spring and summer. During a three-year study on the CWTDNWR, radio-collared fawns suffered a predation rate as high as 86% during the initial ten weeks postpartum (Al Clark, unpublished data). Also, young mammals are generally poor thermoregulators (Bartholomew 1977) and their large surface to volume ratio increases the susceptibility to thermal stress (Bartholomew 1977, Moen 1973). An effective means of reducing thermal stress is via behavioral responses (Bartholomew 1977), such as through habitat selection. The general pattern of frequent use of woodland habitats during late spring and summer, particularly among riparian woodlands, can probably be attributed to more favorable microclimatic conditions. Woodland and brushland habitats also afforded good escape cover.

Typical fawning habitat (during the first week postpartum), as determined from sampling 35 capture sites, represented areas experiencing little or no livestock use, averaged 146.2m ($s_x^2 = 13.5$) from water, supported an Oregon white oak canopy and occurred on sites with little or no incline (<20%) and a northern exposure.

Fawns were captured an average of 3.95m from the base of a tree (DBH>10 cm) in herbaceous vegetation that averaged 38.2 cm ($s_{\bar{x}} = 3.6$) in height. Dominant herbaceous species included hedgehog dogtail, perennial ryegrass and new-growth poison oak; tall fescue, orchard grass and sedges and rushes occurred on the more mesic sites. The dominant shrub species were poison oak and wild rose.

Eighty percent of the fawn capture sites occurred among woodland habitats while a significant disproportion (69%) occurred on portions of the study area (12%) that experienced no livestock use during the fawning season. The closed oak woodland was the most preferred fawning habitat, representing 40% of the capture locations; grasslands were the least preferred habitat representing only 2.8% of the capture sites. The remaining capture sites occurred proportionally among open oak (20%), oak-savanna (11.4%), oak-conifer (5.7%), oak-madrone (2.8%), madrone (2.8%) and riparian (8.6%) habitats.

Generally, yearling and adult CWTB demonstrated a preference for grass-shrub, oak-savanna, riparian and conifer habitats and avoided grassland, oak-conifer, oak-madrone and madrone habitats (Table 6). Adults also displayed a preference for open oak and closed oak habitats; yearlings utilized open oak and closed oak woodlands proportionally (Table 6).

Habitat Use Between Sexes. Adult male and adult female CWTB exhibited similar patterns of habitat use (Fig. 15). Adult males however, occurred significantly less frequently among grass-shrub habitats and demonstrated a significantly greater use of conifer habitats as compared to females (Fig. 15)(comparison of proportions

Figure 15. Proportion of adult Columbian white-tailed deer males and females occurring among the ten habitats represented on the study area in Douglas County, Oregon during the period May 1978-December 1980 (* denotes significant difference, $\underline{P} < 0.05$).

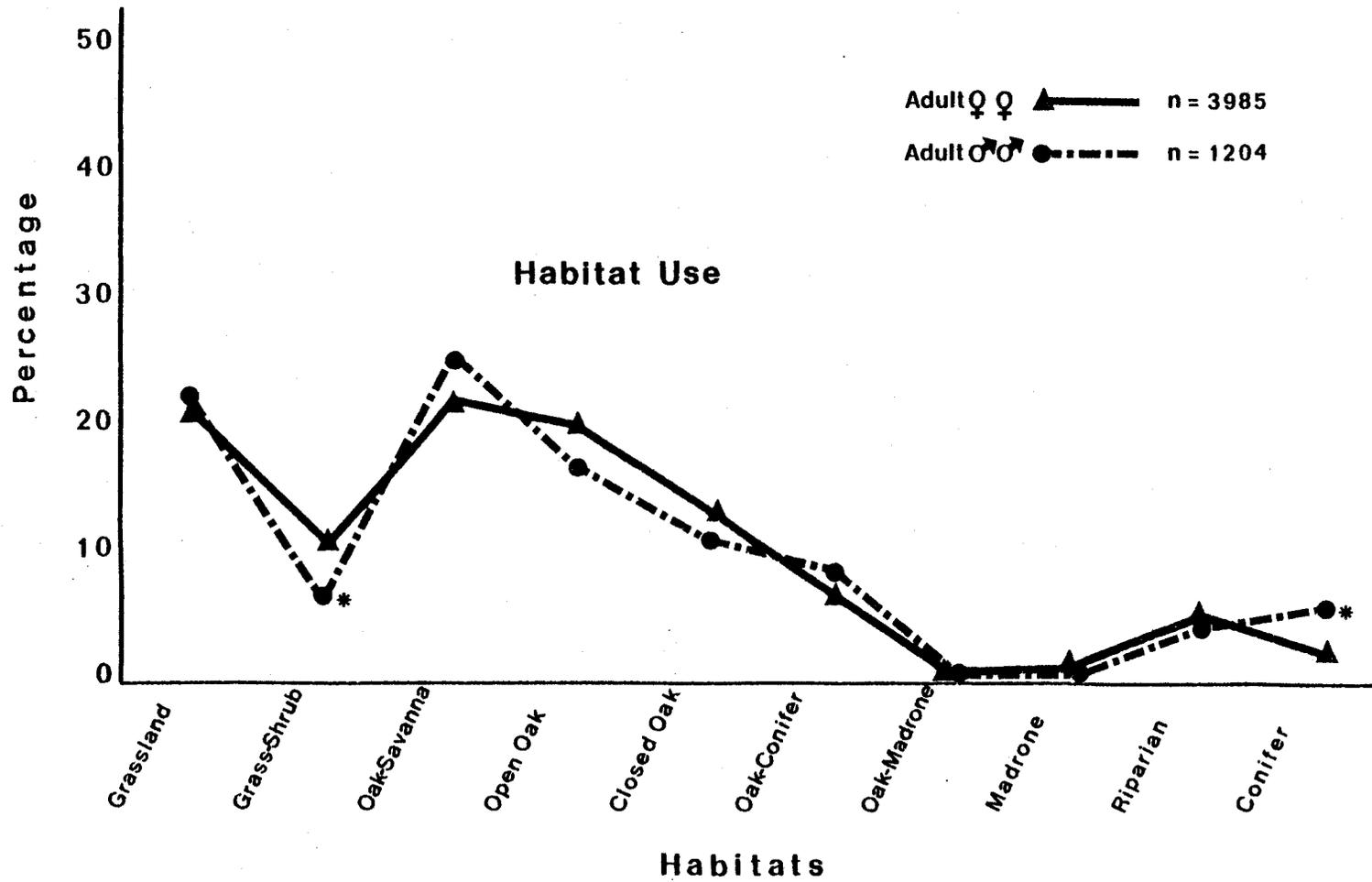


Figure 15.

in independent samples, Snedecor and Cochran 1980:124). Adult males and females demonstrated a preference for grass-shrub, oak-savanna and conifer habitats while generally avoiding madrone, oak-madrone, oak-conifer and grassland habitats (Table 8). Adult females also exhibited a preference for riparian, open oak and closed oak habitats; open oak, closed oak and riparian habitats were used proportionally by adult males (Table 8). The greatest disparity in use of open oak and closed oak habitats between adult males and females occurred during late spring and summer and was probably associated with fawning activities; 60% of the marked fawns in this study were captured in closed oak and open oak habitats.

Seasonal patterns of habitat use revealed that the greatest disparity in grass-shrub and conifer habitat use between adult males and females also occurred during the summer. Adult males increased their use of conifer habitats from 0.030 during spring to 0.050 during summer and significantly decreased their use of grass-shrub habitats from 0.090 to 0.040 during the same period (comparison of proportions in independent samples, Snedecor and Cochran 1980:124). Analysis of diel patterns of habitat use suggested that these seasonal patterns of use by males represented a behavioral response intended to reduce thermal stress; adult males used conifer and other woodland habitats almost exclusively during the hottest part of the day while avoiding grass-shrub and grassland habitats during that same period.

Adult males in this study were on the average 27% larger than adult females; the smaller surface to volume ratio, smaller mass-specific endogenous heat production (Bartholomew 1977) and greater

Table 8. Occurrence of Columbian white-tailed deer adult males and females among the ten habitats represented on the study area, Douglas County, Oregon during the period May 1978-December 1980. (notations from Neu et al. 1974)

Habitat	Proportion Of Total Area ^a (p_{i0})	Proportion Observed In Each Habitat (\bar{p}_i)	95% Family Confidence Interval ^b
ADULT MALES (n = 1204)			
GRASSLAND	0.336	0.220	0.186 $\leq p_i \leq$ 0.254
GRASS-SHRUB	0.044	0.065	0.045 $\leq p_i \leq$ 0.085
OAK-SAVANNA	0.132	0.247	0.212 $\leq p_i \leq$ 0.282
OPEN OAK	0.171	0.164	0.134 $\leq p_i \leq$ 0.194
CLOSED OAK	0.087	0.108	0.083 $\leq p_i \leq$ 0.133
OAK CONIFER	0.113	0.087	0.064 $\leq p_i \leq$ 0.110
OAK MADRONE	0.061	0.003	0.000 $\leq p_i \leq$ 0.007
MADRONE	0.014	0.004	0.000 $\leq p_i \leq$ 0.009
RIPARIAN	0.031	0.042	0.026 $\leq p_i \leq$ 0.058
CONIFER	0.011	0.059	0.040 $\leq p_i \leq$ 0.078
ADULT FEMALES (n = 3985)			
GRASSLAND	0.336	0.211	0.193 $\leq p_i \leq$ 0.229
GRASS-SHRUB	0.044	0.103	0.089 $\leq p_i \leq$ 0.117
OAK-SAVANNA	0.132	0.212	0.194 $\leq p_i \leq$ 0.230
OPEN OAK	0.171	0.194	0.176 $\leq p_i \leq$ 0.212
CLOSED OAK	0.087	0.129	0.114 $\leq p_i \leq$ 0.144
OAK CONIFER	0.113	0.069	0.058 $\leq p_i \leq$ 0.080
OAK MADRONE	0.061	0.101	0.012 $\leq p_i \leq$ 0.021
MADRONE	0.014	0.007	0.003 $\leq p_i \leq$ 0.011
RIPARIAN	0.031	0.046	0.037 $\leq p_i \leq$ 0.055
CONIFER	0.011	0.020	0.014 $\leq p_i \leq$ 0.026

^aProportions of total area represent expected Columbian white-tailed deer observations in corresponding habitat.

^bIndividual habitat proportion estimates represent 99.5% confidence intervals.

thermal inertia (Moen 1968) of adult males would seemingly make them less susceptible to heat stress (Bartholomew 1977). Correspondingly, adult females should on the average experience greater thermal stress during comparable periods; yet, adult females did not exhibit comparable seasonal and diel patterns of habitat use. This apparent contradiction in behavior can perhaps be explained by examining the additional constraints placed on adult females during the summer. Ordinarily, adult females have to contend with the energetic demands of lactation as well as sufficient escape cover for fawns. Conifer habitats did not support much in the way of palatable forage nor was there adequate herbaceous and shrub vegetation for good escape cover (as evidenced by the fact that conifer habitats were rarely if ever used for fawning). Instead, adult females increased their use of open oak and closed oak habitats during summer; both of these habitats supported a well-developed understory (herbaceous forage) and provided good escape cover for neonates while providing reasonably good thermal cover for both adult females and fawns. Thus, while habitat use patterns of adult males during the summer were apparently influenced by a primary concern for maximizing their net energy budget (via minimizing energy expenditures for thermoregulation) during the critical period preceding the breeding season, adult females apparently adopted a strategy that provided an optimum balance among several potentially conflicting needs during an equally critical period.

There are at least two major assumptions inherent in the methods we employed to determine habitat use and preference. First was the assumption that the animal under study was equally observable among

all habitats. The habitats differed significantly with respect to the obstruction-to-vision index and one would suspect that corresponding differences in the observability of CWTD existed. Suring and Vohs (1979) attempted to reduce the bias resulting from differences in visibility among plant communities by dividing the number of observations of deer by the percentage of visibility for each community. Theoretically this procedure should reduce the bias arising from differences in visibility, however in practice multiplying (or dividing) data by a correction factor probably increased the bias by an indeterminable quantity (W. Scott Overton, personal communication).

More important however is the realization that the probability of observing a deer within a specific habitat is not determined solely by the obstructive characteristics of the environment, but rather is determined also by the behavior of deer among the various habitats, and the mode of data collection and how it affects their behavior. Behavioral observations recorded in this study indicated that flight behavior differed significantly among the habitats. Generally, as the density of the habitat increased and visibility decreased, the flight distance of CWTD decreased. Also, deer were much more approachable and observable on horseback than on foot or from a vehicle. Nevertheless, CWTD were probably under-represented in some habitats, particularly in dense monotypic stands of madrone. But my experiences in the field and the behavioral data we collected suggest that the observability of CWTD essentially did not differ noticeably among the habitats.

A key assumption in habitat use and preference studies is that the proportion of the total environment represented by a specific habitat represents the availability of the habitat. In reality, that quantity is the abundance of the habitat; availability is the accessibility of that habitat to the consumer (Johnson 1980) and reflects both the abundance of the habitat and the behavior of the consumer.

In this study, the abundance of each habitat was probably a good index of availability with the exception of grasslands. Behavioral observations indicated that CWTD seldom (16%, 1965/12077) utilized portions of the study area greater than 25m from cover. Thus a large portion of grassland habitats were effectively inaccessible to CWTD and although grasslands represented 33.6% of the total study area, a much smaller portion was available for use. We have no means of determining the effective availability of the grassland habitat and consequently no means of evaluating its relative preference. However, the consistently high frequency of use throughout the year provides some indication of its relative importance.

CWTD habitat use patterns generally reflected a need for vegetative associations that provided both palatable forage and adequate escape cover. Suring and Vohs (1979) reported similar conclusions for CWTD on the CWTDNWR. Seasonal and daily habitat preferences indicated that the specific needs of CWTD changed seasonally and throughout the day. Some habitats received infrequent use generally, but became highly preferred during critical periods of environmental stress or during periods characterized by

specific life history events. Much of the variation in habitat use reflected significant age and sex class preferences. Riparian and closed oak habitats, for example, were much more important to adult females and their fawns than was indicated from general patterns of use. Adult males demonstrated seasonal habitat preferences that were apparently associated with a need for thermal cover during summer. Indeed, the relative importance of each habitat differed with respect to season, time of day, age and sex and availability. Thus an adequate assessment of critical CWTD habitat can not simply be a gross comparison of the proportion of use of each habitat to its corresponding availability, but should also include an in-depth analysis of habitat selection as it might reflect the critical environmental periods and important biological events in the life history of the species.

POPULATION CHARACTERISTICS

Population Size and Density

Crews (1939) estimated the number of whitetails on the White-tailed Deer Refuge (7895 ha) at 200 - 300 individuals during 1937-1939, representing a density of 2.5 - 3.8 deer per km^2 (6.6-9.8/ mi^2). This estimate was derived from a number of censusing techniques including general reconnaissance, close observation of sign and talking with local farmers (Crews 1939). During 1970, William McCaleb (ODFW) via spotlight counts (i.e. number of deer per linear mile) estimated the number of whitetails within the White-tailed Deer Refuge area at approximately 450 - 500 individuals (personal communication), a density of 5.7 - 6.3 deer per km^2 (14.8-16.3/ mi^2). Although these estimates were not obtained through extended field work nor derived from rigorous censusing techniques, they provide some information on general population trend during the 30 year period and reinforce preliminary conclusions in this study regarding high whitetail density areas and the recent center of dispersal.

Schnabel estimates of population size were obtained for the intensive study portion of the study area during November and December 1979 and January and August 1980 (Table 9). Separate early morning and evening estimates obtained during November and December 1979 were not significantly different ($P > 0.05$) and were combined to improve the precision of these monthly estimates. The three monthly winter estimates (November-January) were not significantly different

Table 9. Schnabel estimates of Columbian white-tailed deer population within intensive study area, Douglas County, Oregon during November and December 1979, and January and August 1980. (95% confidence intervals are in parentheses)

	M_i	n_i	x_i	λ^a	Z statistic ^b
1979					
November 17-20	15	317	41	4755	
				$\lambda = 4755$	
				$\hat{N} = 113 (82-157)$	Nov-Dec
December 12-14	16	153	35	4032	Z = 0.093
December 15-18	17	360	48	5950	P(Z>Z ₀) = 0.928
				$\lambda = 9982$	
				$\hat{N} = 119 (97-150)$	
1980					Dec-Jan
January 2-8	17	404	63	6867	Z = -0.50
				$\lambda = 6867$	P(Z>Z ₀) = 0.617
				$\hat{N} = 109 (85-140)$	
					Jan-Aug
August 12-22	19	570	41	5168	Z = 0.626
				$\lambda = 5168$	P(Z>Z ₀) = 0.529
				$\hat{N} = 123 (90-171)$	

^a M_i is the number of marked deer in the population, n_i is the total number of deer observed during census period (i.e. month), and x_i is the number of marked deer observed during the census period; where

$$\hat{N} = \lambda/x + 1; \quad \lambda = \sum_{i=1}^k (n_i M_i), \quad \text{and} \quad x = \sum_{i=1}^k x_i.$$

^b Employed to test for statistically significant differences in population estimates between census periods;

$$Z = \frac{x_0 - (x_0 + x_1) \frac{\lambda_0}{\lambda_0 + \lambda_1}}{(x_0 + x_1) \left(\frac{\lambda_0}{\lambda_0 + \lambda_1} \right) \left(\frac{\lambda_1}{\lambda_0 + \lambda_1} \right)} \pm$$

(Table 9); the mean population estimate for the intensive study area during this period was 114 ($s_{\bar{x}} = 23$). The August 1980 estimate was larger than the early winter estimates and probably reflected an increase in the fawn segment of the population realized through a birth pulse during June–August. Since most of the fawn mortality occurred during the first ten weeks postpartum (see Fawn Survival and Recruitment), the best estimate of year-round population size supported by the intensive study area is given by the August 1980 Schnabel estimate (Table 9); the August 1980 estimate was used to compute an estimate of total population size for the entire study area.

CWTD density estimates for the intensive study area incorporated the August 1980 Schnabel estimate and estimates of total area inhabited by the study population. The two independent techniques employed to estimate total area provided different estimates. The biological technique (i.e. derived from peripheral locations of marked deer) provided 3.97 km^2 as an estimate of total area; the measurement technique used a 50 m tape, a Lietz Range Finder (Forestry Supplies, Inc., Jackson, Mississippi 39204) and aerial photographs, and gave an estimate of 3.37 km^2 as the total area. Respective density estimates for the intensive study area became 31.0 CWTD per km^2 and 36.5 CWTD per km^2 .

The CWTD density estimate for the intensive study area served as the basis for calculating a total population size for the entire study area (2745 ha). Population density coefficients (Table 10) derived from the relative density indices (Table 11) were used to compute population estimates for the respective habitat structure types (i.e. locations) comprising the entire study area (Table 10). These

Table 10. Columbian white-tailed deer population estimates for the different habitat structure types on the study area, Douglas County, Oregon during the period November 1979-December 1980. Estimates were calculated from two independently determined densities derived from a biologically determined area (3.97 km²) and from a measured area (3.37 km²).

Location	Total Area (km ²)	Density Coefficient ^a	Population Estimate ^b	
			3.97 km ²	3.37 km ²
Page Road	2.02	1.00	63	74
Newton Creek Road and Jones' Ranch	3.24	1.14	114	135
Sunshine Road and Lindbloom Ranch	18.22	0.58	328	386
Whistler's Bend Park ^c	<u>3.97</u>	1.00	<u>123</u> ^d	<u>145</u>
TOTAL	27.45		628	740

^a Derived from the following equation:

$$D.C. = \frac{\text{relative density index of location}}{\text{relative density index of intensive study area}}$$

^b Determined from the following equation:

$$N_{loc} = (\text{Total Area})(\text{Density Coefficient}) \left(\frac{\text{Population Estimate of}}{\text{Intensive Study Area}} \right)$$

^c Intensive study area for which Schnabel estimate was obtained.

^d Population estimate derived from Schnabel estimate for August 1980.

Table 11. Relative density indices of Columbian white-tailed deer derived from spotlight counts obtained within calculated sampling areas for the different habitat structure types that occurred on the study area, Douglas County, Oregon during December 1979 and January 1980.

<u>Location^a</u>	<u>Spotlight Counts</u>			<u>Area Sampled (ha)</u>	<u>Relative Density Index</u> (CWTD per hectare)
	<u>\bar{x}</u>	<u>s_x</u>	<u>n</u>		
Page Road	19.3	0.88	3	39.7	0.49
Newton Creek Road and Jones' Ranch	19.2	1.11	4	34.6	0.56
Sunshine Road and Lindbloom Ranch	35.2	0.99	5	124.3	0.28
Whistler's Bend Park ^b	54.4	3.32	7	112.0	0.49

^a Each location represents a major different structure type with respect to abundance and distribution of woodland cover, and use (e.g. livestock, residential, undisturbed).

^b Intensive study area for which Schnabel population estimate was obtained.

values when summed represent the total population size of the entire study area during the period November 1979 through August 1980.

There are several methods available for estimating population size of North American cervids (Rasmussen and Doman 1943; Thomas 1969; Lewis and Farrar 1968). Generally however, ratio estimators are cited as providing the most accurate estimates of total population size (Rasmussen and Doman 1943; Lewis and Farrar 1968). Capture - recapture techniques give an unbiased estimate of population size and variance (Wittes 1972) while multiple recapture techniques have been demonstrated to provide estimates that are within 2% of the known population size (Cook et al. 1967).

The accuracy and precision of population estimates derived from capture-recapture techniques are contingent upon several assumptions (Overton 1971); foremost of which concerns the question of equal observability among individuals of the population during the census period. Unequal observability can result from behavioral differences between marked and unmarked individuals (i.e. prior experience); behavioral differences among age and sex groups within the population; and because the recaptures of marked individuals are not independent of captures (i.e. the probability of observing marked individuals is disproportionately greater because recapture routes include capture sites). Also, there are potential biases associated with individual patterns of behavior independent of age and sex and circumstances surrounding capture; however, these differences would be important only if they affected the mean probability of observing marked or unmarked deer.

Observations of marked deer indicated a decrease in observability for a brief period following capture; presumably a response to the negative experiences associated with capture. Only once (December) during all sampling periods was an individual marked immediately preceding or during a population estimate spotlight census. The individual was not included in the marked deer category (M_1) until the following night's census when it was observed as part of the total sample (n). This was done in order to ensure that the recently marked individual was available for recapture and to minimize bias resulting from subsequent aversive behavior.

Variation in observability among age and sex classes has been documented in white-tailed deer (Gavin 1979; Downing et al. 1977). Both Gavin (1979) and Downing et al. (1977) however noted seasonal patterns in observability such that specific sex and age groups were more equally observable during certain periods. Downing et al. (1977) observed that fawns were always less observable than does during the summer, the time they were most easily differentiated from older deer, and bucks and does were generally observed at the same rate in August and November. Observations of marked deer during the census periods (November-January and August) indicated that age and sex groups were equally observable (Table 12). A significant departure from the expected did occur between males and females during December (Table 12). This significant difference resulted from an increase in the observability of males during this period; apparently a consequence of increased rutting activity, i.e. tending, defending or pursuing estrus females. The percent of observed males

Table 12. Comparison of observability of marked Columbian white-tailed deer within the intensive study area during November and December 1979, and January and August 1980. (asterisk indicates statistically significant, $P < 0.05$)

November			
	<u>No. Marked</u>	<u>No. Observed</u>	<u>No. Expected^a</u>
Adult	12	29	29.1
Yearling	3	10	7.3
Fawns	6	12	14.6
		$\chi^2 = 1.462, df = 2, P > 0.25$	
All Age Classes			
Males	5	18	13
Females	10	21	26
		$\chi^2 = 2.885, df = 1, P > 0.05^b$	
Adults			
Males	3	10	7.2
Females	9	19	21.8
		$\chi^2 = 1.449, df = 1, P > 0.20^b$	
December			
	<u>No. Marked</u>	<u>No. Observed</u>	<u>No. Expected</u>
Adults	13	64	62.0
Yearlings	3	19	14.4
Fawns	6	22	28.6
		$\chi^2 = 3.057, df = 2, P > 0.10$	
All Age Classes			
Males	5	35	25.9
Females	11	48	57.1
		$\chi^2 = 4.647^*, df = 1, P > 0.05$	
Adults			
Males	3	21	14.8
Females	10	43	49.2
		$\chi^2 = 3.378, df = 1, P > 0.05$	

Table 12 continued.

January			
	<u>No. Marked</u>	<u>No. Observed</u>	<u>No. Expected</u>
Adults	14	55	48.1
Yearlings	3	8	10.3
Fawns	6	16	20.6
		$X^2 = 2.531, df = 2, P > 0.25$	
All Age Classes			
Males	5	16	18.5
Females	12	47	44.5
		$X^2 = 0.478, df = 1, P > 0.25$	
Adults			
Males	3	10	11.8
Females	11	45	43.2
		$X^2 = 0.350, df = 1, P > 0.50$	
August			
	<u>No. Marked</u>	<u>No. Observed</u>	<u>No. Expected</u>
Adults	15	35	27.8
Yearlings	4	4	7.4
Fawns	8	11	14.8
		$X^2 = 4.403, df = 2, P > 0.10$	
All Age Classes			
Males	5	8	10.3
Females	14	31	28.7
		$X^2 = 0.785, df = 1, P > 0.25^b$	
Adults			
Males	4	8	9.3
Females	11	27	25.7
		$X^2 = 0.247, df = 1, P > 0.50^b$	

^aDerived from the proportion of marked individuals during census period.

^bYates' continuity correction applied to this test.

engaged in rutting activity was 27% in December as compared to 23% and 19% for November and January respectively.

The location of initial capture sites along or near subsequent recapture census routes would generally increase the probability of observing marked individuals and consequently underestimate the total population size. For this reason, livetraps were distributed throughout the intensive study area independent of the proximity to the predefined census route. Four deer were darted and immobilized along the recapture route; however, five individuals were marked in remote portions of the intensive study area independent of the recapture route. The starting point for each census within a censusing period differed so as to minimize the bias resulting from habitual use of areas by those individuals marked along or near the recapture route.

Two density estimates were derived for the intensive study area, both of which incorporated defensible techniques. The population density derived from the area encompassing the peripheral locations of marked deer provided a more biologically meaningful estimate as it allowed the movements of marked deer to define the population range, a valid corollary of assumption 1 for mark-recapture estimators (Overton 1971). That is, given that there exists a well-defined population of animals containing N individuals, and the marked sample is representative of this population, it follows then that the area defined by the movements of the marked sample should represent the range of the total population. Also, further examination of the alternate method reveals that there may

exist certain biases associated with the inclusion of individuals within a sample (i.e. affinity or aversion to those areas sampled) which may disproportionately represent the population density of the intensive study area if calculated from the measured area within which the sample was obtained. Finally, the biologically derived population range provided the most conservative density estimate, and although this generally should not be a primary concern in biological investigations, it is certainly a worthwhile consideration when managing an endangered species.

Average white-tailed deer density on the 2745 ha study area as derived from the running Schnabel estimate (November 1979 - August 1980) was 21.8 deer per km² (598 deer/27.45 km²). Gavin (1979) employed similar estimating techniques and reported CWTD densities on the 790 ha study area portion of the CWTDNWR as ranging from 30 deer per km² in 1975 to 21.3 deer per km² in 1976. Non-hunted whitetailed deer populations in other regions have attained similar or in many instances higher densities. White (1973) reported approximately 39 deer per km² on the Aransas National Wildlife Refuge in Texas, and White et al. (1972) observed similar densities on the Welder Wildlife Refuge. The highest reported whitetail densities to date occurred on the National Aeronautics and Space Administration's Plum Brook Station in northern Ohio, a density of 115 deer per km² (Rice and Harder 1977). Relatively high densities have been reported for other enclosed whitetail populations: 58 deer per km² on the Rachelwood Wildlife Research Preserve (Woolf and Harder 1979) and 39 deer per km² on the George Reserve (McCullough 1979). In contrast,

the Florida Key Deer (O.v. clavium), the only other endangered subspecies of white-tailed deer, occurred at densities of 8-10 deer per km² on Big Pine Key (Hardin et al. 1976).

Sex and Age Composition

Sex Ratios. Examination of road kill does during winter and spring indicated that the primary (in utero) sex ratio of CWTB in Douglas County did not depart significantly (Chi-square test of independence, Sokal and Rohlf 1969:589) from an expected 1:1 sex ratio. Five adult females and one yearling female carried a total of 10 fetuses: 6 males and 4 females.

The sex ratio of newborn CWTB fawns was determined from descriptive data recorded for individuals that were captured during the fawning season (May-September). Twenty-seven of 42 captured fawns were males, suggesting a skewed sex ratio in favor of males for the period 1978-1980. Statistical analyses of annual fawn sex ratios revealed that a significant disproportion of male fawns (9 males :1 female) was born into the population during 1978. Fawn capture data from 1979 (11 males :6 females) suggested that male fawns were represented disproportionately in the population again, but a Chi-square test of independence failed to substantiate a significant departure ($P>0.10$) from unity. Unlike the previous two years, the sex ratio of fawns captured during 1980 (8 males :9 females) closely paralleled a 1:1 ratio and suggested that male and female fawns were represented equally in the population during that year.

Buck:Doe Ratio. The sex ratio of yearlings and adults was derived from observations recorded while on horseback and during spotlight

censuses in autumn and early winter. Observations of marked individuals indicated that yearlings, adult males and adult females were equally observable during this period (Table 12); the observed sex ratios averaged 30 males per 100 females during November and December. Thus, sex ratio estimates derived from observations conducted during November and December best reflected the actual proportions of yearling-adult males and females in the population.

Fawn:Doe Ratio. The proportion of fawns to yearling-adult females in the population was similarly derived from horseback transects and spotlight censuses. The mean fawn:doe ratio during November and December was 52 fawns per 100 does. As before, observations of marked individuals during autumn and early winter indicated that age groups were most equally observable during this period (Table 12). Thus, fawn:doe ratio estimates derived during November and December best reflected the actual proportions of fawns and yearling-adult females in the population.

Herd Composition. The age and sex composition of the CWTD population was derived from the population estimate obtained for the entire study area (598, from Table 3) and the sex and age class ratios determined from horseback and spotlight censuses (52 fawns:30 bucks:100 does). During November and December 1979, does comprised 55% of the total population while bucks and fawns represented 16.5% and 28.5% of the population, respectively. Thus, the estimated age and sex composition of the CWTD population on the 2745 ha study area during autumn and early winter was 329 does, 99 bucks and 170 fawns.

Much of the data in the literature relating to age and sex

composition of white-tailed deer populations were derived from harvest statistics during the fall (Severinghaus and Cheatum 1956; Mansell 1974; Kirkpatrick et al. 1976). Unfortunately, there are a number of biases inherent in harvest data (Roseberry and Klimstra 1974), biases that compel one to be suspect of the reliability of derived age and sex ratios and that render consequent herd composition estimates incomparable. Even in populations where either-sex hunts were in operation, hunters still exerted selective hunting pressure (Severinghaus and Cheatum 1956; Roseberry and Klimstra 1974). Additionally, sex-specific mortality differences among male and female fawns during the neonatal period and on into autumn bias fawn sex ratios derived from fall harvest statistics.

Gavin (1979) derived sex and age composition estimates for CWTD on the CWTDNWR from herd composition counts during autumn. The reported buck:doe ratio in November ranged from 29-42 males per 100 females, approximately three does for every buck, while fawn:doe ratios ranged from 35-60 fawns per 100 does (Gavin 1979). Thus, bucks on the refuge comprised 17.5-21.2% of the population while does and fawns represented from 49.5-60.2% and 22.3-31.0% of the population, respectively (derived from Table 9, Gavin 1979). Similarly, the CWTD buck:doe ratio in Douglas County approached three females for every male (30M:100F) during autumn and early winter, and represented 16.5% of the population. Also, fawn:doe ratios in this study (52:100) were comparable to the CWTDNWR with fawns and does comprising 28.5% and 55.0% of the Douglas County population, respectively.

It is somewhat surprising that Gavin (1979) did not observe more bucks per 100 does on the CWTDNWR; the refuge population had not experienced a legal harvest since 1967. Correspondingly, the Douglas County herd experienced intensive selective hunting pressure through 1977, pressure that removed as many as 4.5 bucks per km² (11 per mi²) on the study area. Since both CWTD populations experienced different recent treatments (i.e. hunting pressure), one might expect a greater disparity in buck:doe ratios. The degree of similarity between the two populations suggest that CWTD respond quickly to a release from selective mortality pressure. Buck:doe ratios reported for the CWTDNWR during the period 1972-1977 indicated that the population reached a "fixed" yearling and adult sex ratio within five years after a release from hunting pressure and remained relatively constant for the entire study period (Gavin 1979).

The preponderance of males in primary (in utero) and secondary (neonatal) sex ratios has been observed within white-tailed deer populations in different geographic regions (Severinghaus and Cheatum 1956) under varying environmental regimes. In south Texas, Illigie (1951) reported 136M:100F, whereas Dahlberg and Guettinger (1956) reported 151M:100F in Wisconsin. Haugen (1975) observed 122M:100F in Iowa and Kirkpatrick et al. (1976) recorded a sex ratio of 121M:100 whitetail fetuses in Indiana. The largest departures from unity reported for fawn and yearling does (198M:100F) were derived from data presented for white-tailed deer in South Carolina by Dapson et al. (1979:892), and for adult females (175M:100F) in

Ohio by Nixon (1971).

Several explanations have been offered regarding the possible environmental circumstances responsible for eliciting certain sex ratios, and the underlying adaptive significance of specific sex-ratio responses to environmental fluctuations. Trivers and Willard (1973) concluded that as maternal condition declines, such as during periods of environmental stress, natural selection would favor females that produced a larger proportion of female offspring because females generally breed regardless of physical condition whereas males of a polygynous species do not. Generally however, the empirical data reported in the literature are in direct contradiction with the Trivers-Willard hypothesis. Verme (1969) reported that female white-tailed deer maintained on a low nutritional plane, such as that experienced during periods of harsh environmental conditions, produced a significantly larger proportion (70%) of males. Similarly, Robinette et al. (1957) reported that mule deer females (Odocoileus hemionus) occupying poor ranges carried a preponderance of male fetuses (65%). Verme (1969) suggested that the larger proportion of male fawns observed in undernourished does represented a mechanism for natural regulation of population size. Verme's hypothesis however is inadequate also as it suggests that the benefit derived from sex-ratio manipulation (i.e. environmentally mediated response) is attributed to the population, an argument that is inconsistent with fundamental Darwinian principles as it requires invoking the highly criticized group selection hypothesis. Wolf and Harder (1979) suggested that observed departures of fawn sex ratios from unity

represented "localized aberrations of a 50/50 ratio"; however, failure to immediately provide a sound logical explanation for a biological phenomenon does not necessarily imply that those observations were only an artifact of the investigative procedures.

According to the literature, disparity within fawn sex ratios is widespread among North American deer (Odocoileus spp.), and suggests that sex-ratio manipulation (i.e. environmentally mediated response) associated with fluctuations in environmental quality is a real biological phenomenon. Woolf and Harder (1979) reported a significant departure of whitetail fawns from a 1:1 sex ratio and concluded that the disparity in male and female fawns was associated with low reproductive performance, a phenomenon that reportedly results from poor range quality and undernutrition (Robinette et al. 1973; Verme 1969). CWTD females in southern Oregon produced a preponderance of male fawns during the spring of 1978 and 1979 following years when rainfall and presumably forage quality were deficient. Conversely, the rainfall prior to the breeding season in 1979 was above average and the corresponding fawn sex ratio in the spring of 1980 was almost exactly 1:1. Dapson et al. (1979) also reported variations in whitetail fawn sex ratios associated with differences in habitat quality.

The empirical evidence, as reported in the literature, does not consistently support any of the foregoing hypotheses. There are at least two explanations as to why this is so. First, much of the data on fawn sex ratios is not comparable; i.e. it is derived from fall harvest data that are inherently biased by sex-specific mortality

schedules in operation during the neonatal period and on into the fall. More important however is the possibility that the observed disparity in fawn sex ratios represents not just one but several biological phenomena; i.e. the result of two or more mechanisms that may or may not be operating in concert with one another.

Correspondingly, a preponderance of male fawns is produced both when environmental quality is unusually good and when environmental quality is unusually poor, phenomena that are unlikely the result of a single selection pressure. McDowell (1962), Verme (1969) and Dapson et al. (1979) reported that fawn and yearling does produced a preponderance of male fawns. Generally, as the quality of the environment improves the relative contribution of fawns and yearlings to the total population increases (Severinghaus and Cheatum 1956; Mansell 1974), such that during periods when environmental quality is unusually high, the population realizes a substantial disproportionate contribution of male fawns from young does.

Additionally, a second mechanism may be operating through adult females (>28 months) and involves sex ratio manipulation (i.e. realized as a physiological response) by individuals in response to fluctuating environmental quality. Robinette (1957) reported skewed sex ratios favoring males among older does on poor range and Verme reported a high male:female ratio among fawns born to does subjected to a low nutritional plane. Similarly, CWTD in this study produced a significantly larger proportion of male fawns during a year when forage quality was far below average, yet produced equal proportions of male and female fawns when forage quality was above the norm.

Furthermore, Dapson et al. (1979) reported that contiguous populations of white-tailed deer exhibited significantly different fawn sex ratios in response to different habitat quality; apparent shifts in demographic parameters in a surprisingly short period of time were observed in association with subtle changes in the environment.

Thus, unequal fawn sex ratios among populations of Odocoileus apparently represent the result of at least two mechanisms operating in response to fluctuations in environmental quality. But how do individuals benefit from sex-ratio manipulation? Parents should bias the sex ratio of their offspring in response to environmental conditions whenever the disproportionate production of one sex realizes a net increase in Darwinian fitness; i.e. the gain in genetic contribution to future generations realized by producing a preponderance of one sex is greater than the loss in fitness that results from producing fewer of the other sex. The benefit accrued to fawn and yearling does is quite obvious. These individuals are producing males when environmental conditions are ideal, and thus the probability of fawns surviving and attaining prime condition are higher. Prime male offspring of a polygynous species contribute more genes to the population than prime females. Therefore young does are maximizing their contribution to future generations via sex-ratio manipulation, i.e. producing a preponderance of male fawns. It seems then that at least one of the predictions outlined by Trivers and Willard (1973) is consistent with the foregoing observations; females should invest disproportionately in males when environmental quality is high.

The benefit derived from investing one's energy into males when environmental conditions are poor is not quite so apparent. As Trivers and Willard (1973) have already argued, seemingly natural selection would favor adult females that produce a greater proportion of female offspring during periods of environmental impoverishment. This would be true if a female's offspring and their offspring continued to reproduce effectively, i.e. natality and fawn survival would not decrease. In reality, a preponderance of female offspring during hard times would almost certainly result in further degradation of the environment, a consequence of the fact that females often breed in spite of their poor condition. Under these circumstances the natality and fawn survivorship of future generations would decline and therefore the effective contribution of adult females to future generations would decrease.

Might it not be more adaptive to invest one's energy into male offspring whose immediate contribution would not be as great, but whose average genetic impact on the population at a later point in time would perhaps surpass the average contributions of female offspring in a continually degenerating environment? In reality, the immediate benefit accrued to mothers of young does is somewhat dubious as the additional metabolic costs of reproduction on young does (Moen 1978) during a time when energy is limiting would probably reduce their probability of survival (Moen, personal communication) and corresponding genetic contribution to future generations. Also, concomitant with an increase in the proportion of male fawns would be a decrease in the number of fetuses per doe, a response to impoverished environmental conditions (Verme 1969) that would increase the

relative energetic investment to male fawns and apparently the likelihood of male offspring attaining prime condition. The overall effect of these responses would be a decrease in the immediate benefits derived from reproduction in exchange for a potentially greater overall contribution to future generations.

Dispersion

Preliminary observations of CWTB recorded during spotlight censuses May-August 1978 revealed that spatial distribution and relative abundance were disproportionate throughout the study area. Subsequent observations and corresponding locations indicated that CWTB exhibited a distinct affinity to the North Umpqua riparian system (i.e. North Umpqua River and associated vegetation). Of 12031 CWTB locations recorded during the period June 1978-December 1980, 10828 (90%) were observed within 1 km of the North Umpqua River, a portion of the study area representing approximately 50% of the total area (Fig. 16). The numbers of CWTB observed in each portion of the study area, after correcting for sampling intensity, were statistically different (Chi-square test of independence, Sokal and Rohlf 1969:585) and substantiated a positive significant association between relative abundance of CWTB and the North Umpqua riparian system.

Also, the distribution of CWTB fawn capture sites within the intensive study area (Figs. 17a and 17b) was significantly different (Chi-square test of independence, Sokal and Rohlf 1969:585) from a random spatial orientation and reflected an inclination toward selecting woodlands immediately adjacent the North Umpqua River. Moreover, of 32 marked individuals in the population, 29 (91%) exhibited home ranges that were located immediately adjacent to the river and were aligned parallel with the river (eg., Fig. 18).

Seasonal spatial distribution and abundance of CWTB were seeming-

Figure 16. Orientation of the study area with respect to the North Umpqua River, Douglas County, Oregon. (diagonal hashmarks designate portion of the study area within 1 km of the North Umpqua River)

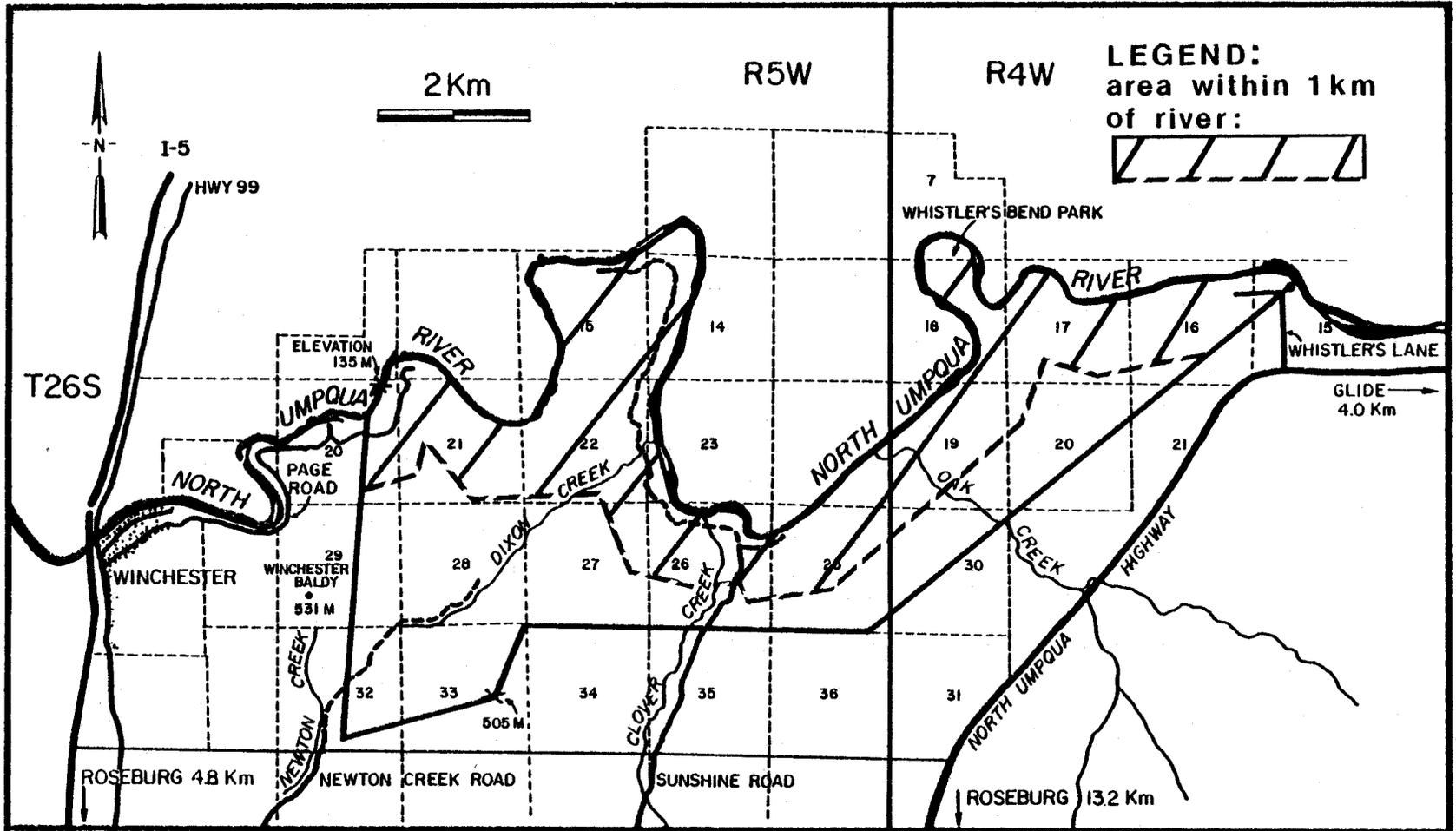


Figure 16.

Figure 17a. Spatial distribution of Columbian white-tailed deer and black-tailed deer fawn capture sites on the intensive study portion of the study area, Douglas County, Oregon for 1978-1980.

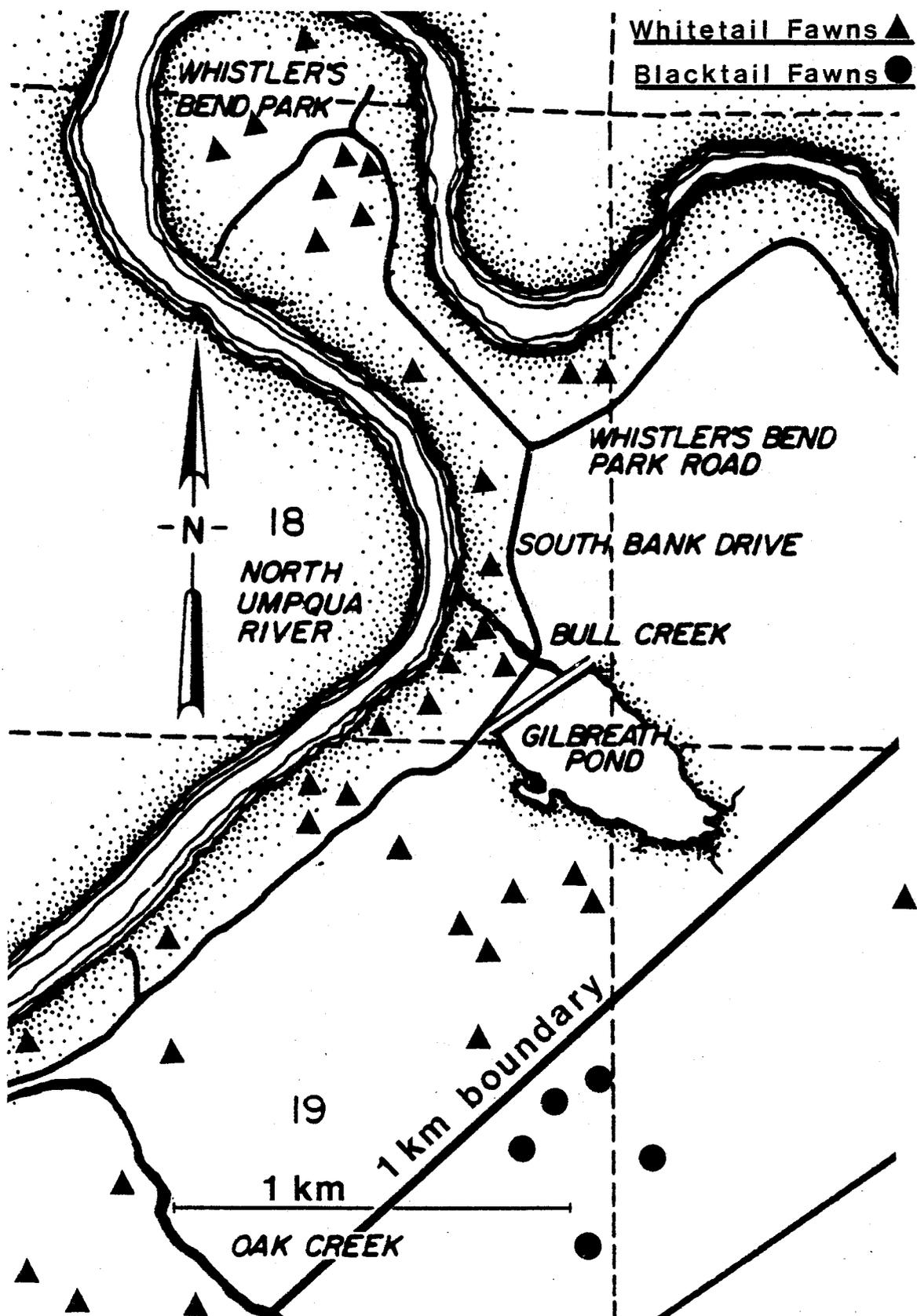


Figure 17a.

Figure 17b. Spatial distribution of Columbian white-tailed fawn capture sites on the intensive study portion of the study area, Douglas County, Oregon for 1978-1980.

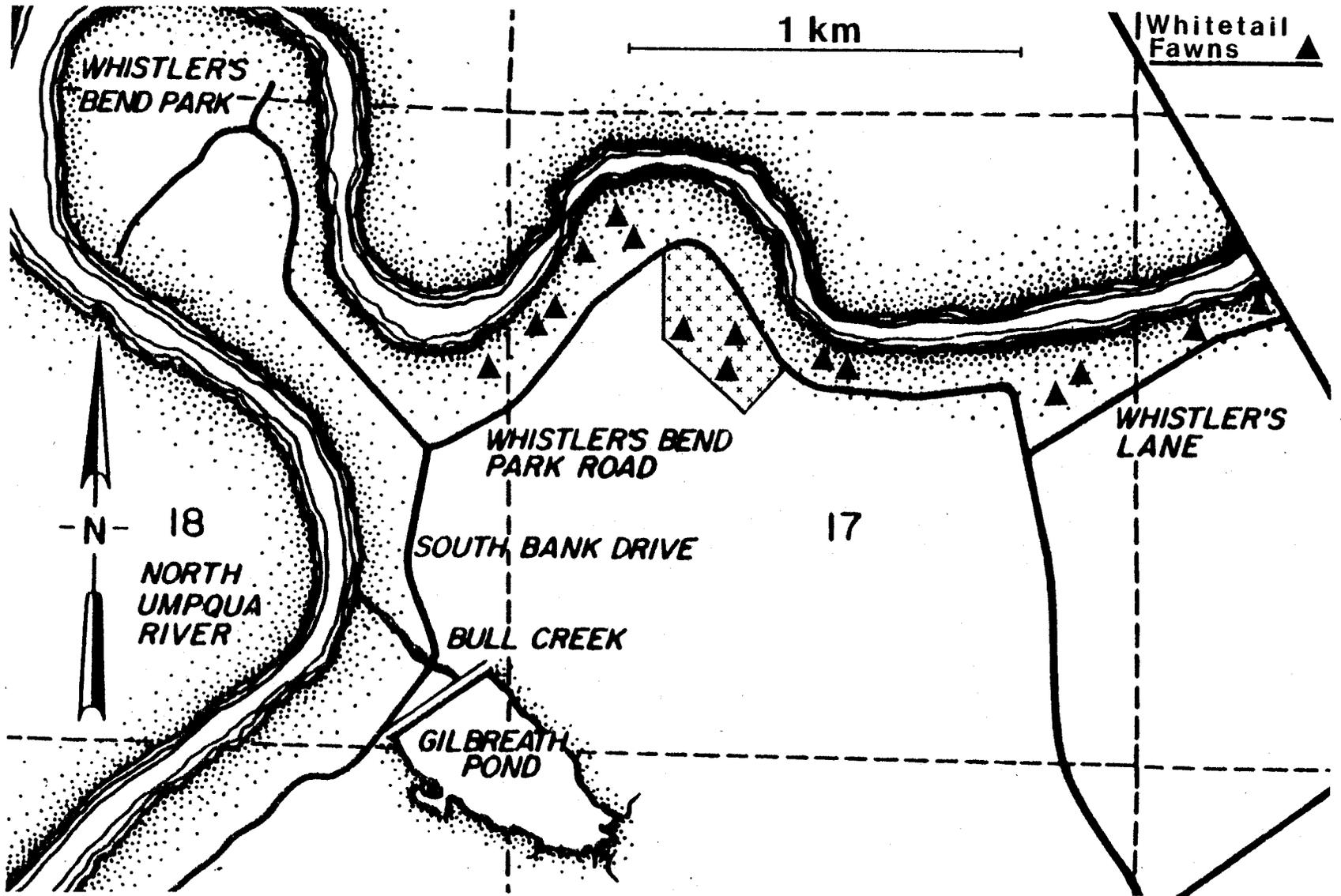


Figure 17b.

Figure 18. Convex polygon and elliptical home range estimates for no. 18, a yearling Columbian white-tailed deer female. Observations conducted during the period May 1978-December 1980, Douglas County, Oregon.

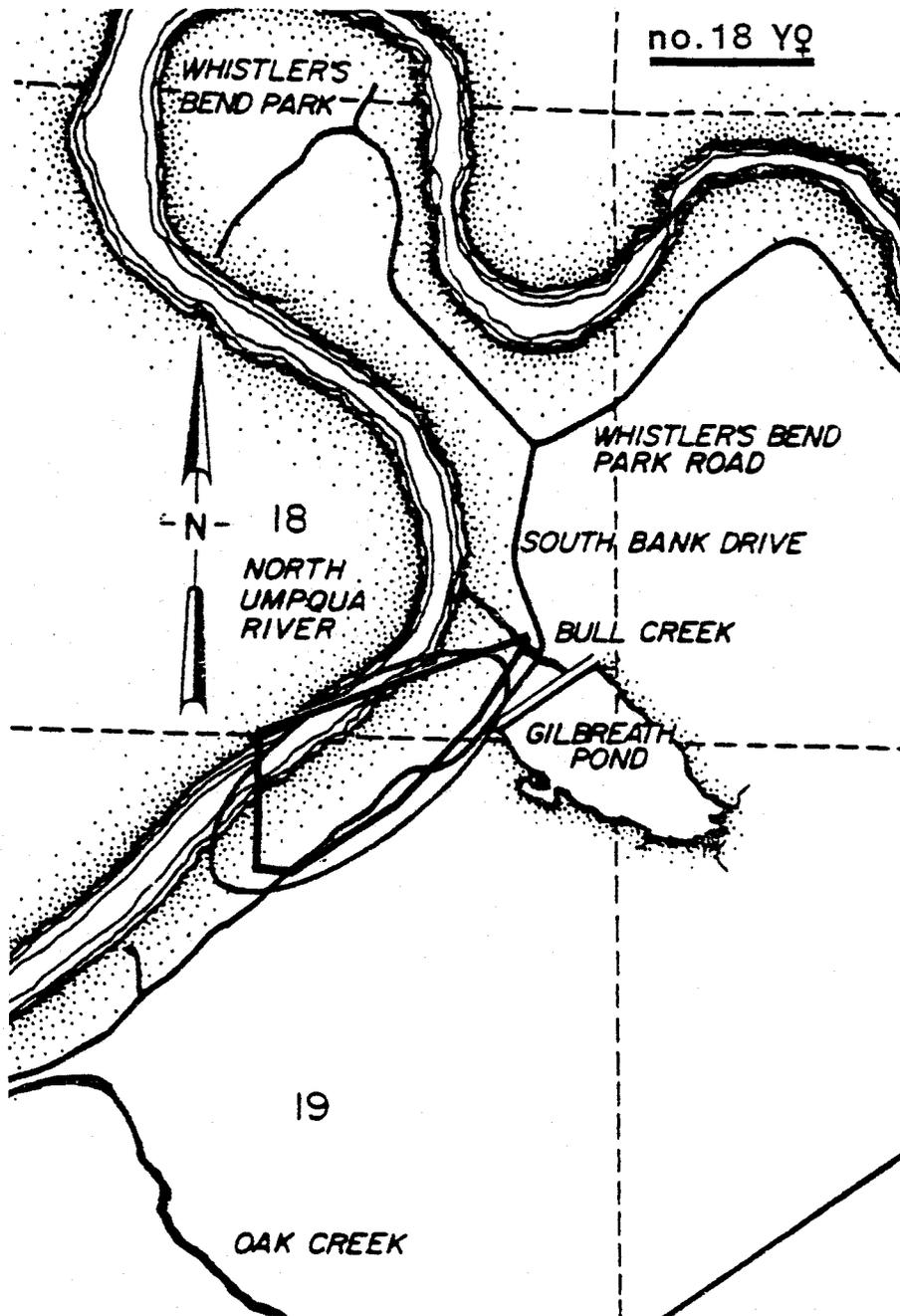


Figure 18.

ly affected by the distribution and intensity of livestock use within the study area. All but approximately 80 ha of the study area was managed primarily for livestock production. An apparent consequence of this was an observed preference by does during the fawning season for areas that were either unavailable to livestock or which received little use. One adult female, for example, established a separate and additional fawning home range within which she reared a pair of male fawns (#12 and #27) for about 3 weeks. Subsequent observations documented that she occupied an annual home range approximately 2.5 km from the neonatal area (see Home Range and Movements). From June 28 to January 16 this adult female and her collared fawns were consistently observed within her annual home range in an oak woodland immediately adjacent to an improved pasture. On January 16 a large number of ewes and newborn lambs were moved into this area, after which fawns 12 and 27 significantly decreased (Chi-square test of independence, Sokal and Rohlf 1969:585) their frequency of use of this area. At least three other adult females exhibited similar behavior and established additional fawning home ranges that represented portions of the intensive study area with little or no livestock use. Additionally, portions of the intensive study area supporting the greatest intensity of livestock use were avoided by CWTD females seeking suitable fawning habitat; fawn capture rates during May-August 1978-1980 averaged 1 fawn per 91.4 man-hours of search time in areas with moderate to heavy livestock use (greater than 6 AUMs^a) as compared to 1 fawn per 7.1 man-hours of

^aAnimal Use Month - equivalent to use of an area by a cow and her calf for a month.

search time in areas with little or no livestock use (less than 4 AUMs^a). Moreover, examination of fawn capture sites revealed a disproportionate spatial distribution within portions of the intensive study area supporting little or no livestock use (Fig. 17b). Chi-square tests of independence substantiated a significant negative association between the intensity of livestock use and the probability of encountering CWTD fawns.

The discrimination of suitable fawning habitat according to the intensity of livestock use probably reflected a general aversion to areas characterized by frequent periods of continued activity and disturbance. Kramer (1973) and Suring and Vohs (1979) reported that white-tailed deer generally avoided a close association with livestock. Also, selection of suitable fawning areas that are inaccessible to livestock may serve as well to eliminate potential competition for palatable and nutritious forage. CWTD demonstrated a significant preference for grassland habitats and grasses and forbs during spring and early summer (see Habitat-Use, Seasonal), the period of greatest energy demand for pregnant and lactating females (Moen 1978). As a consequence, the availability of nutritious forage could influence the survival rate of fawns. Finally, fawns that were reared in areas free of intensive livestock use probably suffered less predation because areas supporting the greatest livestock use also would generally experience a greater frequency and intensity of use by local predators (Danner and Smith 1980).

^a Animal Use Month - equivalent to use of an area by a cow and her calf for a month.

The influence of environmental features on the movements and dispersion of North American cervids has been reported by a number of investigators. Inglis et al. (1979) reported that boundaries created by the occurrence of unusual vegetative types, or barriers such as rivers and lakes limited the movements of white-tailed deer in Texas coastal prairie brushland. Gavin (1979) observed that deer on the CWTDNWR avoided entering water and restricted use of an area to one side of a water boundary. Knowlton (1960) and Mitchell (1961) reported that a number of far-ranging ungulate species, notably moose (Alces alces) and wapiti (Cervus elaphus), exhibited spatial distributions of activity that were restricted to lake shores and river valleys.

Gavin (1979) reported a significant correlation between the density of CWTD and the corresponding percent woodland cover for various portions of the CWTDNWR. Similarly, the relative density of CWTD within each habitat structure type in this study (Fig. 19) was correlated ($r = .85$) with percent woodland cover. The association between CWTD abundance and woodland cover approximated a power function correlation, i.e. the density of CWTD generally increased with increasing woodland cover. However, as percent woodland cover approached 50% corresponding increases in density decreased such that portions of the study area with a woodland cover percentage exceeding 50% supported similar densities of CWTD. This is not surprising as the white-tailed deer is reportedly a successional animal and as its environment becomes increasingly overgrown with woodlands, the amount of suitable habitat diminishes and density of deer decreases.

Figure 19. Relative densities of Columbian white-tailed deer throughout the study area in Douglas County, Oregon during the period May 1978-December 1980. Locations differ with respect to percent woodland cover.

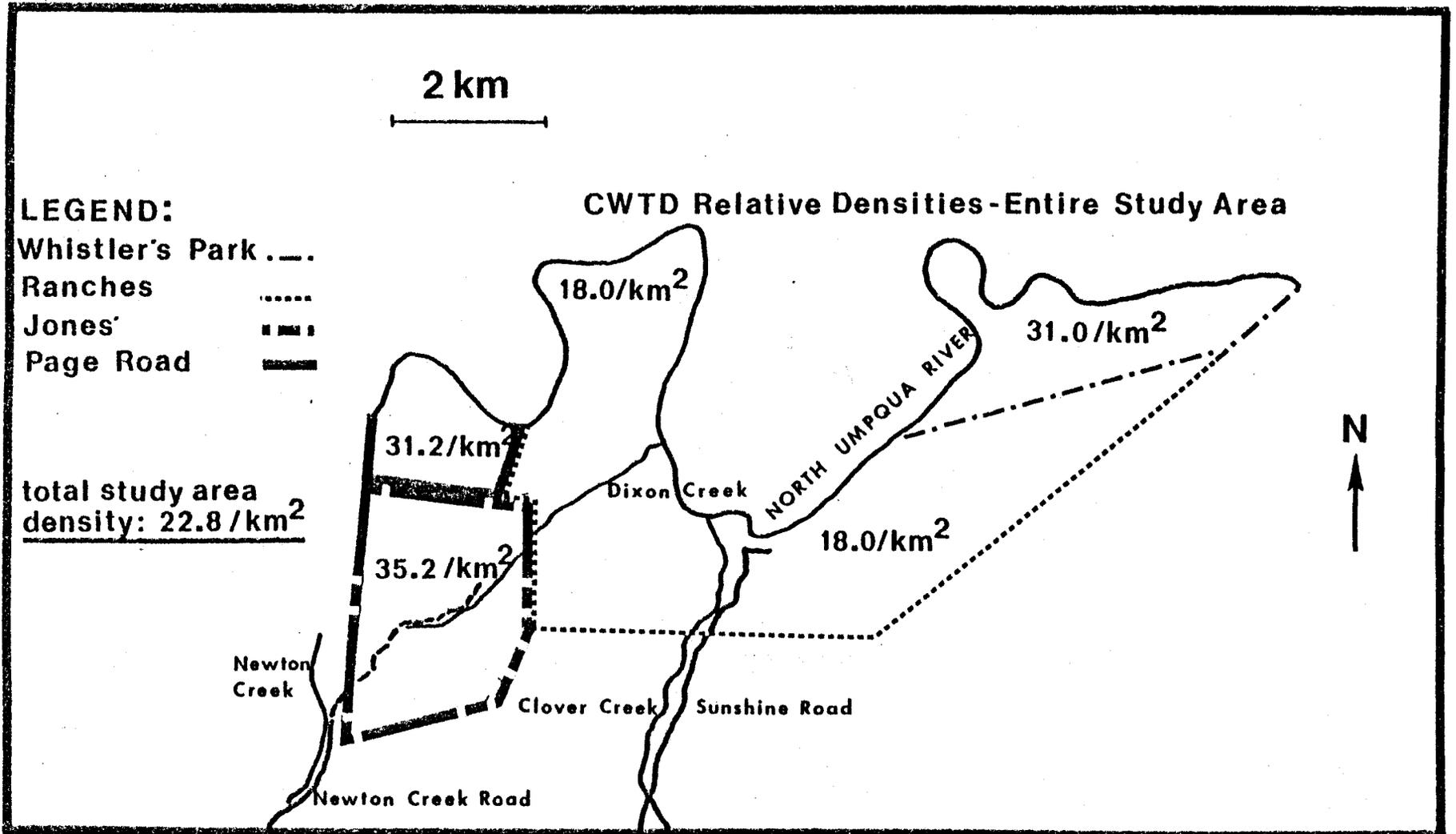


Figure 19.

Mortality

A total of 206 CWTD mortalities were recorded during the period June 1978-September 1980. In addition to an estimate of the month of death and proximate cause of mortality, sex, age and habitat within which each carcass was located were recorded. The age of fawns and yearlings was determined according to tooth replacement (Severinghaus 1949), whereas the age of adults was derived from the number of annuli cementum observed in a stained microtome section of the second premolar (Crowe 1972). Several mortalities were obtained from ODFW and OSP; corresponding cause and time of death were obtained from these agencies. Also, local ranchers often provided information regarding probable cause and time of death for specific individuals. Seven fresh carcasses were examined by veterinary pathologists and complete necropsy reports of these provided an evaluation of physical condition including ultimate and/or proximate cause of death. Field necropsies of some individuals confirmed preliminary conclusions regarding cause of death and provided additional information relating to their general physical condition. Because of the large sample size, the following analyses and results were assumed to be representative of the population during the period of study.

Proximate causes of mortality included malnutrition, collisions with motor vehicles, fence entanglement, predation and disease. Mortalities for which a cause of death could not be determined were recorded as unknown. Individuals suffering from malnutrition were

generally emaciated, exhibited a physical condition index of ≤ 20 (Kistner et al. 1980) and were characterized by depleted femur marrow fat. Frequently, individuals suffering from malnutrition were also burdened with ecto- and endoparasites, and often it was impossible to ascertain which factor had primary importance in contributing to the initial decline in general physical condition. In these situations, unless it was documented (by veterinary pathologists) that parasites were the primary mortality factor, the cause of death was attributed to malnutrition. Also, stillborn and abandoned fawns presumably suffered mortality as a consequence of a nutritional deficiency experienced by their mothers and therefore their cause of death was attributed to malnutrition.

Analysis of the frequency distribution of mortality among the various proximate mortality factors for the entire study period revealed that malnutrition (25.7%) and road kills (25.3%) accounted for the largest portions of known mortality (Fig. 20). Predation, fence entanglement and disease collectively represented only 12.5% of the known mortality (15/120) during this period. Correspondingly, malnutrition and road kills were responsible for the largest proportion of known mortalities during 1978-79 (Fig. 21) and 1979-80 (Fig. 22). During 1978-79 malnutrition (33.4%) accounted for three times the mortality caused by vehicles (11.1%) (Fig. 21); a significant disproportion of CWTD suffered mortality from malnutrition during this period (comparison of proportions in independent samples, Snedecor and Cochran 1980:124). Conversely, the percentage of individuals that experienced malnutrition during 1979-80 (15.8%) was

Figure 20. Monthly frequency distribution of Columbian white-tailed deer mortality among the proximate mortality factors during the period May 1978-December 1980, Douglas County, Oregon.

CWTD MORTALITY DISTRIBUTION

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	TOTAL	%
road kill	4	1	4	1	—	4	10	7	7	5	7	3	53	25.7
malnutrition ^a	7	24	8	—	2	10	—	—	—	—	—	1	52	25.3
predation	—	—	—	—	—	2	1	1	—	2	—	—	6	2.9
fence	—	—	—	—	—	—	—	—	1	2	—	1	4	1.9
disease	—	1	—	—	—	—	—	—	—	2	1	1	5	2.4
unknown	8	13	12	5	4	7	3	2	8	9	5	10	86	41.8
TOTAL	19	39	24	6	6	23	14	10	16	20	13	16	206	
%	9.2	18.9	11.6	2.9	2.9	11.2	6.8	4.9	7.8	9.7	6.3	7.8		

Figure 20.

Figure 21 . Monthly frequency distribution of Columbian white-tailed deer mortality among the proximate mortality factors during 1978-79, Douglas County, Oregon.

**CWTD MORTALITY DISTRIBUTION
1979 - 1980**

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	TOTAL	%
road kill	2		2	1	-	2	2	-	5	5	7	2	28	36.8
malnutrition ^a	3	1	2	-	-	6	-	-	-	-	-	-	12	15.8
predation	-	-	-	-	-	3	-	1	-	1	-	-	5	6.6
fence	-	-	-	-	-	-	-	-	1	2	-	1	4	5.3
disease	-	-	-	-	-	-	-	-	-	2	1	1	4	5.3
unknown	2	1	3	-	-	1	3	-	2	4	1	6	23	30.2
TOTAL	7	2	7	1	-	12	5	1	8	14	9	10	76	
%	9.2	2.6	9.2	1.3	-	15.8	6.6	1.3	10.5	18.4	11.9	13.2		

Figure 22.

Figure 22. Monthly frequency distribution of Columbian white-tailed deer mortality among the proximate mortality factors during 1979-80, Douglas County, Oregon.

**CWTD MORTALITY DISTRIBUTION
1978-1979**

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	TOTAL	%
road kill	2	1	2	—	—	2	3	2	—	—	—	—	12	11.1
malnutrition ^a	4	23	6	—	2	1	—	—	—	—	—	—	36	33.4
predation	—	—	—	—	—	1	—	—	—	—	—	—	1	0.9
fence	—	—	—	—	—	—	—	—	—	1	—	—	1	0.9
disease	—	1	—	—	—	—	—	—	—	—	—	—	1	0.9
unknown	13	7	8	5	4	—	1	1	5	5	4	4	57	52.8
TOTAL	19	32	16	5	6	4	4	3	5	6	4	4	108	
%	17.4	29.6	14.8	4.7	5.6	3.7	3.7	2.8	4.7	5.6	3.7	3.7		

Figure 21.

less than half the percentage of individuals that suffered road kill mortality (36.8%)(Fig. 22), and was significantly less than the number of CWTB that experienced malnutrition during 1978-79 (comparison of proportions in independent samples).

Examination of the climatic statistics for each of the two annual periods disclosed that the mean winter temperature (Jan-Mar) and the mean monthly minimum temperature (Jan) during 1978-79 were below average, while the total number of days in which the minimum temperature was below 0°C and the total number of days in which the maximum temperature was below 0°C were above the norm for the study area (U.S. Department of Commerce 1979-80). Correspondingly, the mean winter temperature during 1979-80 was above average while the total number of days in which the minimum temperature was below 0°C and the total number of days in which the maximum temperature was below 0°C were below the norm. Comparably, the CWTB mortality distribution in 1978-79 differed statistically from the 1979-80 mortality distribution (Chi-square test of independence, Sokal and Rohlf 1969:589), and indicates that during each of these two years there existed a significant association between the severity of winter and the proportion of individuals that suffered mortality from malnutrition.

Monthly distribution among proximate mortality factors. The monthly distribution of CWTB mortality was examined with respect to the various proximate mortality factors (Fig. 20). CWTB suffered significantly more malnutrition during winter and late spring (Fig. 20)(comparison of proportions in independent samples,

Snedecor and Cochran 1980:124); 75% (39/52) of malnutrition-related mortalities for the entire study period occurred during the period January-March whereas 23% (12/52) occurred in May and June. During the severe winter of 1978-79, 92% (33/36) of the mortalities attributed to malnutrition occurred during the winter, while the remaining 8% (3/36) occurred during late spring.

Except for May, CWTB experienced road kill mortality during all months of the year (Fig. 20). However, individuals were apparently most susceptible to vehicle-inflicted mortality during summer and early fall, as a significant disproportion of road kills occurred during the period July-September (comparison of proportions in independent samples, Snedecor and Cochran 1980:124). CWTB experienced predation predominately in the summer, whereas individuals generally suffered mortality attributed to disease and fence entanglement during the fall (Fig. 20).

A significant disproportion of CWTB (33/39) (Chi-square test of independence, Sokal and Rohlf 1969:589) that experienced malnutrition during the winter also suffered a profuse diarrhea. Field necropsies of relatively fresh carcasses and subsequent rumen content analysis revealed that 76% (13/17) of the individuals that experienced diarrhea also had rumens that contained exclusively early spring herbaceous new-growth. During February and early March, the water content of herbaceous vegetation can exceed 90% in western Oregon (Steve Sharrow, personal communication). Even as late as April, water comprises 83% of forage new-growth (Bedell 1971), and although

the relative nutrient content of dry matter is higher during this period, the total amount of energy and other nutrients available per volume consumed is less (Bedell 1971). Correspondingly, Roosevelt elk (Cervus elaphus roosevelti) were observed to suffer nutritional deficiencies while foraging on succulent herbaceous new-growth during winter, reportedly a result of an inability to realize effective digestive rates required to compensate for the low absolute nutrient content of the forage (Mereszczak 1979).

Some of the stress experienced by CWTB during late winter and early spring was probably associated with abrupt changes in diet composition. Ruminants generally require a gradual transition period (2-3 weeks) during major changes in dietary composition (Church 1975); individuals experiencing a low nutritional plane prior to dietary changes, such as during severe winters, need as long as six weeks (D.C. Church, personal communication). The effective digestion of forage hinges on maintaining the proper microfaunal environment within the ruminant digestive system; abrupt changes in diet totally disrupt the microfauna, eliminate effective digestion and often results in profuse diarrhea, acidosis and a number of pathological disorders (D.C. Church, personal communication). Additional complications may stem from reported selenium deficiencies in the forage in Douglas County (Reynolds 1980). Dietary deficiencies in selenium are reported to contribute to the "unthriftiness" of yearling and adult ruminants; many of these animals were observed to develop a profuse diarrhea, were unable to feed properly and in many instances suffered mortality as a result of complications

thereof (Reynolds 1980).

CWTD experienced 45% (24/53) of their road kill mortality during the period July-September (Fig. 20). Seemingly, the greater frequency of road kill mortality during this period was a result of seasonal movement patterns associated with decreasing availability of water and palatable forage. Allen and McCullough (1976) observed an increase in road kill mortality among white-tailed deer in southern Michigan in conjunction with a decrease in forage availability, and Puglisi et al. (1974) noted a significant association between forage availability and vehicle-inflicted mortality among white-tailed deer in Pennsylvania. Southwest Oregon generally experiences semi-drought summers; only 5.8% of the annual precipitation normally falls during the period July-September - of which half occurs in September (U.S. Department of Commerce 1955-1979). Even in years when precipitation was above average, seasonal creeks and watering ponds were completely dry by the end of June (personal observation). Dramatic phenological changes in the vegetation also occurred during the summer (see also Hitchcock and Cronquist 1973), and it became relatively unpalatable and indigestible (see also Hulbert 1955; Harris and Goebel 1976).

Correspondingly, CWTD exhibited significant seasonal movements; deer generally utilized upland regions during late winter and spring, but occupied lowland areas with associated riparian systems during summer, autumn and early winter. Adult female no. 214, for example, exhibited two separate home ranges (Fig. 31); during the period April-July, she occupied wooded uplands and adjacent improved

pasturelands, whereas during the period July-March she occupied woodlands immediately adjacent the North Umpqua River.

CWTD exhibited a significant increase in the use of riparian areas during summer while significantly decreasing the frequency of use of grassland habitats during this period (Fig. 11). They also tended to aggregate along roadside ditches during late summer and early fall. The first autumn rains generally began during this period; much of the rain collected in the roadside ditches and these areas became the first to experience fall green-up. CWTD apparently congregated along roadside ditches during this period to take advantage of the first available new-growth, and thereby increased their susceptibility to vehicle-inflicted injuries.

Distribution of mortality among age and sex groups. The monthly distribution of CWTD mortality was examined with respect to age and sex. The seasonal distributions of yearling-adult male and female mortality were each statistically different from a random frequency distribution (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552); yearling-adult males and females each experienced significant differential mortality among the seasons. Moreover, the respective temporal and age-class distributions of yearling-adult males (Fig. 23) were significantly different from the corresponding mortality distributions of yearling-adult females (Fig. 24) (comparison of proportions in independent samples, Snedecor and Cochran 1980:124). Yearling-adult males experienced 47% (28/60) of their mortality during December-February while yearling-

adult females suffered only 33% (28/85) of their mortality during this period. The remaining female mortality occurred proportionally among the seasons (Fig. 24), whereas the remaining male mortality was distributed disproportionately in late summer and fall (Fig. 23).

Examination of the respective distributions of known mortality for yearling-adult males and females among the various proximate mortality factors disclosed that males and females were equally susceptible to corresponding causes of death. Yearling-adult males suffered 54% (20/37) of their mortality from vehicle-inflicted injuries (Fig. 23) as compared to 55% (26/37) for females (Fig. 24). Malnutrition, predation and fence entanglement accounted for 37.8% (14/37), 5.4% (2/37) and 2.7% (1/37) of yearling-adult male mortality (Fig. 23) while representing 38.2% (18/47), 4.3% (2/47) and 2.1% (1/47) of yearling-adult female mortality, respectively. There were no yearling-adult male or female mortalities attributed to disease.

Generally, yearling CWTB were most susceptible to vehicle-inflicted mortality. Road kills accounted for a significant proportion of known mortality (comparison of proportions in independent samples, Snedecor and Cochran 1980:124) for both male and female yearlings; 73% (8/11) and 80% (4/5) of male and female yearling deaths, respectively, resulted from vehicle-inflicted injuries. Male yearlings experienced a large proportion of their road kill mortality during summer (Fig. 23), whereas females were seemingly more susceptible during the fall and winter (Fig. 24). Both male and female yearlings experienced few mortalities that were

Figure 23. Age-class frequency distribution of male Columbian white-tailed deer mortality among the proximate mortality factors and monthly during the period May 1978-December 1980, Douglas County, Oregon.

CWTD Males

N	Cause of Mortality						AGE CLASS	Chronology												N
	27	3	2	3	22	23		12	12	7	2	1	10	7	2	4	10	6	7	
	unknown	disease	fence	predation	malnutrition ^a	road kill		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
5	1	-	-	-	2	2	5	2	1	-	-	-	1	-	-	-	-	-	1	5
11	5	-	-	1	3	2	4	1	2	1	-	1	1	1	-	1	2	-	1	11
12	3	-	-	-	5	4	3	1	3	2	1	-	1	1	-	-	1	1	1	12
16	9	-	1	-	2	4	2	5	2	1	-	-	-	1	-	-	3	2	2	16
16	5	-	-	1	2	8	1	3	1	-	-	-	-	3	2	2	1	2	2	16
20	4	3	1	1	8	3	0	-	3	3	1	-	7	1	-	1	3	1	-	20

Figure 23.

Figure 24. Age-class frequency distribution of female Columbian white-tailed deer mortality among the proximate mortality factors and monthly during the period May 1978-December 1980, Douglas County, Oregon.

CWTD Females

N	Cause of Mortality						AGE CLASS	Chronology												N
	53	3	2	2	29	27		12	21	16	5	5	6	6	9	11	11	5	9	
2	2	-	-	-	-	-	10	-	-	-	-	1	-	-	-	-	1	-	-	2
5	3	-	-	-	1	1	9	-	2	1	1	-	-	-	1	-	-	-	-	5
13	9	-	-	-	3	1	8	1	2	3	1	-	1	3	1	-	1	-	-	13
9	8	-	-	-	1	-	7	2	3	1	-	-	-	-	-	1	-	-	2	9
9	2	-	-	-	4	3	6	1	2	2	-	-	-	1	2	-	1	-	-	9
9	5	-	-	-	2	2	5	1	2	2	-	-	-	1	1	1	1	-	-	9
10	1	-	1	1	3	4	4	-	2	-	-	1	2	1	1	1	-	1	1	10
13	3	-	-	-	3	7	3	1	2	2	-	-	-	-	2	3	-	2	1	13
8	3	-	-	1	-	4	2	1	-	1	-	1	-	-	1	1	3	-	-	8
7	2	-	-	-	1	4	1	-	1	1	-	-	-	-	-	1	3	-	1	7
31	15	3	1	-	11	1	0	5	5	3	3	2	3	-	-	3	1	2	4	31
	unknown	disease	fence	predation	malnutrition ^a	road kill		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	

Figure 24.

attributed to nutritional deficiencies; however, as with adults, yearlings generally suffered malnutrition during the period January-March.

Malnutrition, road kills and disease accounted for 91% (29/32) of known fawn mortality. The largest proportion of known mortality was attributed to malnutrition (19/32, 59%). Fawns experienced nutrition-deficient mortalities during the period late spring-early summer and during winter; fawns that died during June were either stillborn or succumbed shortly after birth, whereas winter mortalities were seemingly associated with the rigors experienced therein. Disease represented 19% (6/32) of the known fawn mortality and generally occurred among neonates that were born during late summer or early autumn. These fawns were diagnosed as having suffered serofibronous pneumonia, a condition characterized by severe lung congestion, respiratory impairment and a general physical debilitation. Road kills accounted for 12% (4/32) of the known mortality and occurred most frequently during late summer. As with yearlings and adults, vehicle-inflicted fawn mortalities were probably associated with the semi-drought conditions that existed during late summer.

Male CWTB fawns suffered a significantly greater proportion of their mortality (8/20, 40%) (Chi-square test of independence, Sokal and Rohlf 1969:589) during the neonatal period (June-July) as compared to female fawns (3/31, 10%) (Figs. 23 and 24). Additional evidence that male fawns suffered significant differential mortality as neonates was provided by an analysis of the mortality schedules of a marked sample. A significantly greater proportion of male fawns

(10/22, 45%) died during June and July as compared to female fawns (2/14, 14%) (Chi-square test of independence). The incidence of mortality among female fawns was greatest during the period December-February (14/31, 45%) and corresponded with the significant disproportion of known mortality among female fawns (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552) that was attributed to malnutrition (Fig. 24). The incidence of malnutrition among male fawns (8/16, 50%) was also significant (Chi-square goodness-of-fit test), however the temporal distribution of male fawn mortality (Fig. 23) differed from that of female fawns (Fig. 24). Also, male fawns were apparently more susceptible than female fawns to vehicle-inflicted mortality (Figs. 23 and 24).

Analysis of fall and winter mortality distributions (26 fawns: 37 bucks:44 does) with respect to corresponding herd composition estimates (52 fawns:30 bucks:100 does) indicated significant differential mortality among sex and age groups (Chi-square test of independence, Sokal and Rohlf 1969:589). Fawns represented comparable proportions in both herd composition (52/182, 29%) and total mortality estimates (26/107, 24%). Yearling and adult females represented a significantly smaller proportion (44/107, 41%) of the sample of population mortality (Chi-square test of independence) as compared to the herd composition estimate (100/182, 55%), and yearling and adult males accounted for a significantly larger proportion (37/107, 35% vs. 30/182, 16%). Thus, CWTD females suffered significantly less winter mortality than fawns while males experienced significantly greater differential mortality (Chi-square test of

independence). Similarly, Gavin (1979) reported that a significantly greater proportion of yearling and adult males died during fall and winter than would be expected from their representation in the population while females were under-represented in the mortality sample. Moreover, Gavin (1979) observed that the annual mortality rate of yearling and adult males (0.345, p. 84) was nearly twice that of females (0.179, p. 84).

Sex and age specific mortality rates could not be reliably estimated because critical assumptions regarding stationary age distribution were violated (Caughley 1977). A quantitative comparison of male and female age structures was accomplished through the construction of respective ecological longevity curves. Dapson (1971, 1972) described the construction and interpretation of ecological longevity curves, and Gavin (1979) employed this technique to compare age structure of CWTD males and females within the same population. Accordingly, the ages at death of CWTD males and females in this study were examined with respect to their respective frequency of occurrence in the population. A simple linear regression of relative frequency against age at death defined the median ecological longevity (MEL) and maximum ecological longevity (MAX) of males and females in the population. MEL represents the age at which the probability of occurrence (in the mortality sample) is 0.5, i.e. that age at which half the population has died; half the population survives beyond MEL. MAX represents the age at which the probability of occurrence is zero and represents the maximum age attainable under existing ecological conditions (Dapson 1971, 1972).

The age at death of males (N = 80) and females (N = 117) were arranged separately in a chronological fashion from oldest to youngest. Each individual occurred with a relative frequency of $1/N$; relative cumulative frequencies (RCF) were computed for individuals of both sexes (Appendix F) by adding successive individual relative frequencies beginning with the oldest deer. To facilitate graphical interpretation, RCF was plotted on the Y-axis against age at death on the X-axis (Dapson 1971). The equation of the line however was determined through a regression of X on Y. Conventionally, Y is regressed on X; but RCF is a non-random variable (each RCF is dependent upon preceding values) and an accurate regression of a non-random variable on a random variable is not possible (Dapson 1971). Corresponding correlation coefficients (r) defined the goodness-of-fit of each observation to the line. The respective X-intercepts represented MAX, and MEL was obtained by solving the regression equation for $Y = 0.5$; corresponding confidence intervals were computed according to conventional formulae for limits about regression predictions (Dapson 1971).

Several transformations of one or both variables were attempted to obtain the best regression model according to the following criteria: a model that provided a MAX that approximated but was greater than the oldest animal of that sex in the sample; and a model with the highest correlation coefficient (r) (Gavin 1979). A regression of the transformed X variable (age at death) against the respective RCF generated the following equations: $1/\sqrt[50]{X} = 0.96 + 0.06Y$, $r = 0.95$, $MEL = 1.65$ with the $P\{1.54 \leq MEL \leq 1.76\} = 0.95$, $MAX = 7.70$ with the $P\{7.47 \leq MAX \leq 7.93\} = 0.95$ for males (Fig. 25); and $1/\sqrt[50]{X} = 0.95 + 0.07Y$,

Figure 25. Ecological longevity curve for Columbian white-tailed deer males (Dapson 1971). Derived from observations recorded May 1978-December 1980, Douglas County, Oregon.

CWTD MALES: ECOLOGICAL LONGEVITY

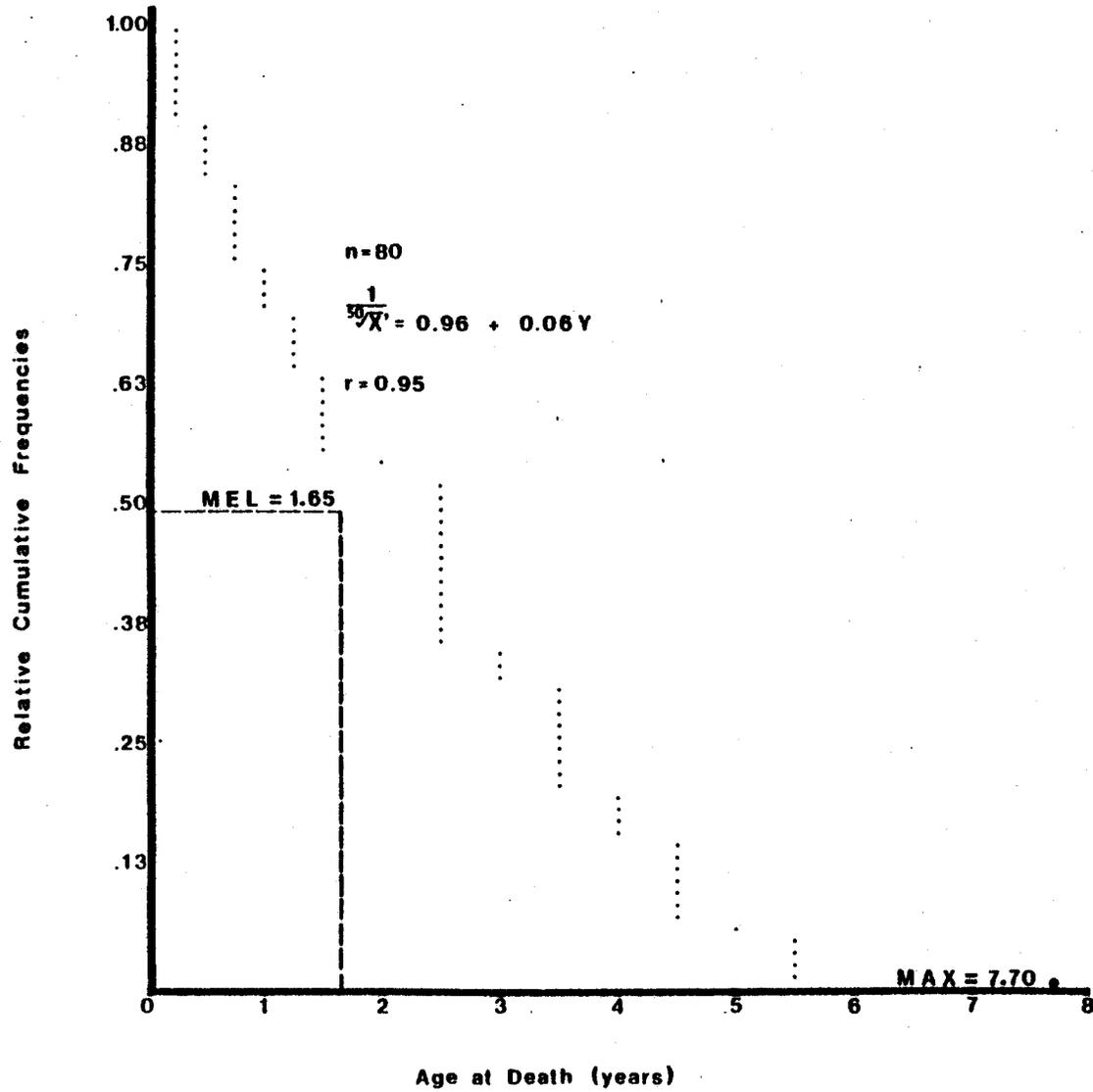


Figure 25.

$r = .95$, $MEL = 2.15$ with the $P\{2.06 \leq MEL \leq 2.24\} = 0.95$, $MAX = 13.0$ with the $P\{12.8 \leq MAX \leq 13.2\} = 0.95$ for females (Fig. 26). A non-parametric test of medians (Zar 1974:114) substantiated that median age at death for females was significantly greater than males; the maximum ecological longevity of females (Fig. 26) was nearly twice that of males (Fig. 25). Correspondingly, the oldest observed male and female in the sample of population mortalities were 5.5 and 10.0 years old, respectively.

Female CWTD were apparently living longer than males. A portion of the disparity in age structure between sexes probably resulted from an intense selective harvest of older males in the population. The hunting pressure on this population was exerted by a small number of local ranchers whose attitudes and hunting philosophy were consistent with such a harvest scheme; trophy bucks were highly prized and sought after. It is unlikely however that hunting was solely responsible for the observed disparity in age structure; a number of non-hunted white-tailed deer populations have exhibited similar male and female age distributions (White 1973; Roseberry and Klimstra 1974; Hardin et al. 1976; Gavin 1979). Also, Klein and Olson (1960) concluded that a skewed sex ratio favoring males in scarcely hunted black-tailed deer populations in Alaska resulted from higher natural mortality among males. There is evidence that sex-specific natural mortality associated with life history activities of white-tailed deer accounts for a significant disproportion of male differential mortality (Gavin 1979).

The temporal distribution of mortality among yearling-adult females and males in this study indicated that the ultimate cause of

Figure 26. Ecological longevity curve for Columbian white-tailed deer females (Dapson 1971). Derived from observations recorded May 1978-December 1980, Douglas County, Oregon.

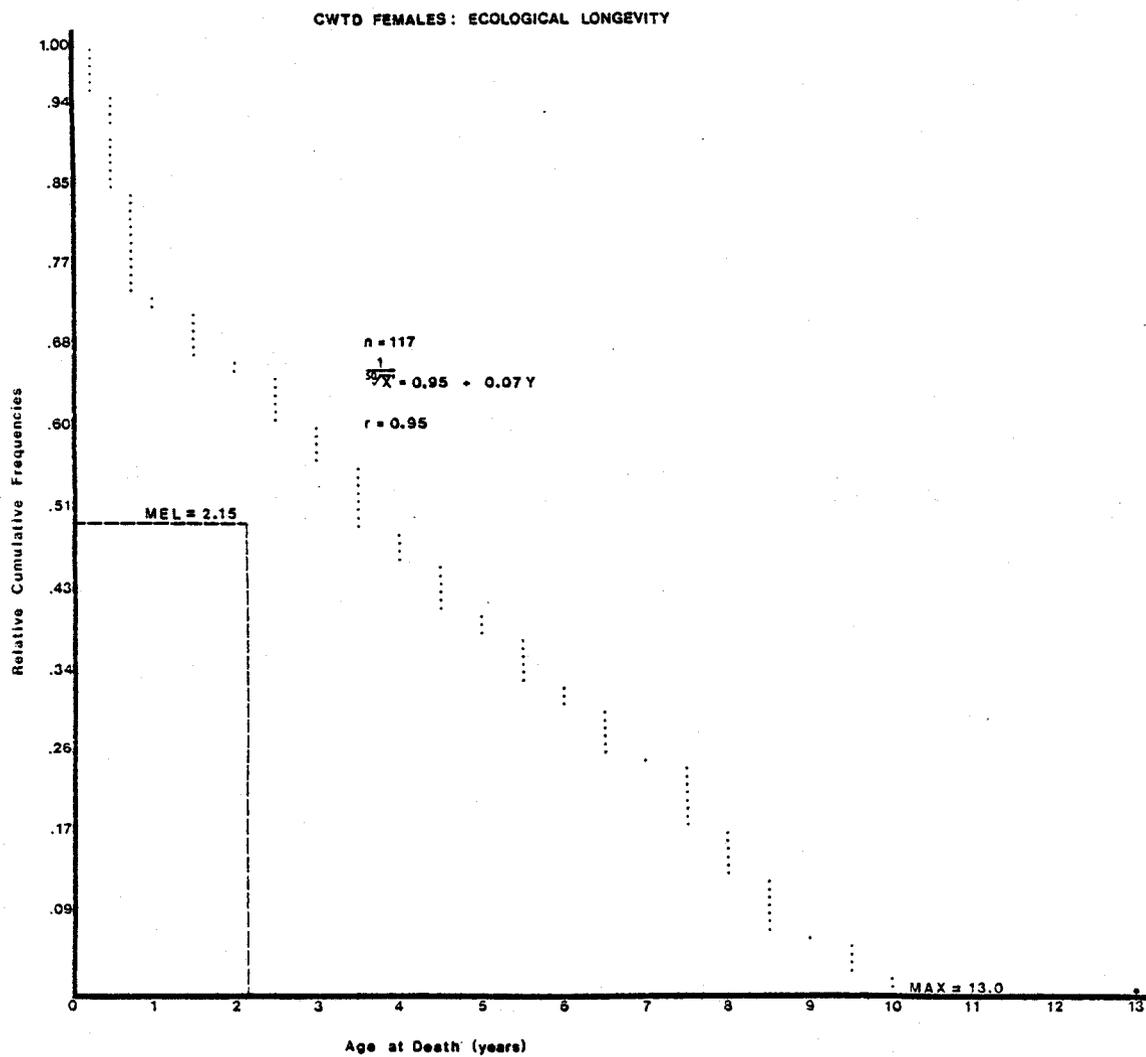


Figure 26.

mortality resulted from the activities and corresponding energetic costs associated with reproduction. A significant disproportion of CWTD males (16/23, 70%) suffered malnutrition during that portion of the year when bucks generally experience the greatest energetic deficit, the rut and ensuing winter (October-March) (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552). CWTD does however, experienced a significant disproportion of their malnutrition-related mortalities (24/29, 83%) during the second half of fetal development and on into the lactation period (February-July) (Chi-square goodness-of-fit test). Similarly, Gavin (1979) reported that natural mortality of males on the CWTDNWR was concentrated during that period following peak rutting activity. Correspondingly, a large proportion of yearling and adult female mortality (71%) on the CWTDNWR reportedly resulted from physiological stress associated with lactation and rearing of young (Gavin 1979).

Gavin (1979) reported that agonistic encounters between CWTD males did not directly influence mortality; but rather high male mortality was associated with increased energy demands and movements. Similarly, male-male encounters during this study appeared stringently ritualistic and were of such low intensity that injury was very unlikely. Additional activity and mobility during this period however apparently increased the incidence of road kill mortality among rutting males. A significant disproportion of vehicle-inflicted male mortality (11/24, 46%) occurred during the period mid-October to mid-January (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552). Similarly, Allen and McCullough (1976) reported an in-

crease in vehicle-inflicted mortality among male white-tailed deer during the rut in southern Michigan. Gavin (1979) concluded that males on the CWTDNWR experienced a greater risk of physical injury due to increased activity during the rut; 67% of the automobile-related mortality occurred among yearling and adult males (Gavin 1979:90).

Physiological stress experienced by males during the rut was seemingly a result of a marked change in the ratio of energy consumption to energy expenditure. Males were more active during this period as indicated by a significant increase in their frequency of occurrence in censuses (Chi-square test of independence, Sokal and Rohlf 1969:589). Gavin (1979) reported that the major stress experienced by males on the CWTDNWR resulted from increased energy expenditure associated with a search for receptive females. Similarly, a significant association between an increased activity of males and rutting behavior was observed in this study (Chi-square test of independence). In conjunction with an increase in energy expenditure, bucks generally decrease energy intake. French et al. (1955) observed that adult white-tailed bucks voluntarily decreased daily consumption of forage during the rut and continually lost weight until March. Wood et al. (1962) reported a similar behavior among several subspecies of O. hemionus. McCullough (1969) observed that Tule elk (C. e. nannodes) decreased the frequency and duration of bedded periods and reduced the proportion of time engaged in foraging after acquiring a harem of cows; subsequent observations indicated a continued decline in the physical condition of harem

bulls. Struhsaker (1967) reported similar behaviors among harem bulls of Rocky Mountain elk (C. e. canadensis); and Flook (1970) reported that adult bull elk experienced a rapid depletion of fat reserves during the rut in association with high physical activity and reduced forage intake.

The apparent consequence of increased energy expenditure concomitant with reduced energy intake among rutting males is higher mortality. Correspondingly, Grubb and Jewell (1974) concluded that a skewed sex ratio as great as eight ewes per ram among Soay sheep on St. Kilda island was a result of higher male mortality that reportedly occurred in association with reduced foraging and increased activity during the peak mating period. Thus higher male mortality during the rut and ensuing winter is apparently a common phenomenon among ungulates exhibiting a polygynous mating system; and to a large extent accounts for the unbalanced yearling and adult sex ratio favoring females.

There are also apparent differences in the demographic characteristics of hunted and non-hunted white-tailed deer populations. Although both the Douglas County and CWTDNWR populations exhibited similar yearling-adult sex ratios (about 3 females per male), the refuge population exhibited an older age distribution. On the CWTDNWR, the median ecological longevity of males (2.97) and females (4.87) (Gavin 1979:81) were significantly greater (non-parametric test of medians, Zar 1974:114) than corresponding male and female estimates for the Douglas County population. Moreover, the maximum ecological longevity of refuge males (8.37) and females (17.49) (Gavin 1979:81)

were nearly twice that of the corresponding estimates in this study.

Intense selective hunting of CWTD in Douglas County apparently exerted an additive, as compared to compensatory (Errington 1956), mortality pressure on the adult male segment of this population, and probably explains much of the disparity in the male age distribution between the CWTDNWR and Douglas County populations. Similarly, females in the Douglas County population were harvested regularly; but females were not subjected to near as intense the hunting pressure as males (ODFW, unpublished data). Caughley (1974) illustrated (via population simulation models) that a decrease in the survival rate of mature animals in the population can over a short period of time increase the proportion of young individuals in the population, a consequence of which would be a decrease in the median age of individuals in the population such as that observed in the Douglas County population. A similar age structure could result from an increase in the survival of sub-adults (Caughley 1974); however in most natural populations, an increase in the survival of one age group is not independent of a decrease in the survival of other age groups in the population (Errington 1956). Nevertheless, one should exercise caution in deriving conclusions regarding the nature of demographic changes involved in producing an observed age distribution, particularly when additional demographic statistics are not available.

Fawn mortality rates among un hunted white-tailed deer populations are apparently higher than comparable populations experiencing perennial harvests. Un hunted populations of white-tailed deer have

fawn mortality rates 2 to 4 times higher; White (1973) reported a summer mortality rate of 60% among white-tailed fawns on the Aransas National Wildlife Refuge and Cook et al. (1971) observed comparable mortality rates of 71% and 72% during a two-year study on Welder Refuge. A.C. Clark (unpublished data) observed summer mortality rates among radio-collared fawns on the CWTDNWR of 85% (16/19), 71% (10/14) and 86% (6/7) during the period 1978-1980, respectively. On the same study site, Gavin (1979) estimated fawn mortality rates to be as high as 75% in 1975 and 1977, and as high as 83% in 1976. Comparable mortality rates of radio-collared fawns in this study were markedly lower; in 1979 only 40% (6/15) of the collared fawns died during the three months following parturition and in 1980 only 13% (2/15) suffered mortality during this period. Similarly, O'Pezio (1978) reported summer mortality rates of 22% among white-tailed deer fawns on the Seneca Army Depot in New York and Teer et al. (1965) observed an average summer mortality rate of 20% for the period 1957-1961 among white-tailed fawns in the Llano Basin, Texas.

Spatial distribution among habitats. The location of 146 CWTD carcasses (excluding road kills) were recorded during the period May 1978-December 1980; subsequent analysis provided a frequency distribution of mortalities among the ten habitats that occurred on the study area. A significant disproportion of carcasses were found in riparian woodlands (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552); 60.3% of the mortalities (88/146) were located in a habitat that represented only 3.1% (85/2745 ha) of the

total study area. Sick and debilitated deer have been reported to travel downhill to lowland regions just prior to dying (Robinette et al. 1954); it appears that CWTD exhibited a preference for riparian lowlands under similar circumstances.

Gavin (1979) reported a significant disproportion of CWTD mortalities on a small portion of the CWTDNWR in 1975-76 and suggested that the apparent concentration of mortalities on such a small area was associated with a concomitant decrease in habitat and forage quality. However, examination of the spatial distribution of yearling and adult white-tailed deer mortalities on the CWTDNWR (Fig. 9, Gavin 1979) revealed that a significant disproportion of the carcasses were found in woodlands associated with riparian areas (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552).

Although not supported by experimental data, I strongly suspect that weakened CWTD were selecting riparian woodlands because these areas provided more cover. Among the four densest habitats (as determined with density board estimates) in this study, the riparian habitat was 1 of 2 multi-strata vegetative associations to not exhibit significant seasonal changes in vegetation density. Furthermore, 93% (54/58) of the remaining deer carcasses were located in the other three dense habitats. Therefore, it seems that wooded riparian areas afforded the best escape cover for sick and debilitated CWTD throughout the year.

Fawn Survival and Recruitment

During the springs and early summers of 1978-1980 CWTD fawns were live-captured and ear-tagged; in 1979 and 1980 fawns were also fitted with motion-sensitive mortality transmitters. Subsequent observations of marked individuals provided a schedule of survival throughout the following year. Annual estimates of recruitment (recruitment to the first anniversary) expressed as yearlings per adult female were derived from intensive observations of marked individuals in the population and from herd composition data recorded during five 6-day periods in June of the following year; the mean of the five 6-day periods provided an estimate of annual recruitment.

Of the ten fawns that were tagged in 1978, three survived through the summer representing a postpartum survival rate of 30% into the fall population; two fawns (20%) survived through the following spring. At the end of the summer there were six fawns remaining among fifteen recognizable adult females representing a fall recruitment rate of 0.40. Annual recruitment as determined from the marked sample was 0.27; the annual recruitment rate derived from herd composition data in the spring was 0.32.

During 1979, fifteen fawns were collared; 60% (9/15) of which survived through the summer. One additional fawn died during the fall and another died during the following spring leaving seven collared fawns, an annual survival rate of 47% (7/15). In 1979, fall recruitment and annual recruitment, as determined from herd

composition data, were 0.52 and 0.60, respectively. The annual recruitment rate derived from the sample of marked individuals was 0.65.

Fifteen fawns were collared during 1980. Subsequent observations recorded through December revealed that 87% (13/15) of the collared fawns survived through the summer; one additional fawn died during the fall representing a survival rate of 80% into the winter. All but one of the remaining fawns was accounted for during brief observation periods conducted in May of 1981. Thus, the survival rate of fawns through the spring of 1981 was 73-80% depending upon the fate of the one unaccounted fawn. The annual recruitment rate as determined from herd composition data recorded during cursory observations conducted during May was 0.68; the recruitment estimate derived from the marked sample was 0.75-0.79.

Annual recruitment rate as defined in this paper is determined by three population parameters: pregnancy rate, conception rate and the rate of survival to one year of age. Although corresponding specific natality rates (Dasman 1964) were unavailable, there are inferences that can be drawn from data gathered in this study. Examination of fawn survival and corresponding annual recruitment rates reveals a close parallel in the annual dynamics of these two population statistics; a two-fold increase in fawn survival from 1978 to 1979 was accompanied by a comparable increase in recruitment suggesting that recruitment during 1978 and 1979 was to a large extent determined by fawn survival rather than natality. Although it was not as apparent, a similar trend seemingly occurred in 1981.

Because of a high recruitment rate in 1979 (0.60), as compared to 1978 (0.32), there was a larger proportion of sub-adult females in the 1981 spring herd composition as compared to 1980. This would have had a tendency to bias the estimate by underestimating the number of fawns per breeding female. An unbiased and probably more accurate estimate of 1980 recruitment was derived from the marked sample (0.75-0.79). The fact that fawn survival (73-80%) and recruitment (0.75-0.79) were essentially identical indicates that again in 1980 fawn survival was largely responsible for the observed recruitment rate.

Fawn survival and recruitment rates in 1979 were significantly greater than corresponding estimates in 1978 (Chi-square test of independence, Sokal and Rohlf 1969:589; and Wilcoxon Mann-Whitney two sample test, Steel and Torrie 1980:542, respectively). During the winter of 1978-79, an estimated 24% of the CWTD population on the study died, a substantial reduction in population density. The significant increase in fawn survival and recruitment in 1979 apparently represented a response to a dramatic decrease in total population size and suggests an inverse density-dependent relationship between recruitment and existing population density. McCullough (1979) reported a similar phenomenon among white-tailed deer on the George Reserve.

Caughley (1976) suggested that the response of ungulate populations to changes in environmental quality (such as that realized through substantial changes in population density) is best characterized by a delayed logistic model, a simulation model of ungulate

population dynamics that incorporates a time lag component. Indeed, in this study the recruitment rate in 1980, two years following the population decrease, was greater than that observed in 1979, and suggests that the population exhibited a one year time-lag response to a decrease in density. During the two years following the winter die-off, it appears that the increase in recruitment was realized primarily through fawn survival; the additional increase in recruitment observed in 1980 over 1979 may reflect differences in pregnancy and conception rates. If the fall density does in fact influence reproductive success as Gavin (1979) observed on the CWTDNWR, then fewer does became pregnant and fewer does produced twins in the fall of 1978, as compared to 1980, a phenomenon that would reduce the recruitment rate independent of fawn survival. Dapson et al. (1979) reported similar responses to differences in habitat quality by contiguous white-tailed deer populations in South Carolina.

CWTD females in the fall of 1979 also experienced lower population densities, however the environment presumably had not recovered from the detrimental effects of higher densities (Caughley 1976). Consequently, females that were recovering from the previous severe winter probably entered the subsequent breeding period in less than prime condition, a phenomenon that directly affects the productivity of white-tailed deer (Verme 1969). Thus, lower pregnancy and conception rates in 1979 probably explains why the response of CWTD to a substantial reduction in density was not fully realized until 1980.

Parasites

External Parasites. During the period May 1978–December 1980, 66 live-captured individuals and 62 recent mortalities were examined for external parasites. Ectoparasites were identified by the U.S. Department of Agriculture, Agricultural Research Service, Animal Health Division and included the following: deer louse fly (Lipoptena depressa), California black-legged tick (Ixodes pacificus), mite (Euschoengastia numerosa), chewing louse (Tricholipeurus lipeuroides) and chewing louse (T. parallelus). Individuals examined were categorized as lightly infested (parasites not readily apparent and localized), moderately infested (parasites locally abundant and apparent throughout) and heavily infested (parasites abundant throughout).

Generally, ectoparasites were most abundant within the lower abdominal and inguinal regions and the axillary regions of the body. Sixty-eight percent (42/62) of the recent mortalities were characterized as lightly infested with ectoparasites while 24% (15/62) fell into the moderate category; only 8% (5/62) of the carcasses examined were categorized as being heavily infested with external parasites. There possibly existed a bias favoring the moderate and light categories as not all carcasses were examined within the same time period after death and some parasites, notably chewing lice, are known to leave the host as the body approaches ambient temperature (T.P. Kistner, personal communication).

Among the live-captured deer examined, young fawns consistently

exhibited the fewest external parasites; 28% (11/40) of the fawns were free of any ectoparasites (as determined from our examination), while 67% (27/40) were described as being lightly infested. There were no fawns classified in the heavily infested category and only 5% (2/40) of the fawns exhibited moderate infestations. Among yearling and adults, 50% (13/26) of the individuals examined were lightly infested with ectoparasites; 46% (12/26) were characterized as moderately infested and one individual was heavily burdened with parasites.

Internal Parasites. Field necropsies were performed on 55 of the 62 recent mortalities; seven carcasses were examined by veterinary pathologists. Among the internal parasites observed, the following helminths were identified and recorded: Trichostrongylus axei in the abomassum, Ostertagia spp., O. mossi, and O. eckerdikmansi in the abomassum and small intestine, Dictyocaulus eckerti in the lungs and bronchi, Fascioloides magnum in the liver, and the abdominal worm Setaria yehi. Nasal bots (Cephenemyia sp.) were observed in the nasal passages, pharynx and upper bronchi. Only one liver fluke (F. magnum) was discovered in the 62 carcasses that were examined. Of the seven carcasses examined by the veterinary pathologist, none were diagnosed as exhibiting pathological conditions and only one individual was described as being moderately infested with internal parasites.

Examination of microbiological slide preparations of fresh fecal samples revealed that the mean number of parasitic species occurring in the feces during late winter-early spring (4.9) was significantly greater (Wilcoxon Mann-Whitney two-sample test,

Steel and Torrie 1980:542) than that observed during late spring-summer (1.1). Moreover, the total number of parasitic eggs and protozoans observed in the winter fecal samples was on the average ten times greater than that recorded from summer samples. These data are consistent with observed seasonal differences in the frequency of malnutrition-related mortalities and the general physical condition of the individuals as determined from PCI indices.

HOME RANGE AND MOVEMENTS

During the period June 1978–December 1980, 1816 locations of marked CWTD were recorded. Convex polygon (C.P.) and bivariate normal (BIV) home range estimates were computed for all ($n = 32$) individuals that were observed on at least 20 independent occasions for a period totaling at least 3 months (Table 13). Whenever possible, both lifetime home ranges (computed from locations recorded during the entire period under observation) and age-class home ranges (computed from observations recorded during a specific age-class period) were computed (Fig. 27). Home range estimates were also computed for an unmarked fawn that was observed in association with a collared adult female. Observations of marked fawns during comparable time periods indicated that fawns were associated with adult females 95.5% (64/67) of the time. On occasions when marked fawns were observed alone, they occurred within the area of the home range defined by the corresponding locational data derived from observations in which they were associated with adult females.

Home Range Size. C.P. estimates ranged from 8.3 – 71.4 ha for females (yearling and adult) and 5.0 – 127.6 ha for males (Table 13). The mean C.P. estimates for females and males were 26.7 and 37.0 ha, respectively. A Wilcoxon Mann-Whitney two sample test (Steel and Torrie 1980:542) indicated that these means were not significantly different ($P > 0.25$). Adult, yearling and fawn C.P. estimates ranged from 1.9 – 65.5, 8.2 – 52.3, and 1.1 – 36.7 ha, respectively. Generally, adults ($\bar{x} = 30.6$ ha), yearlings ($\bar{x} = 34.3$ ha) and fawns

(\bar{x} = 10.8 ha) were significantly different according to a Kruskal-Wallis k-sample test (Steel and Torrie 1980:544). Adult and yearling estimates were significantly larger than fawns, however adult and yearling home ranges were not significantly different ($P > 0.90$) as as determined with Dunn's Multiple Comparison Test (Hollander and Wolfe 1973:125). Home ranges exhibited by adult males (\bar{x} = 43.4 ha) were significantly larger than adult females (\bar{x} = 24.8 ha), whereas fawn male home ranges (\bar{x} = 8.1 ha) and fawn female home ranges (\bar{x} = 12.3 ha) were not significantly different according to a Wilcoxon Mann-Whitney two sample test. Also, adult males demonstrated significantly larger displacements (\bar{x} = 2307 m) (greatest straight-line distance between any two locations) than adult females (\bar{x} = 1743 m) providing additional evidence that adult males ranged farther and occupied larger areas than adult females. Home range estimates were obtained for only three yearlings: two males and one female. The two yearling males exhibited home ranges of 8.2 and 52.3 ha, whereas the yearling female estimate was 42.4 ha.

Bivariate normal home range estimates ranged from 15.1 - 170.6 ha for yearling-adult females and 11.2 - 417.3 ha for males (Table 13). However, only individuals in which the spatial distribution of locations did not depart significantly from bivariate normality were included in further analyses. A Chi-square goodness-of-fit test for bivariate distributions indicated that 12 of 16 fawn spatial distributions and 9 of 16 adult spatial distributions did not depart significantly from bivariate normality; all three yearlings exhibited significant departures. Subsequent tests of skewness with the G_1

Table 13. Home range size indices of Columbian white-tailed deer in Douglas County, Oregon as derived from both the convex polygon method (C.P.) and the bivariate normal model (BIV), and the greatest straight-line distance between any two locations for each deer. (asterisk denotes a significant departure of locational data from bivariate normality)

FEMALES (N = 21)						
Deer #	Age at marking (months) ^a	Inclusive months of observations	No. months observed-No. observations ^b	Home Range Size (ha)		Greatest distance (m)
				C.P.	BIV	
11	1	June 79-Aug 80	14 - 38	36.7	97.2	1524
16	1	June 79-Aug 80	14 - 32	14.7	25.4	564
18	1	July 79-Aug 80	13 - 49	17.7	26.9	864
19	1	July 79-Aug 80	13 - 51	14.1	21.0*	1284
21	1	June 80-Sep 80	4 - 21	2.6	5.1	312
24	1	June 80-Sep 80	4 - 26	4.2	16.8	396
31	1	June 80-Nov 80	6 - 31	17.9	32.3*	648
34	1	July 80-Sep 80	3 - 27	1.9	9.3	264
38	1	June 80-Sep 80	4 - 20	8.9	31.2	624
102	3	Aug 79-Jul 80	11 - 31	7.1	12.3	540
201	24	June 78-Oct 80	28 - 82	38.8	56.0*	1176
205	25	July 78-Aug 80	25 - 42	17.1	31.6	876
207	12	June 79-Sep 80	15 -104	71.4	76.9*	1920
209	25	July 79-Aug 80	13 - 32	50.0	103.6	2004
211	26	Aug 79-Sep 80	13 - 61	11.4	15.1*	1680
212	24	June 79-Aug 80	14 - 74	14.5	19.8	1452
213	26	Aug 79-Oct 80	14 - 56	33.8	77.0*	2676
214	26	Aug 79-Oct 80	14 - 38	37.1	170.6	2304
215	26	Aug 79-Aug 80	12 -102	10.3	16.0	912
218	28	Oct 79-Sep 80	11 - 46	24.2	48.0	2604
220	30	Dec 79-Aug 80	9 - 51	8.3	17.3	1572

Table 13 continued.

MALES (N = 11)						
Deer #	Age at marking (months) ^a	Inclusive months of observations	No. months observed-No. observations ^b	Home Range Size (ha)		Greatest distance (m)
				C.P.	BIV	
8	1	July 78-Sep 80	26 - 79	12.5	41.0*	2280
12	1	June 79-Sep 80	15 - 75	5.0	11.2	2460
22	1	June 80-Sep 80	4 - 26	5.4	19.8	420
27	1	June 79-Mar 80	10 - 52	19.7	45.1*	2388
39	1	June 80-Sep 80	4 - 23	7.3	15.9	420
103	3	Aug 79-Jun 80	10 - 30	7.1	12.2	540
204	24	June 78-Jun 79	12 - 35	65.5	417.3*	2592
208	14	Aug 78-Aug 80	24 - 29	28.0	58.1	1500
401	13	July 79-Sep 80	14 - 109	80.9	78.6*	2664
403	28	Oct 79-Sep 80	11 - 59	52.2	184.6*	3216
404	27	Sept 79-Aug 80	11 - 36	14.9	49.0*	1560
UNKNOWN (N = 1)						
101	3	Aug 79-Jul 80	11 - 42	18.0	42.6*	1476

^a June 1 was selected as the anniversary date for all deer. Age at marking for some individuals was determined by aging skull after death.

^b Number of months in which this deer was observed-total number of observations for all months.

Figure 27. Convex polygon and elliptical (lifetime and adult) home range estimates for no. 401, an adult Columbian white-tailed deer male.

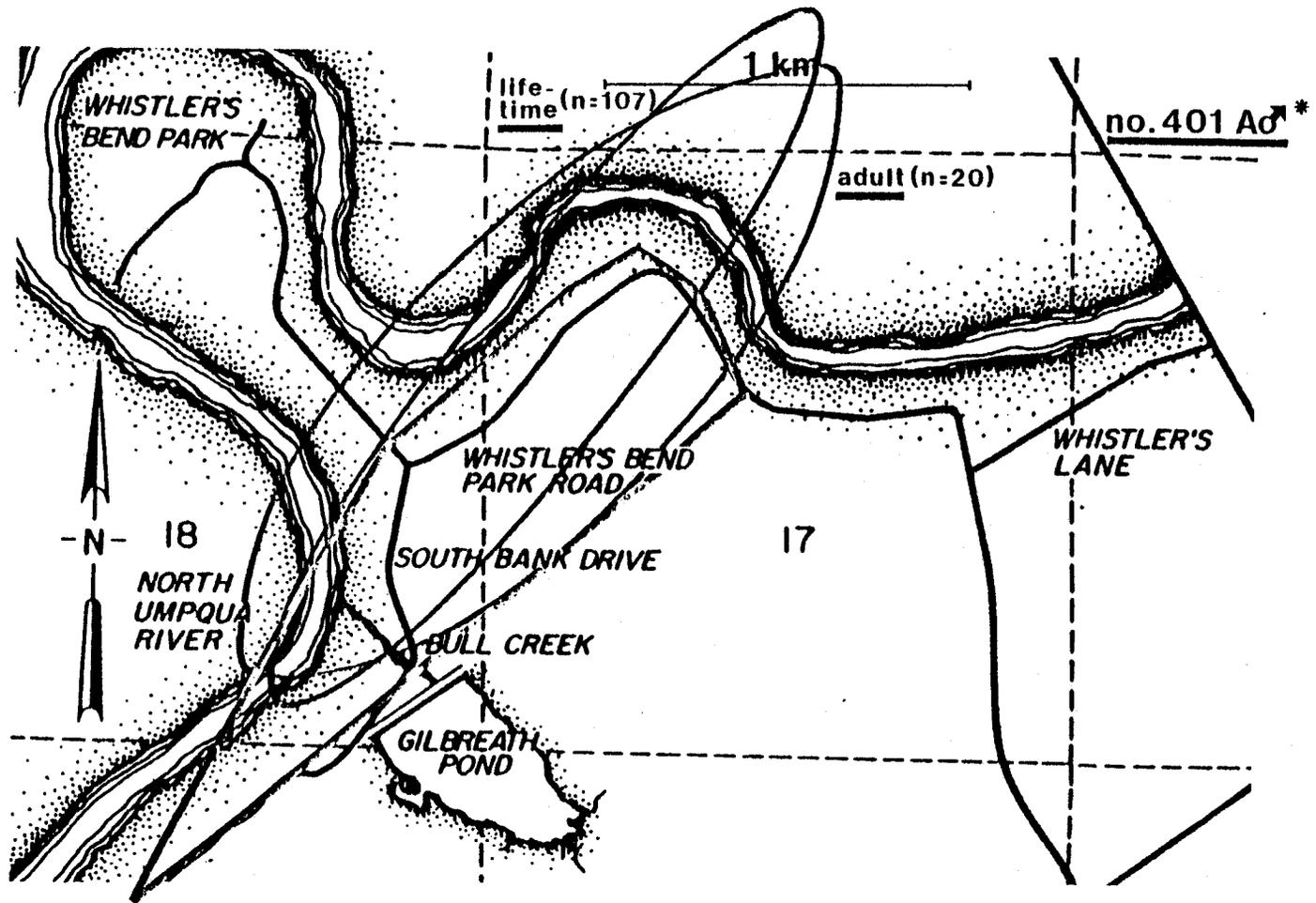


Figure 27.

statistic (Sokal and Rohlf 1969:113) verified prior conclusions regarding bivariate normality.

Female BIV estimates (yearlings and adults) ($\bar{x} = 55.6$ ha) were not significantly different ($P > 0.25$) from male estimates ($\bar{x} = 34.7$ ha) as determined with a Wilcoxon Mann-Whitney two sample test (Steel and Torrie 1980:542). Additional comparisons of sex and/or age class BIV estimates employing a Wilcoxon Mann-Whitney two sample test indicated that adults ($\bar{x} = 66.0$ ha) exhibited significantly larger home ranges than fawns ($\bar{x} = 25.7$ ha), whereas adult males ($\bar{x} = 93.7$ ha) and adult females ($\bar{x} = 58.1$ ha), and fawn males ($\bar{x} = 16.0$ ha) and fawn females ($\bar{x} = 29.4$ ha) exhibited home ranges that were not significantly different ($P > 0.20$ and $P > 0.50$, respectively).

Home Range Shape, Location and Orientation. The shape of the home ranges were greatly influenced by their location and orientation with respect to the North Umpqua River and other riparian areas within the study area. Twenty-nine of the 32 individuals (91%) for which C.P. and BIV estimates were obtained exhibited home ranges that were located immediately adjacent to the North Umpqua River and/or incorporated a portion of the river within the estimated home range area (Fig. 28). Also, 21 of the 29 individuals that were located along the North Umpqua River (72%) exhibited C.P. home ranges that had their longest side immediately adjacent to and parallel with the river. This spatial distribution and orientation of home ranges represents a significant association between the location of individual home ranges and the North Umpqua River and its associated vegetation as determined with a Chi-square test of independence (Sokal and Rohlf

1969:585). Individuals that did not have home ranges along the North Umpqua River displayed spatial distributions of activity that were located immediately adjacent to and/or incorporated portions of riparian areas that were within 1 km of the North Umpqua River (Fig. 29).

Spatio-Temporal Activity Patterns. The straight-line distance between annual geometric centers of activity for CWTB observed as fawns and yearlings (fawns), yearlings and two-year olds (yearlings), and as adults in consecutive years (adults) (Table 14) served as an index of spatio-temporal stability of home ranges between years. Distance between seasonal centers of activity provided information concerning the spatio-temporal activity patterns of individuals among seasons within a specific year (Table 15).

Generally, CWTB exhibited stable home ranges between years as indicated by the nominal shifts in annual centers of activity (Table 14). Annual center of activity displacements for all males ($\bar{x} = 150.3$ m) and females ($\bar{x} = 157.1$ m) were not significantly different ($P > 0.90$) according to a Wilcoxon Mann-Whitney two sample test (Steel and Torrie 1980:542). A Kruskal-Wallis k-sample test (Steel and Torrie 1980:544) indicated that annual center of activity displacements among adults ($\bar{x} = 162.0$ m), yearlings ($\bar{x} = 173.8$ m) and fawns ($\bar{x} = 129.0$ m) were not significantly different ($P > 0.25$). Also, adult males ($\bar{x} = 174.0$ m) and adult females ($\bar{x} = 159.2$ m), and fawn males ($\bar{x} = 75.5$ m) and fawn females ($\bar{x} = 155.8$ m) were not significantly different ($P > 0.25$ and $P > 0.15$, respectively) as determined with a Wilcoxon Mann-Whitney two sample test.

Figure 28. Convex polygon and elliptical home range estimates for no. 208, an adult Columbian white-tailed deer male.

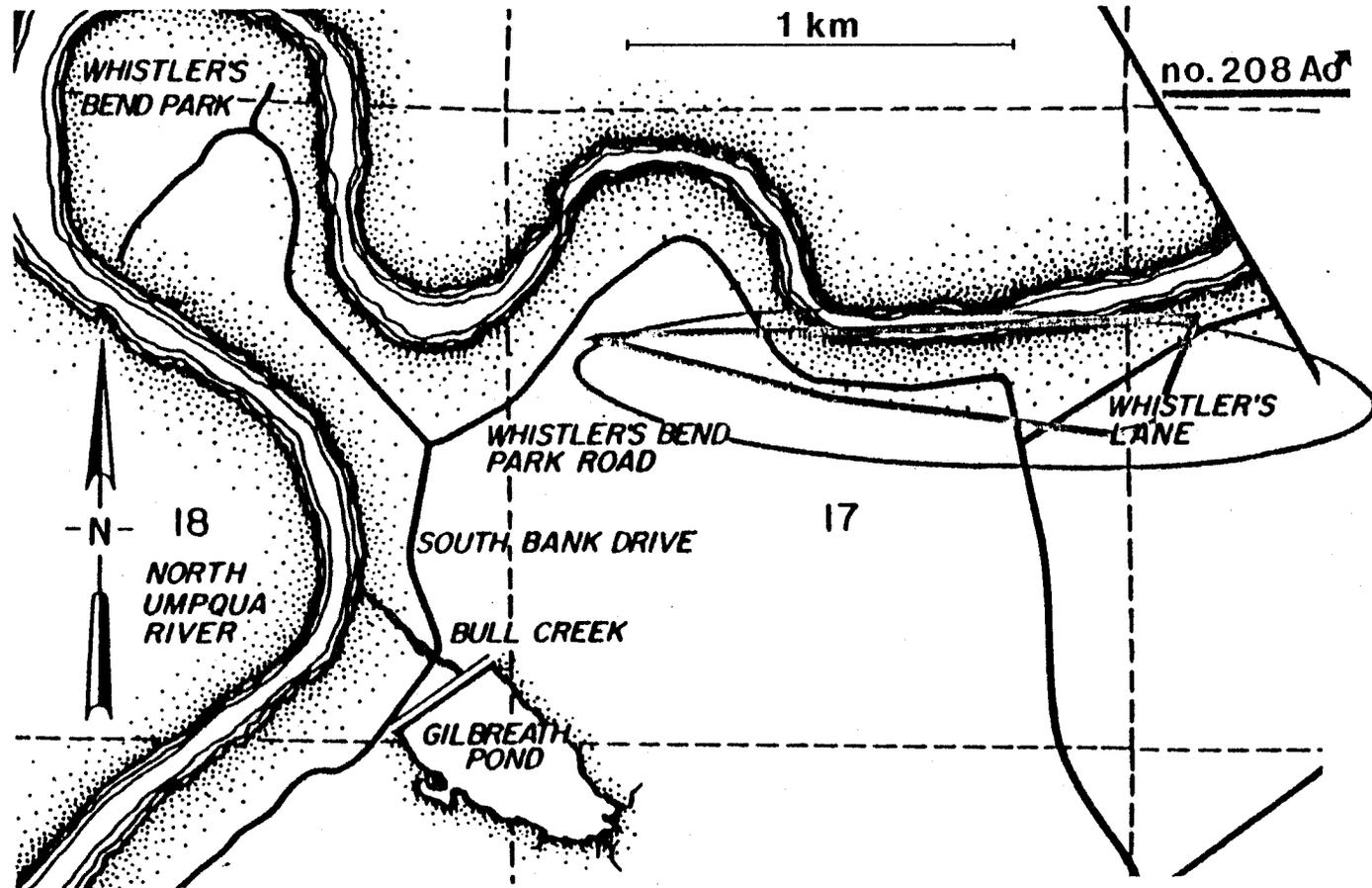


Figure 28.

Figure 29. Convex polygon and elliptical home range estimates for no. 11, a yearling Columbian white-tailed deer female.

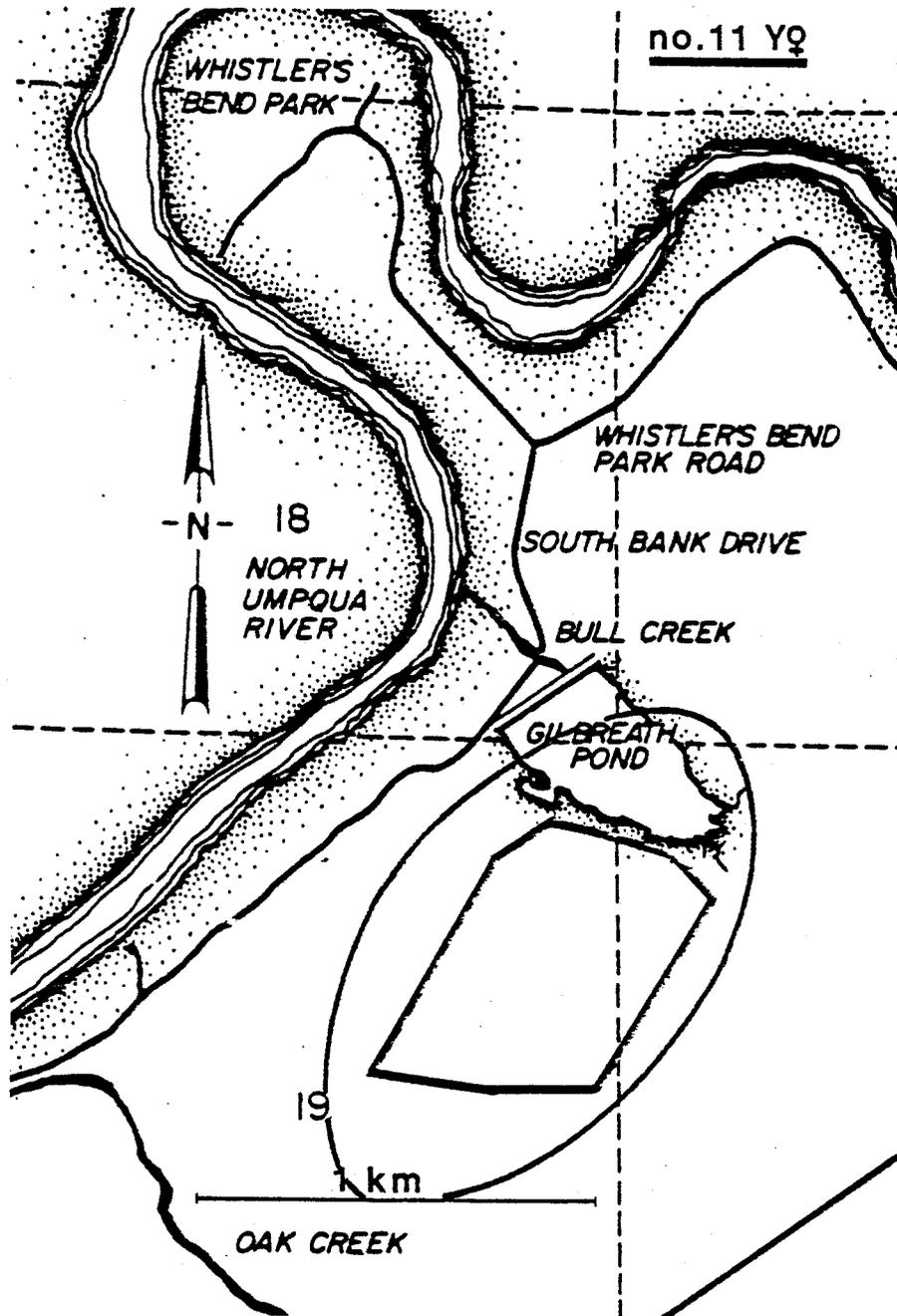


Figure 29.

Table 14. Straight-line distance between annual geometric centers of activity during comparable time periods for Columbian white-tailed deer observed as fawns and yearlings, yearlings and two-year-olds, and as adults in consecutive years.

FAWN-YEARLING OBSERVATIONS ^a			
FEMALES			
<u>Deer #</u>	<u>Fawn (\bar{X}, \bar{Y})</u>	<u>Yearling (\bar{X}, \bar{Y})</u>	<u>Distance (m)^b</u>
11	(148.7, 127.1)	(133.7, 111.9)	260
16	(104.5, 145.8)	(100.0, 154.0)	115
18	(108.0, 151.4)	(122.6, 155.6)	185
19	(111.1, 267.3)	(115.1, 263.9)	63
MALES			
8	(106.3, 144.5)	(109.2, 146.2)	42
12	(259.6, 235.2)	(266.7, 230.4)	109
YEARLING-TWO-YEAR-OLD OBSERVATIONS ^a			
FEMALES			
<u>Deer #</u>	<u>Yearling (\bar{X}, \bar{Y})</u>	<u>Two-Year-Old (\bar{X}, \bar{Y})</u>	<u>Distance (m)</u>
207	(172.6, 242.2)	(179.7, 251.4)	142
MALES			
8	(109.2, 146.2)	(86.2, 121.8)	409
208	(254.1, 231.8)	(250.7, 233.1)	44
401	(166.8, 235.4)	(170.9, 242.5)	100
ADULT-ADULT OBSERVATIONS ^a			
FEMALES			
<u>Deer #</u>	<u>Adult (\bar{X}, \bar{Y})_t</u>	<u>Adult (\bar{X}, \bar{Y})_{t+1}</u>	<u>Distance (m)</u>
201 ^c	(65.2, 99.3)	(61.8, 92.4)	94
201 ^d	(61.8, 92.4)	(51.3, 89.1)	134
205	(109.7, 132.7)	(94.7, 119.3)	245
209	(139.1, 176.6)	(134.4, 123.8)	647

Table 14. Female adult-adult observations continued.

Deer #	Adult $(\bar{X}, \bar{Y})_t$	Adult $(\bar{X}, \bar{Y})_{t+1}$	Distance (m)
211	(215.1, 247.3)	(209.1, 247.2)	73
212	(169.8, 240.2)	(170.7, 240.8)	13
213	(234.5, 240.2)	(232.2, 241.2)	31
214	(231.4, 240.5)	(251.0, 234.3)	251
215	(117.4, 150.2)	(116.5, 152.2)	27
218	(280.4, 234.2)	(285.8, 231.0)	77
MALES			
208	(277.8, 234.8)	(283.1, 229.3)	93
403	(66.5, 100.1)	(54.3, 83.1)	255

^aCenter of activity is reported for individuals for which coefficient of variation did not exceed 20%.

^bComputed from the following equation: $Distance = (\bar{X}_1 - \bar{X}_2)^2 + (\bar{Y}_1 - \bar{Y}_2)^2$.
The computed grid units are multiplied times 12.2 m (i.e. the grid unit scale).

^cDerived from observations recorded June 1978-May 1979.

^dDerived from observations recorded June 1979-May 1980.

Table 15. Straight-line distance between seasonal geometric centers of activity for Columbian white-tailed deer observed in Douglas County, Oregon during the period June 1978-December 1980. (asterisk denotes largest displacement for a specific individual)

FEMALES							
Deer #	Summer-Fall (m)	Fall-Winter (m)	Winter-Spring (m)	Spring-Summer (m)	Fall-Spring (m)	Winter-Summer (m)	
18	92.8*	50.8	---	---	---	78.9	
19	85.0	25.4	282.4	171.1	307.8*	61.7	
201	126.3	143.5	---	---	---	148.9*	
205	150.3	23.4	96.0	108.9	75.3	153.6*	
207	248.5*	140.9	95.1	136.7	233.7	123.9	
209	170.6	621.9	319.4	476.0	940.0*	787.1	
211	48.4	66.7	179.9	133.9	245.9*	20.9	
212	189.0	191.4	59.4	96.4	239.6*	35.6	
213	---	---	---	78.8	140.1*	---	
215	31.7	76.8	55.5	54.8	24.7	101.3*	
218	---	46.6	65.7	96.8*	23.2	---	
220	---	75.5	153.5	---	226.2*	---	
Mean \bar{x}	127.0	133.0	145.2	150.4	245.7	96.0	Grand Mean $\bar{\bar{x}}$ 152.2
MALES							
8	104.5	133.2	76.6	301.1*	207.9	31.9	
12	70.5	163.8*	120.8	97.6*	47.1	111.9	
27	27.1	613.8	---	---	---	640.0*	
204	242.3	1016.6*	614.6	---	420.8	777.4	
208	593.5*	---	---	---	---	---	

Table 15 Males continued.

MALES							
Deer #	Summer-Fall (m)	Fall-Winter (m)	Winter-Spring (m)	Spring-Summer (m)	Fall-Spring (m)	Winter-Summer (m)	
401	34.2	134.9	33.2	104.5	163.1*	162.8	
403	2107.9	2336.1	126.0	369.9	2446.6*	---	
Mean \bar{x}	<u>454.3</u>	<u>733.1</u>	194.2	218.3	<u>657.1</u>	344.8	Grand Mean $\bar{\bar{x}}$ <u>418.9</u>

CWTD exhibited significantly larger displacements in center of activity among seasons ($\bar{x} = 265.9$ m) than between years ($\bar{x} = 155.0$) according to a Wilcoxon Mann-Whitney two sample test (Steel and Torrie 1980:542). Also, displacements in center of activity among the seasons (Table 14) were significantly different for both males and females according to a Kruskal-Wallis k-sample test (Steel and Torrie 1980:544), and seasonal displacements for all males ($\bar{x} = 418.9$ m) were significantly larger than seasonal displacements for all females ($\bar{x} = 152.2$ m) as determined with a Wilcoxon Mann-Whitney two sample test.

Males demonstrated significantly larger displacements (Wilcoxon Mann-Whitney two sample test, Steel and Torrie 1980:542) among periods of comparison in which the fall season was included ($\bar{x} = 603.6$ m) than periods in which fall was not included ($\bar{x} = 254.9$ m). These observations were consistent with spatio-temporal patterns of activity displayed by individual yearling and adult males during the rut. Five of the 6 (83%) collared bucks, for example, exhibited the largest single displacement ($\bar{x} = 1623$ m) from their respective annual center of activity during the rutting period (November-January), a significant association between individual patterns of movement and the male phenomena according to a Chi-square test of independence (Sokal and Rohlf 1969:585). Home range expansion by bucks in the fall was substantiated further by observations recorded for an individual that established an additional home range during the rut (Fig. 30).

Female CWTD displayed the largest seasonal movements during the

Figure 30. Annual and rutting convex polygon and elliptical home range estimates for no. 403, an adult Columbian white-tailed deer male.

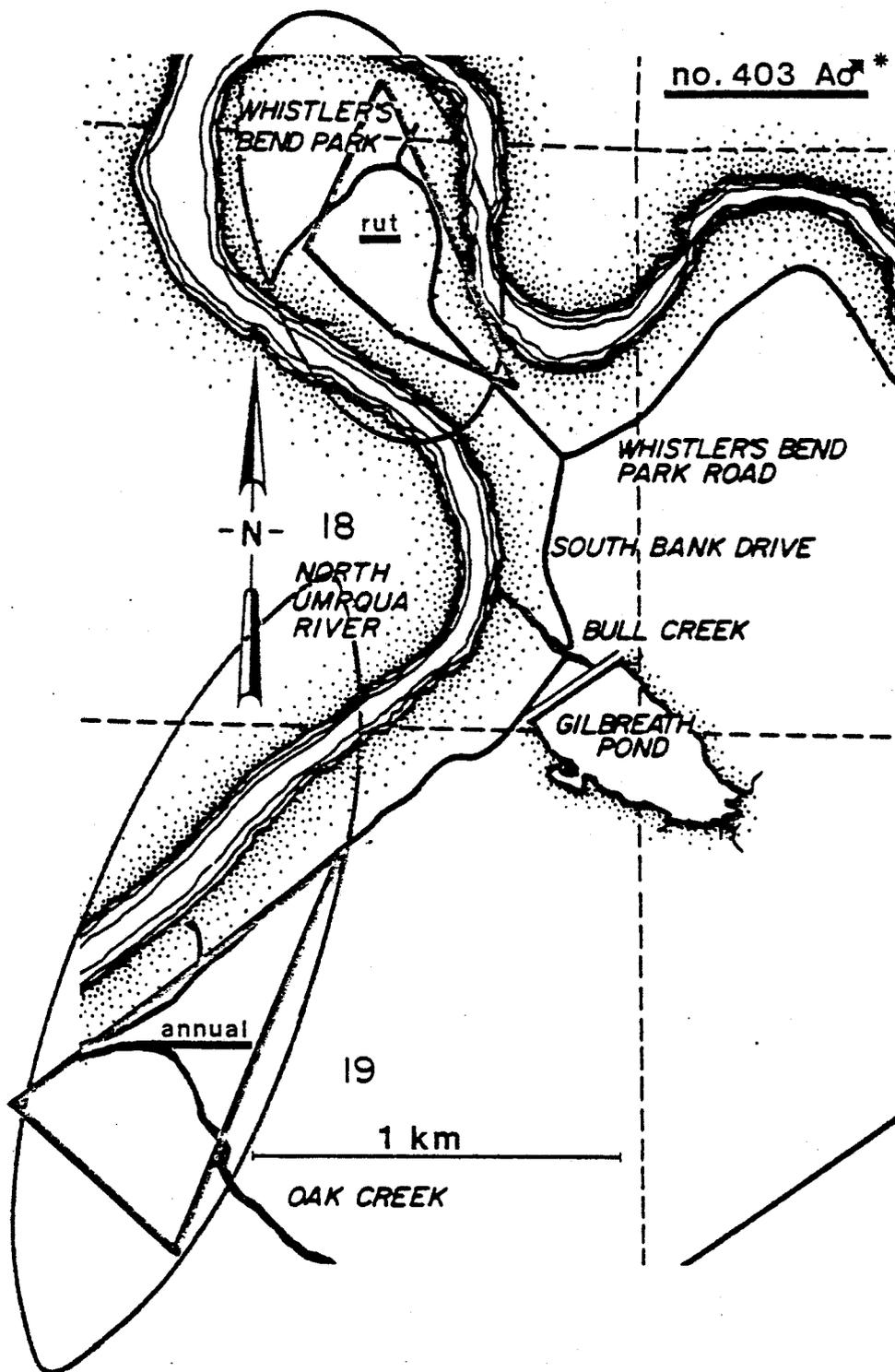


Figure 30.

period just prior to fawning. Eight of 11 does (73%) exhibited the longest seasonal displacements among periods of comparison that included spring (Table 15); there was a significant association between individual patterns of movement and this time period (Chi-square test of independence, Sokal and Rohlf 1969:585). Evidence that these movements were associated with fawning activities was provided by observations in which 7 adult females undertook extended excursions during the period April 25 - May 20. These movements represented a mean displacement of 1445 m from their respective annual centers of activity. Also, 3 adult females established separate fawning home ranges (eg. Fig. 31) whose centers of activity averaged 1926 m from the respective annual home range center of activity.

Generally two methods of evaluating white-tailed deer home ranges have been employed: non-statistical techniques that require no assumption about the spatial distribution of the locational data, and statistical models that calculate home range with the assumption that the locational data follow some probabilistic distribution. Non-statistical methods (convex polygon and smallest polygon) are reported to have a sample size bias, i.e. their estimates tend to increase as the number of locations increases (Jennrich and Turner 1969), whereas elliptical models are reported to be free of sample size bias (Koepl et al. 1975). However, with increasing sample size the expected error of elliptical estimates decreases such that home range values derived from the Koepl et al. model, for example, decrease on the average with increasing sample size (Madden and

Marcus 1978). Age-class home range estimates computed from subsets of locational data used to compute respective lifetime estimates were invariably smaller ($\bar{x} = 51.6$ ha) than corresponding lifetime estimates ($\bar{x} = 73.8$ ha) (e.g., Fig. 27), substantiation that elliptical estimates are in reality not totally independent of sample size. Biases associated with polygon methods become negligible when the sample size exceeds 20 (Jennrich and Turner 1969). However, when locational data do not conform to bivariate normality, elliptical models provide tenuous estimates from which spurious conclusions will almost certainly arise. For this reason, analyses and subsequent comparisons of age and sex class BIV estimates were performed only with individuals whose spatial distribution of activity did not depart significantly from bivariate normality. Because elliptical and polygon methods measure similar home-range properties (Madden and Marcus 1978), home range estimates derived from the smallest polygon technique are probably more biologically meaningful when bivariate normality is violated and sample size stipulations have been satisfied.

Generally, the BIV and C.P. estimates resulted in similar conclusions regarding sex and age class home ranges. Examination of corresponding BIV and C.P. estimates revealed that BIV home ranges were invariably larger than C.P. estimates (Table 13). Gavin (1979) reported similar conclusions with elliptical and convex polygon estimates. Also, the statistically projected elliptical home ranges incorporated areas with undocumented locations in regions that were not readily accessible (across the river) to individuals (Fig. 32)

Figure 31. Annual and fawning convex polygon and elliptical home range estimates for no. 214, an adult Columbian white-tailed deer female.

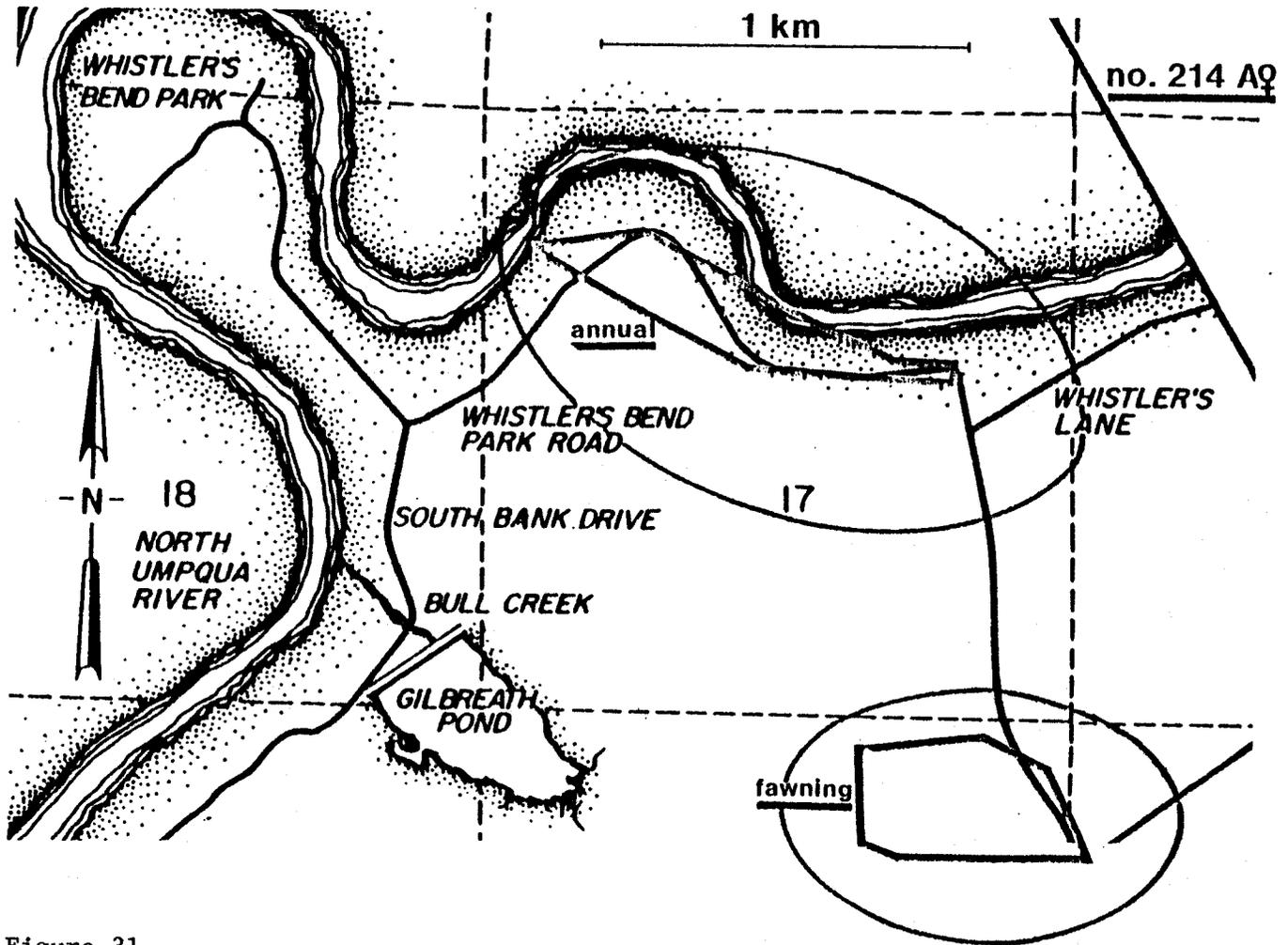


Figure 31.

in 25 of 30 instances. C.P. estimates incorporated relatively inaccessible regions in only 8 of 30 instances, and in each example represented a much smaller total area of undocumented home range than the corresponding ellipse (egs., Fig. 32 and Fig. 33).

Gavin (1979) reported elliptical estimates for CWTB yearling-adult males ($\bar{x} = 192.2$ ha) and females ($\bar{x} = 158.5$ ha) that were significantly larger (Wilcoxon Mann-Whitney two sample test, Steel and Torrie 1980:542) than home ranges for adult-yearling males ($\bar{x} = 34.7$ ha) and females ($\bar{x} = 55.6$ ha) in Douglas County. Convex polygon estimates obtained for CWTB yearling-adult males ($\bar{x} = 137.7$ ha) and females ($\bar{x} = 112.2$ ha) on the CWTBNWR (Gavin 1979) were significantly larger (Wilcoxon Mann-Whitney two sample test) than comparable convex polygon estimates obtained for CWTB males ($\bar{x} = 27.1$ ha) and females ($\bar{x} = 21.1$ ha) in Douglas County. Also, all age and sex class elliptical home ranges reported for the CWTBNWR were larger than corresponding estimates reported herein. I suspect that possibly some of the reported differences between convex polygon estimates for the 2 populations were due to appreciable differences in the average number of observations recorded for CWTBNWR ($\bar{x} = 97.2$) as compared to the number of observations for Douglas County deer ($\bar{x} = 49.3$). However, the observed significant differences in corresponding elliptical estimates and the magnitude to which the respective convex polygon home ranges differed indicate real biological differences in the home range sizes of CWTB on the CWTBNWR as compared to the individuals within the Douglas County population.

Additionally, home ranges of Douglas County CWTB were smaller

Figure 32. Convex polygon and elliptical home range estimates for no. 204, an adult Columbian white-tailed deer male (asterick denotes individuals whose locational data departed significantly from bivariate normality).

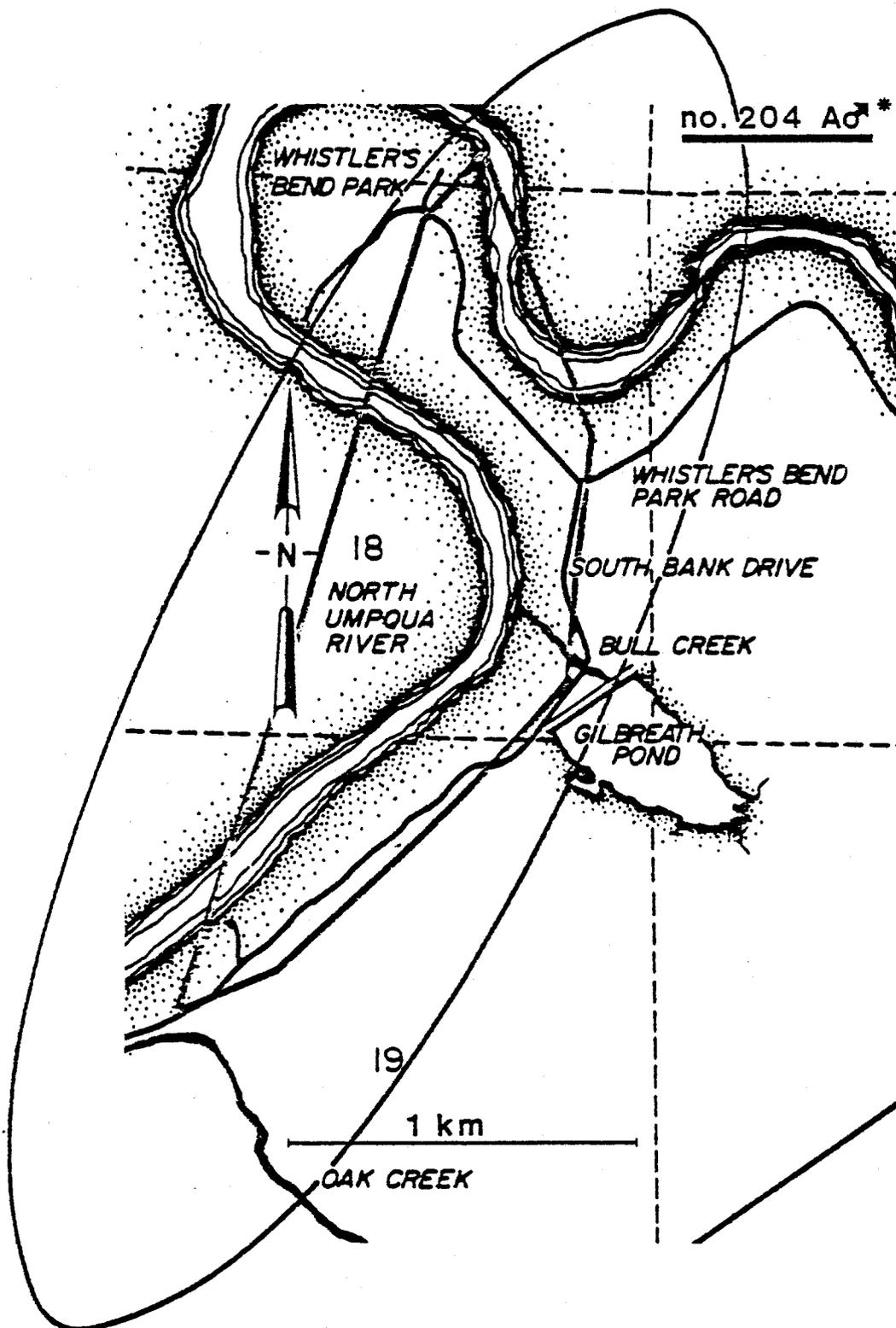


Figure 32.

Figure 33. Convex polygon and elliptical home range estimates for no. 207, an adult Columbian white-tailed deer female. (asterick denotes individuals whose locational data departed significantly from bivariate normality)

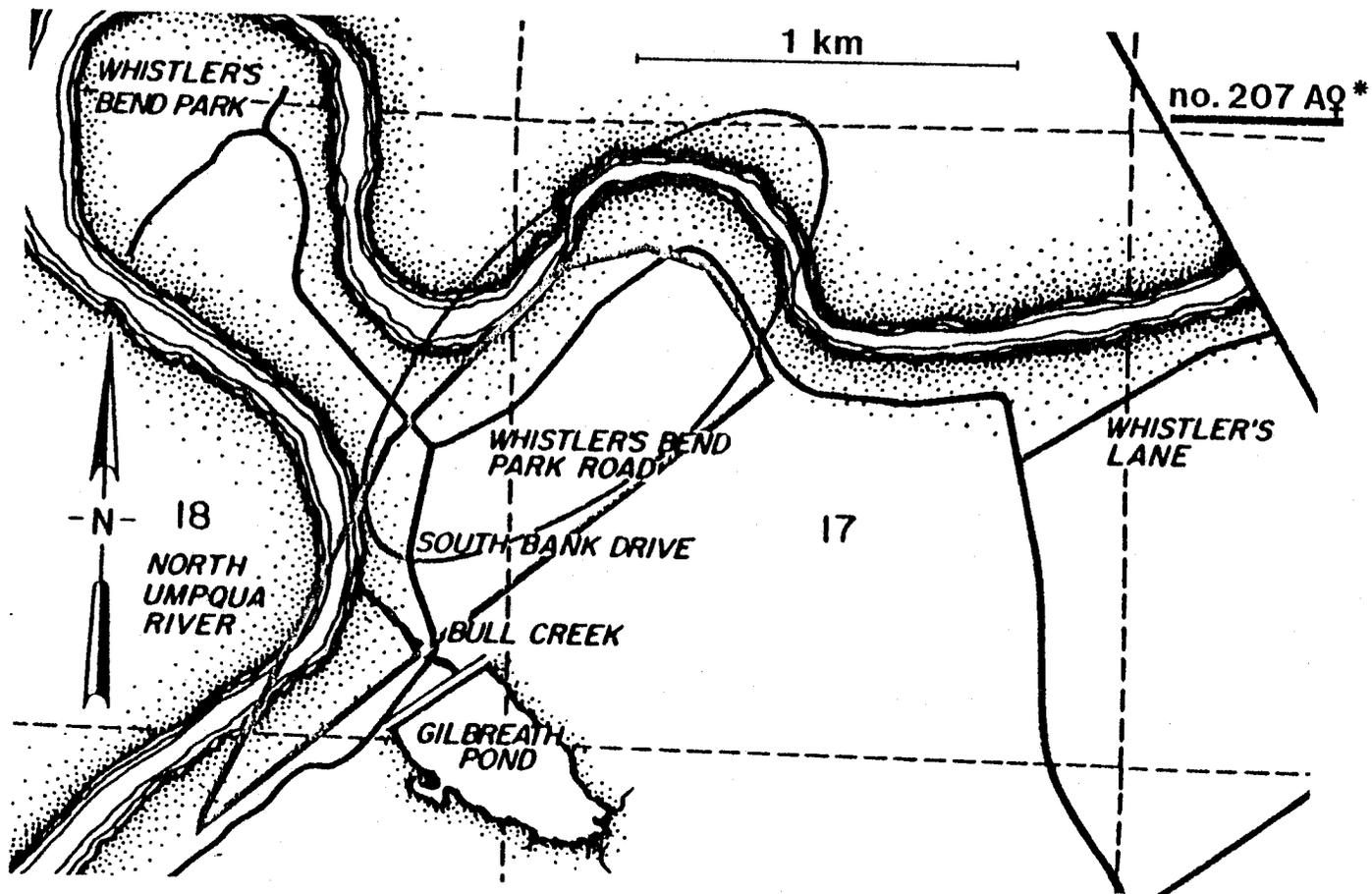


Figure 33.

than home ranges reported for white-tailed deer in the literature (Severinghaus and Cheatum 1956; Progulske and Baskett 1958; Thomas et al. 1964; Michael 1965; Alexander 1968; Marshall and Whittington 1968; Sparrowe and Springer 1970; Inglis et al. 1979). Progulske and Baskett (1958) reported adult male and adult female home ranges (\bar{x} = 281 ha and 162 ha, respectively) that were an order of magnitude larger than corresponding home ranges obtained for CWTD in Douglas County. CWTD home ranges were most similar to estimates reported by Kirkpatrick et al. (1976) for white-tailed deer in Indiana. Carlsen and Farnes (1957) presented evidence that home ranges of white-tailed deer varied with respect to vegetative type, whereas Marchinton (1968) reported that home range size varied inversely with density. Similarly, CWTD exhibited relatively small home ranges in conjunction with locally high densities, and generally displayed larger home ranges in upland regions nonadjacent the North Umpqua River where woodlands were discontinuous.

Invariably, home ranges reported in the literature for bucks were larger than corresponding estimates for does (Progulske and Baskett 1958; Thomas et al. 1964; Michael 1965; Alexander 1968; Marshall and Whittington 1968; Sparrowe and Springer 1970; Inglis et al. 1979), a generalization consistent with CWTD observations. Also, yearling white-tailed deer have been reported to range farther and occupy larger areas than older individuals (Carlsen and Farnes 1957). Both Gavin (1979) and Sparrowe and Springer (1970) observed that yearlings exhibited the longest displacements. In Douglas County, two of three yearling CWTD home ranges were considerably

larger (36%) than the mean estimate for adults, suggesting a similar trend for Douglas County CWTD. Sparrowe and Springer (1970) suggested that this behavior among yearlings represented an "age-characteristic" phenomenon, a predisposition to wander and roam associated with dispersal. Subsequent observations of marked fawns by Michael (1965) demonstrated that natal areas did not become the centers of home ranges for the respective yearlings. The consequence of far-ranging movements by yearling white-tailed deer and its proposed role in dispersal has not been documented. However, the evidence certainly implies that during a period of time following expulsion by the adult female yearlings tend to wander and range over relatively large geographic areas, a behavior that apparently is associated with the procurement of an established home range.

The movements and home ranges of white-tailed deer are affected by geographic features of the environment (Michael 1965). Inglis et al. (1979) reported that the spatial distribution of suitable habitat influenced the "linearity of home ranges"; deer whose home ranges were associated with homogeneous vegetation types displayed spatial distributions that "ranged out equally in all directions", whereas deer whose ranges included several discontinuous vegetation types displayed home ranges that approached linearity. Similarly, CWTD in Douglas County exhibited home ranges that reflected the outstanding geographic features and ultimately the relative availability and spatial distribution of the various vegetation types. Individuals that utilized relatively large continuous vegetation types displayed distributions that approached bivariate normality, whereas locational

data that departed significantly from bivariate normality characterized individuals that occupied discontinuous habitats. Water boundaries also greatly influence the movements and ultimately the shape of white-tailed deer home ranges. Gavin (1979) reported that CWTD on the CWTDNWR avoided water and consequently exhibited home ranges that were restricted to one side of a water boundary. In Douglas County, the spatial distribution and orientation of home ranges with respect to the North Umpqua River indicates that the North Umpqua riparian system (river and associated vegetation) played a vital role in the home range dynamics of CWTD.

Throughout much of their range in North America, white-tailed deer are generally sedentary and characteristically occupy year-round home ranges (Severinghaus and Cheatum 1956). Seasonal migrations associated with severe winter conditions have been reported in Montana (Severinghaus and Cheatum 1956), Minnesota (Hoskinson and Mech 1976; Nelson 1977) and Michigan (Verme 1973). In South Dakota, Sparrowe and Springer (1970) observed larger displacements during fall, winter and early spring, and characterized the behavior as a response to seasonally changing habitat. Michael (1965) observed the greatest mobility of whitetails on Welder Wildlife Refuge during the period January-April, whereas Progulske and Baskett (1958) reported that white-tailed deer in Missouri exhibited significant seasonal shifts exclusively in the fall. Generally, CWTD in Douglas County and on the CWTDNWR were relatively sedentary and occupied year-round home ranges that were comparably stable between years. However, in Douglas County significant seasonal shifts were displayed by bucks

during the fall and does during the spring, behaviors that were associated with rutting and fawning activities, respectively. Home range expansion by bucks during the rut has been reported by a number of investigators (Severinghaus and Cheatum 1956), and apparently represents a fairly common behavioral phenomenon. But extensive seasonal movements by does during the spring in conjunction with the establishment of additional fawning home ranges had not been documented previously. Sparrowe and Springer (1970) reported extensive movements by a number of young whitetails during spring and summer, but these observations probably represented the movements of evicted yearlings just prior to and following fawning. I strongly suspect that the seasonal shifts displayed by adult female CWTB in Douglas County represented a local response to the relative abundance and spatial distribution of preferred natal areas and reflected the availability of suitable fawning habitat.

NICHE SEPARATION BETWEEN CWTD
AND BLACK-TAILED DEER

CWTD and black-tailed deer occur sympatrically within the interior valleys of the Umpqua River in Douglas County, Oregon. To my knowledge, this is the only area in North America where white-tailed and black-tailed deer co-occur. Sympatric populations of mule deer and white-tailed deer have been investigated by a number of researchers (Krämer 1973, Krausman 1978, Anthony and Smith 1979); however very little if any information is available regarding the ecology of sympatric populations of white-tailed and black-tailed deer.

Historically, the two species apparently maintained a local segregation; CWTD occupied the river valleys and bottomlands of western Oregon and southwestern Washington while black-tailed deer occurred at higher elevations along slopes of the foothills and along the slopes and high meadows of the mountains (Douglas 1829, Nash 1877). In western Oregon, blacktails have primarily inhabited the coniferous forests whereas CWTD were typically a woodland-brushland species, an inhabitant of the oak-savanna complex. The settlement of European man in western Oregon was responsible for dramatic changes in the natural vegetation, particularly in the river valleys and bottomlands of the Willamette Valley (Thilenius 1968). Extensive cultivation of western Oregon in recent times has supplanted most of the native associations, a consequence of which has been the extirpation of CWTD from most of its historic range. Since that time,

black-tailed deer have invaded much of the Willamette Valley; today, blacktails occur throughout most of the range previously occupied by CWTD.

In Douglas County, black-tailed deer and CWTD have remained ecologically segregated. The dispersion of the two species throughout the study area departed significantly from a random spatial distribution; CWTD occurred significantly more frequently within 1 km of the North Umpqua River (Chi-square goodness-of-fit test, Sokal and Rohlf 1969:552). Further analysis indicated that the two species were spatially segregated on a smaller scale; i.e. once one species was encountered the probability of encountering the same species was significantly greater than encountering the second (Runs test, Siegel 1956). In over 13000 observations, only once were the two species ever observed in close association, i.e. less than 25m apart.

There were apparent differences in habitat use between the two species (Fig. 34). Generally, black-tailed deer utilized grasslands and the more open upland habitats more frequently while CWTD occurred more frequently among the woodland habitats. Black-tailed deer displayed a preference for grass-shrub, oak-savanna and conifer habitats while avoiding closed oak, oak-conifer, oak madrone and riparian habitats; grassland, open oak and madrone habitats were used proportionally (Table 16). Black-tailed deer and CWTD differed significantly in their use of grassland, grass-shrub, open oak, closed oak, oak conifer and riparian habitats (Fig. 34)(comparison of proportions in independent samples, Snedecor and Cochran 1980:124).

Figure 34. Proportion of occurrence of Columbian white-tailed deer and black-tailed deer among the ten habitats represented on the study area in Douglas County, Oregon during the period May 1978-December 1980.

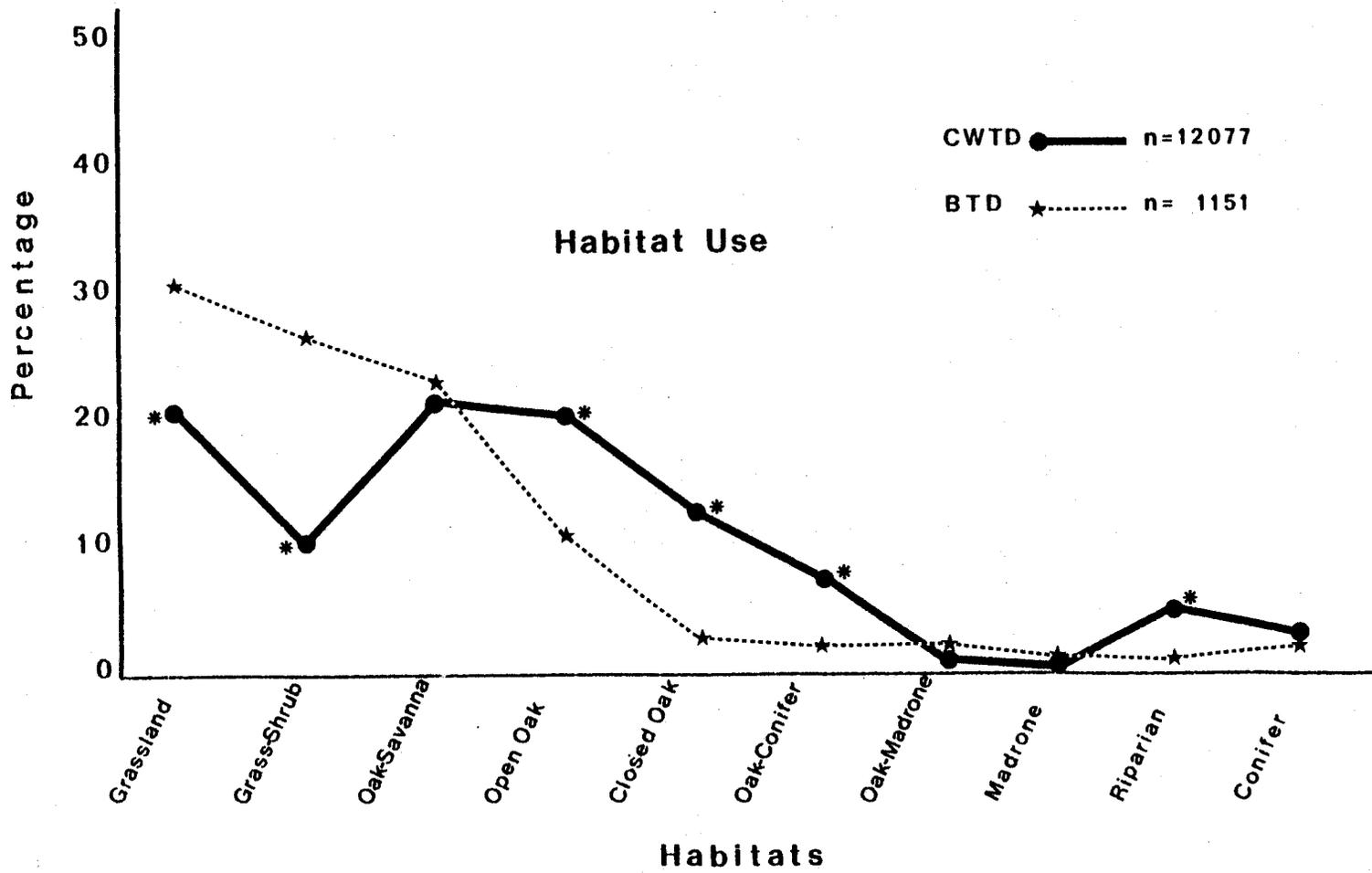


Figure 34.

Table 16. Occurrence of black-tailed deer among the ten habitats represented on the study area in Douglas County, Oregon during the period May 1978-December 1980. (notations from Neu et al. 1974)

Habitats	Proportion Of Total Area ^a (p_{i0})	Proportion Observed In Each Habitat (\bar{p}_i)	95% Family Confidence Intervals ^b
GRASSLAND	0.336	0.295	$0.257 \leq p_i \leq 0.338$
GRASS-SHRUB	0.044	0.257	$0.221 \leq p_i \leq 0.293$
OAK-SAVANNA	0.132	0.222	$0.188 \leq p_i \leq 0.256$
OPEN OAK	0.171	0.106	$0.081 \leq p_i \leq 0.131$
CLOSED OAK	0.087	0.030	$0.016 \leq p_i \leq 0.044$
OAK-CONIFER	0.113	0.022	$0.010 \leq p_i \leq 0.034$
OAK-MADRONE	0.061	0.022	$0.010 \leq p_i \leq 0.034$
MADRONE	0.014	0.015	$0.005 \leq p_i \leq 0.025$
RIPARIAN	0.031	0.010	$0.002 \leq p_i \leq 0.018$
CONIFER	0.011	0.021	$0.009 \leq p_i \leq 0.033$

^aProportions of total area represent expected Columbian white-tailed deer observations in corresponding habitat.

^bIndividual habitat proportion estimates represent 99.5% confidence intervals.

Although we have no experimental evidence, our data strongly suggest that the occurrence of CWTB within portions of the study area precluded extensive use of those areas by black-tailed deer. For example, black-tailed deer were seldom observed within portions of the study area supporting high densities of CWTB; indeed, there was a significant inverse correlation ($r = 0.93$) between the relative densities of the two species. Also, the relative density of each species differed significantly with respect to the second species (Wilcoxon Mann-Whitney two sample test, Steel and Torrie 1980:542); black-tailed deer density in areas supporting relatively low CWTB densities averaged 6.2 deer per mile as compared to 0.6 deer per mile in areas supporting an average CWTB density of 9.2 deer per mile.

Additionally, black-tailed deer utilized a greater diversity of habitats in comparable environments supporting lower CWTB densities. Interstate-5 apparently represented a substantial barrier to CWTB as their density on the west side of the freeway ($\bar{x} = 1.1/\text{mile}$) was significantly less than that observed on the east side ($\bar{x} = 9.2/\text{mile}$) (Wilcoxon Mann-Whitney two sample test, Steel and Torrie 1980:542). Correspondingly, black-tailed deer were observed within riparian and associated woodland habitats more frequently on the west side (0.248) as compared to the east side of the freeway (0.168). Also, the spatial distribution of black-tailed fawn capture sites within the intensive study portion of the study area (Fig. 176) strongly suggested that black-tailed females avoided those portions of the study area that experienced intensive use by CWTB.

Black-tailed deer are apparently able to utilize a relatively

broad array of habitats; they occur from the crest of the Cascade Mountains, throughout the interior river valleys to the coastal woodlands along the Pacific Ocean. CWTB however, are restricted to the river bottomland regions of the interior valleys, achieving their highest densities in brushland and woodland communities adjacent major riparian systems. In ecological terms, black-tailed deer appear to be more of a generalist whereas CWTB have seemingly evolved a specialist life history strategy. Miller (1964) described an included niche model for species that exhibited similar ecological needs; the niche of the specialist was included within the niche of a species that displayed a more generalist approach to making a living. Accordingly, the generalist is able to make use of a broader spectrum of environmental resources; however, within the region of overlap, the generalist is outcompeted and effectively excluded by the specialist. It may prove useful to view CWTB and black-tailed deer as behaving according to Miller's included niche model.

In addition to providing further insight into the ecological relationships of the two species, there are some important management implications. According to Miller's hypothesis, resources exploited by CWTB are completely contained within the array of environmental resources exploited by black-tailed deer; thus the potential for intense competition is greatest. More important however, is the realization that within that portion of the environment that influences both species, environmental perturbations will generally favor black-tailed deer. Since blacktails are able to exploit a greater diversity of habitats, changes in the environment will more likely

provide additional black-tailed deer habitat. Moreover, some of the changes will almost certainly occur within portions of the environment that include optimum CWTD habitat. Under these circumstances, blacktails are favored directly as a result of the creation of more suitable habitat and indirectly from a subsequent reduction in CWTD. The invasion of the Willamette Valley and other interior valleys by black-tailed deer following the local extirpation of CWTD is an excellent example of what might occur with major alterations of the native environment.

SUMMARY AND CONCLUSIONS

The present geographic range of Columbian white-tailed deer in southwestern Oregon encompasses 1199 km² (463 mi²), approximately 25% of its native range in Douglas County. The whitetail distribution is not contiguous, owing to the interspersed small mountains and associated coniferous forests; the highest densities were observed in the region between Glide and Winchester, north of Buckhorn Road and south of the North Umpqua River in which Quercus woodland predominated. In 1939 Crews reported that the CWT distribution was limited to approximately 79 km²; however, observations recorded during the 1960's and 1970's by the Oregon Department of Fish and Wildlife documented a recent expansion in geographic range. The present geographic distribution in Douglas County together with recent patterns of dispersal indicate that CWT relied on riparian zones as avenues for dispersal and suggest that further geographic expansion depends upon the distribution and availability of these riparian corridors and their juxtaposition to suitable habitat.

The natural vegetation of the study area is classified as Quercus woodland community and is typical of the Interior Valley Zone of western Oregon. A general reconnaissance of the study area during the initial field season provided the basis for delineating ten distinct habitats according to species composition and/or structural characteristics: grassland, grass-shrub, oak-savanna, open oak, closed oak, oak-conifer, oak-madrone, madrone, riparian and conifer. Grassland habitats comprised the largest portion of the

study area representing 36.6% (922 ha) of the total area; the most abundant woodland habitat was open oak representing 17.1% (469 ha) of the total study area. Generally, the habitats differed with respect to percent cover of the three vegetative strata, obstruction-to-vision (vertical density) and density of trees. Mean percent herbaceous cover ranged from 81.1% in grasslands to 25.0% in madrone habitats. Grass-shrub habitats supported the densest shrub layer averaging 34.4% shrub cover, while conifer stands exhibited the densest overstory with an average of 92.3% canopy cover. Madrone and oak-conifer habitats exhibited the greatest vertical vegetation density; corresponding obstruction-to-vision indices averaged 3.04 and 5.15, respectively. Dominant herbaceous species included hedgehog dogtail, medusahead, soft brome, perennial ryegrass and tall fescue. California oatgrass was the only common native grass. Common shrubs were poison oak, wild rose, ocean-spray and wild lilac, while the dominant tree species included Oregon white oak, California black oak, Douglas-fir and madrone. Significant seasonal differences in percent herbaceous cover occurred among all the habitats; grassland, grass-shrub, closed oak, oak-madrone, madrone and conifer habitats exhibited concomitant changes in vertical vegetation density.

CWTD utilized the ten habitats disproportionately with respect to corresponding availabilities; 95% family confidence intervals computed for the proportion of occurrence in each habitat revealed that CWTD demonstrated a significant preference for grass-shrub, oak-savanna, open oak, closed oak, riparian and conifer habitats. Grassland, oak-conifer, oak-madrone and madrone habitats were utilized

significantly less than was commensurate with respective availabilities. CWTD exhibited seasonal trends in habitat use that corresponded with seasonal climatic and phenological patterns. The most apparent pattern occurred among grassland habitats; percent use of grasslands increased throughout the spring in proportion to increases in biomass production of grasses and forbs while frequency of grassland use during the fall varied with respect to mean monthly precipitation (i.e. fall green-up). CWTD exhibited a similar bimodal pattern of forage utilization; grasses and forbs were consumed most often during late spring and autumn. An increase in grazing accompanied a significantly greater frequency of grassland habitat use during autumn and suggests that CWTD relied more heavily on herbaceous forage during the fall. Monthly habitat-use patterns also conformed to specific seasonal climatic trends. The frequency of use among woodland habitats, particularly riparian woodlands, varied with temperature and in some instances precipitation. Daily patterns of habitat use reflected seasonal daylight-darkness regimes and climatic trends and corresponded with diel patterns of behavior and activity.

CWTD exhibited significant differences in habitat use among sex and age classes. Fawns utilized woodland and brushland habitats more often and occurred in grasslands less frequently than yearlings and adults. Yearlings and adults differed significantly in their frequency of occurrence among grassland and grass-shrub habitats; yearlings utilized grasslands more often than adults while occurring in grass-shrub habitats less frequently. During the first week post-partum, fawns were observed most frequently in woodland habitats;

80% of the fawn capture sites occurred in woodland habitats with closed oak being the most preferred. Typical fawning habitat represented areas that had little or no livestock use, averaged 146.2 m ($s_{\bar{x}} = 13.5$) from water, supported an Oregon white oak canopy and occurred on sites with little or no incline (<20%) and a northern exposure. Yearlings and adults preferred grass-shrub, oak-savannas, riparian and conifer habitats; adults also preferred open oak and closed oak habitats.

Adult males and females exhibited similar patterns of habitat use; males however, occurred significantly less frequently in grass-shrub habitats, and significantly more frequently in conifer habitats. Females occurred more frequently in open oak and closed oak habitats. Seasonal and diel patterns of habitat use suggested that the observed disparity between males and females was associated with differences in thermal stress and fawning activities. Adult males and females preferred grass-shrub, oak-savanna and conifer habitats; adult females also preferred riparian, open oak and closed oak habitats.

CWTD habitat use patterns generally reflected a need for plant communities that provided both palatable forage and adequate escape cover. The relative importance of each habitat differed with respect to season, time of day, age and sex and availability. It is apparent that a realistic assessment of critical CWTD habitat can not simply be a gross comparison of the proportion of use of each habitat to its corresponding availability, but should also include an in-depth analysis of habitat selection as it might reflect the critical environmental periods and important biological events in the life

history of the species.

Schnabel estimates of population size were obtained for the intensive study portion of the study area; density estimates incorporated the cumulative Schnabel estimate (November 1979–January 1980 and August 1980) and estimates of the total area inhabited by the intensive study site population. The total area estimate derived from peripheral locations of marked deer provided a density estimate of 31.0 CWT/D per km² while an estimate of total area derived from measurements of the sampling area provided a density estimate of 36.5 CWT/D per km². Density estimates for the entire study area were obtained by extrapolating the cumulative Schnabel population estimate over the total study area taking into account relative density indices obtained for the various cover types represented on the study area. The weighted mean density estimates for the 2745 ha study area were 22.9 and 27.0 CWT/D per km² representing a total population size of 628 and 740 individuals, respectively.

The dispersion of CWT/D throughout the study area was influenced by the major environmental features characterizing the region. Generally, the relative density of CWT/D within each portion of the study area was positively correlated with percent woodland cover with maximum densities observed in areas supporting approximately 50% woodlands. Also, there existed a significant association between spatial distribution and corresponding relative abundance of CWT/D and the juxtaposition of suitable habitat to the North Umpqua River. Seasonal dispersion was seemingly affected by the distribution and intensity of livestock use within the study area.

Herd composition data obtained during November and December of

1979 provided ratio estimates of 52 fawns:100 does and 30 bucks:100 does. Accordingly, does comprised 55% of the total population while bucks and fawns represented 16.5% and 28.5%, respectively; the estimated age and sex composition of the population during this period was 329 does, 99 bucks and 170 fawns. Secondary (neonatal) sex ratios departed from unity favoring males during years when precipitation was abnormally low while approaching unity when precipitation was normal suggesting an association between environmental quality and disparity among fawn sex ratios.

Proximate causes of mortality included malnutrition, road kill, fence entanglement, predation and disease. Malnutrition (43.3%) and road kills (44.2%) accounted for the largest proportion of known mortality. Malnutrition accounted for significantly more mortality during the severe winter of 1978-79 as compared to 1979-80; 75% of the malnutrition related mortalities occurred during the period January-March. Some of the stress experienced by CWTD during late winter and early spring was apparently associated with abrupt changes in diet composition. Generally, CWTD experienced road kill mortality during all months of the year, but were most susceptible to vehicle-inflicted injuries during late summer and early fall. A significant disproportion of road kill mortality during this period was probably a result of seasonal movement and activity patterns associated with decreasing availability of water and palatable forage.

The temporal distribution of mortality among yearling-adult females and males indicated that the ultimate cause of mortality resulted from the activities associated with reproduction; a significant

disproportion of bucks suffered mortality during the rut and ensuing winter whereas does experienced significantly more mortality during the second half of fetal development and on into the lactation period. Yearling and adult males experienced significant differential mortality during the fall and winter suggesting that the activities and corresponding energetic costs associated with reproduction were more demanding on males than females. The median age at death for males (1.65) was significantly less than that observed for females (2.15) and probably reflected the differential natural mortality experienced by males.

Generally, yearling CWTB were most susceptible to vehicle-inflicted mortality; road kills accounted for 73% and 80% of male and female yearling deaths, respectively. Malnutrition, road kills and disease accounted for 91% of known fawn mortality; 59% of the deaths were attributed solely to malnutrition. Summer mortality rates derived from radio-collared fawns were 40% and 13% for 1979 and 1980, respectively, and were markedly lower than comparable estimates reported for white-tailed fawns in un hunted populations.

Fawn survival and recruitment varied inversely with existing population densities and winter severity. Annual survival rates for 1978-1980 were 20%, 47% and 73-80%, respectively. Corresponding estimates of annual recruitment determined from observations of a marked sample were 0.27, 0.65 and 0.75-0.79, while estimates of annual recruitment derived from spring herd composition data were 0.32, 0.60 and 0.68, respectively.

External parasites were most abundant within the lower abdominal

and inguinal regions and axillary regions of the body; 68% (42/62) of the carcasses examined were characterized as lightly infested whereas only 8% (5/62) were heavily burdened with ectoparasites. Analyses of microbiological preparations of fresh fecal samples revealed that the number of parasitic species and the total number of parasites recorded were greater in winter samples; these data were consistent with observed seasonal differences in the physical condition of CWTD.

Convex polygon estimates of home range size for CWTD females and males averaged 21.1 ha and 32.8 ha, respectively. Elliptical home ranges were derived with a bivariate normal statistical model. Individuals whose locational data did not depart significantly from bivariate normality were subjected to further analysis; female and male home ranges averaged 44.5 ha and 47.1 ha, respectively. Examination of sex and age class estimates resulted in similar conclusions with both the convex polygon and bivariate normal methods; fawn males exhibited the smallest home ranges (\bar{x} = 8.1 ha and 14.4 ha, respectively) and adult males displayed the largest home ranges (\bar{x} = 43.4 ha and 93.7 ha, respectively). Home ranges of CWTD in Douglas County were appreciably smaller than corresponding estimates for CWTD on CWTDNWR and home ranges reported in the literature for white-tailed deer. The shape, location and orientation of home ranges indicated that the North Umpqua riparian system played a vital role in the home range dynamics of CWTD. Distance between geometric centers of activity indicated that home ranges were relatively stable between years, however both males and females demonstrated significant shifts

among the seasons. Average seasonal shifts displayed by males ($\bar{x} = 418.9$ m) were significantly larger than corresponding shifts displayed by females ($\bar{x} = 152.2$ m). Males exhibited significantly larger displacements during autumn whereas females exhibited larger displacements significantly more often during periods of comparison that included spring, behaviors observed to be associated with rutting and fawning activities, respectively.

CWTD and black-tailed deer demonstrated a local geographic and ecological segregation; whitetails exhibited a strong affinity for riparian systems, occurring significantly more often within portions of the study area that were less than 1 km from the North Umpqua River. There existed a significant inverse correlation in the relative densities of the two species; i.e., high densities of CWTD precluded extensive use of corresponding portions of the study area by black-tailed deer. Comparable environments supporting low densities of CWTD supported significantly higher densities of black-tailed deer. Wherever black-tailed deer and CWTD occurred sympatrically, they differed significantly in their frequency of occurrence among the ten habitats; CWTD preferred woodland and brushland habitats while blacktails occurred more often in grasslands and open uplands. In areas supporting few or no CWTD, black-tailed deer utilized woodland habitats more frequently.

Historic and current geographic distributions of the two species suggest that black-tailed deer exploit a broad array of environmental resources while CWTD are restricted to a narrow range of habitats; i.e., black-tailed deer have adopted a more generalist approach to

making a living whereas CWTD have evolved as specialist. Habitat-use patterns indicated that within preferred CWTD habitats, black-tailed deer were competitively excluded; however, modification of the native environment has historically favored black-tailed deer and resulted in local extinctions of CWTD.

It is apparent that lowland riparian systems have played a major role in the ecology of CWTD. The rivers and streams of the interior Umpqua valleys provided corridors of dispersal through which CWTD have expanded their geographic range in the last 30 years. Riparian systems also represented an important component of the CWTD environment; indeed, the dispersion of CWTD throughout the study area was significantly influenced by the North Umpqua River. The location and orientation of individual home ranges, seasonal movement and activity patterns and the spatial distribution of fawning sites are evidence of the critical role that riparian systems have played in the life history of this species. The continued existence of CWTD in western Oregon is clearly contingent upon the existence and availability of native riparian systems within an environment that affords additional suitable habitat.

LITERATURE CITED

- Alexander, B. G. 1968. Movements of deer in northeast Texas. *J. Wildl. Manage.*, 32(3):618-620.
- Anthony, R. G. and N. S. Smith. 1977. Ecological relationships between mule deer and white-tailed deer in southeastern Arizona. *Ecological Monographs*, 47:255-277.
- Allen, R. E. and D. R. McCullough. 1976. Deer-car accidents in southern Michigan. *J. Wildl. Manage.*, 40(2):317-325.
- Bailey, V. 1936. The mammals and life zones of Oregon. *North American Fauna* 55. 416pp.
- Bartholomew, G. A. 1977. Body temperature and energy metabolism. Pp. 364-449 in M. S. Gordon (ed.) *Animal Physiology: Principles and adaptation*. MacMillan Publishing Co., Inc. New York. 699pp.
- Bedell, T. E. 1971. Nutritive value of forage and diets of sheep and cattle from Oregon sub-clover-grass mixtures. *J. Range Manage.*, 24(2):125-133.
- Bryant, M. M. 1943. Area determination with modified acreage grid. *J. Forestry*, 41:764-765.
- Canfield, R. 1941. Application of the line interception method in sampling range vegetation. *J. Forestry* 39:388-394.
- Carlsen, J. C. and R. E. Farnes. 1957. Movements of white-tailed deer tagged in Minnesota. *J. Wildl. Manage.*, 21:397-401.
- Caughley, G. 1974. Interpretation of age ratios. *J. Wildl. Manage.*, 38(3):557-562.
- Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pp. 183-246, in T. H. Coaker (ed.), *Applied Biology*. Vol. 1. Academic Press. London. 358pp.
- Caughley, G. 1977. *Analysis of vertebrate populations*. John Wiley and Sons. London. 234pp.
- Chapman, D. G. and W. S. Overton. 1966. Estimating and testing differences between population levels by the Schnabel estimation method. *J. Wildl. Manage.*, 30(1):173-180.

- Church, D. C. 1975. The digestive physiology and nutrition of ruminants. Second edition. Volume 1-Digestive physiology. D. C. Church. Corvallis. 350pp.
- Cook, L. M., L. P. Brower and H. J. Croze. 1967. The accuracy of a population estimation from multiple recapture data. *J. Animal Ecology*. 36(1):57-60.
- Cook, R. S., M. White, D. O. Trainer and W. C. Glazener. 1971. Mortality of young white-tailed deer fawns in south Texas. *J. Wildl. Manage.*, 35(1):47-56.
- Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology*. 17(3):451-460.
- Crews, A. K. 1939. A study of the Oregon white-tailed deer, Odocoileus virginianus leucurus (Douglas). M. S. Thesis, Oregon State College, Corvallis. 45pp.
- Crowe, D. M. 1972. The presence of annuli in bobcat tooth cementum layers. *J. Wildl. Manage.*, 36(4):1330-1332.
- Dahlberg, B. L. and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin. *Tech. Wildlife Bull.*, Wisconsin Conserv. Dept., Madison, 14:1-282.
- Daniel, W. W. 1978. Applied nonparametric statistics. Houghton Mifflin Company. Boston. 503pp.
- Danner, D. A. and N. S. Smith. 1980. Coyote home range, movement and relative abundance near a cattle feedyard. *J. Wildl. Manage.*, 44(2):484-486.
- Dapson, R. W. 1971. Quantitative comparison of populations with different age structures. *Ann. Zool. Fennici*, 8:75-79.
- Dapson, R. W. 1972. Age structure of six populations of old-field mice, Peromyscus polionotus. *Res. Popul. Ecol.*, 13:161-169.
- Dapson, R. W., P. R. Ramsey, M. H. Smith and D. F. Urbston. 1979. Demographic differences in contiguous populations of white-tailed deer. *J. Wildl. Manage.*, 43(4):889-898.
- Dasman, R. F. 1959. Environmental Conservation. John Wiley and Sons. New York. 307pp.
- Dasman, R. F. 1964. Wildlife biology. John Wiley and Sons, Inc. New York. 231pp.

- Daubenmire, R. F. 1959. Canopy coverage method of vegetation analysis. Northwest Sci., 33:45-64.
- Douglas, D. 1829. Observations on two undescribed species of North American mammalia (Cervus leucurus et Ovis californianus). Zool. J., 4:330-332.
- Douglas, D. 1914. Journal kept by David Douglas during his travels in North America 1823-27. W. Wesley and Son, London. 364pp.
- Downing, R. L. and B. S. McGinnes. 1969. Capturing and marking white-tailed deer fawns. J. Wildl. Manage., 33(3):711-714.
- Downing, R. L., E. D. Michael and R. J. Poux, Jr., 1977. Accuracy of sex and age ratio counts of white-tailed deer. J. Wildl. Manage., 41(4):709-714.
- Errington, P. L. 1956. Factors limiting higher vertebrate populations. Science, 124(3216):304-307.
- Flook, D. R. 1970. A study of sex differential in the survival of wapiti. Can. Wildl. Serv. Rep. Series No. 11. 71pp.
- Franklin, J. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. 417pp.
- French, C. E., L. C. McEwen, N. D. Magruder, R. H. Ingram and R. W. Swift. 1955. Nutritional requirements of white-tailed deer for growth and antler development. Pa. St. U. AES Bull. 600. 50pp.
- Gavin, T. A. 1979. Population ecology of the Columbian white-tailed deer. Ph.D. Thesis. Oregon State University, Corvallis. 149pp.
- Grubb, P. and P. A. Jewell. 1974. Movement, daily activity and home range of Soay sheep. Pp. 160-194, in P. A. Jewell, C. Milner and J. M. Boyd (eds.), Island survivors: The ecology of the Soay sheep of St. Kilda. The Athlone Press. London. 386pp.
- Halls, L. K. 1978. White-tailed deer. Pp. 43-65, in J. L. Schmidt and D. L. Gilbert (eds.), Big game of North America. Ecology and management. Stackpole Books. Harrisburg, Pa. 494pp.
- Hardin, J. W., N. J. Silvy and W. D. Klimstra. 1976. Group size and composition of the Florida Key deer. J. Wildl. Manage., 40(3): 454-463.
- Harris, G. and C. J. Goebel. 1976. Factors of plant competition in seeding Pacific Northwest bunchgrass ranges. Ag. Res. Center Bull. No. 820. Washington State University, Pullman. 22pp.

- Haugen, A. O. 1975. Reproductive performance of white-tailed deer in Iowa. *J. Mammal.*, 56(1):151-159.
- Haugen, A. O. and D. W. Speake. 1958. Determining age of young fawn white-tailed deer. *J. Wildl. Manage.*, 22(3):319-321.
- Hitchcock, C. L. and A. Conquist. 1973. *Flora of the Pacific Northwest*. U. of Wash. Press. Seattle. 730pp.
- Hollander, M. and D. A. Wolfe. 1973. *Nonparametric statistical methods*. John Wiley and Sons. New York. 503pp.
- Hoskinson, R. L. and L. D. Mech. 1976. White-tailed deer migration and its role in wolf predation. *J. Wildl. Manage.*, 40(3):429-441.
- Hulbert, L. 1955. Ecological studies of Bromus tectorum and other brome grasses. *Ecological Monographs*. 25:181-213.
- Illigie, D. 1951. An analysis of the reproductive pattern of white-tail deer in south Texas. *J. Mammal.*, 32:411-421.
- Inglis, J. M., R. E. Hood, B. A. Brown and C. A. DeYoung. 1979. Home range of white-tailed deer in Texas costal prairie brushland. *J. Mammal.*, 60(2):377-389.
- Jennrich, R. I. and F. B. Turner. 1969. Measurement of non-circular home range. *J. Theoret. Biol.*, 22:227-237.
- Jewett, S. G. 1914. The white-tailed and other deer in Oregon. *The Oregon Sportsman*. 2(8):5-9.
- Kirkpatrick, C. M., C. M. White, T. W. Hoekstra, F. A. Stormer and H. P. Weeks, Jr. 1976. White-tailed deer of US Naval Ammunition Depot Crane. *Purdue University AES Res. Bull.* No. 932. 42pp.
- Kistner, T. P., C. E. Trainer, and N. A. Hartman. 1980. A field technique for evaluating physical condition of deer. *Wildl. Soc., Bull.*, 8(1):11-17.
- Klein, D. R. and S. T. Olson. 1960. Natural mortality patterns of deer in southeast Alaska. *J. Wildl. Manage.*, 24(1):80-88.
- Knowlton, F. F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. *J. Wildl. Manage.*, 24(2):162-170.
- Koepl, J. W., N. A. Slade and R. S. Hoffman. 1975. A bivariate home range model with possible application to ethological data analysis. *J. Mammal.*, 56(1):81-90.

- Krämer, A. 1973. Interspecific behavior and dispersion of two sympatric deer species. *J. Wildl. Manage.*, 37(3):288-300.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science*, 2(1):314-320.
- Lewis, J. C. and J. W. Farrar. 1968. An attempt to use the Leslie census method on deer. *J. Wildl. Manage.*, 32(4):760-764.
- Madden, R. and L. F. Marcus. 1978. Use of the F distribution in calculating bivariate normal home ranges. *J. Mammal.*, 59(4):870-871.
- Mansell, W. D. 1974. Productivity of white-tailed deer on the Bruce Peninsula, Ontario. *J. Wildl. Manage.*, 38(4):808-814.
- Marchinton, R. L. 1968. Telemetric study of white-tailed deer movement-ecology and ethology in the southeast. Ph.D. dissertation Auburn University, Auburn. 153pp.
- Markell, E. K. and M. Voge. 1965. Medical parasitology. W. B. Saunders Co. Philadelphia. (revised) 317pp.
- Marshall, A. D. and R. W. Whittington. 1968. A telemetric study of deer home ranges and behavior of deer during managed hunts. *Proc. S. E. Assoc. Game and Fish Comm.*, 22:30-46.
- McCullough, D. R. 1969. The Tule elk: Its history, behavior and ecology. University of California Pub. Zool. V. 88. 209pp.
- McCullough, D. R. 1979. The George Reserve deer herd. The University of Michigan Press. Ann Arbor 271pp.
- McDowell, R. 1962. Relationship of maternal age to prenatal sex ratios in white-tailed deer (Report IV). *Proc. N. E. Sect. Wildl. Soc.* 14. 3pp.
- Merezcak, I. M. 1979. The effects of three levels of range improvement on Roosevelt elk nutrition. M. S. Thesis. Oregon State University, Corvallis. 86pp.
- Michael, E. D. 1965. Movements of white-tailed deer on the Welder Wildlife Refuge. *J. Wildl. Manage.*, 29(1):44-52.
- Miller, R. S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. *Ecology*, 45:256-272.
- Mitchell, J. L. 1961. Mink movements and populations on a Montana river. *J. Wildl. Manage.*, 25(1):48-54.
- Moen, A. N. 1968. Energy balance of white-tailed deer in the winter. *Trans. 33rd. N. A. Wildl. Conf.*, 224-236.

- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism and forage intake of white-tailed deer. *J. Wildl. Manage.*, 42(4):715-738.
- Moore, D. and J. B. Stubblebine. (In press). Chi-square test for multivariate normality with applications in common stock prices. *Communications in Statistics*.
- Mosby, H. S. 1971. Reconnaissance mapping and map use. Pp. 119-134, in R. H. Giles, Jr.(ed), *Wildlife management techniques*. 3rd ed. The Wildlife Society. Washington, D. C. 623pp.
- Nash, W. (1877) 1976. Oregon: There and back in 1877. Oregon State University Press. 290pp.
- Nash, W. 1882. Two years in Oregon. O. Appleton, New York. 327pp.
- Nelson, M. E. 1977. Migration and social organization of white-tailed deer in northeastern Minnesota. M. S. Thesis. University of Minnesota. St. Paul. 119pp.
- Neter, J. and W. Wasserman. 1974. *Applied linear statistical models*. Richard D. Irwin, Inc. Homewood, Illinois. 842pp.
- Neu, C. W., C. R. Byers and J. M. Peck. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.*, 38(3):541-545.
- Nixon, C. M. 1971. Productivity of white-tailed deer in Ohio. *Ohio J. Sci.*, 71:217-225.
- O'Pezio, J. P. 1978. Mortality among white-tailed deer fawns on the Seneca Army depot. *N. Y. Fish and Game J.*, 25(1):1-15.
- Overton, W. S. 1971. Estimating the numbers of animals in wildlife populations. Pp. 403-455, in R. H. Giles, Jr. (ed.), *Wildlife management techniques*. 3rd ed. The Wildlife Society. Washington, D. C. 623pp.
- Pieper, R. D. 1978. *Measurement techniques for herbaceous and shrubby vegetation*. New Mexico State University Bookstore, Inc. Las Cruces. (revised) 148pp.
- Progulske, D. R. and T. S. Baskett. 1958. Mobility of Missouri deer and their harassment by dogs. *J. Wildl. Manage.*, 22(2):184-192.
- Puglisi, M. J., J. S. Lindzey and E. D. Bellis. 1974. Factors associated with highway mortality of white-tailed deer. *J. Wildl. Manage.*, 38:(4):799-807.
- Rampton, H. 1945. *Alta fescue production in Oregon*. Oregon AES Bull. No. 427. Corvallis. 22pp.

- Rasmussen, D. I. and E. R. Doman. 1943. Census methods and their application in the management of mule deer. Trans Eighth N. A. Wildl. Conf., pp.369-380.
- Reynolds, G.E. 1980. White muscle and other selenium responsive diseases of livestock. Pacific Northwest Publication No. 157. 8pp.
- Rice, W. R. and J. D. Harder. 1977. Application of multiple aerial sampling to a mark-recapture census of white-tailed deer. J. Wildl. Manage., 40(3):454-463.
- Robinette, W. L., C. H. Baer, R. E. Pillmore and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. J. Wildl. Manage., 37(3):312-336.
- Robinette, W. L., J. S. Gashwiler and C. M. Aldous. 1954. Methods for censusing winter-lost deer. Trans. N. A. Wildl. Conf., 19:511-525.
- Robinette, W. L., J. S. Gashwiler, D. A. Jones and H. S. Crane. 1955. Fertility of mule deer in Utah. J. Wildl. Manage., 19(1):115-136.
- Robinette, W. L., J. B. Low and D. A. Jones. 1957. Differential mortality by sex and age among mule deer. J. Wildl. Manage., 21(1): 1-16.
- Roseberry, J. L. and W. D. Klimstra. 1974. Differential vulnerability during a controlled deer harvest. J. Wildl. Manage., 38(3): 499-507.
- Sanders, K. 1965. The seasonal yield, quality and utilization of Trifolium subterraneum in mixture with Festuca arundinacea and Lolium perenne in Western Oregon. M. S. Thesis. Oregon State University, Corvallis. 61pp.
- Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Manage; 13(1):195-216.
- Severinghaus, C. W. and E. L. Cheatum. 1956. Life and times of the white-tailed deer. Pp. 59-186, in W. P. Taylor (ed.), The deer of North America. The Stackpole Co. Harrisburg, Pa. 668pp.
- Sharrow, S. 1979. Sheep stocking intensity for hill pastures. Sheep and wool days. Oregon AES Special Rep. No. 539. pp.35-41.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co. New York. 312pp.
- Snedecor, G. W. and W. G. Cochran. 1980. Statistical methods. Seventh edition. The Iowa State University Press. Ames. 507pp.

- Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co. San Francisco. 776pp.
- Sparrowe, R. D. and P. F. Springer. 1970. Seasonal activity patterns of white-tailed deer in eastern South Dakota. J. Wildl. Manage., 34(2):420-431.
- Steel, R. G. D. and J. H. Torrie. 1980. Principles and procedures of statistics. (second ed.) McGraw-Hill Book Company, Inc. New York. 633pp.
- Struhsaker, T. T. 1967. Behavior of elk (Cervus canadensis) during the rut. Zeit. für Tierspy., 24(1):80-114.
- Suring, L. H. and P. A. Vohs, Jr. 1979. Habitat use by Columbian white-tailed deer. J. Wildl. Manage., 43(3):610-619.
- Teer, J. G., J. W. Thomas and E. A. Walker, 1965. Ecology and management of white-tailed deer in the Llano Basin of Texas. Wildlife Monographs. No. 15. 62pp.
- Thilenius, J. F. 1968. The Quercus Garryana forests of the Willamette Valley, Oregon. Ecology, 49(6):1124-1133.
- Thomas, D. C. 1969. Population estimates of Barren-Ground caribou March to May 1967. Can. Wild. Serv. Report Ser. 9. pp2-44.
- Thomas, J. W., J. G. Teer and E. A. Walker. 1964. Mobility and home range of white-tailed deer on the Edwards Plateau in Texas. J. Wildl. Manage., 28(3):463-472.
- Trivers, R. L. and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science, 179: 90-92.
- United States Department of Commerce. 1955-1980. Climatological Data, Oregon. Annual Summary. National Oceanic and Atmospheric Administration, Environmental Data Service, Asheville, N. C. Volumes 61-86.
- Verme, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. J. Wildl. Manage., 33(4):881-887.
- Verme, L. J. 1973. Movements of white-tailed deer in upper Michigan. J. Wildl. Manage., 37(4):545-552.
- Verts, B. J. 1978. Keys to the mammals of Oregon. Oregon State University Book Store, Inc. Corvallis, 82pp.
- Wheatley, W. B. 1951. A rapid staining procedure of intestinal amoebae and flagellates. Amer. J. Clin. Pathol., 21:990-991.

- White, M. 1973. The whitetail deer of the Aransas National Wildlife refuge. *Texas J. Science*, 24(4):457-498.
- White, M., F. F. Knowlton and W. C. Glazener. 1972. Effects of dam-newborn fawn behavior on capture and mortality. *J. Wildl. Manage.*, 36(3):897-906.
- Wight, H. M. 1938. Field and laboratory technics in wildlife management. University of Michigan Press. Ann Arbor. 105pp.
- Wittes, J. T. 1972. On the bias and variance of Chapman's two-sample capture-recapture population estimate. *Biometrics*. 28(2):592-597.
- Wood, A. J., I. Mct. Cowan and H. C. Nordan. 1962. Periodicity of growth in ungulates as shown by deer of the genus Odocoileus. *Can. J. Zool.*, 40:593-603.
- Wolf, A. and J. D. Harder. 1979. Population dynamics of a captive white-tailed deer herd with emphasis on reproduction and mortality. *Wildlife Monographs*. No. 67. 53pp.
- Zar, J. H. 1974. *Biostatistical analysis*. Prentice Hall. Englewood Cliffs, N. J. 620pp.

APPENDIX


```

X(I) = X(I)*COS(THETA) + Y(I)*SIN(THETA)
Y(I) = Y(I)*COS(THETA) - (SAVEI)*SIN(THETA)
SUMX = SUMX + X(I)
SUMY = SUMY + Y(I)
SUMXR2 = SUMXR2 + X(I)*X(I)
SUMYR2 = SUMYR2 + Y(I)*Y(I)
20 CONTINUE

```

```

42 NON WILL TRANSLATE (STANDARDIZE) THE POINTS.
XBAR = SUMX/NOBS
YBAR = SUMY/NOBS
SSXR = SUMXR2 - (SUMX)**2/(NOBS)
SSYR = SUMYR2 - (SUMY)**2/(NOBS)
SSXYR = SUMXYR - (SUMX)*(SUMY)/(NOBS)
D1 = SQRT(SSXR)
D2 = SQRT(SSYR)
D3 = 30
I = 1, NOBS
X(I) = (X(I) - XBAR)/D1
Y(I) = (Y(I) - YBAR)/D2
30 CONTINUE

```

THE X'S AND Y'S ARE NOW ROTATED AND TRANSLATED.
 WE ARE NOW READY TO BEGIN CALCULATIONS FOR THE COMPARISON WITH THE
 BIVARIATE NORMAL DISTRIBUTION. THE DATA POINTS WILL BE ASSIGNED TO
 ONE OF SEVERAL CONCENTRIC ELLIPTICAL CELLS. THE NUMBER OF THIN
 CELLS IS DETERMINED BY THE NUMBER OF OBSERVATIONS WITHIN A DATA SET.

```

READ(16,900)CELLNO
K = CELLNO

```

THE FOLLOWING DO CALCULATES THE VALUE CORRESPONDING TO THE ITH CELL.

```

DO 60 I = 1, NCELL
  XCELL(I) = 2*ALOG(1 - I/CELLNO)
60 CONTINUE

```

CELL(K) IS UNDEFINED -- WE CANNOT CALCULATE ITS VALUE.

THE FOLLOWING NESTED DO DETERMINES WHICH CELL EACH OBSERVATION FALLS
 INTO AND TALLIES THE NUMBER OF TIMES AN OBSERVATION FALLS IN A PARTICULAR
 CELL. THE NUMBER OF OBSERVATIONS FALLS IN THE KTH CELL. THE COUNT IS KEPT IN
 NCELL(K).

```

DO 100 J = 1, NOBS
  X = X(J)
  Y = Y(J)
  DO 110 I = 1, NCELL
    IF (X**2 + Y**2 .GT. XCELL(I)**2) GO TO 110
    NCELL(I) = NCELL(I) + 1
  110 CONTINUE
  100 CONTINUE
  EXPECT = NOBS/CELLNO
  180 WRITE(*,180) 'THE FOLLOWING LIST GIVES THE NUMBER OF * * * OBSERVATI  

  * * * IN EACH CELL * * *'
  DO 175 K = 1, NCELL
    WRITE(*,181) NCELL(K)
  181 FORMAT(12,13)
  175 CONTINUE
  175 WRITE(*,175) 'WE EXPECT TO HAVE * , F4.1, * OBSERVATIONS PER CELL *'
  EXPECT GIVES THE NUMBER OF OBSERVATIONS WE WOULD EXPECT TO FIND IN  

  EACH CELL.

```

THE NEXT DO CALCULATES THE CHI-SQUARE VALUE FOR THE DATA SET.

```

SUM = 0.0
DO 70 K = 1, NCELL
  DIFF = NCELL(K) - EXPECT
  SUM = SUM + DIFF*DIFF
70 CONTINUE
CHISQ = SUM/EXPECT
WRITE(*,190) NOBS, NOBJ, CHISQ, L
190 FORMAT(18,2)
WRITE(*,191) 'HERE WERE * , I3, * OBSERVATIONS FOR OBJECT NUMBER * , I3, *'
191 FORMAT(13,13)

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* * * THE CHI-SQUARE VALUE IS * , F10.5, * WITH * , I3, * DEGREES OF FRE  

* * *
200 FORMAT(13,0)
200 CONTINUE
END

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Appendix B. Species composition of the respective vegetative strata for each of the habitats on the study area.

GRASSLAND HABITAT-L¹

<u>Herbaceous</u>			
Species	Frequency	% Cover	Relative Dominance
<u>Cynosurus echinatus</u>	0.887	17.495	0.2089
<u>Taeniatherum asperum</u>	0.693	15.736	0.1879
<u>Bromus mollis</u>	0.800	7.966	0.0951
<u>Lolium perenne</u>	0.340	5.900	0.0704
<u>Danthonia californica</u>	0.373	5.739	0.0685
<u>Trifolium dubium</u>	0.480	4.842	0.0578
<u>Festuca megalura</u>	0.427	3.317	0.0396
<u>Linum angustifolium</u>	0.513	3.240	0.0387
<u>Juncus bufonius</u>	0.300	2.466	0.0294
<u>Briza minor</u>	0.527	2.233	0.0267
<u>Trifolium subterraneum</u>	0.173	1.861	0.0222
<u>Juncus effusus</u>	0.187	1.530	0.0183
<u>Juncus patens</u>	0.060	1.416	0.0169
<u>Geranium spp.</u>	0.267	1.000	0.0119
<u>Plantago lanceolata</u>	0.140	0.935	0.0112
<u>Navaretia squarrosa</u>	0.307	0.933	0.0111
<u>Cerastium viscosum</u>	0.333	0.917	0.0109
<u>Stachys palustris</u>	0.040	0.583	0.0070
<u>Leontodon nudicaulis</u>	0.133	0.567	0.0068
<u>Erodium cicutarium</u>	0.173	0.517	0.0062
<u>Bromus rigidus</u>	0.093	0.483	0.0058
<u>Bromus sterilis</u>	0.027	0.483	0.0056
<u>Agrostis tenuis</u>	0.020	0.450	0.0054
<u>Sherardia arvensis</u>	0.127	0.400	0.0048
<u>Centaureum umbellatum</u>	0.093	0.317	0.0038
<u>Galium spp.</u>	0.100	0.250	0.0030
<u>Holcus lanatus</u>	0.060	0.233	0.0028
<u>Hypericum perforatum</u>	0.080	0.200	0.0024

¹L denotes grassland areas which were subjected to livestock use during the study period.

Appendix B. Grassland Habitat-L, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Caucalis microcarpa</u>	0.040	0.183	0.0022
<u>Vicia angustifolia</u>	0.040	0.183	0.0022
<u>Brodiaea coronaria</u>	0.067	0.167	0.0020
<u>Rumex acetosella</u>	0.033	0.167	0.0020
<u>Carex spp.</u>	0.020	0.133	0.0016
<u>Madia spp.</u>	0.040	0.100	0.0011
<u>Poa pratensis</u>	0.040	0.100	0.0011
<u>Sisyrinchium angustifolium</u>	0.040	0.100	0.0011
<u>Lathyrus spp.</u>	0.033	0.083	0.0010
<u>Penstemon spp.</u>	0.033	0.083	0.0010
<u>Veronica arvensis</u>	0.033	0.083	0.0010
<u>Achillea millefolium</u>	0.020	0.050	0.0006
<u>Epilobium spp.</u>	0.020	0.050	0.0006
<u>Leontodon autumnalis</u>	0.020	0.050	0.0006
<u>Myosotis discolor</u>	0.020	0.050	0.0006
<u>Eremocarpus setigerus</u>	0.013	0.033	0.0004
<u>Matricaria chamomilla</u>	0.013	0.033	0.0004
<u>Capsella bursa-pastoris</u>	0.007	0.017	0.0002
<u>Cirsium arvense</u>	0.007	0.017	0.0002
<u>Cirsium vulgare</u>	0.007	0.017	0.0002
<u>Eriophyllum lanatum</u>	0.007	0.017	0.0002
<u>Potentilla spp.</u>	0.007	0.017	0.0002
<u>Sidalcea virgata</u>	0.007	0.017	0.0002
<u>Zigadenus venenosus</u>	0.007	0.017	0.0002

Summary Statistics

	Mean	95% C.I.	$s_{\bar{x}}$	n
Herbaceous % Cover	81.1	78.2-84.0	1.48	150
Obstruction Index	20.5	20.4-20.6	0.04	150

Appendix B. continued.

GRASSLAND HABITAT-WL¹

<u>Herbaceous</u>			
Species	Frequency	% Cover	Relative Dominance
<u>Bromus mollis</u>	0.720	8.982	0.1692
<u>Cynosurus echinatus</u>	0.760	7.650	0.1441
<u>Lolium perenne</u>	0.400	6.540	0.1232
<u>Taeniatherum asperum</u>	0.610	4.699	0.0885
<u>Danthonia californica</u>	0.290	3.622	0.0682
<u>Festuca megalura</u>	0.380	3.050	0.0574
<u>Holcus lanatus</u>	0.200	1.850	0.0348
<u>Bromus rigidus</u>	0.290	1.824	0.0344
<u>Festuca arundinacea</u>	0.060	1.224	0.0231
<u>Bromus spp.</u>	0.110	0.900	0.0170
<u>Rhus diversiloba</u>	0.060	0.852	0.0160
<u>Cerastium viscosum</u>	0.290	0.849	0.0160
<u>Juncus bufonius</u>	0.170	0.799	0.0150
<u>Linum angustifolium</u>	0.190	0.725	0.0137
<u>Briza minor</u>	0.230	0.700	0.0132
<u>Geranium spp.</u>	0.200	0.625	0.0118
<u>Poa spp.</u>	0.050	0.600	0.0113
<u>Centaurium umbellatum</u>	0.220	0.550	0.0104
<u>Brodiaea coronaria</u>	0.210	0.525	0.0099
<u>Myosotis discolor</u>	0.180	0.450	0.0085
<u>Caucalis microcarpa</u>	0.130	0.450	0.0085
<u>Navarretia squarrosa</u>	0.130	0.450	0.0085
<u>Galium spp.</u>	0.160	0.400	0.0075
<u>Potentilla spp.</u>	0.110	0.400	0.0075
<u>Trifolium dubium</u>	0.140	0.350	0.0066
<u>Veronica arvensis</u>	0.140	0.350	0.0066
<u>Juncus effusus</u>	0.090	0.350	0.0066
<u>Carex spp.</u>	0.130	0.325	0.0061
<u>Leontodon nudicaulis</u>	0.080	0.325	0.0061
<u>Sisyrinchium angustifolium</u>	0.110	0.275	0.0052
<u>Hypericum perforatum</u>	0.100	0.250	0.0047

¹WL denotes grassland areas which have not had recent livestock use.

Appendix B. Grassland Habitat-WL, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Madia</u> spp.	0.090	0.225	0.0042
<u>Cirsium</u> <u>vulgare</u>	0.040	0.225	0.0042
<u>Stachys</u> <u>palustris</u>	0.040	0.225	0.0042
<u>Bromus</u> <u>sterilis</u>	0.030	0.200	0.0038
<u>Erodium</u> <u>cicutarium</u>	0.030	0.200	0.0038
<u>Plantago</u> <u>lanceolata</u>	0.070	0.175	0.0033
<u>Eremocarpus</u> <u>setigerus</u>	0.060	0.150	0.0028
<u>Trichostema</u> <u>lanceolatum</u>	0.060	0.150	0.0028
<u>Vicia</u> <u>angustifolia</u>	0.040	0.100	0.0019
<u>Achillea</u> <u>millefolium</u>	0.030	0.075	0.0014
<u>Eriophyllum</u> <u>lanatum</u>	0.030	0.075	0.0014
<u>Sherardia</u> <u>arvensis</u>	0.030	0.075	0.0014
<u>Astragalus</u> spp.	0.020	0.050	0.0009
<u>Prunella</u> <u>vulgaris</u>	0.020	0.050	0.0009
<u>Rumex</u> <u>acetosella</u>	0.020	0.050	0.0009
<u>Zigadenus</u> <u>venenosus</u>	0.020	0.050	0.0009
<u>Agrostis</u> <u>tenuis</u>	0.010	0.025	0.0005
<u>Elymus</u> <u>glaucus</u>	0.010	0.025	0.0005
<u>Juncus</u> <u>patens</u>	0.010	0.025	0.0005

Summary Statistics

	Mean	95% C.I.	$s_{\bar{x}}$	n
Herbaceous % Cover	78.1	74.7-81.5	1.69	100
Obstruction Index	19.6	19.4-19.8	0.12	100

Appendix B. continued.

GRASS-SHRUB HABITAT

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.987	33.130	0.9624
<u>Rosa elganteria</u>	0.220	1.277	0.0371
<u>Ceanothus intergerrimus</u>	0.020	0.017	0.0005

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.707	23.083	0.3685
<u>Cynosurus echinatus</u>	0.787	10.135	0.1618
<u>Festuca arundinacea</u>	0.207	4.649	0.0742
<u>Danthonia intermedia</u>	0.173	2.999	0.0479
<u>Taeniatherum asperum</u>	0.260	2.020	0.0322
<u>Bromus mollis</u>	0.367	1.982	0.0316
<u>Linum angustifolium</u>	0.373	1.790	0.0286
<u>Briza minor</u>	0.447	1.533	0.0244
<u>Galium spp.</u>	0.227	1.384	0.0221
<u>Festuca megalura</u>	0.187	0.883	0.0141
<u>Hypericum perforatum</u>	0.273	0.850	0.0136
<u>Bromus rigidus</u>	0.200	0.750	0.0120
<u>Danthonia californica</u>	0.202	0.750	0.0120
<u>Caucalis microcarpa</u>	0.293	0.733	0.0117
<u>Myosotis discolor</u>	0.187	0.716	0.0114
<u>Lolium perenne</u>	0.113	0.700	0.0112
<u>Pteridium aquilinum</u>	0.087	0.550	0.0088
<u>Plantago lanceolata</u>	0.107	0.517	0.0083
<u>Elymus glaucus</u>	0.127	0.483	0.0077
<u>Veronica arvensis</u>	0.180	0.450	0.0072
<u>Lathyrus spp.</u>	0.047	0.433	0.0069
<u>Geranium spp.</u>	0.167	0.417	0.0067

Appendix B. Grass-Shrub Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Poa pratensis</u>	0.067	0.417	0.0067
<u>Astragalus</u> spp.	0.020	0.366	0.0058
<u>Trifolium dubium</u>	0.107	0.350	0.0056
<u>Festuca</u> spp.	0.013	0.349	0.0056
<u>Polystichum munitum</u>	0.020	0.300	0.0048
<u>Achillea millefolium</u>	0.080	0.283	0.0045
<u>Cerastium viscosum</u>	0.100	0.250	0.0040
<u>Holcus lanatus</u>	0.033	0.250	0.0040
<u>Carex</u> spp.	0.027	0.233	0.0037
<u>Madia</u> spp.	0.087	0.217	0.0035
<u>Sherardia arvensis</u>	0.087	0.217	0.0035
<u>Leontodon nudicaulis</u>	0.053	0.217	0.0035
<u>Iris tenax</u>	0.020	0.133	0.0021
<u>Brodiaea coronaria</u>	0.047	0.117	0.0019
<u>Bromus carinatus</u>	0.013	0.117	0.0019
<u>Erodium cicutarium</u>	0.040	0.100	0.0016
<u>Lolium multiflorum</u>	0.007	0.100	0.0016
<u>Stachys palustris</u>	0.007	0.100	0.0016
<u>Sisyrinchium angustifolium</u>	0.033	0.083	0.0013
<u>Centaureum umbellatum</u>	0.027	0.067	0.0010
<u>Eriophyllum lanatum</u>	0.027	0.067	0.0010
<u>Fragaria</u> spp.	0.027	0.067	0.0010
<u>Koeleria cristata</u>	0.027	0.067	0.0010
<u>Trientalis latifolia</u>	0.027	0.067	0.0010
<u>Dactylis glomerata</u>	0.020	0.050	0.0008
<u>Navarretia squarrosa</u>	0.020	0.050	0.0008
<u>Myosotis</u> spp.	0.020	0.050	0.0008
<u>Potentilla</u> spp.	0.020	0.050	0.0008
<u>Juncus effusus</u>	0.013	0.033	0.0005
<u>Agrostis tenuis</u>	0.007	0.017	0.0003
<u>Berberis repens</u>	0.007	0.017	0.0003
<u>Phleum pratense</u>	0.007	0.017	0.0003
<u>Vicia angustifolia</u>	0.007	0.017	0.0003

Appendix B. Grass-Shrub Habitat continued.

	<u>Summary Statistics</u>			
	Mean	95% C.I.	$s_{\bar{x}}$	n
Shrub % Cover	34.4	30.9-37.9	1.76	150
Herbaceous % Cover	73.1	69.6-76.6	1.77	150
Obstruction Index	10.1	8.77-11.4	0.67	150

Appendix B. continued.

OAK-SAVANNA HABITAT

Trees

Species	Basal Area (m ²)	Relative Dominance
<u>Quercus garryana</u>	29.969	0.9538
<u>Quercus kelloggii</u>	1.323	0.0421
<u>Fraxinus latifolia</u>	0.129	0.0041

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.270	5.575	0.9489
<u>Rosa elganteria</u>	0.060	0.300	0.0511

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Taeniatherum asperum</u>	0.550	12.615	0.2154
<u>Cynosurus echinatus</u>	0.890	12.054	0.2059
<u>Danthonia californica</u>	0.280	5.721	0.0977
<u>Rhus diversiloba</u>	0.200	4.643	0.0793
<u>Bromus mollis</u>	0.680	4.426	0.0756
<u>Lolium perenne</u>	0.230	4.274	0.0730
<u>Linum angustifolium</u>	0.520	2.550	0.0436
<u>Briza minor</u>	0.600	2.374	0.0406
<u>Festuca arundinacea</u>	0.090	1.926	0.0329
<u>Festuca megalura</u>	0.320	1.300	0.0222
<u>Bromus rigidus</u>	0.240	1.099	0.0188
<u>Sherardia arvensis</u>	0.160	1.025	0.0175
<u>Geranium spp.</u>	0.140	0.600	0.0103
<u>Elymus glaucus</u>	0.080	0.450	0.0077
<u>Caucalis microcarpa</u>	0.150	0.375	0.0064
<u>Veronica arvensis</u>	0.150	0.375	0.0064
<u>Achillea millefolium</u>	0.130	0.325	0.0056

Appendix B. Oak-Savanna Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Cerastium viscosum</u>	0.130	0.325	0.0056
<u>Navarretia squarrosa</u>	0.100	0.250	0.0043
<u>Myosotis discolor</u>	0.090	0.225	0.0038
<u>Trifolium dubium</u>	0.080	0.200	0.0034
<u>Erodium cicutarium</u>	0.030	0.200	0.0034
<u>Eremocarpus setigerus</u>	0.020	0.175	0.0030
<u>Koeleria cristata</u>	0.020	0.175	0.0030
<u>Poa prantensis</u>	0.060	0.150	0.0026
<u>Astragalus spp.</u>	0.010	0.150	0.0026
<u>Hypericum perforatum</u>	0.050	0.125	0.0021
<u>Galium spp.</u>	0.030	0.075	0.0013
<u>Plantago lanceolata</u>	0.030	0.075	0.0013
<u>Centaurium umbellatum</u>	0.020	0.050	0.0009
<u>Lathyrus spp.</u>	0.020	0.050	0.0009
<u>Madia spp.</u>	0.020	0.050	0.0009
<u>Brodiaea coronaria</u>	0.010	0.025	0.0004
<u>Carex spp.</u>	0.010	0.025	0.0004
<u>Dactylis glomerata</u>	0.010	0.025	0.0004
<u>Festuca idahoensis</u>	0.010	0.025	0.0004
<u>Fragaria spp.</u>	0.010	0.025	0.0004

Summary Statistics

	Mean	95% C.I.	$s_{\bar{x}}$	n
Canopy % Cover	25.5	19.6-31.3	2.94	100
Tree Density (stems/ha)	95.6	54.8-136.4	20.59	100
Diameter at Breast Height (cm)	32.9	31.2-34.6	0.87	400
Shrub % Cover	5.9	3.3-8.5	1.33	100
Herbaceous % Cover	76.8	72.2-81.4	2.32	100
Obstruction Index	18.4	17.5-19.3	0.46	100

Appendix B. continued.

OPEN OAK HABITAT

Trees

Species	Basal Area (m ²)	Relative Dominance
<u>Quercus garryana</u>	7.782	0.774
<u>Quercus kelloggii</u>	1.770	0.176
<u>Arbutus menziesii</u>	0.291	0.029
<u>Pseudotsuga menziesii</u>	0.155	0.015
<u>Pinus ponderosa</u>	0.048	0.005
<u>Pyrus malus</u>	0.004	0.001

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.300	3.724	0.6093
<u>Rosa elganteria</u>	0.340	2.304	0.3770
<u>Amelanchier alnifolia</u>	0.020	0.083	0.0137

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Cynosurus echinatus</u>	0.900	14.880	0.3125
<u>Danthonia californica</u>	0.493	6.369	0.1338
<u>Lolium perenne</u>	0.320	4.204	0.0883
<u>Rhus diversiloba</u>	0.260	2.619	0.0550
<u>Geranium spp.</u>	0.267	1.749	0.0367
<u>Bromus mollis</u>	0.320	1.717	0.0361
<u>Caucalis microcarpa</u>	0.527	1.317	0.0277
<u>Festuca arundinacea</u>	0.073	1.316	0.0276
<u>Trifolium dubium</u>	0.193	1.233	0.0259
<u>Bromus rigidus</u>	0.167	0.999	0.0210
<u>Holcus lanatus</u>	0.080	0.997	0.0209
<u>Veronica arvensis</u>	0.340	0.949	0.0199
<u>Plantago lanceolata</u>	0.080	0.700	0.0147

Appendix B. Open Oak Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Carex</u> spp.	0.047	0.683	0.0143
<u>Cerastium viscosum</u>	0.187	0.633	0.0133
<u>Linum angustifolium</u>	0.200	0.583	0.0122
<u>Juncus effusus</u>	0.060	0.550	0.0116
<u>Briza minor</u>	0.133	0.417	0.0088
<u>Hypericum perforatum</u>	0.153	0.383	0.0080
<u>Bromus sterilis</u>	0.047	0.367	0.0077
<u>Myosotis discolor</u>	0.140	0.350	0.0074
<u>Sherardia arvensis</u>	0.093	0.317	0.0067
<u>Poa pratensis</u>	0.060	0.317	0.0067
<u>Taeniatherum asperum</u>	0.060	0.317	0.0067
<u>Koeleria cristata</u>	0.033	0.315	0.0066
<u>Elymus glaucus</u>	0.087	0.300	0.0063
<u>Galium</u> spp.	0.120	0.300	0.0063
<u>Potentilla</u> spp.	0.080	0.283	0.0059
<u>Poa</u> spp.	0.047	0.283	0.0059
<u>Festuca megalura</u>	0.067	0.250	0.0053
<u>Vicia angustifolia</u>	0.093	0.233	0.0049
<u>Lolium multiflorum</u>	0.027	0.233	0.0049
<u>Festuca</u> spp.	0.020	0.216	0.0045
<u>Sisyrinchium angustifolium</u>	0.047	0.200	0.0042
<u>Deschampsia elongata</u>	0.013	0.200	0.0042
<u>Eriophyllum lanatum</u>	0.027	0.150	0.0032
<u>Fragaria</u> spp.	0.053	0.133	0.0028
<u>Achillea millefolium</u>	0.040	0.100	0.0021
<u>Leontodon nudicaulis</u>	0.007	0.100	0.0021
<u>Madia</u> spp.	0.033	0.083	0.0017
<u>Juncus bufonius</u>	0.020	0.050	0.0010
<u>Lathyrus</u> spp.	0.020	0.050	0.0010
<u>Navarretia squarrosa</u>	0.020	0.050	0.0010
<u>Brodiaea coronaria</u>	0.013	0.033	0.0007
<u>Centaureum umbellatum</u>	0.013	0.033	0.0007
<u>Iris tenax</u>	0.007	0.017	0.0004
<u>Prunella vulgaris</u>	0.007	0.017	0.0004
<u>Stachys palustris</u>	0.007	0.017	0.0004

Appendix B. Open Oak Habitat continued.

	<u>Summary Statistics</u>			
	Mean	95% C.I.	$s_{\bar{x}}$	n
Canopy % Cover	69.9	65.5-74.2	2.21	150
Tree Density (stems/ha)	665.0	543-787	61.97	150
Diameter at Breast Height (cm)	22.1	20.9-23.3	0.59	600
Shrub % Cover	6.1	4.7-7.5	0.72	150
Herbaceous % Cover	71.3	66.6-76.0	2.38	150
Obstruction Index	14.2	13.0-15.4	0.61	150

Appendix B. continued.

CLOSED OAK HABITAT

Trees

Species	Basal Area (m ²)	Relative Dominance
<u>Quercus garryana</u>	6.753	0.6918
<u>Quercus kelloggii</u>	2.395	0.2454
<u>Pseudotsuga menziesii</u>	0.511	0.0523
<u>Fraxinus latifolia</u>	0.063	0.0064
<u>Abies grandis</u>	0.040	0.0041

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.720	33.875	0.7117
<u>Rosa elganteria</u>	0.520	9.355	0.1965
<u>Symphoricarpos albus</u>	0.120	2.660	0.0559
<u>Amelanchier alnifolia</u>	0.060	1.285	0.0270
<u>Holodiscus discolor</u>	0.030	0.425	0.0089

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.660	10.736	0.3206
<u>Dactylis glomerata</u>	0.430	4.521	0.1350
<u>Cynosurus echinatus</u>	0.590	4.348	0.1298
<u>Holcus lanatus</u>	0.270	3.550	0.1060
<u>Festuca arundinacea</u>	0.170	1.522	0.0455
<u>Elymus glaucus</u>	0.230	1.200	0.0358
<u>Danthonia californica</u>	0.100	0.976	0.0291
<u>Bromus sterilis</u>	0.200	0.874	0.0261
<u>Caucalis microcarpa</u>	0.320	0.800	0.0239
<u>Lolium perenne</u>	0.060	0.688	0.0206
<u>Satureja douglasii</u>	0.150	0.624	0.0186
<u>Iris tenax</u>	0.040	0.476	0.0142
<u>Galium spp.</u>	0.190	0.475	0.0142

Appendix B. Closed Oak Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Deschampsia elongata</u>	0.020	0.400	0.0119
<u>Pteridium aquilinum</u>	0.020	0.300	0.0090
<u>Vicia angustifolia</u>	0.070	0.300	0.0090
<u>Danthonia intermedia</u>	0.040	0.224	0.0067
<u>Festuca rubra</u>	0.010	0.150	0.0045
<u>Poa spp.</u>	0.050	0.125	0.0037
<u>Achillea millefolium</u>	0.040	0.100	0.0030
<u>Myosotis discolor</u>	0.040	0.100	0.0030
<u>Oxalis spp.</u>	0.040	0.100	0.0030
<u>Potentilla spp.</u>	0.040	0.100	0.0030
<u>Hypericum perforatum</u>	0.030	0.075	0.0022
<u>Juncus effusus</u>	0.030	0.075	0.0022
<u>Phleum pratense</u>	0.030	0.075	0.0022
<u>Sherardia arvensis</u>	0.030	0.075	0.0022
<u>Thalictrum occidentale</u>	0.030	0.075	0.0022
<u>Linum angustifolium</u>	0.020	0.050	0.0015
<u>Madia spp.</u>	0.020	0.050	0.0015
<u>Poa pratensis</u>	0.020	0.050	0.0015
<u>Veronica arvensis</u>	0.020	0.050	0.0015
<u>Athyrium filix-femina</u>	0.010	0.025	0.0007
<u>Bromus mollis</u>	0.010	0.025	0.0007
<u>Bromus rigidus</u>	0.010	0.025	0.0007
<u>Centaureum umbellatum</u>	0.010	0.025	0.0007
<u>Cerastium viscosum</u>	0.010	0.025	0.0007
<u>Fragaria spp.</u>	0.010	0.025	0.0007
<u>Lathyrus spp.</u>	0.010	0.025	0.0007
<u>Lolium multiflorum</u>	0.010	0.025	0.0007
<u>Polystichum munitum</u>	0.010	0.025	0.0007

Summary Statistics

	Mean	95% C.I.	s _x	n
Canopy % Cover	90.3	87.3-93.3	1.53	100
Tress Density (stems/ha)	1266	1032-1500	118	100
Diameter at Breast Height (cm)	21.2	19.9-22.5	0.66	400

Appendix B. Closed Oak Habitat, Summary Statistics continued.

	Mean	95% C.I.	$s_{\bar{x}}$	n
Shrub % Cover	47.6	41.0-54.2	3.34	100
Herbaceous % Cover	58.4	53.9-62.9	2.25	100
Obstruction Index	9.3	7.8-10.8	0.75	100

Appendix B. continued.

OAK-CONIFER HABITAT

Trees

Species	Basal Area (m ²)	Relative Dominance
<u>Pseudotsuga menziesii</u>	3.594	0.4020
<u>Quercus garryana</u>	2.586	0.2893
<u>Arbutus menziesii</u>	1.635	0.1829
<u>Quercus kelloggii</u>	1.086	0.1215
<u>Acer macrophyllum</u>	0.032	0.0036
<u>Fraxinus latifolia</u>	0.006	0.0007

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.440	20.135	0.9493
<u>Arbutus menziesii</u>	0.060	0.480	0.0227
<u>Rosa elganteria</u>	0.070	0.270	0.0127
<u>Holodiscus discolor</u>	0.030	0.225	0.0106
<u>Corylus cornuta</u>	0.010	0.100	0.0047

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.660	9.686	0.3860
<u>Polystichum munitum</u>	0.130	4.952	0.1974
<u>Cynosurus echinatus</u>	0.510	3.726	0.1485
<u>Festuca spp.</u>	0.230	1.200	0.0478
<u>Caucalis microcarpa</u>	0.460	1.150	0.0458
<u>Athyrium filix-femina</u>	0.080	0.826	0.0329
<u>Danthonia intermedia</u>	0.220	0.550	0.0219
<u>Astragalus spp.</u>	0.020	0.524	0.0209
<u>Thalictrum occidentale</u>	0.170	0.425	0.0169

Appendix B. Oak-Conifer Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Holcus lanatus</u>	0.010	0.375	0.0149
<u>Galium</u> spp.	0.110	0.275	0.0110
<u>Festuca arundinacea</u>	0.090	0.225	0.0090
<u>Iris tenax</u>	0.020	0.175	0.0070
<u>Madia</u> spp.	0.060	0.150	0.0060
<u>Elymus glaucus</u>	0.050	0.125	0.0050
<u>Geranium</u> spp.	0.050	0.125	0.0050
<u>Satureja douglasii</u>	0.040	0.100	0.0040
<u>Hypericum perforatum</u>	0.030	0.075	0.0030
<u>Achillea millefolium</u>	0.020	0.050	0.0020
<u>Bromus rigidus</u>	0.020	0.050	0.0020
<u>Cerastium viscosum</u>	0.020	0.050	0.0020
<u>Sherardia arvensis</u>	0.020	0.050	0.0020
<u>Veronica arvensis</u>	0.020	0.050	0.0020
<u>Vicia angustifolium</u>	0.020	0.050	0.0020
<u>Cirsium vulgare</u>	0.010	0.025	0.0010
<u>Lathyrus</u> spp.	0.010	0.025	0.0010
<u>Poa pratensis</u>	0.010	0.025	0.0010
<u>Poa</u> spp.	0.010	0.025	0.0010
<u>Trientalis latifolia</u>	0.010	0.025	0.0010

Summary Statistics

	Mean	95% C.I.	s _x	n
Canopy % Cover	89.7	86.3-93.1	1.72	100
Tree Density (stems/ha)	1364	1094-1634	136.	100
Diameter at Breast Height (cm)	21.5	20.0-23.0	0.78	400
Shrub % Cover	21.2	14.9-27.5	3.20	100
Herbaceous % Cover	30.5	24.6-36.4	2.99	100
Obstruction Index	5.15	3.80-6.50	0.68	100

Appendix B. continued.

OAK-MADRONE HABITAT

Trees

Species	Basal Area (m ²)	Relative Dominance
<u>Quercus garryana</u>	2.237	0.4354
<u>Arbutus menziesii</u>	1.648	0.3208
<u>Pseudotsuga menziesii</u>	0.662	0.1290
<u>Quercus kelloggii</u>	0.537	0.1044
<u>Pinus ponderosa</u>	0.054	0.0104

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.827	28.530	0.9012
<u>Arbutus menziesii</u>	0.180	2.227	0.0704
<u>Rosa elganteria</u>	0.167	0.587	0.0185
<u>Ceanothus intergerrimus</u>	0.033	0.313	0.0099

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.660	10.586	0.3768
<u>Cynosurus echinatus</u>	0.783	6.861	0.2442
<u>Festuca arundinacea</u>	0.173	1.812	0.0645
<u>Elymus glaucus</u>	0.267	1.167	0.0415
<u>Danthonia californica</u>	0.133	1.066	0.0379
<u>Caucalis microcarpa</u>	0.313	0.866	0.0308
<u>Satureja douglasii</u>	0.080	0.617	0.0220
<u>Iris tenax</u>	0.140	0.600	0.0214
<u>Holcus lanatus</u>	0.053	0.383	0.0136
<u>Festuca spp.</u>	0.040	0.350	0.0125
<u>Veronica arvensis</u>	0.127	0.317	0.0113
<u>Linum angustifolium</u>	0.093	0.317	0.0113

Appendix B. Oak-Madrone Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Astragalus</u> spp.	0.027	0.300	0.0107
<u>Bromus mollis</u>	0.073	0.266	0.0095
<u>Briza minor</u>	0.093	0.233	0.0083
<u>Hypericum perforatum</u>	0.093	0.233	0.0083
<u>Fragaria</u> spp.	0.087	0.217	0.0077
<u>Madia</u> spp.	0.053	0.217	0.0077
<u>Festuca idahoensis</u>	0.020	0.216	0.0077
<u>Cerastium viscosum</u>	0.073	0.183	0.0065
<u>Galium</u> spp.	0.067	0.167	0.0058
<u>Lathyrus</u> spp.	0.067	0.167	0.0058
<u>Danthonia intermedia</u>	0.047	0.117	0.0042
<u>Myosotis discolor</u>	0.047	0.117	0.0042
<u>Vicia angustifolia</u>	0.047	0.117	0.0042
<u>Achillea millefolium</u>	0.033	0.083	0.0030
<u>Poa pratensis</u>	0.033	0.083	0.0030
<u>Trifolium dubium</u>	0.027	0.067	0.0024
<u>Centaurium umbellatum</u>	0.020	0.050	0.0018
<u>Plantago lanceolata</u>	0.020	0.050	0.0018
<u>Taeniatherum asperum</u>	0.020	0.050	0.0018
<u>Rumex acetosella</u>	0.013	0.033	0.0012
<u>Sherardia arvensis</u>	0.013	0.033	0.0012
<u>Sisyrinchium angustifolium</u>	0.013	0.033	0.0012
<u>Trientalis latifolia</u>	0.013	0.033	0.0012
<u>Bromus rigidus</u>	0.007	0.017	0.0006
<u>Geranium</u> spp.	0.007	0.017	0.0006
<u>Juncus effusus</u>	0.007	0.017	0.0006
<u>Lolium perenne</u>	0.007	0.017	0.0006
<u>Polystichum munitum</u>	0.007	0.017	0.0006

Summary Statistics

	Mean	95% C.I.	$s_{\bar{x}}$	n
Canopy % Cover	78.0	74.0-82.0	2.04	150
Tree Density (stems/ha)	1283	1122-1444	81.2	150
Diameter at Breast Height (cm)	15.7	14.8-16.6	0.46	600

Appendix B. continued.

MADRONE HABITAT

Trees

Species	Basal Area (m ²)	Relative Dominance
<u>Arbutus menziesii</u>	1.852	0.9105
<u>Pseudotsuga menziesii</u>	0.107	0.0526
<u>Quercus garryana</u>	0.039	0.0192
<u>Quercus kelloggii</u>	0.028	0.0138
<u>Pinus ponderosa</u>	0.008	0.0039

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Rhus diversiloba</u>	0.710	27.805	0.9785
<u>Rosa elganteria</u>	0.180	0.610	0.0215

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Festuca arundinacea</u>	0.350	8.260	0.3837
<u>Rhus diversiloba</u>	0.490	6.186	0.2873
<u>Cynosurus echinatus</u>	0.460	4.333	0.2013
<u>Iris tenax</u>	0.190	0.475	0.0221
<u>Danthonia californica</u>	0.070	0.425	0.0197
<u>Danthonia intermedia</u>	0.060	0.275	0.0128
<u>Poa pratensis</u>	0.030	0.200	0.0093
<u>Poa spp.</u>	0.070	0.175	0.0081
<u>Hypericum perforatum</u>	0.060	0.150	0.0070
<u>Linum angustifolium</u>	0.060	0.150	0.0070
<u>Caucalis microcarpa</u>	0.050	0.125	0.0058

Appendix B. Madrone Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Briza minor</u>	0.040	0.100	0.0046
<u>Achillea millefolium</u>	0.030	0.075	0.0035
<u>Cerastium viscosum</u>	0.030	0.075	0.0035
<u>Deschampsia elongata</u>	0.030	0.075	0.0035
<u>Elymus glaucus</u>	0.030	0.075	0.0035
<u>Trifolium dubium</u>	0.030	0.075	0.0035
<u>Centaurium umbellatum</u>	0.020	0.050	0.0022
<u>Holcus lanatus</u>	0.020	0.050	0.0022
<u>Madia spp.</u>	0.020	0.050	0.0022
<u>Dactylis glomerata</u>	0.010	0.025	0.0012
<u>Fragaria spp.</u>	0.010	0.025	0.0012
<u>Lathyrus spp.</u>	0.010	0.025	0.0012
<u>Lolium perenne</u>	0.010	0.025	0.0012
<u>Sherardia arvensis</u>	0.010	0.025	0.0012

Summary Statistics

	Mean	95% C.I.	$s_{\bar{x}}$	n
Canopy % Cover	79.3	74.3-84.3	2.52	100
Tree Density (stems/ha)	3762	2710-4814	530.	100
Diameter at Breast Height (cm)	10.3	9.81-10.8	0.25	400
Shrub % Cover	28.4	22.9-33.9	2.76	100
Herbaceous % Cover	25.0	19.7-30.3	2.69	100
Obstruction Index	3.04	2.18-3.90	0.43	100

Appendix B. continued.

RIPARIAN HABITAT

Trees

Species	Basal Area (m ²)	Relative Dominance
<u>Quercus garryana</u>	11.253	0.7016
<u>Frasinus latifolia</u>	4.566	0.2846
<u>Quercus kelloggii</u>	0.109	0.0068
<u>Alnus rubra</u>	0.086	0.0054
<u>Pyrus malus</u>	0.016	0.0010
<u>Pseudotsuga menziesii</u>	0.006	0.0004
<u>Pyrus communis</u>	0.003	0.0002

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Rosa elganteria</u>	0.360	1.940	0.4193
<u>Viburnum ellipticum</u>	0.060	1.423	0.3076
<u>Rhus diversiloba</u>	0.080	1.007	0.2176
<u>Holodiscus discolor</u>	0.020	0.217	0.0468
<u>Ceanothus intergerrimus</u>	0.013	0.040	0.0087

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Juncus effusus</u>	0.500	15.813	0.3571
<u>Festuca arundinacea</u>	0.413	7.253	0.1638
<u>Holcus lanatus</u>	0.373	4.212	0.0951
<u>Cynosurus echinatus</u>	0.433	2.900	0.0655
<u>Carex spp.</u>	0.227	2.505	0.0566
<u>Carex densa</u>	0.127	2.063	0.0466
<u>Rhus diversiloba</u>	0.207	1.350	0.0305

Appendix B. Riparian Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Festuca</u> spp.	0.113	1.321	0.0298
<u>Lolium perenne</u>	0.113	1.017	0.0230
<u>Danthonia californica</u>	0.093	0.733	0.0166
<u>Lolium multiflorum</u>	0.040	0.600	0.0135
<u>Dactylis glomerata</u>	0.073	0.517	0.0117
<u>Caucalis microcarpa</u>	0.200	0.500	0.0113
<u>Poa pratensis</u>	0.073	0.349	0.0079
<u>Juncus patens</u>	0.013	0.349	0.0079
<u>Bromus rigidus</u>	0.100	0.333	0.0075
<u>Stachys palustris</u>	0.053	0.300	0.0068
<u>Daucus carota</u>	0.020	0.283	0.0064
<u>Bromus mollis</u>	0.093	0.233	0.0053
<u>Veronica arvensis</u>	0.067	0.167	0.0038
<u>Galium</u> spp.	0.060	0.150	0.0034
<u>Cynosurus cristatus</u>	0.013	0.117	0.0026
<u>Prunella vulgaris</u>	0.013	0.117	0.0026
<u>Fragaria</u> spp.	0.040	0.100	0.0023
<u>Lathyrus</u> spp.	0.040	0.100	0.0023
<u>Mentha</u> spp.	0.040	0.100	0.0023
<u>Elymus glaucus</u>	0.027	0.067	0.0015
<u>Geranium</u> spp.	0.027	0.067	0.0015
<u>Trifolium dubium</u>	0.027	0.067	0.0015
<u>Vicia angustifolia</u>	0.027	0.067	0.0015
<u>Centaureum umbellatum</u>	0.020	0.050	0.0011
<u>Cirsium vulgare</u>	0.020	0.050	0.0011
<u>Linum angustifolium</u>	0.020	0.050	0.0011
<u>Myosotis discolor</u>	0.020	0.050	0.0011
<u>Plantago lanceolata</u>	0.020	0.050	0.0011
<u>Sherardia arvensis</u>	0.020	0.050	0.0011
<u>Cerastium viscosum</u>	0.013	0.033	0.0007
<u>Phleum pratense</u>	0.013	0.033	0.0007
<u>Senecio jacobaea</u>	0.013	0.033	0.0007
<u>Thalictrum occidentale</u>	0.013	0.033	0.0007
<u>Achillea millefolium</u>	0.007	0.017	0.0004
<u>Danthonia intermedia</u>	0.007	0.017	0.0004
<u>Juncus bufonius</u>	0.007	0.017	0.0004
<u>Juncus oxymersis</u>	0.007	0.017	0.0004
<u>Poa</u> spp.	0.007	0.017	0.0004
<u>Trientalis latifolia</u>	0.007	0.017	0.0004

Appendix B. Riparian Habitat continued.

	<u>Summary Statistics</u>			
	Mean	95% C.I.	$s_{\bar{x}}$	n
Canopy % Cover	81.5	77.1-85.9	2.21	150
Tree Density (stems/ha)	622.	463.-781.	80.2	150
Diameter at Breast Height (cm)	28.1	26.7-29.5	0.72	600
Shrub % Cover	4.63	3.03-6.23	0.81	150
Herbaceous % Cover	69.1	65.2-73.0	1.95	150
Obstruction Index	10.9	9.65-12.1	0.63	150

Appendix B. continued.

CONIFER HABITAT

Trees

Species	Basal Area (m ²)	Relative Dominance
<u>Pseudotsuga menziesii</u>	31.992	0.9051
<u>Quercus garryana</u>	1.465	0.0414
<u>Quercus kelloggii</u>	0.854	0.0241
<u>Pinus ponderosa</u>	0.720	0.0204
<u>Abies grandis</u>	0.193	0.0055
<u>Fraxinus latifolia</u>	0.048	0.0014
<u>Arbutus menziesii</u>	0.042	0.0012
<u>Alnus rubra</u>	0.032	0.0009

Shrubs

Species	Frequency	% Cover	Relative Dominance
<u>Corylus cornuta</u>	0.130	2.550	0.4374
<u>Rosa elganteria</u>	0.200	1.730	0.2967
<u>Rhus diversiloba</u>	0.040	1.550	0.2659

Herbaceous

Species	Frequency	% Cover	Relative Dominance
<u>Cynosurus echinatus</u>	0.630	7.118	0.3951
<u>Polystichum munitum</u>	0.100	2.522	0.1400
<u>Athyrium filix-femina</u>	0.090	1.872	0.1039
<u>Holcus lanatus</u>	0.100	1.204	0.0668
<u>Rhus diversiloba</u>	0.290	1.100	0.0611
<u>Caucalis microcarpa</u>	0.420	1.050	0.0583
<u>Danthonia intermedia</u>	0.190	0.600	0.0333
<u>Festuca arundinacea</u>	0.110	0.400	0.0222

Appendix B. Conifer Habitat, Herbaceous continued.

Species	Frequency	% Cover	Relative Dominance
<u>Bromus rigidus</u>	0.150	0.375	0.0208
<u>Madia</u> spp.	0.050	0.375	0.0208
<u>Galium</u> spp.	0.140	0.350	0.0194
<u>Elymus glaucus</u>	0.120	0.300	0.0167
<u>Festuca</u> spp.	0.101	0.150	0.0083
<u>Marah oreganus</u>	0.010	0.150	0.0083
<u>Hypericum perforatum</u>	0.040	0.100	0.0056
<u>Geranium</u> spp.	0.030	0.075	0.0041
<u>Trifolium dubium</u>	0.030	0.075	0.0041
<u>Pteridium aquilinum</u>	0.020	0.050	0.0028
<u>Cerastium viscosum</u>	0.010	0.025	0.0014
<u>Linum angustifolium</u>	0.010	0.025	0.0014
<u>Lolium perenne</u>	0.010	0.025	0.0014
<u>Satureja douglasii</u>	0.010	0.025	0.0014
<u>Veronica arvensis</u>	0.010	0.025	0.0014
<u>Vicia angustifolia</u>	0.010	0.025	0.0014

Summary Statistics

	Mean	95% C.I.	$s_{\bar{x}}$	n
Canopy % Cover	92.3	89.8-94.8	1.26	100
Tree Density (stem/ha)	541.	441.-641.	50.5	100
Diameter at Breast Height (cm)	41.8	39.8-43.8	1.00	400
Shrub % Cover	5.83	3.14-8.52	1.36	100
Herbaceous % Cover	21.4	16.5-26.3	2.49	100
Obstruction Index	12.0	10.3-13.7	0.84	100

Appendix C. Basal area (m^2) per hectare for each tree species among the various habitats on the study area.

Species	GRASSLAND-L ¹	GRASSLAND-WL ²	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Quercus garryana</u>	-	-	-	7.75	19.75	30.91	14.33	10.81	0.60	27.06	3.08
<u>Pseudotsuga menziesii</u>	-	-	-	-	0.39	2.34	19.91	3.20	1.65	0.01	67.20
<u>Quercus kelloggii</u>	-	-	-	0.34	4.49	10.96	6.02	2.60	0.43	0.26	1.79
<u>Arbutus menziesii</u>	-	-	-	-	0.74	-	9.06	7.97	28.54	-	0.09
<u>Fraxinus latirfoli</u>	-	-	-	0.03	-	0.29	0.03	-	-	10.98	0.10
<u>Pinus ponderosa</u>	-	-	-	-	0.11	-	-	0.26	0.12	-	1.51
<u>Abies grandis</u>	-	-	-	-	-	0.18	-	-	-	-	0.41
<u>Alnus rubra</u>	-	-	-	-	-	-	-	-	-	0.21	0.07
<u>Acer macrophyllum</u>	-	-	-	-	-	-	0.18	-	-	-	-
<u>Pyrus malus</u>	-	-	-	-	0.01	-	-	-	-	0.04	-
<u>Pyrus communis</u>	-	-	-	-	-	-	-	-	-	0.01	-
TOTAL	-	-	-	8.12	25.49	44.68	49.53	24.84	31.34	38.57	74.25

¹L denotes grassland areas that were subjected to livestock use during the study period.

²WL denotes grassland areas that have not experienced recent livestock use.

Appendix D. The frequency of occurrence and percent crown cover for each shrub species among the habitats on the study area.

Species	FREQUENCY										
	GRASSLAND-L ¹	GRASSLAND-WL ²	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Rhus diversiloba</u>	-	-	0.987	0.270	0.300	0.720	0.440	0.827	0.710	0.080	0.040
<u>Rosa elganteria</u>	-	-	0.220	0.060	0.340	0.520	0.070	0.167	0.180	0.360	0.200
<u>Arbutus menziesii</u>	-	-	-	-	-	-	0.060	0.180	-	-	-
<u>Holodiscus discolor</u>	-	-	-	-	-	0.030	0.030	-	-	0.020	-
<u>Corylus cornuta</u>	-	-	-	-	-	-	0.010	-	-	-	0.130
<u>Symphoricarpos albus</u>	-	-	-	-	-	0.120	-	-	-	-	-
<u>Amelanchier alnifolia</u>	-	-	-	-	0.020	0.060	-	-	-	-	-
<u>Ceanothus intergerrimus</u>	-	-	0.020	-	-	-	-	0.033	-	0.013	-
<u>Viburnum ellipticum</u>	-	-	-	-	-	-	-	-	-	0.060	-

¹L denotes grassland areas that were subjected to livestock use during the study period.

²WL denotes grassland areas that have not experienced recent livestock use.

Appendix D. continued. Percent crown cover.

Species	PERCENT CROWN COVER										
	GRASSLAND-L ¹	GRASSLAND-WL ²	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Rhus diversiloba</u>	-	-	33.130	5.575	3.724	33.875	20.135	28.530	27.805	1.007	1.550
<u>Rosa elganteria</u>	-	-	1.277	0.300	2.304	9.355	0.270	0.587	0.610	1.984	1.730
<u>Holodiscus discolor</u>	-	-	-	-	-	0.425	0.225	-	-	0.217	-
<u>Arbutus menziesii</u>	-	-	-	-	-	-	0.480	2.227	-	-	-
<u>Symphoricarpos albus</u>	-	-	-	-	-	2.660	-	-	-	-	-
<u>Corylus cornuta</u>	-	-	-	-	-	-	0.100	-	-	-	2.550
<u>Viburnum ellipticum</u>	-	-	-	-	-	-	-	-	-	1.423	-
<u>Amelanchier alnifolia</u>	-	-	-	-	0.083	1.285	-	-	-	-	-
<u>Ceanothus integerrimus</u>	-	-	0.017	-	-	-	-	0.313	-	0.040	-

¹L denotes grassland areas that were subjected to livestock use during the study period.

²WL denotes grassland areas that have not experienced recent livestock use.

Appendix E. The frequency of occurrence and percent crown cover for each herbaceous species among the habitats on the study area.

Species	FREQUENCY										
	GRASSLAND-L ¹	GRASSLAND-WL ²	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Cynorurus echinatus</u>	0.887	0.760	0.787	0.890	0.900	0.590	0.510	0.783	0.460	0.433	0.630
<u>Rhus diversiloba</u>	-	0.060	0.707	0.200	0.260	0.660	0.660	0.660	0.490	0.207	0.290
<u>Bromus mollis</u>	0.800	0.720	0.367	0.680	0.320	0.010	-	0.073	-	0.093	-
<u>Caucalis microcarpa</u>	0.040	0.130	0.293	0.150	0.527	0.320	0.460	0.313	0.050	0.200	0.420
<u>Taeniztherum asperum</u>	0.693	0.610	0.260	0.550	0.060	-	-	0.020	-	-	-
<u>Briza minor</u>	0.527	0.230	0.447	0.600	0.133	-	-	0.093	0.040	-	-
<u>Linum angustifolium</u>	0.513	0.190	0.373	0.520	0.200	0.020	-	0.093	0.060	0.020	0.010
<u>Danthonium californica</u>	0.373	0.290	0.020	0.280	0.493	0.100	-	0.133	0.070	0.093	-
<u>Festuca arundinacea</u>	-	0.060	0.207	0.090	0.073	0.170	0.090	0.173	0.350	0.413	0.110
<u>Lolium perenne</u>	0.340	0.400	0.113	0.230	0.320	0.060	-	0.007	0.010	0.113	0.010
<u>Festuca megalura</u>	0.427	0.380	0.187	0.320	0.067	-	-	-	-	-	-
<u>Bromus rigidus</u>	0.093	0.290	0.200	0.240	0.167	0.010	0.020	0.007	-	0.100	0.150
<u>Galium spp.</u>	0.100	0.160	0.227	0.030	0.120	0.190	0.110	0.067	-	0.060	0.140
<u>Holcus lanatus</u>	0.060	0.200	0.033	-	0.080	0.270	0.010	0.053	0.020	0.373	0.100
<u>Cerastium viscosum</u>	0.333	0.290	0.100	0.130	0.187	0.010	0.020	0.073	0.030	0.013	0.010
<u>Geranium spp.</u>	0.267	0.200	0.167	0.140	0.267	-	0.050	0.007	-	0.027	0.030
<u>Trifolium dubium</u>	0.480	0.140	0.107	0.080	0.193	-	-	0.027	0.030	0.027	0.030

¹ L denotes grassland areas that were subjected to livestock use during the study period.
² WL denotes grassland areas that have not experienced recent livestock use.

Appendix E. continued. Frequency.

Species	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Veronica arvensis</u>	0.033	0.140	0.180	0.150	0.340	0.020	0.020	0.127	-	0.067	0.010
<u>Elymus glaucus</u>	-	0.010	0.127	0.080	0.087	0.230	0.050	0.267	0.030	0.027	0.120
<u>Hypericum perforatum</u>	0.080	0.100	0.273	0.050	0.153	0.030	0.030	0.093	0.060	-	0.040
<u>Juncus effusus</u>	0.187	0.090	0.013	-	0.060	0.030	-	0.007	-	0.500	-
<u>Trichostema lanceolatum</u>	-	0.060	-	-	-	-	-	-	-	-	-
<u>Trientalis latifolia</u>	-	-	0.027	-	-	-	0.010	0.013	-	0.007	-
<u>Phleum pratense</u>	-	-	0.007	-	-	0.030	-	-	-	0.013	-
<u>Koeleria cristata</u>	-	-	0.027	0.020	-	-	-	-	-	-	-
<u>Prunella vulgaris</u>	-	0.020	-	-	0.007	-	-	-	-	0.013	-
<u>Mentha spp.</u>	-	-	-	-	-	-	-	-	-	0.040	-
<u>Oxalis spp.</u>	-	-	-	-	-	0.040	-	-	-	-	-
<u>Agrostis tenuis</u>	0.020	0.010	0.007	-	-	-	-	-	-	-	-
<u>Penstemon spp.</u>	0.033	-	-	-	-	-	-	-	-	-	-
<u>Festuca idahoensis</u>	-	-	-	0.010	-	-	-	0.020	-	-	-
<u>Zigadcnus venenosus</u>	0.007	0.020	-	-	-	-	-	-	-	-	-
<u>Daucus carota</u>	-	-	-	-	-	-	-	-	-	0.020	-
<u>Epilobium spp.</u>	0.020	-	-	-	-	-	-	-	-	-	-
<u>Leontodon autumnalis</u>	0.020	-	-	-	-	-	-	-	-	-	-
<u>Myosotis spp.</u>	-	-	0.020	-	-	-	-	-	-	-	-
<u>Bromus carinatus</u>	-	-	0.013	-	-	-	-	-	-	-	-
<u>Cynosurus cristatus</u>	-	-	-	-	-	-	-	-	-	-	-
<u>Matricaria chamomilla</u>	0.013	-	-	-	-	-	-	-	-	-	-
<u>Senecio jacobaea</u>	-	-	-	-	-	-	-	-	-	0.013	-
<u>Festuca rubra</u>	-	-	-	-	-	0.010	-	-	-	-	-

Appendix E. continued. Frequency.

Species	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Lathyrus</u> spp.	0.033	-	0.047	0.020	0.020	0.010	0.010	0.067	0.020	0.040	-
<u>Polystichum munitum</u>	-	-	0.020	-	-	0.010	0.130	0.007	-	-	0.100
<u>Potentilla</u> spp.	0.007	0.110	0.020	-	0.080	0.040	-	-	-	-	-
<u>Sisyrinchium angustifolium</u>	0.040	0.100	0.033	-	0.047	-	-	0.013	-	-	-
<u>Fragaria</u> spp.	-	-	0.027	0.010	0.053	0.010	-	0.087	0.010	0.040	-
<u>Poa</u> spp.	-	0.050	-	-	0.047	0.050	0.010	0	0.070	0.007	-
<u>Thalictrum occidentale</u>	-	-	-	-	-	0.030	0.170	-	-	0.013	-
<u>Athyrium filix-femina</u>	-	-	-	-	-	0.010	0.080	-	-	-	0.090
<u>Trifolium subterraneum</u>	0.173	-	-	-	-	-	-	-	-	-	-
<u>Stachys palustris</u>	0.040	0.040	0.007	-	0.007	-	-	-	-	0.053	-
<u>Pteridium aquilinum</u>	-	-	0.087	-	-	0.020	-	-	-	-	0.020
<u>Carex densa</u>	-	-	-	-	-	-	-	-	-	0.127	-
<u>Bromus</u> spp.	-	0.110	-	-	-	-	-	-	-	-	-
<u>Astragalus</u> spp.	-	0.020	0.020	0.010	-	-	0.020	0.027	-	-	-
<u>Eremocarpus setigerus</u>	0.013	0.060	-	0.020	-	-	-	-	-	-	-
<u>Eriophyllum lanatum</u>	0.007	0.030	0.027	-	0.027	-	-	-	-	-	-
<u>Lolium multiflorum</u>	-	-	0.007	0	0.027	0.010	-	-	-	0.040	-
<u>Juncus patens</u>	0.060	0.010	-	-	-	-	-	-	-	0.013	-
<u>Cirsium vulgare</u>	0.007	0.040	-	-	-	-	0.010	-	-	0.020	-
<u>Rumex acetosella</u>	0.033	0.020	-	-	-	-	-	0.013	-	-	-
<u>Deschampsia elongata</u>	-	-	-	-	0.013	0.020	-	-	0.030	-	-

Appendix E. continued. Frequency.

Species	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Danthonia intermedia</u>	-	-	0.173	-	-	0.040	0.220	0.047	0.060	0.007	0.190
<u>Myosotis discolor</u>	0.020	0.180	0.187	0.090	0.140	0.040	-	0.047	-	0.020	-
<u>Sherardia arvensis</u>	0.127	0.030	0.087	0.160	0.093	0.030	0.020	0.013	0.010	0.020	-
<u>Navarretia squarrosa</u>	0.307	0.130	0.020	0.100	0.020	-	-	-	-	-	-
<u>Dactylis glomerata</u>	-	-	0.020	0.010	0.033	0.430	-	-	0.010	0.073	-
<u>Juncus bufonius</u>	0.300	0.170	-	-	0.020	-	-	-	-	0.007	-
<u>Madia spp.</u>	0.040	0.090	0.087	0.020	0.033	0.020	0.060	0.053	0.020	-	0.050
<u>Plantago lanceolata</u>	0.140	0.070	0.107	0.030	0.080	-	-	0.020	-	0.020	-
<u>Carex spp.</u>	0.020	0.130	0.027	0.010	0.047	-	-	-	-	0.227	-
<u>Centaureium umbellatum</u>	0.093	0.220	0.027	0.020	0.013	0.010	-	0.020	0.020	0.020	-
<u>Achillea millefolium</u>	0.020	0.030	0.080	0.130	0.040	0.040	0.020	0.033	0.030	0.007	-
<u>Festuca spp.</u>	-	-	0.013	-	0.020	-	0.230	0.040	-	0.113	0.010
<u>Iris tenax</u>	-	-	0.020	-	0.007	0.040	0.020	0.140	0.190	-	-
<u>Poa pratensis</u>	0.040	-	0.067	0.060	0.060	0.020	0.010	0.033	0.030	0.073	-
<u>Vicia angustifolia</u>	0.040	0.040	0.007	-	0.093	0.070	0.020	0.047	0.010	0.027	0.010
<u>Brodiaea coronaria</u>	0.067	0.210	0.047	0.010	0.013	-	-	-	-	-	-
<u>Bromus sterilis</u>	0.027	0.030	-	-	0.047	0.200	-	-	-	-	-
<u>Satureja douglasii</u>	-	-	-	-	-	0.150	0.040	0.080	-	-	0.010
<u>Erodium cicutarium</u>	0.173	0.030	0.040	0.030	-	-	-	-	-	-	-
<u>Leontodon nudicaulis</u>	0.133	0.080	0.053	-	0.007	-	-	-	-	-	-

Appendix E. continued. Frequency.

Species	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Marah oreganus</u>	-	-	-	-	-	-	-	-	-	-	-
<u>Berberis repens</u>	-	-	-	-	-	-	-	-	-	-	0.010
<u>Capsella bursa-pastoris</u>	0.007	-	0.007	-	-	-	-	-	-	-	-
<u>Cirsium arvense</u>	0.007	-	-	-	-	-	-	-	-	-	-
<u>Juncus oxymetris</u>	-	-	-	-	-	-	-	-	-	-	-
<u>Sidalcea virgata</u>	0.007	-	-	-	-	-	-	-	-	0.007	-

Appendix E. continued. Percent crown cover.

Species	PERCENT CROWN COVER										
	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Cynosusus echinatus</u>	17.495	7.650	10.135	12.054	14.880	4.348	3.776	6.861	4.333	2.900	7.118
<u>Rhus diversiloba</u>	-	0.852	23.083	4.643	2.619	10.736	9.686	10.586	6.186	1.350	1.100
<u>Taeniatherum asperum</u>	15.736	4.699	2.020	12.615	0.317	-	-	0.050	-	-	-
<u>Festuca arundinacea</u>	-	1.224	4.649	1.926	1.316	1.552	0.225	1.812	8.260	7.253	0.400
<u>Bromus mollis</u>	7.996	8.982	1.982	4.426	1.717	0.025	-	0.266	-	0.233	-
<u>Danthonia californica</u>	5.739	3.622	0.750	5.721	6.369	0.976	-	1.066	0.425	0.733	-
<u>Lolium perenne</u>	5.900	6.540	0.700	4.274	4.204	0.689	-	0.017	0.025	1.017	0.025
<u>Juncus effusus</u>	1.530	0.350	0.033	-	0.550	0.075	-	0.017	-	15.813	-
<u>Holcus lanatus</u>	0.233	1.850	0.250	-	0.997	3.550	0.375	0.383	0.050	4.212	1.204
<u>Linum angustifolium</u>	3.240	0.725	1.790	2.550	0.583	0.050	-	0.317	0.150	0.050	0.025
<u>Festuca megalura</u>	3.317	3.050	0.883	1.300	0.250	-	-	-	-	-	-
<u>Polystichum munitum</u>	-	-	0.300	-	-	0.025	4.952	0.017	-	-	2.522
<u>Briza minor</u>	2.233	0.700	1.533	2.374	0.417	-	-	0.233	0.100	-	-
<u>Caucalis microcarpa</u>	0.183	0.450	0.733	0.375	1.317	0.800	1.150	0.866	0.125	0.500	1.050
<u>Trifolium dubium</u>	4.842	0.350	0.350	0.200	1.233	-	-	0.067	0.075	0.067	0.075
<u>Bromus rigidus</u>	0.483	1.824	0.750	1.099	0.999	0.025	0.050	0.017	-	0.333	0.375
<u>Dactylis glomerata</u>	-	-	0.050	0.025	-	4.521	-	-	0.025	0.517	-
<u>Danthonia intermedia</u>	-	-	2.999	-	-	0.225	0.550	0.117	0.275	0.017	0.600
<u>Geranium spp.</u>	1.000	0.625	0.417	0.600	1.749	-	0.125	0.017	-	0.067	0.075
<u>Elymus glaucus</u>	-	0.025	0.483	0.450	0.300	1.200	0.125	1.167	0.075	0.067	0.300

Appendix E. continued. Percent crown cover.

Species	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Carex</u> spp.	0.133	0.325	0.233	0.025	0.683	-	-	-	-	2.505	-
<u>Galium</u> spp.	0.250	0.400	1.384	0.075	0.300	0.475	0.275	0.167	-	0.150	0.350
<u>Festuca</u> spp.	-	-	0.349	-	0.216	-	1.200	0.350	-	1.321	0.150
<u>Cerastium viscosum</u>	0.917	0.849	0.250	0.325	0.633	0.025	0.050	0.183	0.075	0.033	0.025
<u>Juncus bufonius</u>	2.466	0.799	-	-	0.050	-	-	-	-	0.017	-
<u>Veronica arvensis</u>	0.083	0.350	0.450	0.375	0.949	0.050	0.050	0.317	-	0.167	0.025
<u>Athyrium filix-femina</u>	-	-	-	-	-	0.025	0.826	-	-	-	1.872
<u>Plantago lanceolata</u>	0.935	0.175	0.517	0.075	0.700	-	-	0.050	-	0.050	-
<u>Hypericum perforatum</u>	0.200	0.250	0.850	0.125	0.383	0.075	0.075	0.233	0.150	-	0.100
<u>Sherardia arvensis</u>	0.400	0.075	0.217	1.025	0.317	0.075	0.050	0.033	0.025	0.050	-
<u>Carex densa</u>	-	-	-	-	-	-	-	-	-	-	-
<u>Myosotis discolor</u>	0.050	0.450	0.716	0.225	0.350	0.100	-	0.117	-	2.063	-
<u>Bromus sterilis</u>	0.483	0.200	-	-	0.367	0.874	-	-	-	0.050	-
<u>Iris tenax</u>	-	-	0.133	-	0.017	0.476	0.175	0.600	0.475	-	-
<u>Trifolium subterraneum</u>	1.861	-	-	-	-	-	-	-	-	-	-
<u>Juncus patens</u>	1.416	0.025	-	-	-	-	-	-	-	-	-
<u>Navarretia squarrosa</u>	0.933	0.450	0.050	0.250	0.050	-	-	-	-	0.349	-
<u>Poa pratensis</u>	0.100	-	0.417	0.150	0.317	0.050	0.025	0.083	0.200	0.349	-
<u>Madia</u> spp.	0.100	0.225	0.217	0.050	0.083	0.050	0.150	0.217	0.050	-	0.375
<u>Astragalus</u> spp.	-	0.050	0.366	0.150	-	-	0.524	0.300	-	-	-

Appendix E. continued. Percent crown cover.

Species	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Satureja douglasii</u>	-	-	-	-	-	0.624	0.100	0.617	-	-	0.025
<u>Poa spp.</u>	-	0.600	-	-	0.283	0.125	0.025	-	0.175	0.017	-
<u>Stachys palustris</u>	0.583	0.225	0.100	-	0.017	-	-	-	-	0.300	-
<u>Leontodon nudicaulis</u>	0.567	0.325	0.217	-	0.100	-	-	-	-	-	-
<u>Centaurium umbellatum</u>	0.317	0.550	0.067	0.050	0.033	0.025	-	0.050	0.050	0.020	-
<u>Achillea millefolium</u>	0.050	0.075	0.283	0.325	0.100	0.100	0.050	0.083	0.075	0.017	-
<u>Vicia angustifolia</u>	0.183	0.100	0.017	-	0.233	0.300	0.050	0.117	0.025	0.067	0.025
<u>Erodium cicutarium</u>	0.517	0.200	0.100	0.200	-	-	-	-	-	-	-
<u>Lathyrus spp.</u>	0.083	-	0.433	0.050	0.050	0.025	0.025	0.167	0.025	0.100	-
<u>Lolium multiflorum</u>	-	-	0.100	-	0.233	0.025	-	-	-	0.600	-
<u>Pteridium aquilinum</u>	-	-	0.550	-	-	0.300	-	-	-	-	0.050
<u>Bromus spp.</u>	-	0.900	-	-	-	-	-	-	-	-	-
<u>Brodiaea coronaria</u>	0.167	0.525	0.117	0.025	0.033	-	-	-	-	-	-
<u>Potentilla spp.</u>	0.017	0.400	0.050	-	0.283	0.100	-	-	-	-	-
<u>Deschampsia elongata</u>	-	-	-	-	0.200	0.400	-	-	0.075	-	-
<u>Sisyrinchium angustifolium</u>	0.100	0.275	0.083	-	0.200	-	-	0.013	-	-	-
<u>Fragaria spp.</u>	-	-	0.067	0.025	0.133	0.025	-	0.217	0.025	0.100	-
<u>Koeleria cristata</u>	-	-	0.067	0.175	0.315	-	-	-	-	-	-
<u>Thalictrum occidentale</u>	-	-	-	-	-	0.075	0.425	-	-	0.033	-
<u>Agrostis tenuis</u>	0.450	0.025	0.017	-	-	-	-	-	-	-	-

Appendix E. continued. Percent crown cover.

Species	GRASSLAND-L	GRASSLAND-WL	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Eremocarpus setigerus</u>	0.033	0.150	-	0.175	-	-	-	-	-	-	-
<u>Eriophyllum lanatum</u>	0.017	0.075	0.067	-	0.150	-	-	-	-	-	-
<u>Cirsium vulgare</u>	0.017	0.225	-	-	-	-	0.010	-	-	0.050	-
<u>Daucus carota</u>	-	-	-	-	-	-	-	-	-	0.283	-
<u>Rumex acetosella</u>	0.167	0.050	-	-	-	-	-	0.033	-	-	-
<u>Festuca idahoensis</u>	-	-	-	0.025	-	-	-	0.216	-	-	-
<u>Prunella vulgaris</u>	-	0.050	-	-	0.017	-	-	-	-	0.117	-
<u>Festuca rubra</u>	-	-	-	-	-	0.150	-	-	-	-	-
<u>Marah oreganus</u>	-	-	-	-	-	-	-	-	-	-	0.150
<u>Trichostema lanceolatum</u>	-	0.150	-	-	-	-	-	-	-	-	-
<u>Trientalis latifolia</u>	-	-	0.067	-	-	-	0.025	0.033	-	0.017	-
<u>Phleum pratense</u>	-	-	0.017	-	-	0.075	-	-	-	0.033	-
<u>Bromus carinatus</u>	-	-	0.117	-	-	-	-	-	-	-	-
<u>Cynosurus cristatus</u>	-	-	-	-	-	-	-	-	-	0.117	-
<u>Mentha spp.</u>	-	-	-	-	-	-	-	-	-	0.100	-
<u>Oxalis spp.</u>	-	-	-	-	-	0.100	-	-	-	-	-
<u>Penstemon spp.</u>	0.083	-	-	-	-	-	-	-	-	-	-
<u>Zigadenus venenosus</u>	0.017	0.050	-	-	-	-	-	-	-	-	-
<u>Epilobium spp.</u>	0.050	-	-	-	-	-	-	-	-	-	-
<u>Leontodon autumnalis</u>	0.050	-	-	-	-	-	-	-	-	-	-

Appendix E. continued. Percent crown cover.

Species	GRASSLAND-L ¹	GRASSLAND-WL ²	GRASS-SHRUB	OAK-SAVANNA	OPEN OAK	CLOSED OAK	OAK-CONIFER	OAK-MADRONE	MADRONE	RIPARIAN	CONIFER
<u>Myosotis</u> spp.	-	-	0.050	-	-	-	-	-	-	-	-
<u>Matricaria chamomilla</u>	0.033	-	-	-	-	-	-	-	-	-	-
<u>Senecio jacobaea</u>	-	-	-	-	-	-	-	-	-	0.033	-
<u>Berberis repens</u>	-	-	0.017	-	-	-	-	-	-	-	-
<u>Capsella bursa-pastoris</u>	0.017	-	-	-	-	-	-	-	-	-	-
<u>Cirsium arvense</u>	0.017	-	-	-	-	-	-	-	-	-	-
<u>Juncus oxymiris</u>	-	-	-	-	-	-	-	-	-	0.017	-
<u>Sidalcea virgata</u>	0.017	-	-	-	-	-	-	-	-	-	-

¹L denotes grassland areas that were subjected to livestock use during the study period.

²WL denotes grassland areas that have not experienced recent livestock use.

Appendix F. Age at death and relative cumulative frequency (RCF) of Columbian white-tailed deer mortalities arranged chronologically from oldest to youngest. Relative frequency = $1/N$ and RCF = n/N , where $n = 1$ to N . RCF was plotted against age at death to derive male and female ecological longevity curves.

MALES (N = 80)

<u>Age (yr)</u>	<u>RCF</u>	<u>Age (yr)</u>	<u>RCF</u>	<u>Age (yr)</u>	<u>RCF</u>
5.50	0.0125	3.00	0.3500	1.25	0.6875
5.50	0.0250	2.50	0.3625	1.25	0.7000
5.50	0.0375	2.50	0.3750	1.00	0.7125
5.50	0.0500	2.50	0.3875	1.00	0.7250
5.00	0.0625	2.50	0.4000	1.00	0.7375
4.50	0.0750	2.50	0.4125	1.00	0.7500
4.50	0.0875	2.50	0.4250	0.75	0.7625
4.50	0.1000	2.50	0.4375	0.75	0.7750
4.50	0.1125	2.50	0.4500	0.75	0.7875
4.50	0.1250	2.50	0.4625	0.75	0.8000
4.50	0.1375	2.50	0.4750	0.75	0.8125
4.50	0.1500	2.50	0.4875	0.75	0.8250
4.00	0.1625	2.50	0.5000	0.75	0.8375
4.00	0.1750	2.50	0.5125	0.50	0.8500
4.00	0.1875	2.50	0.5250	0.50	0.8625
4.00	0.2000	2.50	0.5375	0.50	0.8750
3.50	0.2125	2.00	0.5500	0.50	0.8875
3.50	0.2250	1.50	0.5625	0.50	0.9000
3.50	0.2375	1.50	0.5750	0.25	0.9125
3.50	0.2500	1.50	0.5875	0.25	0.9250
3.50	0.2625	1.50	0.6000	0.25	0.9375
3.50	0.2750	1.50	0.6125	0.25	0.9500
3.50	0.2875	1.50	0.6250	0.25	0.9625
3.50	0.3000	1.50	0.6375	0.25	0.9750
3.50	0.3125	1.25	0.6500	0.25	0.9875
3.00	0.3250	1.25	0.6625	0.25	1.0000
3.00	0.3375	1.25	0.6750		

Appendix F. continued.

FEMALES (N = 117)

<u>Age (yr)</u>	<u>RCF</u>	<u>Age (yr)</u>	<u>RCF</u>	<u>Age (yr)</u>	<u>RCF</u>
10.00	0.0085	5.50	0.3419	1.50	0.6752
10.00	0.0171	5.50	0.3504	1.50	0.6838
9.50	0.0256	5.50	0.3590	1.50	0.6923
9.50	0.0342	5.50	0.3675	1.50	0.7009
9.50	0.0427	5.50	0.3761	1.50	0.7094
9.50	0.0513	5.00	0.3846	1.50	0.7179
9.00	0.0598	5.00	0.3932	1.00	0.7265
8.50	0.0684	5.00	0.4017	1.00	0.7350
8.50	0.0769	4.50	0.4103	0.75	0.7436
8.50	0.0855	4.50	0.4188	0.75	0.7521
8.50	0.0940	4.50	0.4274	0.75	0.7607
8.50	0.1026	4.50	0.4359	0.75	0.7692
8.50	0.1111	4.50	0.4444	0.75	0.7777
8.50	0.1197	4.50	0.4530	0.75	0.7863
8.00	0.1282	4.00	0.4615	0.75	0.7949
8.00	0.1368	4.00	0.4701	0.75	0.8034
8.00	0.1453	4.00	0.4786	0.75	0.8120
8.00	0.1538	4.00	0.4872	0.75	0.8205
8.00	0.1624	3.50	0.4957	0.75	0.8291
8.00	0.1709	3.50	0.5043	0.75	0.8376
7.50	0.1795	3.50	0.5128	0.75	0.8462
7.50	0.1880	3.50	0.5214	0.50	0.8547
7.50	0.1966	3.50	0.5299	0.50	0.8632
7.50	0.2051	3.50	0.5385	0.50	0.8718
7.50	0.2137	3.50	0.5470	0.50	0.8803
7.50	0.2222	3.50	0.5555	0.50	0.8888
7.50	0.2308	3.00	0.5641	0.50	0.8974
7.50	0.2393	3.00	0.5726	0.50	0.9060
7.00	0.2479	3.00	0.5812	0.50	0.9145
6.50	0.2564	3.00	0.5897	0.50	0.9231
6.50	0.2650	3.00	0.5983	0.50	0.9316
6.50	0.2735	2.50	0.6068	0.50	0.9402
6.50	0.2821	2.50	0.6154	0.50	0.9487
6.50	0.2906	2.50	0.6239	0.25	0.9573
6.50	0.2991	2.50	0.6325	0.25	0.9658
6.00	0.3077	2.50	0.6410	0.25	0.9744
6.00	0.3162	2.50	0.6496	0.25	0.9829
6.00	0.3248	2.00	0.6581	0.25	0.9914
5.50	0.3333	2.00	0.6666	0.25	1.0000
